



Migrant Birds in the Neotropics

ECOLOGY, BEHAVIOR, DISTRIBUTION, and CONSERVATION

Edited by

ALLEN KEAST and
EUGENE S. MORTON

THE SYMPOSIA OF
THE NATIONAL ZOOLOGICAL PARK

Smithsonian Institution

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Title page and material

Dedication to Paul Schwartz

Contents

Foreword by S. Dillon Ripley

List of contributors with their addresses as of 1980

Introduction by Keast and Morton

Complete introductory paper by John W. Terborgh

Complete paper by Paul Schwartz, to whom the volume is dedicated

Abstracts of all other papers

Complete concluding paper by Eugene S. Morton

Complete concluding paper by Allen Keast

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This volume is dedicated to the memory of Paul Schwartz, whose studies of territoriality in Northern Waterthrushes in Venezuela have stimulated many ornithologists to study migrant birds as integral components of tropical ecosystems.

THE SYMPOSIA OF THE NATIONAL ZOOLOGICAL PARK

Neotropics: ECOLOGY, BEHAVIOR, DISTRIBUTION, and CONSERVATION

Edited by

**ALLEN KEAST and
EUGENE S. MORTON**

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Foreword

Thirty years ago and earlier, publications on avian biology in the earth's tropical zones were largely confined to resident species. Interest in temperate zone migrants was rare; mention of such species largely incidental. With the coming of an intensive field of research in theoretical ecology involving spatial arrangements, territory, and competition, a good deal of interest in smaller passerine species, especially migrants, has shifted to speculation on the evolution and life history of such species in the tropics and their dispersal and foraging strategies in different competitive situations with resident congeners.

This interest led us at the Smithsonian to organize a symposium on the avifauna of northern Latin America in 1966, in which one of the major participants was the late Robert H. MacArthur, colleague of many years, whose interest in spatial separation of New World warblers and their evolution, during his graduate work at Yale, had led to his development into one of our foremost theoretical ecologists. The results of this seminar were published in 1970.

Now, nearly 10 years later, we have had a second Smithsonian seminar on the problems of migrant temperate species wintering in the New World tropics. This event, of compelling interest in the field of comparative ecology, has been a source of particular satisfaction to me. The symposium and this volume have combined research of great fascination with a new sense of urgency, including work by Professor John W. Terborgh, a highly appropriate successor to our friend, Professor MacArthur.

As President of the International Council for Bird Preservation, I take especial satisfaction that ecologists of all persuasions are alert to the threat presented to their field of research by the violent and steady degradation of avian habitats. The tropical zones of the world are threatened as never before by the massive assist of technology in the conquest of primary forests. As forests dwindle and disappear from the terrestrial tropics, the relative balance of bird species shifts and crucially changes in the temperate zones as well. The pesticides and herbicides of capital-intensive agriculture complete the destruction of the original flora and fauna, whether resident or, in this case, migratory.

Those of us concerned with conservation fear that we are witnessing an irreversible series of shifts in biotic balance. I pray that the Smithsonian will continue this seminar, in a cyclical series, so that we may document these massive environmental events, if we cannot arrest them. If only an institution had been witness to the degradation and desertification of the Middle East. What a tremendous amount we would have learned if those events, far slower in time, to be sure, could have been documented. Now we know enough to list these current events in the neotropics in detail. Perhaps in a generation the message of this research and scientific reporting will have sunk in. One could wish ecologists of a generation ago had had the intuition and the persuasive power to be able effectively to counsel governments to control careless proliferation of technology and growth of population.

S. Dillon Ripley

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Introduction

The nearctic-neotropical migration system is one of the world's greatest and most complex, birds from the whole length and width of the North American continent being compressed into Middle America and northern South America, a land area a fraction of the breeding area's size. The neotropics are, nevertheless, extremely rich as bird habitat, supporting the world's richest endemic avifauna. These features pose fascinating questions. Where do the different northern migrants winter, what are their spatial utilization patterns in the wintering grounds, how is competition between congeners minimized? Are the adaptations of migrants different in any way from tropical residents; do they exclude each other from certain habitats? What collective devices might be operative to minimize interspecific competition for limited resources?

Many of us who have spent time in the neotropics in winter have asked ourselves these questions. This volume, and its antecedent symposium, came into being thanks to the Smithsonian Institution's National Zoological Park and Friends of the National Zoo who, in October 1977, made funds available to bring together a range of tropical workers at Front Royal, Virginia.

As anyone who has ever organized a symposium knows, there are inevitable gaps (and commonly important gaps) in content. This symposium was no exception. We were however, singularly fortunate to have a dozen or so younger workers who were completing Ph.D. theses on migrant-resident interactions in the neotropics. The book, accordingly, suddenly acquired a highly topical aspect. We tried to find colleagues willing to review such aspects of the migration system as the evolution of migratory and resident races, climatic history in the main overlap zones, and the biology of (admittedly few) migrants within Neotropica. In the interests of making the book relatively complete, the two editors developed syntheses sum-

marizing, or drawing attention to, a series of additional facets of migration systems. A most important facet of the whole story, the future of migrants in a region of the world subject to rapid clearing and biological change was, however, advanced to the preeminent position of the opening chapter. Here, Dr. John W. Terborgh draws on the joint findings of the 40 authors in a synthesis: "The Conservation Status of Neotropical Migrants: Present and Future."

The arrangement followed in the book is for a pair of introductory chapters (Terborgh, Schwartz) to be followed by a series of treatments of specific groups: the shorebirds (that winter in the far south of Neotropica) in associations of austral species (Myers); hawks, where only four species extensively penetrate Neotropica (Smith), and three groups of small insectivores (flycatchers, vireos, and warblers) that together make up the bulk of the northern breeders wintering in Neotropica (Fitzpatrick, Keast, Barlow). A series of regional treatments follow. Here successive authors consider migrant-resident interactions in particular areas: Florida and the Bahamas (Emlen); West Indies (Terborgh and Faaborg); Yucatán Peninsula of Mexico (Waide); Barro Colorado Island, Panama, (Willis); Panamanian forests (Hespenheide); lowlands and highlands of northern Colombia (Russell, Johnson); western Colombian forests (Orejuela, Raitt, Alvarez, and Hilty), and Ecuador, Peru, and Bolivia (Pearson). Resource partitioning between migrant and resident in Mexico is the subject of a chapter by Hutto and comparative foraging ecology (in Costa Rica) of one by Tramer and Kemp. Three studies on specific warbler species follow: Black-throated Green Warbler (Rabenold), Blackburnian Warbler (Chipley), and American Redstart (Bennett), in which the ecology and behavior of these species in breeding and wintering grounds are contrasted. Rappole and Warner review a detailed study on ecological aspects of bird

behavior at a specific study site (southern Veracruz, Mexico). Two papers on the comparative ecology of resident and migrant nectar-feeding hummingbirds follow (DesGranges and Grant; Feinsinger). General discussions of the evolutionary implications of habitat relations of migrants and residents by Stiles, and seasonal changes in migrant behavioral ecology (Morton) follow.

Five papers away from the main theme but of particular relevance in the evolutionary context conclude the series. These are the influence of meteorological patterns on trans-Gulf migration patterns (Buskirk); demographic aspects of long-distance migration (Greenberg); population limitation in migrants (Morse); migration relative to the regulation of bird numbers (Fretwell); food abundance (Janzen), and a comparative survey of Old and New World migrants (Karr).

We hope that this volume will answer some of the above questions and, especially, that it will provide the stimulus for much more research in this rich and diversified area of fast-shrinking avian habitat.

We are indebted to the staff of the N.Z.P. Conservation and Research Center at Front Royal for their help during the symposium and to Kathleen A. Lynch for her professional copy editing.

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The Conservation Status of Neotropical Migrants: Present and Future

ABSTRACT

There is far more reason to be alarmed about the status of land birds wintering in the neotropics than of water birds. Deforestation is occurring more rapidly than is destruction of water bird habitats.

About half of all land birds breeding in North America go to Mexico, the Bahamas, Cuba, and Hispaniola. Migrants commonly make up 50 percent of bird numbers in these northern areas and lesser percentages as one goes south into southern Middle America. Since many migrants are concentrated in winter, clearing 1 ha of forest in Mexico is probably equivalent to clearing 5-8 ha in northeastern United States.

Many migrant species prefer tropical highlands and these areas are rapidly being preempted for agriculture. Forest habitats are, in general, more important for many migrant species than was previously thought. Continued tropical deforestation will result in major reductions in many species.

Two-thirds of the breeding pairs of birds of many North American forests and woodlands migrate to the neotropics. The annual pilgrimages of this vast avian hoard to and from its tropical retreat are spectacles of such compelling richness and variety that they entice even the most indolent birdwatcher into the field. Yet in spite of our intense preoccupation with their goings and comings, it was not until comparatively recently that we took more than a casual notice of where all the birds go and what they do there.

This symposium, splendidly conceived in its timeliness, presents the first comprehensive information on both these questions, and offers the earliest glimpses of an overview of how more than 150 species sort themselves into their winter homes. My aim here is to draw upon the available information to formulate some broad generalities relating to the present and prospective conservation status of Neotropical migrants.

Before launching into specifics, I will preface my remarks with the qualification that apart from the following paragraphs, they will pertain to land birds only. The fact that only one of the 38 papers given at Front Royal digressed from a staple fare of land birds (Myers' article on shorebirds) suggests that this is where the main focus of interest lies. But more importantly from a conservation standpoint, there is far more reason to be alarmed about the status of land birds. It is the land in the neotropics that is being transformed before our eyes, not so much the water. Shorebirds, ducks, herons, terns, and others tend to scatter widely in the off season and to concentrate opportunistically wherever good feeding sites are discovered. Many live near or in salt water, which, relative to fringing land masses, is a virtually undisturbed environment. Local deterioration due to pesticide runoff or the sluicing of industrial wastes may result in the loss of some feeding areas, or even occasional mass die-offs. But a few widely scattered blots on the shoreline are unlikely to affect the status of whole species populations. It is only when persistent toxic chemicals such as DDT begin to contaminate the seas on a regional or global scale that whole populations become endangered. It is hoped that we are now alert to the threat of global contamination and prepared to take international action to prevent it.

As for the freshwater environments used by grebes, rails, gallinules, some waterfowl, herons, and others, most of these are not currently in serious jeopardy either. Wetlands beyond the limits of North America are largely intact. Drainage, filling, and canalization are in the main conveniences (vices?) of affluent societies. To be sure, there is cause for concern as marshes in Cuba, Colombia, and elsewhere are converted to

rice paddies, but as yet the transformation of wetlands has not reached the massive and near universal scale of deforestation. It is the consequences of deforestation that will be our primary concern.

Distribution of Migrants in the Neotropics

Before we consider the effects of habitat destruction per se, it will be helpful to have a general picture of where migrant land birds go. Prior to this symposium, one could have given only a vague account. Now there are some real data (table 1). In terms of absolute numbers, clearly near areas are preferred to far ones. Using the density of resident birds as a gauge against which to calibrate migrant concentrations, the role of distance as a decisive factor in the choice of wintering grounds is obvious. In Mexico and the Bahamas, migrants commonly make up 50 percent or more of the winter populations in a broad spectrum of both natural and disturbed habitats. Progressively more remote destinations in the Caribbean harbor fewer and fewer migrants: Hispaniola—20–40 percent (various habitats); Puerto Rico—10–20 percent; Lesser Antilles, Trinidad and Tobago—1 percent or less. A similar pattern holds along the Central American isthmus and into South America. Decreasing from the high proportions found in Mexico, values of 20–40 percent are reported for Costa Rica and Panama, of 5–15 percent for Colombia, of <1 percent for forested habitats in Venezuela, and presumptively similar values for Ecuador, Peru, and Bolivia.

It seems likely that as much as half of all the land birds that go south of the United States each winter funnel into Mexico, the Bahamas, Cuba, and Hispaniola, which offer a combined area of 2,175,000 km² as compared to 16,200,000 km² for North America south of the tree line. Rough as these numbers are, they strongly imply that many migratory populations are concentrated severalfold on their wintering grounds. In the case of shorebirds wintering on the Argentine pampas (which may be extreme) the concentration factor can be as much as 10 or more (Myers this volume). The obvious and unsettling implication of this is that the effects of tropical habitat destruction are amplified several times; clearing 1 ha of forest in Mexico is equivalent to expanding urban sprawl by perhaps 5–8 ha in the Northeast. With over half the natural vegetation of Central America and the Greater Antilles already converted to cropland and pasture, and the remainder disappearing at a rate of a few percent a year, we seriously face the prospect that suitable habitat will no longer be available for many migrant species by the end of the century (cf. Food and Agricultural Organization [FAO] estimates in the article by D. H. Morse).

While it may be true that forests are disappearing, it does not follow necessarily that the total amount of usable habitat for migrants is being reduced. Indeed, there is at least one sanguine forecast that opening up of the primary forest may result in a higher carrying capacity for migrants (Monroe 1970). Let us see how the information at hand bears on such predictions.

Habitats Used by Overwintering Migrants

There are two oft-repeated statements about the habitat choice of migrants in the neotropics that lie somewhere between myth and fact. They are that migrants concentrate at middle elevations (1,000–2,000 m; Miller 1963; Willis 1966; Leck 1972; Smith 1975) and in second growth, such as in fragmented woodlands and along edges, more than in primary vegetation (e.g., Slud 1960; Willis 1966; Karr 1976). Results of this symposium provide a basis for evaluating both statements.

Middle Elevation vs Lowlands

The conventional wisdom here appears to be true for some areas and not for others. In west central Mexico, for example, the situation seems quite the reverse. High concentrations of migrants winter in the Pacific lowlands, and declining numbers occur in the interior plateaus and mountains (Hutto this volume). At this latitude (ca 20°N), winter temperatures may be low enough at elevations above 1,500 m to depress insect activity, an interpretation that is in accord with Hutto's data. In southern Mexico (latitude 16–18°), it is probable that larger numbers of migrants occur in the mountains. However, the lowlands at this latitude harbor impressive concentrations (up to >50 percent; Waide et al this volume) so that numbers in the highlands are unlikely to be noticeably higher. In Hispaniola and Jamaica, the only two Caribbean islands with appreciable areas above 1,500 m, the density of migrants appears to be nearly independent of elevation (Terborgh and Faaborg this volume; Lack and Lack 1972).

The initial impressions that migrants prefer highlands came from studies in Panama, Costa Rica, and northern South America. In these regions the generalization does indeed seem to stand up (e.g., Tramer and Kemp; Orejuela et al; Russell; Johnson, all this volume). The reasons for the attraction of mountain habitats at these latitudes is obscure. While a more amenable winter temperature regime may contribute to the preferential concentration of individuals in the northern Mexican lowlands, it is clear that a different explanation will have to be invoked to account for the

pattern at lower latitudes. Migrants abandoned a tract of lowland thorn scrub in Colombia when the vegetation became leafless with the onset of the dry season (Russell this volume). Several sets of measurements agree that insect densities in Panama and Costa Rica reach an annual minimum in the December to March dry season (Janzen 1973; Smythe 1974; Ricklefs 1975; Buskirk and Buskirk 1976). Perhaps the impact of seasonality is reduced at higher elevations, with a consequently better and more reliable supply of harvestable resources. Moreover, Janzen (1973, 1976) has found, both in Costa Rica and in Venezuela, that insect densities are substantially higher in mid-elevation vegetation than in the lowlands or at very high elevation (>2,500 m). This may well be the decisive consideration, because an individual bird's feeding rate will depend, more than on anything else, on the absolute abundance of available prey. Other things being equal, one would expect wintering birds to concentrate in regions offering the greatest abundance of food resources. The number of competitors becomes important only when prey are at low density or are being exploited at greater than the recruitment rate.

There is little consolation to be had in the finding that large numbers of migrants do winter in tropical highlands, for it is the highlands that are preferentially preempted for agricultural use (Monroe 1970; Howell 1970; Terborgh 1977). Very little natural vegetation remains between 1,000 m and 2,000 m in Hispaniola, southern Mexico, the central Andes of Colombia, the Pacific slope of Costa Rica, and Panama, for example, and what little remains in other areas is being rapidly reduced. Thus, one prediction that can be made with confidence is that species which use or concentrate in primary forest in the neotropical highlands can be expected to be among the first to come under heavy pressure due to loss of habitat (e.g., Blackburnian Warbler, Black-throated Green Warbler, Cerulean Warbler).

Primary Vegetation vs Disturbed Habitats

Another oft-repeated assertion is that migrants gravitate to disturbed sites such as clearings, second growth, and edges, because such places are presumptively underutilized by resident species (Willis 1966). Some support for this impression is contained in data presented in this volume by Emlen (Bahamas), Hutto (Western Mexico), Pearson (Ecuador, Peru, Bolivia), Waide (Southern Yucatan), and Willis (Panama). All these results are concordant in showing greater concentrations of migrants in disturbed or successional vegetation than in nearby undisturbed tracts. However, in some other regions, migrants seem to be

Table 1. Proportional representation of North American migrants in winter bird populations in the neotropics

<i>Location</i>	<i>Elevation¹</i>	<i>Vegetation</i>	<i>Method²</i>	<i>Number of sites</i>
Middle America				
West Central Mexico	Low	Gallery forest	Strip count	2
" " "	"	Mangrove	" "	3
" " "	"	Plantation	" "	1
" " "	"	Second growth	" "	2
" " "	"	Forest edge	" "	1
" " "	"	Thorn scrub	" "	2
" " "	"	Tropical deciduous forest	" "	2
" " "	Mid	Oak woodland	" "	3
" " "	"	Pine-oak	" "	5
" " "	"	Pine	" "	1
" " "	High	Pine-oak-fir	" "	2
" " "	"	Fir	" "	1
North Yucatán	Low	Disturbed	" "	3
" " "	"	Partly disturbed	" "	3
" " "	"	Semi-deciduous forest	" "	3
Campeche	"	Old field	Nets	3
"	"	Semi-evergreen forest	"	3
Yucatán Peninsula	"	Semi-evergreen forest	"	2
" " "	"	Semi-evergreen forest	Strip count	8
Costa Rica	Mid	Disturbed	? ?	?
" " "	"	Cloud forest	?	?
Panama	Low	Moist forest	Nets	1
" (Canal Zone)	"	Late scrub	"	1
" " "	"	Disturbed forest	"	1
Panama (Puerco Island)	Low	Semi-deciduous forest	Nets	1
" (Canal Zone)	"	Moist forest	Strip count	1
" " "	"	Dry forest	" "	1
" (Barro Colorado Island)	"	Moist forest	" "	1
" " "	"	Young moist forest	" "	1
" " "	"	Scrub	" "	1
" " "	"	Grass, trees	" "	1
" " "	"	Lake edge	" "	1
" " "	"	Marsh	" "	1
Caribbean Islands				
Bahamas	"	Mature pines	Strip count	?
"	"	Young pines	" "	?
"	"	Old fields	" "	?
"	"	Broadleaf thicket	" "	?
"	"	Marsh	" "	?
"	"	Mangrove flat	" "	?
"	"	Coastal dunes	" "	?
Jamaica	"	Dry limestone forest	" "	?
"	"	Arid limestone scrub	" "	?
"	"	Cut over arid scrub	" "	?
"	"	Cut over limestone forest	" "	?
"	"	Secondary limestone forest	" "	?
"	"	Riverine forest	" "	?
"	"	Gardens, etc.	" "	?
"	Mid	Gardens, etc.	" "	?
"	High	Gardens, etc.	" "	?
"	Low	Mangroves	" "	?
"	"	Evergreen forest	" "	?

Percentage
migrants³

Reference

68	Hutto ⁵
81	"
51	"
62	"
48	"
57	"
19	"
33	"
43	"
32	"
24	"
37	"
34	Tramer 1974
22	" "
26	" "
54	Waide ⁶
38	"
53	Waide et al. ⁶
29	" " "
20-30	Tramer & Kemp ⁶
<5	" " "
5	Karr 1976
4	" "
7	" "
25	Karr 1976
6	Hespenheide ⁶
18	"
8	Willis ⁶
17	"
100?	"
24	"
17	"
8	"
39	Emlen ⁶
28	"
40	"
43	"
47	"
50	"
50	"
31 ⁴	Lack & Lack 1972
21 ⁴	" " " "
5 ⁴	" " " "
42 ⁴	" " " "
32 ⁴	" " " "
33 ⁴	" " " "
13 ⁴	" " " "
29 ⁴	" " " "
16 ⁴	" " " "
49 ⁴	" " " "
33 ⁴	" " " "
13 ⁴	Lack & Lack 1972

equally abundant in various types of primary and secondary vegetation, e.g., Bahamas [Emlen, this volume], Jamaica [Lack and Lack 1972], northern Yucatán [Tramer 1974]). But before we jump to the conclusion that habitat destruction is not a serious threat to migratory populations, let us consider how such findings should be qualified.

First, we should be aware that only minor quantitative differences in the proportions of migrants are involved. In some instances, this could be explained by the presence of relatively fewer residents as well as by increased absolute densities of migrants.

Another, and far more vital consideration, is the identity of the species themselves. It is not surprising that large numbers of Palm Warblers, Yellow Warblers, Orchard Orioles, and Indigo Buntings can be found in settled areas and in early successional growth. But such species are not at present a source of concern. It is the species that shun disturbance that are being threatened by deforestation, and there are a large number of these (table 2). A sizeable fraction of our migrants are intrinsically forest-dwelling species. Those that nest in forest tend to winter in them as well, although on the wintering grounds some of them may be able to make greater opportunistic use of edges and openings than is the case when they are confined to breeding territories.

Finally, it is necessary to take into account the relative areas, and the rates of change in area, of suitable wintering habitat. The weight given to different types of vegetation in the census data reported in this volume is surely biased. Not one observer reported on the birds seen in a fenced cattle pasture, canefield, or rice paddy, yet a large and increasing fraction of the land in tropical America is being occupied by "habitats" such as these. The emphasis on "edge" is certainly exaggerated by the frequency with which roads and paths pass along them, indeed, create them. Unbroken expanses of forest are often inaccessible, lacking trails, and present serious impediments to the ease of bird detection, especially in the canopy. Even if edges and second growth do contain greater concentrations of birds, their combined area in the neotropics as a whole is still a small fraction of that of semi-mature to mature forest. This means that most individuals are wintering in mature vegetation, as Pearson (this volume) has rightfully emphasized, notwithstanding their somewhat greater dispersion.

Land-Use Trends in Temperate and Tropical America and Their Implications for Migratory Populations

Since the arrival of settlers in North America, all but perhaps 1 percent of the landscape east of the great plains and south of 50° latitude has been logged, and

Table 1. (cont.)

<i>Location</i>	<i>Elevation¹</i>	<i>Vegetation</i>	<i>Method²</i>	<i>Number of sites</i>
Jamaica	Mid	Evergreen forest	Strip count	?
"	High	Evergreen forest	" "	?
"	Low	Riverine forest	" "	1
Hispaniola	"	Moist forest	Nets	1
"	Mid	Moist forest	"	2
"	Low	Limestone forest	"	2
"	"	Arid scrub	"	1
"	"	Open pine forest	Strip count	2
"	Mid	Open pine forest	" "	2
"	High	Open pine forest	" "	1
"	Low	Limestone forest	" "	2
"	"	Secondary scrub	" "	2
"	"	Arid thorn scrub	" "	2
Puerto Rico	"	Limestone scrub	Nets	1
(Mona Island)	"	Limestone scrub	"	1
St. Kitts	"	Montane forest	"	1
" "	"	Shrubby field	"	1
Montserrat	"	Montane forest	"	1
Guadeloupe	"	Montane forest	"	1
"	"	Sclerophyll scrub	"	5
Dominica	"	Montane forest	"	1
Trinidad	Low	Moist forest	"	1
"	"	Semi-deciduous forest	"	1
"	"	Shrubby field	"	1
Tobago	"	Secondary forest	"	1
"	"	Maritime forest	"	1
San Andres	"	Disturbed scrub	"	1
South America				
Northern Colombia	Low	Thorn scrub	Nets	1
" "	"	Mangroves	"	1
" "	"	Disturbed forest	"	1
" "	Mid	Cloud forest	"	1
Southern Colombia	Low	Wet forest	"	1
" "	"	Dry forest	"	1
" "	Mid	Cloud forest	"	1
" "	Low	Wet forest	Strip count	1
" "	"	Dry forest	" "	1
" "	Mid	Cloud forest	" "	1
" "	"	Disturbed oak forest	" "	1
Northern Venezuela	Low	Deciduous forest	Nets	1
" "	Mid	Montane forest	"	1
" "	High	Montane forest	"	1
Ecuador	Low	Moist forest	Strip count	1
"	"	Secondary vegetation	" "	1
Peru	"	Evergreen forest	" "	1
"	"	Secondary vegetation	" "	1
Bolivia	"	Evergreen forest	" "	1
"	"	Secondary vegetation	" "	1

¹ Low 0–1,000 m; Mid 1,000–2,000 m; High >2,000 m.² Included under strip count are many individual variants; most commonly an observer walks slowly along a course, recording all individual birds detected, whether seen or heard.³ Percentage of North American migrants in the total of all birds detected.⁴ Lack and Lack recorded the percentage of migrants among passerines only, hence their figures are higher than would be the case if they had included all birds (as nearly all migrants in Jamaica are passerines).⁵ Pearson only provided encounter rates (in birds per hr) for migrants, with no data on residents.⁶ This volume.

<i>Percentage migrants³</i>	<i>Reference</i>
17 ⁴	Lack & Lack 1972
38	Gochfeld 1979
46	Terborgh & Faaborg ⁶
22	" " "
31	" " "
3	" " "
29	" " "
40	" " "
28	" " "
16	" " "
25	" " "
3	" " "
14	" " "
7	" " "
1	" " "
4	" " "
0.5	" " "
2	" " "
0.4	" " "
0	" " "
0	" " "
0	" " "
1	" " "
2	" " "
1	" " "
32	Russell & Johnson ⁶
(Oct–Nov) 24	Russell & Johnson ⁶
(Dec) 0	" " "
46	" " "
6	" " "
5	Hilty ⁶
0	Orejuela et al. ⁶
24	" " "
14	" " "
0	" " "
22	" " "
14	" " "
46	Chiple ⁶
2	Terborgh & Faaborg ⁶
0	" " "
0	" " "
0.29b/h ⁵	Pearson ⁶
5.29b/h	"
0.07b/h	"
2.68b/h	"
0.00b/h	"
0.16b/h	"

most of it has been cleared at one time or another. The west has not been ravaged to the same extent because of the low agricultural potential of most naturally forested land in that part of the continent. At no time has the total extent of forest in North America decreased to less than half the original amount. Many eastern states report increasing amounts of forest cover, often exceeding 50 percent of their areas (Aldrich and Robbins 1970). Drastic alterations in the ratio of forested to open land since colonial times have certainly had profound impacts (both positive and negative) on the abundances of many terrestrial species. Many distributions have also changed, although historical documentation is scanty. Taking North America as a whole, the total acreage in forest has decreased by perhaps 30–40 percent since pre-Columbian times. We can expect proportional reductions in the populations of most forest-dwelling birds. Further reductions have probably occurred in some regions due to the fragmentation of forest into discrete woodlots. A growing body of evidence indicates that these insular patches do not provide acceptable habitat for many obligate forest birds (Forman et al 1976; Galli et al 1976; Whitcomb et al 1976; Whitcomb 1977). Species whose population centers lie in the crowded and highly agricultural states of the mid-Atlantic region and Midwest will of course have suffered by greater margins than those that occupy the comparatively undisturbed boreal regions and western mountains.

The wave of agricultural settlement that passed across eastern North America in the nineteenth century did not lead to permanent occupancy because of the availability of even more productive lands farther west. The effects on our forests were partial, transitory, and spread out over more than a century. Such cannot be said of the tropical regions that constitute the winter homes of many forest-dwelling migrants. Settlement of new land is being propelled by rapid population growth, just as it was in nineteenth-century North America, but population densities in many countries are well above current, much less historical, North American levels. Moreover, the best terrain is already under cultivation, and settlement is being pushed by hunger and crowding onto ever more marginal soils and steeper slopes. In my experience, clearing is not selective and confined to the richest hollows as it was, say, in the Appalachians, but instead it advances as a front that consumes the entire landscape, except perhaps for the steepest ridgetops and ravines. Even these are often subject to gradual denudation as the sole remaining sources of firewood in the landscape.

After a few cycles of cropping, cattle or goats are turned onto the land which is periodically burned to

keep the weeds in check. I could see this pattern plainly in a recent flight along the Pacific slope of Panama from David to Tocumen. Cattle raising has taken over the whole scene; the land is being used just as intensively as it is in Illinois or Iowa; little or no forest remains, and there is very little that could be called second growth. The Dominican Republic is in much the same state, and Haiti is even worse. Environmental deterioration has not progressed so far in some countries (Guatemala, Nicaragua) but with accelerating population pressure everywhere, it is only a question of time.

The notion that second growth will provide a haven for migratory populations is, I think, largely fallacious. Current land-use practices in tropical America may favor a few species, such as the Yellow Warbler and Indigo Bunting as I suggested above, but most migrants prefer tree crowns or the cool dark recesses of the forest interior. The habitat requirements of the latter categories of species are not met by shrubby pastures or canefields.

Because most migrant species and individuals are essentially forest dwelling birds, it seems clear that the gross carrying capacity of the neotropics is decreasing. This is evident in the FAO statistics quoted by Morse which show that the sum total of primary and secondary forest is declining rapidly as ever greater areas are brought under cultivation or converted to pasture. Even with no acceleration in the rate of deforestation over the 1955-70 average, the remaining primary forest in Central America will have disappeared completely by the end of the century unless control measures are promptly instituted. This presents a gloomy prospect for migrant and resident species alike.

The likelihood that conditions will stabilize, as they have in North America, with a sizeable portion of the landscape covered by middleaged second growth, seems remote. Under the traditional system of slash-and-burn agriculture, such an equilibrium was possible; indeed it existed in parts of a number of countries. However, the current trend is away from extensive land-use practices and toward more intensive ones. A shifting slash-and-burn economy was possible in low density peasant cultures, or on the frontier. But the frontier era is coming to an end in much of tropical America today, just as it did in North America about a century ago. Central governments are extending their control and services into the remotest villages. Increasingly, land is coming under title, and rural peasants are adapting to a more sedentary way of life for the sake of being close to roads, villages, and schools. These structural transformations in rural society assure ever more intensive exploitation of the landscape.

Table 2. North American migrants wintering in mature tropical forest¹

Mississippi Kite	Blue-winged Warbler
Swallow-tailed Kite	Bachman's Warbler
Broad-winged Hawk	Tennessee Warbler
Chuck-will's-widow	Parula Warbler
Whip-poor-will	Magnolia Warbler
Yellow-billed Cuckoo	Cape May Warbler
Black-billed Cuckoo	Townsend's Warbler
Yellow-bellied Sapsucker	Black-throated Green Warbler
Great Crested Flycatcher	Hermit Warbler
Yellow-bellied Flycatcher	Black-throated Blue Warbler
Acadian Flycatcher	Cerulean Warbler
Western Flycatcher	Yellow-throated Warbler ³
Eastern Wood Pewee	Grace's Warbler ³
Western Wood Pewee	Blackburnian Warbler
Wood Thrush	Chestnut-sided Warbler
Swainson's Thrush	Bay-breasted Warbler
Gray-cheeked Thrush	Blackpoll Warbler
Veery	Ovenbird
Blue-gray Gnatcatcher	Northern Waterthrush ²
Solitary Vireo	Louisiana Waterthrush
Yellow-throated Vireo	Kentucky Warbler
Red-eyed Vireo	Hooded Warbler
Philadelphia Vireo	Canada Warbler
Black-and-white Warbler	American Redstart
Prothonotary Warbler ²	Western Tanager ³
Swainson's Warbler	Scarlet Tanager
Worm-eating Warbler	Hepatic Tanager ³
Golden-winged Warbler	

¹ Many of the species listed have broad habitat tolerances and may winter in middleaged second growth, such as along borders. Only a relative few show strong partiality for undisturbed forest.

² Primarily in mangroves.

³ Primarily in pines.

Other trends reinforce this projection: continued population growth, replacement of labor-intensive farming by capital-intensive agriculture, rising land values, and the existence of inexhaustible export markets for certain commodities, notably timber and beef.

Prospectus

What do these trends presage for the future? Certainly the amount of habitat that is attractive to migrants will diminish, probably drastically. Even generous allotments for parks and reserves will not prevent a very major deterioration of the overall picture. The

best that could be hoped for would be 10–20 percent of the land under some kind of protected status. Because migrant populations are already more crowded on their wintering grounds than in their summer ranges, this amounts to little more than a token solution.

One could anticipate that the landscape of a typical Middle American country by the end of the twentieth century might resemble that of one of our more crowded eastern states. Consider, for example, my own, New Jersey, with a population density of 370 persons per km². Virtually all its prime land is under cultivation or engulfed by urban sprawl. Sizeable tracts of forest persist in only two areas of negligible agricultural value. These are the pine barrens and the series of steep rocky ridges transecting the northwestern corner of the state. Elsewhere, the existing forest is highly fragmented into scattered woodlots that show conspicuous signs of pathology with respect to their nesting birdlife (Forman et al 1976; Galli et al 1976). To the extent that it is permissible to project this pattern onto developing countries, we can anticipate that the land will be exploited to the fullest except where rugged topography or infertile soils raise cost/benefit ratios to prohibitive levels. Something akin to natural vegetation will persist longer in the least desirable sectors of the landscape, but eventually the demands for charcoal, firewood, building materials, and ultimately goat range will overtake even the most inhospitable terrain, as indeed they already have in Haiti. This final stage of utter devastation seems to set in when rural population densities reach approximately 150 persons per km.² Some countries (El Salvador, Haiti, Jamaica) have already passed this threshold, while others are only a generation or two away from it. The situation may not be desperate yet, but there is no room for complacency.

Reforestation, as currently practiced in tropical countries, offers little hope of restoring useful habitat to overworked lands. Monocultures of exotic species such as pine, eucalyptus, and teak are notoriously barren of birds. Coffee and cacao plantations provide far more amenable environments. Mixed silviculture, which at this point in the tropics is more a dream than a reality, would go a good step further.

Another source of relief would be possible if some species could shift the focus of their populations into less-disrupted portions of the tropics. This is a plausible prospect for a few species, such as Swainson's Thrush, Black-and-white Warbler, and Redstart that winter from Mexico well into South America, and which demonstrably possess the ability to live in sympatry with a broad spectrum of potential competitors. The winter ranges of many others, however, are far more

limited, and appear frequently to be constrained by the presence of close competitors in adjacent regions (c.f. Fitzpatrick, Keast, Terborgh, and Faaborg, this volume). It is unlikely that many of these would be successful in accomplishing major range shifts.

Conclusion

My own assessment of the situation is that continued deforestation in the near neotropics will result in major reductions in the numbers of many forest-dwelling migrants. We are, in effect, about to play observers in a massive experiment in which there will be dramatic alterations in the relative population sizes of numerous common species. No one can yet say which species will be most affected, or what all the consequences will be.

The most obvious prediction is that in North America permanent residents and temperate migrants will be enabled to expand their populations in substitution for missing tropical migrants. There are already signs that this is taking place in some fragmented eastern woodlands (Whitcomb et al 1976; Whitcomb 1977). We can expect further that the species most versatile at wintering successfully in a wide variety of disturbed habitats will be able to expand into niches left vacant by competitors with more inflexible requirements for mature vegetation. It would be risky to go beyond this level of generality in making more specific predictions. No species, except perhaps for the Bachman's and Kirtland's Warblers, seems under imminent threat of extinction (Terborgh 1973). Indeed, for the foreseeable future, the possibility of outright extinctions seems remote. Some species will surely become rarer, others more abundant. The total biomass of birds breeding in the North American continent will probably change little. What will change is the familiar ambience of our forests in springtime. It just won't sound the way it used to.

Literature Cited

- Aldrich, J. W., and C. S. Robbins.
1970. Changing abundance of migratory birds in North America. In: *The Avifauna of Northern Latin America*, eds. H. K. Buechner and J. H. Buechner, Smithsonian Contrib. Zool. 26:17–25.
- Buskirk, R. E., and W. H. Buskirk
1976. Changes in arthropod abundance in a highland Costa Rica forest. *Amer. Midland Natur.* 95:288–98.
- Chipley, R. M.
1976. The impact of wintering migrant wood warblers on resident insectivorous passerines in a subtropical Colombian oak woods. *Living Bird* 15:119–41.

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Some Considerations on Migratory Birds

ABSTRACT Migrant species should not be considered "invaders" to the tropics but as species that have tropical niches the same as resident species.

When reading publications relating to the question of the role of migrant birds in tropical ecosystems, and in conversations on this topic, I have been impressed by the apparent belief that such migrants must constitute a rather disturbing force on their wintering grounds. The word impact is used generally, and the migrants are not infrequently referred to as invaders. To some degree this may be a matter of semantics, but it is evident that the implication is in full accord with the basic meaning of the words impact and invader. That implication is not consistent with the true situation.

I make clear that my field work has not been directed specifically to the question at hand. Beginning some 20 years ago, however, I conducted a 6-year study of the Northern Waterthrush (*Seiurus noveboracensis*) on its wintering grounds in northern Venezuela. That study included some work with the American Redstart (*Setophaga ruticilla*) and observations of other migrants from North America. At that time considerations of interspecific competition in regulating animal distributions, now prominent in ecological and speciation research, had barely entered the scene. My investigation was motivated by a desire to determine concretely, using banded birds, if wintering migrants showed intraspecific territoriality and if so whether they returned to occupy the same territories in successive years. Circumstantial evidence from previous observations had suggested that might be the case.

Among the results of that study I found that individual Northern Waterthrushes were commonly present on their winter territories for at least six months and some American Redstarts for at least seven months (Schwartz 1964:172-75). Note that these are residence times of individual birds. The species as a whole is present in northern South America more than eight months. This long period of residence becomes even more significant when we consider that it includes that portion of the year, the dry season, when the food supply for many birds is at a minimum level.

Competition, Resource Levels, and Migrant Niches

At the lower elevations subject to a strong seasonal influence, the depression of resources, at least for insectivorous birds, is readily apparent to the human observer. In riparian or analogous situations, or in montane regions where cloud cover maintains an evergreen vegetation, a depression of such resources is less apparent, but it is necessary only to experience the resurgence of invertebrate life with the return of the rains to realize that there is fluctuation in invertebrate abundance in the annual cycle in the evergreen montane areas.

I shall not discuss the why and how of migration. It is enough for our consideration to think that present

patterns of migration and of seasonal climate and resource availability have probably been in effect for thousands of years; and at some time or times in the past the now-migratory species or their ancestral forms may have been resident in tropical areas for even longer periods.

At some times in the past, probably relating to the times of glaciation, the normal processes of evolution have determined which species have survived and the ecological niches they have forged for themselves. The now-migratory species have been subject to selective pressures in the tropics, and in many of the same places, as have the species that are tropical breeding residents. Together with the tropical breeding species, they have been subject also to the effects of climatic cycles that resulted in significant contractions and expansions of wooded areas in the tropics. In that competitive situation, some now-migratory birds won their place, and it seems probable they may have done so at the expense of some tropical breeding residents. Those niches won are still occupied by their winners for almost 70 percent of the year and have been so occupied every year for thousands of years. The competitive situations just mentioned involved not only migratory species vs tropical breeding species but also interspecies interactions among the migratory species themselves (and among the tropical breeding species themselves) which have bearing on the tropical distributions as we find them today.

During the relatively short annual absences of the waterthrush and the redstart I have not seen that their niches are occupied by tropical breeding residents. It should not be inferred from this that these are necessarily marginal niches. They are obviously rewarding niches in communities of dozens of resident breeding species that would almost surely include one to occupy these niches if they had not been won by the migratory species in ecological evolutionary history.

Besides the waterthrush and the redstart, several other migratory species appear to be intraspecifically territorial or competitive in their tropical homes, to judge from circumstantial evidence in casual observation over many years' field work in Venezuela. I have not observed active competition between these species and tropical breeding residents. That some tropical breeding species may sometimes or in some places forage in niches temporarily abandoned by migratory species is not grounds to suppose that they are otherwise being crowded out by migrant "invaders." They may be only exploiting opportunistically a resource area to which they do not have access during the major portion of the time, one that does not really belong to them. It is possible that in some regions seasonal replacement may even have evolved as a fixed

pattern. It is difficult to evaluate this aspect today. Man-wrought changes to natural tropical habitats during the past 100 years (or longer), and especially during the past 15–20 years, have altered conditions to the extent that we are today witnessing a new chapter in ecological evolution.

Of course, not all migratory species (nor all tropical breeding species) are individually territorial in fixed areas during their nonbreeding period. Some, such as the Tennessee Warbler (*Vermivora peregrina*), are partially or largely nectar or fruit eaters. Social behavior and flexible mobility are apparently the most successful strategies for exploiting such resources, which may provide abundant food but are spatially and temporally scattered (Morton 1971; Snow 1971, 1976:72–74). Flocking by some largely insectivorous birds has also, no doubt, its reason for being.

The concepts of impact and invasion are, of course, associated primarily with the time of fall migration, the idea being that, at a time of year when the tropical ecosystem is presumably already saturated with the resident breeders and their offspring of the year, it is invaded by a horde of migrants. The real situation does not conform to that concept.

In those regions subject to seasonal influence, the period of minimum resource availability (the dry season) almost certainly constitutes an important force regulating the density of populations. Even assuming saturation at the minimum resource level, given the low reproduction rate of tropical breeding birds, the population can not expand itself in one season to exploit fully the “normal” resource level; and, anyway, it seems probable that this could be undesirable, as suggested by Willis (1966: 221). The result is that vast portions of habitat apparently appropriate to one or another species are not occupied during the periods of normal abundance (the rainy season). In much of the lower north Tropical Zone, north of the equatorial rain belt, September and October are among the months of greatest rainfall. Insect life, while not at its maximum, is still ample. There are also fruiting and flowering trees. Therefore, at the time of fall migration the tropical ecosystem is in a state of normal abundance and is not saturated by the tropical breeding birds. This, however, is largely irrelevant, for as previously mentioned the tropical breeding species and the migratory species have their respective niches long since established.

The competition during the fall migration is among the migrants, mainly if not entirely at the intraspecific level in recent time. Even this is less than it might seem, for not all the migrants arrive simultaneously; they are spread over a period of two months or more centering around mid-October, so that some migrants

of passage have already left a given area before others arrive. And at this time resources are still at normal levels. It is after this time that any separation due to competition occurs. The birds most affected are the offspring of the year. During the previously mentioned Northern Waterthrush study, I could see year after year the effect on November population levels as habitat deteriorated in December and January with the advancing dry season. Bear in mind that those birds over a year old that survive to return to their tropical homes have territories awaiting them that have been proven to hold valuable resources the previous year(s). Besides, the birds have learned something of the hazards and dangers in those territories. Not all losses are attributable directly to insufficient resources; many, maybe most, may be due to inexperience. Under deteriorating conditions, the young birds are continuously more exposed than the old birds to new, unknown conditions.

With regard to the long-running debate as to why birds breeding in northern regions lay more eggs than their tropical breeding counterparts, it has been suggested that an important pressure leading to this may be losses sustained in competition on the tropical wintering grounds. So far as it concerns migratory species I have long believed, and the little evidence available suggests although it cannot prove it, that the most important pressures contributing to evolution to larger clutch size in northern breeders relate directly to the migration process itself. To the obvious hazards deriving from various variable natural phenomena, we may add individual variation in preparation for the migration: individual birds, perhaps influenced by the behavior of their fellows, depart on migratory flights before they are physiologically fully prepared. Also, during the transient period of migration not only the young but also the older individuals are frequently exposed to the inexperience factor in regions where they may descend briefly or through which they may travel during their movements between their tropical homes and their breeding grounds.

Several other topics could be developed under the general theme treated in this paper, but they would do little more than illustrate the many manifestations of the evolutionary process; or would amount mainly to mental exercise, for the fact is that we know little or nothing of the basic material thrown into the process at its beginning. The important point to be made is that during two-thirds of the year, including the periods of least resources for insectivorous birds, the neotropics harbors and has harbored for thousands of years an avifauna that is best treated as a single unit. Some of the species of that avifaunal unit depart for a brief period each year to reproduce. They return to

the tropics not as invaders with a disturbing impact but to their long-ago won places.

Literature Cited

Morton, E. S.

1971. Food and migration habits of the Eastern Kingbird in Panama. *Auk* 88:925-26.

Schwartz, P.

1964. The Northern Waterthrush in Venezuela. *Living Bird* 3:169-184.

Snow, D. W.

1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113:194-202.

Snow, D. W.

1976. *The Web of Adaptation*. New York: Quadrangle/New York Times.

Willis, E. O.

1966. The role of migrant birds at swarms of army ants. *Living Bird* 5:187-231.

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The Pampas Shorebird Community: Interactions Between Breeding and Nonbreeding Members

ABSTRACT The shorebird community in coastal Buenos Aires Province, Argentina, includes nonbreeding migrants from North and South America as well as locally nesting species. Data indicate that the nonbreeding birds are numerically dominant through the year, and that they have major effects on the breeding community: 1) local breeders are taxonomically and ecologically distinct from migrants present during the breeding season; 2) those that migrate south from coastal Buenos Aires Province wintering grounds to breed in Patagonia in austral spring are more similar to North American migrants (present during austral spring and summer) than are species which do not leave; 3) the distributions of several potential competitors among South American (breeding) and North American (nonbreeding) species resemble geographic replacement patterns, and 4) aggressive interactions occur repeatedly between North and South American species. High densities of nonbreeding birds may prevent scolopacids from establishing local breeding populations: breeding attempts would be unsuccessful because of behavioral and competitive interactions with "wintering" scolopacids. Patterns in resource use by migrants vs resident shorebirds do not support the generalization that migrants depend on more ephemeral resources than do residents.

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Hawk and Vulture Migrations in the Neotropics

ABSTRACT

Nearly all Swainson's and most migratory Broad-winged Hawks pass through Panama during October–November along with Turkey Vultures. Broad-winged hawks spend four months breeding, six months in the tropics and two months on migration. Swainson's Hawk spends four months breeding, four months in South America, and four months on migration. Migrant and resident Turkey Vultures coexist in Panama during November to April.

Thermal soaring is the dominant flight strategy for migration. Heights of 3,600 to 4,000 m are commonly attained, occasionally 6,400 m.

Few aggressive interactions are seen even though large concentrations occur. Migrating Swainson's Hawks and Turkey Vultures were not seen to feed.

Numbers for the three species, censused by photography, were 958,634 in 1972 and 871,286 in 1973. Competition for Broad-winged Hawks that remain in Panama is mainly intraspecific. Use of invertebrate food is characteristic of migratory birds.

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Wintering of North American Tyrant Flycatchers in the Neotropics

ABSTRACT

Twenty-two of 32 flycatcher species winter south of their North American breeding ranges. Only 8 reach South America where no more than 6 are sympatric. Most flycatchers winter in habitat similar to breeding habitat. Food and social habits are discussed.

In some places, migrant species use peripheral habitats, in others, resident species seem peripheral. In Mexico, migrants may prevent the northward spread of more southerly species.

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Patterns of Ecological Interactions Among Migrant and Resident Vireos on the Wintering Grounds

ABSTRACT

Basic adaptive patterns minimize interspecific competition among migrant and resident vireos. Eleven of the 43 vireo species breed in North America. Competition is reduced by foraging differently and in different strata, habitat differences, and spatial separation.

Winter ranges and habitats are described and a history of vireo distribution and migration patterns is suggested.

Spatial Relationships Between Migratory Parulid Warblers and Their Ecological Counterparts in the Neotropics

ABSTRACT

Consideration of the spatial relationships of the migratory and resident parulids in winter shows that: 1) geographic and habitat separation of congeneric species amongst the migrants is marked; 2) a significant segment of migrants winter at the southern limits of the nearctic region, i.e. do not "compete" with resident neotropical birds, and there is a marked north-south attenuation in numbers of species and absolute numbers of migrants southward through central America and into South America; 3) this attenuation matches a progressive increase in numbers of small foliage-gleaning tyrannids, greenlets, etc., the ecological counterparts of the parulids in Neotropica proper. This also applies to formicariids and furnariids, but these larger-bodied (and especially larger-billed) birds mainly occupy different feeding zones from the parulids; 4) where migratory and resident species of parulids co-occur they tend to differ either in feeding zone or habitat. There are, however, foliage gleaners and low-shrub dwellers among both in the highland areas of central and northern South America; 5) spatial and ecological separation patterns between migrant and resident warblers, and between the various species of migrants, are sufficiently clear-cut to indicate a long period of coevolution. In this respect, it can be noted that the migratory warblers spend six to seven months of the year in their wintering grounds.

Interactions of Migrant and Resident Land Birds in Florida and Bahama Pinelands

ABSTRACT

Florida and the northern Bahama Islands experience a heavy invasion of northern land-bird migrants each winter. At a series of 13 pine forest sites in 1971 community densities (sum of all species densities) were more than doubled in Florida and nearly doubled in the Bahamas. The number of species was nearly doubled at most sites. Bird species diversity (H') remained essentially unchanged due to the low equitability of the migrant element. The proportion of migrants was higher in open habitats than in forests, higher in tree crowns than in shrubs, and higher in the aerial and ground insectivore guilds than in the granivore and bark-gleaning guilds. Migrant and resident species were similar in the amplitude of their dispersion through the habitats, compartments, and guilds.

Analyses of these distribution and abundance patterns suggest that the mixed winter assemblages of migrant and resident species represent full, integrated ecological communities and that resident species do not fill the available niche space after the migrants leave. Winter integration is considered to have evolved by selective processes of displacement and extinction; few traces of unresolved competition persist. Food shortage is probably not a critical factor in population regulation for most species and guilds. Habitat complexity is seasonally stable, a factor that may account for the stability of bird species diversity (H') in the face of marked seasonal changes in species richness and in population density.

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Factors Affecting the Distribution and Abundance of North American Migrants in the Eastern Caribbean Region

ABSTRACT

In the first part we evaluate several factors that could plausibly affect the abundance and distributions of overwintering populations in the eastern Caribbean region. These are: climate, distance from the North American mainland, size of landmass, density of resident species, and habitat quality.

The fraction of North American migrants in winter bird populations in the Caribbean region shows a strong inverse dependence on distance from the mainland (Florida). The mean value for a large array of censuses in Hispaniola is roughly 35 percent. The incidence of migrants drops toward the east to ca 10 percent in Puerto Rico and to 1 percent or less in more distant locations: Lesser Antilles, Trinidad, Tobago, and the Venezuelan mainland.

Area effects are difficult to factor out of the data because of the tight negative correlation between island area and distance from the mainland in the Greater and Lesser Antilles. Nevertheless, comparisons of nearby large and small islands do reveal a moderate tendency for migrants to gravitate to larger islands, although the number of comparisons is insufficient to permit a quantification of the tendency. The major factor controlling the abundance of migrants is clearly the combined effect of area and distance: the diminishing returns to be realized in flying farther and farther to reach smaller and smaller targets. The influence of the remaining factors considered, climate, habitat quality, and local density of resident species, was found to be slight or undetectable.

The second part investigates the possibility of competitive interactions between residents and migrants, and between the migrants themselves. Several lines of evidence suggest that the distributions of resident parulids in the Greater Antilles are drastically truncated by the impact of large overwintering populations of migrants. Thus, at least in the Antilles, migrants seem to exert strong pressures on resident species that are not evenly reciprocated. Interactions among the 15 species of migrant parulids that commonly winter in Hispaniola are manifested by segregation into different habitats and in the formation of stratified species complexes. Two habitats that lie near the extremes of the island's vegetation gradient, lowland rainforest and open montane pine forest, contain nonoverlapping, functionally integrated parulid complexes of 7 species each. These represent a higher level of syntopy than is normally achieved by parulids in North American habitats. If, as we predict, equivalent complexes of migrant species occur in Central and South America, their tight ecological packing will effectively exclude other species and thereby provide a mechanism for the delimitation of winter ranges. The related problem of why each species winters where it does, however, remains largely inaccessible to analysis due to our ignorance of the evolutionary history of today's migratory populations.

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Patterns of Migration in the West Indies

ABSTRACT

We begin by showing that the collection of birds that winters in the West Indies is a nonrandom subset of all North American species that migrate to the tropics. Small gleaning insectivores are strikingly overrepresented while hawking, aerial and large gleaning insectivores, frugivores and granivores are absent or conspicuously underrepresented. Most of the species that breed in the West Indies and migrate to South America for the winter are aerial or hawking insectivores or large gleaners. The pattern is consistent in the two groups of migrants, but at present it is not known whether different categories of prey (e.g., large vs small insects) vary differentially through the year.

West Indian breeding bird communities differ from mainland communities in having much higher proportions of frugivores and in having frugivore guilds that are more tightly packed than insectivore guilds. The arrival of large numbers of migrant parulids reverses this pattern in the winter.

A severe drought at Guanica, Puerto Rico, resulted in a drastic and precipitous decline of frugivores and a less extreme and more prolonged decline of insectivores. We postulate that this can be explained by a lack of buffering between climate and fruits, which are an immediate product of photosynthesis, and a substantial buffering between climate and insects, which are one or two trophic levels removed from primary production. Given the large geographic scale of climatic patterns, it may be that fruits are effectively an unreliable resource within the confined space of an island, while insects, being

more buffered from perturbations, are a reliable resource that assures a high probability of survival.

There are still a number of unresolved problems in the interpretation of migratory patterns in the West Indies. We close with a brief discussion of these.

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Distribution of Migrant Birds in the Yucatán Peninsula: A Survey

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ABSTRACT

Censuses from 21 study sites show that migrants comprise a greater proportion of mixed wintering communities in the Yucatán Peninsula than they do in Central and South America. Within the peninsula, migrants are relatively more common in wetter and less populated areas. Common migrants are widely distributed geographically through the peninsula but may be restricted to a particular habitat. Different census methods are differentially effective for a given species, and bias in migrant-resident ratios may be introduced by full dependence on either mist-netting or transect counts. Insufficient data exist to evaluate seasonal or yearly changes in migrant abundance.

SUMARIO

Censos de 21 sitios muestran que aves migratorias componen una proporción más grande de comunidades invernales en la Península de Yucatán de que en otras partes de Centro y Sur America. En la península, aves migratorias son más comunes en lugares más lluviosos y menos poblados. Las aves migratorias más comunes tienen una distribución amplia en la península, pero pueden ser restringidas a habitats particulares. Diferentes métodos de censo son diferencialmente efectivos para una especie, y el uso de un sólo método puede influir en la proporción relativa de aves migratorias y residentes. Pocos datos existen para evaluar cambios estacionales o anuales en la abundancia de aves migratorias.

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Analysis of North American Subspecies of Migrant Birds Wintering in Los Tuxtlas, Southern Veracruz, Mexico

ABSTRACT

In this paper we presented data concerning the subspecific composition of some North American migrant birds wintering in the Tuxtla Mountains of Southern Veracruz, Mexico. Eight species are included. When more than one race or population was found wintering there, their relative abundances are given. Observations concerning habitat use are also included and compared with those in the literature. Some species were found to have eastern and western races wintering together, and others just had eastern or western representatives. We conclude that the wintering grounds play an important role in the evolutionary history of the bird species, and additional efforts should be made for their conservation.

RESÚMEN

En éste trabajo presentamos datos acerca de la composición subspecifica de algunas aves migratorias de Norte America que invernan en la region de los Tuxtlas al sur de Veracruz, México. Ocho especies son incluídas y se dan datos acerca de la abundancia relativa cuando más de una subespecie o población de la misma especie se encontraron invernando juntas. Observaciones acerca del habitat y su uso son tambien incluídas y comparadas con la literatura. Encontramos que algunas especies tienen subespecies tanto del Este como del Oeste de Norte America invernando juntas, mientras que otras solo tienen de uno o del otro lado. Concluimos que las areas de invernación juegan un papel muy importante en la historia evolutiva de las especies de aves y por lo tanto mayores esfuerzos deben hacerse para su conservación.

Winter Habitat Distribution of Migratory Land Birds in Western Mexico, with Special Reference to Small Foliage-Gleaning Insectivores

ABSTRACT

Winter censuses were conducted in 26 sites among 13 habitat types over an elevational gradient in western Mexico. The numbers and proportions of migratory species and individuals varied considerably between habitats. There are significant inverse correlations between numbers or proportions of migrants and elevation, but more important differences between sites (particularly lowland sites) due to the level of human disturbance. Disturbed lowland sites supported greater densities (to 150/ha) and proportions (to 83 percent) of migrants than those reported by other researchers for African or Neotropical sites. Furthermore, one subset of the total migratory bird pool—small foliage-gleaning insectivores—comprised 100 percent of the wintering birds within that guild in 4 sites and averaged 95 percent over 14 lowland sites.

Within the guild of small foliage-gleaners, there seems to be little species turnover between habitats among the migrants. With the exception of only one pair of species, migrants occupy all potentially utilizable habitats and avoid those habitats which are inappropriate for reasons apparently unassociated with migrant competitors.

Although migrants appear not to influence the choice of habitats within which other migrants winter, residents and migrants seem to avoid one another in at least two respects. The small migrant and resident foliage gleaners show a degree of between-habitat avoidance since there is an inverse correlation between the numbers of migrants and residents over the 13 habitat types ($r = -.43$, $P < .05$). This same guild also

shows within-habitat avoidance in 2 mature lowland habitats (mangroves and tropical evergreen forests); here the migrants are most abundant where roads, edges, or other clearings exist while the residents are least abundant in these locations. Resident bird density increases and migrant bird density decreases upon entering the interiors of these forests.

The situation is somewhat different in highland coniferous forests since an edge effect is absent, and the small insectivores join with the residents in the interior of the forests to form mixed-species flocks which are larger and more diverse than any I have seen reported for other parts of the world. As many as 30 species (more usually 17–20) and two to four times as many individuals participate in these flocks which are composed of about 30 percent migrants, on average.

After the departure of migrants during the northern summer, there is, in the small foliage-gleaner guild, an apparent ecological vacuum which remains unfilled by resident species in the lowlands; the same areas which supported 64 individuals/ha in winter harbored only 1.7 individuals/ha in summer. This "vacuum" is filled rather more effectively in the highland habitats where there may actually be more individuals/ha in summer than winter. This difference between lowland and highland habitats can be explained in part by different seasonal changes in insect densities. There is a general correspondence between the summer-to-winter changes in insect density within seven habitat types (as

Ecological Roles of Migratory and Resident Birds on Barro Colorado Island, Panama

ABSTRACT

An estimate of species, individuals and biomasses of birds on forested Barro Colorado Island (14.8 km²), Panama, indicates that migrants, even though there are many species, are only about 1 out of 16 individuals in the avifauna on an annual basis; at the October peak, migrants are 1 out of 7 birds. Migrants average one-third the weight of residents, and thus are only about 2 percent of the biomass on an annual basis and 5 percent at the October peak.

Migrants tend to concentrate in scrub patches and along the lake shore, but residents also concentrate along shore. Migrants are moderately common in young forest and uncommon in old forest, while residents decrease only slightly in old forest. However, many individual migrants (in a large area) and several migrant species use forest, so that human cutting of tropical forests can have drastic effects on migratory birds as well as resident ones.

Migrants tend to use low levels slightly more than do residents and average much less in weight on the ground and in the canopy. This is largely caused by the fact that migrants scarcely use large fruits, concentrating instead on small insects—which many small resident species and individuals (but a low biomass) also use. Resident biomass is 40 percent in heavy birds that eat large fruit on the ground or in the canopy. Directly or indirectly, large and small fruit account for the food of over half the resident biomass. Foods provided by rather than stolen from the plants thus become important in a tropical forest among residents, though not for migrants.

Migrants of the lake and clearing edge tend not to use large insects, perhaps because a large proportion of the resident birds of edge eat large insects flying out of the forest. Migrants eating large insects are few and smaller than residents, and thus form a small fraction even in the forest. However, migrants eating small insects tend to outweigh residents eating such insects.

Some cases where migrants are rare or fail to winter on Barro Colorado seem due to failure of food supplies in the dry season. Other cases may be due to competition with other migrants or residents. Migrants do seem slightly displaced from peak habitats, levels, and foods used by residents. Perhaps migrants use in fairly normal ways the most abundant foods that they can without encountering aggressive residents or problems of unpredictable fluctuations better exploited by motile resident species. They are least able to use large fruits and insects, foods relatively unavailable in temperate zones.

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Bird Community Structure in Two Panama Forests: Residents, Migrants, and Seasonality During the Nonbreeding Season

ABSTRACT

Trailside censuses of birds were made in two forests in Panama over the transition from wet to dry seasons and during both (October through March) to determine the structure of nonbreeding resident communities and to observe the roles of north temperate migrants. The two forests—only about 20 miles apart—differed somewhat in vegetation structure and age, but primarily in rainfall (70 vs 105 in. per year) and the intensity of the wet and dry seasons. The drier forest was 1) dominated by a small set of common species which 2) were relatively sedentary, and 3) contained a higher proportion of North American migrants which were also more frequent in flocks. The wetter forest 1) showed no pattern of dominance by a few species and had a large number of infrequent species, 2) was characterized by mixed-species flocks which at times included most of individuals observed, and 3) contained few migrants. The term migrants includes a diversity of roles, both temporal—as transients, winter residents and extended transients—and ecological—as insectivores that are territorial, intra- or interspecific flock members, or species that change from predominantly insect to predominantly fruit or nectar diets during winter. The period of winter residency in Panama coincides with the period of minimal insect density.

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Resident and North American Migrant Bird Interactions in the Santa Marta Highlands, Northern Colombia

ABSTRACT

In a subtropical zone lower montane wet forest, North American migrant species numbers peaked in March–April and were about 1.6 times the numbers present in October. This is believed to be a result, in part, of altitudinal migration by migrants wintering in the lowlands as the highlands dry season progresses. The difference in numbers may also be a reflection of different autumn and spring migration routes, but data are presently inadequate to support this hypothesis. Migrants exhibited protracted arrival times in autumn. Numbers of species and individuals increased dramatically in spring, and departures were abrupt. Migrants contributed a higher percentage of individuals to flocks than to the non-flocking community. Migrants were subordinate in their social relations with residents in flocks. Mean numbers of individuals and species of migrants in flocks showed a tendency toward an inverse relationship to those of residents (the more residents, the fewer migrants). The competitive impact of migrants upon the resident community is believed to be small.

RESÚMEN

En un bosque bajo montano muy húmedo de la zona subtropical, los números de especies migratorias norteamericanas alcanzaron a su número máximo en Marzo y Abril y eran más o menos de 1.6 veces los que se encontraron en Octubre. Se cree que resultaba, en parte, de una migración altitudinal por las migratorias que inicialmente se lograron en las lomas, pero cuales subieron durante la estación seca. Quizás refleje la diferencia de números una diferencia de rutas de migración entre el otoño y la primavera, pero los datos son tan escasos que no es posible apoyar la hipótesis esta. Las migratorias mostraron unos tiempos inconsistente en llegar en el otoño. No obstante, los números de especies y individuos aumentaron muy dramáticamente por la primavera, cuando se vea que eran muy abruptos las salidas. Las migratorias contribuyeron un porcentaje más grande de individuos a las bandadas de aves que a la comunidad fuera de las bandadas. Las migratorias mostraron subordinación a los residentes en las relaciones sociales, cuando se encontraron en las bandadas. Los números promedios de individuos y de especies migratorias en bandadas mostraron una tendencia a la relación inversa al compararlos a los de las especies residentes. Se cree que el impacto en competencia de migratorias con la comunidad residente es muy pequeño.

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Distribution and Abundance of North American Migrants in Lowlands of Northern Colombia

ABSTRACT

In a lowland thornscrub community, North American migrants occurred in numbers in fall when leaves were abundant. Coincident with leaf shedding and declining precipitation in December, the migrants departed. The thornscrub is dry and leafless during the time of spring migration, and migrants did not utilize it. In mangroves, *Protonotaria citrea* winters abundantly and must compete with local insectivores. On Isla San Andres, many migrants were found in April without fat reserves and were doubtless unable to complete a journey north, but local potential competitors were in good condition.

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Differential Use by North American Migrants of Three Types of Colombian Forests

ABSTRACT

Migrants' use of three Colombian forests was studied through mist netting, visual, and auditory counts. Seasonality of resources was assessed. Most migrants used the Cauca Valley and premontane forest sites. None used the lowland forest site. Differential occurrence of migrants is discussed in relation to competition in avian communities as influenced by species composition, sedentariness, and seasonality.

RESÚMEN

En un esfuerzo para adquirir una mejor comprensión de los cambios estacionales en las comunidades de aves neotropicales, nosotros comenzamos en Mayo de 1976 un estudio de algunas características de las aves que viven en 3 tipos diferentes de bosques en el departamento del Valle del Cauca, Colombia. Después de una extensa búsqueda de posibles zonas de trabajo, seleccionamos los siguientes sitios: 1) una mancha del bosque que anteriormente cubría el piso del valle de Rio Cauca, a 950 m de elevación, cerca de la ciudad de Jamundí, clasificado como bosque seco-tropical de acuerdo con el sistema de Holdridge; 2) un bosque apreciablemente grande y bien preservado a unos 1,600 m en la ladera oriental de la cordillera occidental, llamado bosque de Yotoco de tipo premontano-húmedo, y 3) una sección del bosque húmedo-tropical del litoral pacífico, recientemente abierto y perturbado, a 40 m y situado cerca de la Estación Agroforestal del Bajo Calima a unos 20 km al nordeste de Buenaventura.

En cada sitio se demarcaron parcelas rectangulares de 2 ha en las cuales se realizaron censos de aves y estudios de vegetación en períodos trimestrales. Las aves se muestrearon de acuerdo con el método de Karr: capturas con 12 redes de nylon durante 3-4 días sucesivos con suplementos visuales y auditivos realizados en recorridos sistemáticos y periódicos de las parcelas.

El resultado más importante fue la utilización por las aves migratorias de los bosques tropical-seco y premontano-húmedo pero no del tropical-húmedo. De un total de 78 especies observadas

en Jamundí, 16 (20.5 por ciento) fueron migratorias transcontinentales. En Noviembre nosotros estimamos 33 individuos de 15 especies que se reproducen en Norte America, pero en Marzo, el número descendió a 21 individuos de 13 especies. Las aves migratorias constituyeron el 21.6 y el 14.5 por ciento de las densidades totales para los meses de Noviembre y Marzo, respectivamente. En términos de biomasa, las aves migratorias representaron 11.5 y 3.4 por ciento de los totales estimados para Noviembre y Marzo respectivamente. Las aves residentes de Jamundí están dominadas por tiránidos y las familias endémicas neotropicales están pobremente representadas.

En Yotoco, de un total de 80 especies, 11 (13.8 por ciento) anidan en Norte America. Los números de individuos migratorios estimados en Diciembre y en Marzo fueron 13 y 5, lo cual representó el 14 y el 6 por ciento de las densidades totales. De las 11 especies, 5 ocurrieron también en Jamundí. En términos de biomasa las aves migratorias representaron 9.8 y 10.8 por ciento de las densidades totales en Diciembre y en Marzo. En Yotoco los tiránidos son nuevamente importantes pero los tucanes, trogones, motmots, formicáridos y pípridos también están representados.

En Bajo Calima no se registraron aves migratorias en censos realizados en Junio, Octubre, Enero, y Marzo. Las familias neotropicales endémicas están altamente representadas y conforman el principal componente de la diversidad aviaria.

Para dar una explicación de la variación en números de individuos y especies migratorios transcontinentales entre las zonas de estudio, se examinaron características ecológicas de los diversos habitats. En términos generales hay un paralelo entre el número de aves migratorias, que es alto en Jamundí, mediano en Yotoco y nulo en Bajo Calima, y el grado de estacionalidad, insularidad, perturbación histórica de los habitats, y probablemente la impredecibilidad.

Es poco probable que estos factores tengan una incidencia directa sobre el número de aves migratorias; mas bien, estos factores pueden ejercer su efecto via los recursos alimenticios o bien, del efecto de éstos sobre el nivel de competencia que pueda ofrecer la porción de aves no-migratorias de la comunidad respectiva.

La relación inversa que se encontró entre al número de miembros locales del group de insectívoros del follaje, que puedan actual o poten-

cialmente ofrecer competencia a los parúlidos migratorios transcontinentales y el número de tales aves migratorias ofrece apoyo a la hipótesis que la competencia limita el número de aves migratorias transcontinentales.

Otro aspecto de las comunidades aviarias que mostró variación entre las zonas de estudio, fue el grado de movilidad de las especies locales y la forma como esta movilidad pueda afectar a las aves migratorias de larga distancia. Una comparación de las avifaunas muestra a la de Jamundí como la más sedentaria y a la de Bajo Calima como la más nomádica. Estas especies tan móviles producen cambios recurrentes (renovación) en la composición de especies en Bajo Calima que bien excede el flujo de especies de Jamundí con su sustancial proporción de migratorios de larga distancia. El efecto competitivo de especialistas locales de alta movilidad sobre las aves que regresan de zonas de reproducción puede, quizás, impedir su reingreso. Pero las causas de las diferencias de grado de movilidad ya sea a nivel local ó a nivel transcontinental quedan por fijarse. Es muy probable que estén relacionados a patrones de disponibilidad de recursos alimenticios sobre los cuales sabemos todavía muy poco.

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Relative Abundance of North Temperate Zone Breeding Migrants In Western Colombia and Their Impact At Fruiting Trees

ABSTRACT

Migrant densities are rather uniform from October through February, averaging about 8.8 percent of the total species and 5.1 percent of the total avifaunal biomass in the upper Anchicayá Valley. Densities were slightly higher in March. Some migrants were not regularly present in the upper Anchicayá Valley until December or January, and the significance of this late arrival is discussed. Migrants were more frequently encountered at a disturbed highland site than at a disturbed lowland site, and only two species were encountered frequently enough to be classified as common. Some elevational replacement of migrant species occurs on the Pacific slope; two species were recorded chiefly in the lowlands and two species chiefly in the highlands. The importance of migrants as competitors for fruit is believed minor. Only 4 of 22 species in the upper Anchicayá Valley were observed taking fruit and migrants accounted for only 1.3–4.2 percent of the total feeding visits to two species of fruiting trees.

ABSTRACTO

Un estudio acerca de las densidades de emigrantes y las explotaciones de arboles con frutas fue realizado durante el período de Agosto de 1972 hasta Mayo de 1973 en el húmedo estacionamiento del pacífico de Colombia. Las densidades de los emigrantes fueron uniformes de Octubre hasta Febrero, promediando acerca de 8.8 por ciento del total de todas especies y 5.1 por ciento de la biomasa de la avifauna en total. El registro del número de individuos capturados mostró un período de máxima abundancia en marzo. Algunos emigrantes no fueron presente regularmente en el Valle del Anchicayá hasta Diciembre o Enero y la significación de esta llega tarde del migrantes es discutida. Emigrantes fueron encontrados con más frecuencia por un sitio subtropical alterado que en un sitio tropical alterado, pero la abundancia en todos los sitios parece bajo. Algún reemplazo elevacional de emigrantes fue observado por la vertiente del pacífico; 2 especies fueron registradas principalmente por una selva tropical alterada y 2 especies por una selva subtropical alterada. La importancia de los emigrantes como competidores por las frutas disponibles de arboles en una elevación mediana por la vertiente del pacífico de Colombia fue insignificante, resultando en no más de 1.3–4.2 por ciento del uso de todas las aves. Únicamente 4 de 22 emigrantes fueron observados comiendo frutas.

Bird Migration in Amazonian Ecuador, Peru, and Bolivia

ABSTRACT

Long-range migrants that breed in northern and southern temperate regions make up a small proportion of the total species occurring in western Amazonia. They appear to be able to winter in this area by 1) using secondary habitats, 2) moving within this area to take advantage of changing resource availability, and 3) using primary forest by being rare or in essence dilute in any given area. The presence of these long-range migrants is complicated by the local and/or altitudinal movement of several "resident" species. As more long-term studies are conducted, the extent and implication of these short-range migrants will likely become important in interpreting the presence or absence of long-range migrants in western Amazonia.

SUMARIO

Las aves de migraciones extensas que anidan en las regiones templadas del norte y sur forman una pequeña proporción del total de las especies que existen en la Amazonía occidental. Apparently pueden ellas invernar en esta area 1) usando habitats secundarios, 2) movilizándose dentro de esta area para aprovechar la disponibilidad de los cambios de recursos, y 3) usando bosques primarios siendo raras o en esencia diseminadas en cualquier área dada. La presencia de estas aves de extensas migraciones se complica con la movilización local y/o altitudinal de varias especies "residentes." A medida que se vayan efectuando estudios prolongados, la extensión e implicación de estas aves de migraciones cortas serán probablemente más importantes al interpretarse la presencia o ausencia de aves de migraciones extensas en la Amazonía occidental.

Foraging Ecology of Migrant and Resident Warblers and Vireos in the Highlands of Costa Rica

ABSTRACT

We studied habitat selection, foraging behavior, and social interactions among migrant and resident warblers and vireos at Monteverde, Costa Rica during the winter of 1976–77. Monteverde lies within a steep moisture gradient at an elevation of 1,300–1,550 m. Migrants were abundant in the drier (lower) portion of the gradient, where the dominant habitats were forest edge, parkland, pastures, and patches of mature premontane moist forest. Four residents (two vireos, the Golden-crowned Warbler, and the Slate-throated Redstart) were also restricted primarily to this zone. At higher elevations, virgin wet forest and edge comprised the major habitats. Migrants were scarce, resident vireos were absent, and Three-striped Warblers and Collared Redstarts largely replaced their congeners.

Mixed-foraging flocks were characteristic of all forest and forest-edge habitats, but their composition varied with elevation. In drier forests, flocks were led by Golden-crowned Warblers, with other warblers and vireos as frequent attendant species. In this zone, migrants often foraged alone as well as in mixed flocks. In higher wet forests, flocks were led by Three-striped Warblers and Common Bush-tanagers, with Collared Redstarts and a variety of Furnariids and Dendrocolaptids as the common attendant species. An analysis of frequencies of co-occurrence further revealed that greenlets, Philadelphia Vireos, and Tennessee Warblers frequently foraged with conspecifics, while Brown-capped Vireos, Black-and-white Warblers, and Golden-winged Warblers most commonly joined multispecies flocks.

Assessment of three components of foraging behavior (method, height, and speed) showed that migrants tended to be more variable in foraging height than residents. With the exception of Black-and-white and Golden-winged Warblers, this also appeared to hold for flexibility of feeding methods. Variations in foraging speed were generally greater in migrants, although the relationship fell just short of statistical significance. Resident warblers in wet forest flocks had less specialized foraging behavior than their congeners, suggesting the possibility that competition with migrants affected foraging of residents where migrants were common; observations when migrants are absent are needed to clarify this. There was no evidence that lone migrants foraged differently from migrants in flocks nor was there evidence of seasonal changes in foraging. Agonistic interactions involving migrants were rare, and the only territoriality observed was a small minority of Tennessee Warblers defending blooming *Erythrina* trees.

Our data suggest that at Monteverde, at least, most migrants were assimilated into the avifauna by being flexible enough to take whatever resources are most available in a given situation. The virtual lack of territoriality and the scarcity of agonistic encounters suggest that migrants are not normally experiencing food-mediated competition at this locality. Comparisons with the data of other workers suggest that the situation may be different elsewhere, especially in lowland areas with more pronounced dry seasons.

The Black-throated Green Warbler in Panama: Geographic and Seasonal Comparison of Foraging

ABSTRACT

I compare the foraging behavior of Black-throated Green Warblers (*Dendroica virens*) wintering in Chiriqui Province, Panama, with that of breeding populations in Maine and North Carolina. Quantitative behavioral observations of the heights and tree parts used in foraging, repertoire of techniques, directionality of flights and probing, and patchiness of habitat use indicate significant seasonal differences in foraging. Seasonal shifts in the spatial distribution of foraging are not wholly attributable to differences in the structure of the forests.

Foraging was more generalized spatially in Panama than in Maine, and all other measures of foraging showed greater generalization in Panama than in the two breeding habitats, particularly in foraging technique. Foraging was also more generalized in North Carolina than in Maine. Generalization is produced in part by greater behavioral diversity of each individual. These results, and similar observations by others, suggest that competitive pressures in diverse tropical faunas can produce niche expansion rather than contraction in wintering migrants, as compared to breeding migrants.

I suggest that a foraging optimization response to lower food availability in southern temperate and tropical systems, due to seasonal constancy and efficient consumer tracking, explains such generalization better than proposed ecological release from congeners or increased intraspecific competition. Behavioral plasticity, probably even greater in other migrants, may be favored by temporary insinuation into a diverse and stable community of tropical residents, as well as by rigors of annual colonization of the temperate zone.

Nonbreeding Ecology of the Blackburnian Warbler

ABSTRACT

Migrant warblers have been generally thought to choose the same subunits of habitat on their wintering grounds as on the breeding grounds. However, in this study of the Blackburnian Warbler in an oak woods near Popayán, Colombia, where it was particularly common from October to April, this species, which prefers the upper vegetational levels during breeding, was commonly observed at all levels. At low densities, when the vanguard arrived and the stragglers departed, it preferred the upper levels. Its use of all vegetational levels at high densities is presumably due to intraspecific competition and the absence on its wintering grounds of congeneric species with which it is sympatric during breeding. The hypothesis is presented and discussed that this species and others of its genus may avoid intrageneric competition during winter by geographical isolation from one another.

Interspecific Competition and the Niche of the American Redstart (*Setophaga ruticilla*) in Wintering and Breeding Communities

ABSTRACT

This study represents an investigation of the role of interspecific competition in the year-round ecology of a common and widely-occurring neotropical migrant, the American Redstart (*Setophaga ruticilla*). The evidence obtained, though indirect, is consistent with the hypothesis that the morphology, behavior, and distribution of this species reflect both ultimate and proximate effects of competition in both its wintering and breeding communities.

At eight sites throughout its winter and summer range, the densities and foraging characteristics of the redstart and other species in the guild of small flycatching/foliage-gleaning birds to which it belongs were quantified. From these data, redstart niche breadth and redstart niche overlap with the rest of the guild were calculated for each site. To interpret the significance of niche overlap, a technique originally suggested by Sale (1974) was used to compare the observed value of redstart overlap in each area with the expected distribution of this value among comparable, but randomly associated (and hence, competition-free), hypothetical species.

In summer sites, redstart density and redstart niche breadth were both inversely correlated with the ecological similarity (an index based on morphological and behavioral criteria) of the other species in its guild. In winter sites, redstart niche breadth, but not density, was inversely correlated with guild similarity. Total overlap in resource use between the redstart and other species was lower in the winter than in the summer, primarily because redstart densities at this time were lower. The observed overlaps of breeding

RESÚMEN

Esta investigación es un análisis del papel de competición interspecífica en la ecología de la candelita (*Setophaga ruticilla*), una especie común y extendida de ave migratoria neotropical. La evidencia obtenida, aunque indirecta, es consistente con la hipótesis de que la morfología, el comportamiento, y la distribución de esta especie reflejan efectos últimos y próximos de competición en sus comunidades de verano y también de invierno.

En ocho sitios en todas partes de su alcance, las densidades y características de forrajear de la candelita y otras especies en su gremio de papamoscas y espigadoras de follaje pequeñas estuvieron cuantificadas. Con estos datos, la anchura del nicho de la candelita y la coincidencia del nicho de la candelita y de los nichos del resto del gremio estuvieron calculadas para cada sitio. En interpretando el significado de la última, una técnica sugerida originalmente para Sale (1974) estuvo empleada para comparar lo que estuvo observada en cada área con la distribución esperada de esta variable entre unas especies hipotéticas que eran comparables, pero asociadas al azar (y por tanto sin competición).

En los sitios de verano, la densidad y la anchura del nicho de la candelita eran las dos correlacionadas negativamente con la semejanza ecológica (un índice basado en criterios morfológicos y comportamentales) de las otras especies en su gremio. En los sitios de invierno, la anchura del nicho de la candelita, si no la densidad, era correlacionada con la semejanza del gremio. La coincidencia en uso de recursos entre la candelita y otras especies era menos en el invierno, prin-

redstarts were generally higher than what would be expected among randomly associated species; winter overlaps were generally lower than randomly generated overlaps. Although these trends were not statistically significant, the redstart niche is significantly more divergent from other species' in nonbreeding than in breeding communities.

Despite the evidence that the redstart experiences competition in both winter and summer situations, winter competition seems to have been more intense in both ecological and evolutionary time. The greater displacement of the redstart niche away from those of other species in its guild in winter, in conjunction with lower total overlap then, suggests that the limits to similarity between this species and those with which it coexists are greater during this season. Moreover, redstarts' flycatcher-like beaks seem most closely adapted to their winter foraging behavior: at this time, they hawk significantly more often than in summer.

principalmente porque la densidad de la candelita era menos en este tiempo. Las coincidencias de nichos observadas de candelitas engendradas eran en general más grande de lo que se esperaría entre especies asociadas al azar; las del invierno, menos. Aunque estas tendencias no eran significantes estadísticamente, el nicho de la candelita está significativamente más divergente de los de otras especies en comunidades invernales que en comunidades de verano.

A pesar de la evidencia que la candelita experimenta la competición en invierno y también en verano, la competición del invierno parece haber sido más intensa en tiempo ecológico y evolutivo. La desalojamiento más grande del nicho de la candelita de los de otras especies en su gremio en invierno, en conjunción con menos coincidencia de nicho luego, sugiere que los límites de semejanza entre esta especie y las con que coexiste son más grandes durante este tiempo. Además, los picos anchos y aplanados de las candelitas parecen adaptados más precisamente para su manera de forrajear en invierno, cuando se comportan más como papamoscas.

Resource Partitioning between Migrant and Resident Birds: The Use of Irregular Resources

ABSTRACT

Students of avian community ecology in the neotropics have suggested that wintering migrant birds avoid direct competition with resident species on their shared wintering ranges by focusing on under-exploited resources. Hypothetically, these resources are under-exploited because they occur in 1) mountaintop habitats too small to support year-round resident populations; 2) seasonal or unpredictably-shifting patches which sedentary resident birds cannot exploit; or 3) new habitat types to which residents have not yet adapted. The literature provides little support for the first and second hypotheses; data presented here from southeastern Campeche, Mexico, generally fail to support the predictions of the third. Mist-net samples of bird populations in old fields and mature forest stands reveal a positive correlation between migrant and resident abundance rather than the negative correlation predicted by the third hypothesis. In the 0-2 m level sampled by mist nets, both resident and migrant projected populations are greater in old fields than in forests. In old fields and disturbed forests, resident and migrant communities are dominated by one or two species while in less-disturbed forests species evenness is higher for both subsets of the avifauna. Ordination of the mist-net samples suggests that resident species discriminate more strongly between forests and old fields and between various stages of old field succession than do migrant species. The presence of resident species adapted to old field habitats in southeastern Campeche may be in part a result of the long history of human disturbance in the area. The proportion of migrants in

RESÚMEN

Autores anteriores han sugerido la hipótesis que las aves migratorias usan recursos que son irregulares en su distribución espacial ó temporal. Tres razones han sido propuestas para esta preferencia: 1) las aves migratorias escogen como habitat regiones montañosas, pequeñas y aisladas dado que el número de aves residentes es relativamente escaso en estos habitats; 2) las aves migratorias, al ser más móviles, explotan recursos que son irregulares en tiempo (árboles frutales u hormigueros) más eficientemente que las aves residentes; y 3) las aves migratorias pueden explotar habitats alterados por el hombre antes que las aves residentes alcancen a adaptarse a condiciones cambiántes. El siguiente resumen de la literatura sugiere que las dos primeras hipótesis todavía deben ser adecuadamente comprobados. Datos obtenidos en México durante este estudio contradicen las predicciones de la tercera hipótesis.

En un estudio de la familia Parulidae en Jamaica, Lack y Lack (1972) descubrieron que las aves migratorias prefirieron tierras bajas o de media altura a selvas montañosas. Los pocos datos que existen de Centro y Sud America no son suficientes para demostrar un efecto claro de la elevación en la abundancia de las aves migratorias. Antes de hacer generalizaciones acerca de la relacion entre la abundancia de aves migratorias y elevación, más datos son necesarios.

Datos sobre las aves migratorias que utilizan frutas u hormigueros sugieren que algunas especies pueden usar alimentos que son más abundantes en ciertas estaciones. Puesto que la may-

samples from Campeche forests is greater than reported from lowland rain forests in Central America. This latter result suggests that migrants may play a more important role in bird communities of tropical dry forests than they do in lowland rain forests, and that conclusions drawn from lowland forest studies may not apply to dry forest sites.

oría de las aves migratorias son insectívoras, dependen por lo tanto de alimentos que son relativamente escasos durante la temporada de Diciembre a Febrero.

La sugerencia que las aves migratorias móviles son más eficientes en explotar recursos presentes en pequeños espacios accidentales está basada en datos de un estudio aves seguidoras de hormigas en Panamá (Willis 1966). Otra evidencia sugiere que tanto ambas aves migratorias y residentes usan la estrategia de migración local en condiciones apropiadas.

Datos de Campeche, México, contradicen la sugerencia que la competencia de las aves residentes relega a las aves migratorias a habitats alterados (Willis 1966). Muestreos de aves con redes en bosques y acahuales muestran que las aves migratorias usan ambos habitats alterados y naturales, y que la abundancia de aves migratorias y residentes aumenta en acahuales. En acahuales, una ó dos especies dominan ambas comunidades residentes y migratorias. Las especies residentes distinguen entre ellos. La diferencia entre estos resultados y los de otros estudios en Centro America sugiere que las aves migratorias tienen funciones diferentes en comunidades del bosque seco y húmedo.

La larga historia de perturbación humana en Campeche podría haber conducido a la acumulación de especies residentes adaptadas a acahuales. Situaciones similares pueden existir en otras partes de Latinoamérica donde existieron grandes poblaciones precolombianas.

Ecological Aspects of Migrant Bird Behavior in Veracruz, Mexico

ABSTRACT

Avian migrants at three primary forest sites in the Tuxtla Mountains of southern Veracruz, Mexico, were investigated during 1973–75. Mist-netting and banding were used for censusing populations and ascertaining movements of individuals within populations; observations supplemented these data for niche structure and intra- and interspecific interactions.

Individuals of both sexes of 14 non-gregarious migrant species defended separate, small (2–5 ha) feeding territories throughout the winter season and returned to the same territory in subsequent seasons. In populations of all species studied, some individuals of both sexes were unable to obtain territories and moved randomly through suitable habitat as floaters, assuming defense of a territory if given the opportunity. Individuals of these 14 species were able to compete for resources on a long-term basis in a primary tropical forest habitat, indicating that earlier theories describing migrants as nomadic opportunists subsisting in disturbed or marginal habitats on temporarily superabundant resources are incorrect.

Differences in resource use between migrants and permanent residents were not seen, but there were relationships between food resource distribution, social system, and use of fattening as a physiological and behavioral response to concentrated resources.

A comparison of foraging niches between migrant and resident species showed no basis for the claim that migrants are competitively inferior to permanent resident species. Migrant species occupy characteristic niches which are not used by permanent residents, even when migrants are absent.

Individuals of most migrant species took part

in interspecific flocks only while the flocks were present on their territories. Presumed advantages of joining interspecific flocks are increased foraging efficiency and avoidance of predators. There was no evidence that individuals of the different species within these flocks behaved as “ecologically the same species,” as has been claimed by some workers.

Although some investigators have maintained that the breeding period is the most critical part of the migrant’s life cycle and others claim that winter is the critical period, there are yet no conclusive data that any one period is more important than any other. Since competition is continuous, as evidenced by the presence of floaters, the migrant must use an optimization strategy to compete well on the breeding ground, during migration and on the wintering ground.

We hypothesize that most nearctic, long distance migrants evolved from historically tropical species which were able to exploit niches common to many different forest types. With low breeding success and intense competition for resources in tropical communities, individuals of these species took advantage of reduced competition in seasonal niches in temperate areas to increase reproductive success.

Migrants use specific niches in tropical communities, a fact with important implications concerning community structure and function that has been overlooked by workers in this field. The effects of new resources, environmental stability, and community productivity are discussed in light of information on migrants and other groups not normally included in species diversity studies. We conclude that productivity is an important ultimate factor in the development of biological heterogeneity in tropical systems.

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Migrant Hummingbirds' Accommodation into Tropical Communities

ABSTRACT

In this study we examine seven ways in which coexistence of resident and migrant hummingbirds might be achieved. A total of eight months was spent observing hummingbird foraging patterns in four habitats of the State of Colima in Mexico. Evidence from this study suggests that the time when migrant hummingbirds are present in the tropics coincides with a seasonal abundance of food in excess of the needs of resident species. Population levels of resident hummingbirds are probably limited by food availability at times of the year when migrants are not present. Territorial behavior is widespread among both resident and migrant species, but the latter are almost always subordinate to the resident species which tend to monopolize the most favorable territories. It follows that migrants display "fugitive" behavior. They settle in a territory until displaced by a dominant species, and then search for an unoccupied territory.

RESÚMEN

En este estudio hemos analizado siete formas de cómo puede ser conseguida una coexistencia entre colibríes no migratorios y colibríes migratorios. Hemos dedicado un total de 8 meses a la observación de las distintas formas de alimentación de los colibríes en 4 distintos habitats del Estado de Colima en México. Los resultados de nuestro estudio nos permiten pensar que la época de estancia de los colibríes migratorios en la zona tropical coincide con una de abundancia estacional del alimento superior para las necesidades de la especie no migratoria. El nivel de población de los colibríes no migratorios puede que esté limitado por la disponibilidad del alimento en épocas de año cuando los colibríes migratorios no están presentes. La conducta territorial está extendida tanto entre la especie no migratoria como en la migratoria, pero está suele quedar casi siempre subordinada a quella que tiende a acaparar los territorios más favorables. La especie migratoria, como resultado, presenta una conducta "de fuga." Se establece en un territorio hasta que se vea desplazada por la especie dominante y tenga que ir a la búsqueda de un territorio inocupado.

Asynchronous Migration Patterns and the Coexistence of Tropical Hummingbirds

ABSTRACT

The complex vegetation of tropical mountains creates a mosaic of habitat patches among which numerous short-billed hummingbird species migrate. Calculation of "seasonal overlaps" among hummingbird populations at two Costa Rican sites, Monteverde (Feinsinger 1976) and the Cerro de la Muerte (Wolfe, Stiles, and Hainsworth 1976) demonstrates that in each patch the population density of each hummingbird species fluctuated in a unique temporal pattern. During seasons of flower scarcity, one or a few species could control all resources. Therefore, the ability of other hummingbirds to locate alternate resources through migration was crucial to their survival. I conclude that asynchronous migration patterns are instrumental in permitting the regional coexistence of large numbers of short-billed hummingbird species.

It follows that regions lacking such habitat mosaics must suffer reduced hummingbird diversity. This factor, among others, may lead to such contrasts in hummingbird diversity as that between the Andes and the Amazon Basin, be-

tween eastern and western North America, or between the tropical mainland and various islands. Data from studies in progress on Trinidad and Tobago support this reasoning. Several extensive nonforested habitats exist on Trinidad; seven short-billed hummingbird species, in particular abundant *Amazilia tobaci* and *Chrysolampis mosquitus*, travel between habitats in different spatiotemporal patterns. In contrast, Tobago has but one extensive habitat type; not only must *Chrysolampis* and *Amazilia* coexist nearly year-around, but they also migrate synchronously to exploit what flower bursts occur in peripheral habitat patches. Individuals of only two other shorter-billed species, which normally forage high in trees, enter the Tobago study sites.

The relationship between diverse migration strategies and the regional coexistence of hummingbirds follows predictions of theoretical models for fugitive species. In this sense it parallels the evolution and ecology of latitudinal migrations by other bird groups.

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Evolutionary Implications of Habitat Relations Between Permanent and Winter Resident Landbirds in Costa Rica

ABSTRACT

In this paper I explore distributional patterns of migrant landbirds in relation to those of permanent residents, with respect to altitude, rainfall, and habitat utilization. The latter is assessed according to a simple habitat classification based on the position and orientation of the foliage-air interface, for birds of 5 localities on the humid Caribbean slope of Costa Rica ranging from 100 to 3,000 m elevation; and for a locality in the dry Pacific lowlands at 100 m elevation. Altitudinal distributions are estimated over 10 Caribbean localities that approximate a transect from 0 to 3,500 m.

The numbers and habitat distributions of winter resident species at the five intensively studied Caribbean localities varied with altitude in the same manner as did those of permanent resident species; no consistent relation was found for fall migrants. In general, migrants occurred less frequently in forest interior and more in nonforest-edge habitats than permanent residents, but this is in part a function of taxonomic affinities: the permanent residents ecologically most similar to winter residents are also closest taxonomically. In fact, the great majority of migrants have close relatives that are tropical residents. Ecological amplitudes (in terms of number of habitat categories occupied at a site, or number of sites along an altitudinal transect at which a species is resident) of winter residents average slightly greater than those of permanent residents as a whole but are similar to those of permanent residents occurring outside the forest interior.

The striking degree of concordance between ecological distributions of permanent and winter residents suggests that the migrants are an inte-

ABSTRACTO

En este artículo se comparan las distribuciones de las aves terrestres migratorias con las de las especies residentes, con respecto a la elevación, la lluvia, y el uso del hábitat. Para esta última comparación se emplea una clasificación simple del hábitat según la posición de la interfase follaje-aire. Datos sobre uso del hábitat se presentan para las aves de 5 localidades en la vertiente del Atlántico de Costa Rica, que incluyen un rango de elevaciones de 100 a 3,000 m, y para una localidad de clima mucho más seco en la vertiente del Pacífico a 100 m de altura. Las distribuciones altitudinales se estimaron en el lado Atlántico agregando datos de 10 localidades adicionales, para tener el equivalente de un transecto desde el nivel del mar hasta 3,500 m de elevación.

Los números y distribuciones ecológicas (según la clasificación de los hábitats) varían con la elevación en la misma manera para las especies que son residentes invernales, que para los residentes permanentes, en las cinco localidades estudiadas más intensivamente (Nota: en este artículo la palabra "invierno" y sus derivados se usan en el sentido del invierno o época fría de la zona templada del norte, aproximadamente Noviembre a Marzo, y no como sinónimo de la época lluviosa—Mayo a Noviembre—como se la usa corrientemente en Centroamérica). No hay ningún patrón altitudinal muy definido con respecto a estos parámetros para las especies que solamente se encuentran de paso otoñal. Por lo general, los residentes invernales se encontraron menos dentro del bosque, y más al borde o afuera del bosque, que los residentes permanentes. Sin embargo, esta diferencia se debe en gran parte a

gral part of tropical communities rather than an extraneous element superimposed upon them. Although the migrants leave the tropics for up to six months each year, the timing of their departure and return tends to preclude invasion of their niches by permanent residents. The high degree of integration of winter residents into tropical communities bespeaks a long tropical history and possibly tropical origins for many migrant taxa: they are basically tropical birds that have been able to increase breeding success by taking advantage of the summer burst of productivity at high latitudes. Given the great seasonal mobility of many "resident" tropical birds, especially canopy-edge oscines, it is difficult to draw a clear ecological distinction between "migrants" and "endemics". However one views the origin of migrant taxa, I would argue that the time is ripe for a fresh look at migration and winter residency— and at the structure of tropical bird communities—from the point of view that the migrants form an ecologically important part of these communities.

afinidades taxonómicas: las especies de residentes permanentes más parecidas ecológicamente a los residentes invernales, también son más cercanas taxonómicamente. Más bien la gran mayoría de especies migratorias tienen parientes muy cercanos entre los residentes permanentes. Las amplitudes ecológicas (en términos de los números de hábitats ocupados en un sitio, o los números de sitios ocupados a través de un transecto altitudinal) de residentes invernales son ligeramente más grandes que las de los residentes permanentes en total, pero muy parecidas a las de las especies de éstos que no ocurren solamente adentro del bosque.

El grado de coincidencia de las distribuciones ecológicas de los residentes permanentes e invernales es muy alto, y sugiere que éstos son miembros integrales de las comunidades y no un elemento ajeno sobrepuesto en ellas. Aunque los migratorios se van de los trópicos hasta por seis meses del año, sus salidas y regresos caen temporalmente de tal manera que se dificulta mucho la invasión de sus nichos por las especies residentes. Los residentes invernales son bien integrados a las comunidades tropicales, que muy posiblemente tienen sus orígenes evolutivos en estas comunidades. Incluso se puede llamarlos aves tropicales que han logrado aumentar el éxito de la reproducción, aprovechando la productividad grande y transitoria del verano norteno, a través de la migración. Dado el grado de movilidad de muchos "residentes" tropicales, especialmente oscines del borde y dosel del bosque, es evidente que se no sería fácil distinguir ecológicamente entre "migratorios" y "endémicos." Sea como sea el origen de los migratorios, yo creo que es hora de reexaminar los fenómenos de la migración y la residencia invernal, desde el punto de vista de que los migratorios constituyen una parte importante de muchas comunidades tropicales.

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Adaptations to Seasonal Changes by Migrant Land Birds in the Panama Canal Zone

ABSTRACT

Migrants that winter in the Panama Canal Zone experience about equal portions of the wet and dry seasons. At 14 study areas across the Canal Zone, changes in migrant numbers, diets, foraging behaviors, and social tolerances, were studied in relation to seasonal changes. Territorial insectivorous species initially chose the wetter habitats and microclimates such as on the ground in mature forest, mangrove swamps; being sedentary, they chose areas least affected by dry conditions. Foliage-gleaning species tended to move from young and mature forest exclusively into mature forest during the seasonal changeover in early January, then back to young as well as mature forest when fruit became available in March. Some foliage gleaners were territorial in young forest but socially tolerant in mixed species flocks in mature forest at the same time of year.

Stomach content data for Bay-breasted and Tennessee Warblers show that they eat smaller insects in the dry season relative to the wet season, even though most of their energy comes from fruit in the dry season. This is the opposite of what would be predicted from optimal foraging theory.

Food habits and social behavior of the 11 most common migrants in Panama are described. General and local effects of tropical wet and dry seasons are discussed in relation to migratory patterns.

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Migratory Parulidae: What Can Species Co-occurrence in the North Reveal About Ecological Plasticity and Wintering Patterns?

ABSTRACT

In contrast with resident species that occupy one habitat throughout their lives, migrants must adapt to distinct winter and summer habitats and a variety of different living conditions while on migration. The nearctic Parulidae, the largest single group of nearctic-breeding species wintering in Neotropica average three months on the breeding grounds, two to three months on migration, and six to seven months in the wintering grounds. Each, accordingly, must exercise a strong moulding influence. This, and a variety of other aspects of the biology demand a high degree of adaptiveness and ecological plasticity. These include capacity to associate with different sets of congeners on breeding and wintering grounds, ability to fit into the neotropical communities, live in close contact with other species as members of mixed species flocks on migration and, to a degree, adjust feeding zone according to circumstances.

It is argued that migrants, although they do show the full range of "species separation" devices have somewhat different life strategies compared to residents. They are opportunists and have many of the basic characteristics of the island-colonizing species described by Ricklefs and Cox (1972), and Diamond (1975). Their fitting into the neotropical ecosystem must be viewed in this light.

Migrant Participation in Neotropical Mixed Species Flocks

No abstract.

Introduction

One interesting facet of resident-migrant relationships in the neotropics is their potential interaction in mixed species flocks. The ubiquitous occurrence of resident flocks in the neotropics allows most forest birds the opportunity to participate in groups irrespective of habitat selection. Flocks are found from sea level to montane forests throughout the spectrum of primary to heavily disturbed habitat. Therefore, most migrants wintering in the neotropics utilize habitat traversed by resident flocks. However, despite a universal accessibility of flocks, the propensities of migrants to flock with residents varies markedly. While some migrants regularly join flocks, many follow inconsistently or ignore them completely. A few form flocks composed exclusively of migrants, but most forage singly or occasionally join into small loosely associated groups. The basis for this variation is not immediately obvious and warrants examination.

In this presentation, I use the term flock in a strict sense excluding feeding assemblages that are chance aggregations of species at resource-rich patches. Loci of aggregations include such diverse forms as fruiting trees (Leck 1971), burning grasslands (Winterbottom 1949), and army ant swarms (Willis 1972). In contrast, flocks are defined as foraging groups that are generated by intrinsic attraction between members (Morse 1970); they are identified by coordinated movement in the absence of external resource cues. Flocks may be monospecific or polyspecific in composition; they may be formed entirely by residents, or migrants, or a mixture of both.

Birds that flock presumably derive some benefit(s) from the presence of other participants. Hypothetical advantages accrued from flocking are numerous, and a complete discussion of their applicability to migrants is beyond the scope of this presentation (for a recent review of hypotheses see Morse 1977). These hy-

potheses are not universally applicable to all types of flocks. Some predict advantages for new arrivals that obtain information by associating with resident flocks (R), but not for flocks consisting entirely of migrants (M). Briefly, flocking is thought to enhance foraging efficiency and/or decrease the likelihood of being captured by a predator. Foraging efficiency may be enhanced by facilitating the location of food-rich areas (primarily R-type flocks, Moynihan 1962), or areas with few competitors (M and R, Morse 1970). Proximal flock members may flush prey (M and R, Belt 1874), or demonstrate the availability of new prey species (primarily R, Leck 1971). Flocking may permit more systematic resource harvesting (M and R, Cody 1971), reduce interspecific aggression (M and R, Austin and Smith 1972), or facilitate reduction of niche overlap (M and R, Morse 1967). The potential for flocks to reduce predation susceptibility is as diverse. Flocks may produce confusion or threat of physical damage for the predator (M and R, Tinbergen 1946). They may make prey more difficult to locate (M and R, Olson 1964) and surprise (M and R, Bates 1863). Following flocks may allow birds to learn the locations likely to harbor predators (primarily R, Moynihan 1962).

The advantages of flocking with residents are potentially great for migrants regardless of whether foraging enhancement or predation evasion hypotheses are invoked. As new arrivals, migrants may use resident flocks to learn local food types and abundances, to assess levels of competition, or to obtain information about types and local densities of predators. Even migrants that are returning to previous wintering sites are likely to encounter conditions sufficiently different to warrant reassessment of resource or predator status. Despite these potential benefits, migrant participation in resident flocks is limited. Only about half of approximately 40 species of migrants that regularly winter in forest habitats of Costa Rica, Panama, and

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Influence of Meteorological Patterns and Trans-Gulf Migration on the Calendars of Latitudinal Migrants

ABSTRACT

A large proportion of the birds migrating between eastern North America and the Central American tropics cross the Gulf of Mexico in spring and fall. This 1,000-km overwater flight is energy-expensive and hazardous. Selection is assumed to have optimized the calendars of trans-Gulf migration relative to the probabilities of birds encountering unfavorable flight conditions over water. The peak of spring trans-Gulf migration and the greatest frequency of high magnitude autumnal flights coincide with recognizable improvement in flight conditions during mid-April and at the beginning of October. Improved trans-Gulf flight conditions cannot be unambiguously discriminated from changes in seasonal climatic conditions in eastern North America. Yet, the coincidence of these changes in climate and the timing of migration indicate a temperate zone-based determination of the calendars of latitudinal migrants. If, however, tropical phenomena exist that influence the duration of winter residence, then the periods of April-May and September-October should be times of changing competitive pressure from permanent residents and/or changing resource abundance throughout the neotropics. That this is not the case lends support to the conclusion that migration calendars are determined by temperate-zone phenomena.

Demographic Aspects of Long-distance Migration

No abstract.

Introduction

Migration is a spectacular attribute of birds. While it has attracted the attention of research probing its mechanisms, the selective bases for the evolution of migration and patterns of migration, such as partial, disjunct, leap-frog (Salomonsen 1955), only recently have been given more than superficial treatment. In particular, little consideration has been given the trade-offs in demographic parameters such as productivity or adult and juvenile survivorship. Lack (1968) considered the primary trade-off to be between risk of migration and the increase in reproduction accrued to a migrant. Von Haartman (1968) viewed increase in survivorship and increase in productivity to be conflicting factors in the evolution of migration. Basically, he contended that residency in proximity to breeding range will confer certain reproductive advantages which have to be weighed against the decrease in survivorship associated with wintering in a more rigorous area. Ketterson and Nolan (1976) suggested that reproductive advantage associated with proximity to the breeding ground was one of the factors that might contribute to more northerly wintering of male than female Dark-eyed Junco (*Junco hyemalis*).

This paper reviews life history consequences of long-distance migration in birds. I concentrate on two major considerations: 1) what general demographic patterns characterize species undergoing long-distance, mainly neotropical, migrations; and 2) what changes in life history might be involved in the evolution of migratory habits. Consideration of the interplay of demographic parameters will be the basis for postulating selective forces in the evolution of migration and migratory patterns.

Survival of Migrants

Good estimates of survivorship in wild bird popula-

tions are difficult to obtain. Annual adult survivorship is far more easily determined than first-year survivorship and is more commonly presented in the literature. First year survivorship (S_1) can be calculated based on data for adult mortality (M_a) and female productivity (P) using the formula $S_1 = M_a/P$ (Ricklefs 1973). Major methods for obtaining adult survivorship (S_a) are discussed below.

1) The *recapture* method involves the proportion of a population that has been previously marked; it is usually based on resightings or recaptures on the breeding ground, but on occasions winter banding studies have been used to estimate survivorship (Diamond and Smith 1965). Recapture data give a minimum estimate of survivorship and the accuracy depends on the degree of philopatry displayed by individuals in a population. In addition, survivorship may be estimated based on the frequency of recaptures of birds of different age classes (Haldane 1955; Boyd 1965; Roberts 1971).

2) The *recovery* method employs large regional banding samples. The estimate is based on the recovery of dead marked birds in different year classes. Frankhauser (1971) compares the results from recovery and recapture data and concludes that recovery data give higher and more accurate estimates, but are restricted by small sample size. This increased accuracy is because recoveries are not dependent upon the tenure of operation of banding stations.

3) The *ratio* method is generally based on the proportion of adults in a prebreeding or breeding sample of museum skins. If a population is of stable size, the proportion of adults present during the breeding season should equal the annual adult survival rate; this method has been little used (for a good discussion see Snow 1956). The technique suffers from potential collecting biases. Immatures must be unidentifiable in the field, yet distinguishable in the hand. Nonbreeding

Population Limitation: Breeding or Wintering Grounds?

ABSTRACT

No single explanation will account for population limitation of all neotropical migrant populations. Further, factors affecting Old World migrants differ fundamentally from those dominating in the New World.

If population limitation were initially to occur either on the breeding or wintering grounds, consequent accommodation (ecological release) of resident birds or other animals should take place in the initially limited area. Over evolutionary time, few remaining opportunities would thus occur in the previously non-limited area. This argument predicts a dynamic equilibrium between the breeding and wintering grounds, regardless of the area in which limitation initially took place and the limiting factor might be.

Contingencies encountered during migration may further affect some species, although rates of increase usually appear adequate to replenish such losses quickly. The condition of being migratory may, however, place morphological and behavioral constraints upon a bird that are not advantageous during the rest of its year, and which may compromise its performance at those times.

Man-modified habitats may have a major impact upon migratory birds. Lest we assume that presently occurring changes constitute a unique phenomenon, we should keep in mind the role that pre-Columbian Indians may have played in altering the landscape of Mexico and Central America.

Evolution of Migration in Relation to Factors Regulating Bird Numbers

ABSTRACT

Our most plausible working hypothesis to answer the question "Why do some but not all birds migrate?" is: 1) birds usually leave the area where they wintered to breed elsewhere to find safe nest sites; 2) birds usually migrate from the area where they breed to winter elsewhere to find more nonbreeding season food; 3) birds are usually resident in order to maintain (through site dominance) a social advantage in contests for resources during either the breeding season or the nonbreeding season (but not necessarily both). Several untested or weakly tested predictions are offered, and some case histories are reviewed. The Field Sparrow is offered as a winter-limited species sometimes migratory to find predator free nesting habitat and sometimes resident to enhance winter survival. The Dickcissel is offered as a winter limited tropical species unable to generate sufficient site dominance to be resident and which migrates to find predator-free nesting habitats.

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Patterns in the Migration System Between the North Temperate Zone and the Tropics

ABSTRACT

Seasonal occupation of different portions of a species' range is a common phenomena and is generally associated with occupation of two distinct regions; one for breeding and the other as nonbreeding range. About 400 species have breeding ranges that are restricted to the North Temperature Zone and winter (occupy nonbreeding areas) in the tropics. Relatively wet and nonseasonal regions in the tropics (Southeast Asia and the neotropical region) host about 25 percent more nonbreeding species than drier and/or highly seasonal areas (Indian subcontinent and Africa). Species richness of migrants does not seem to be correlated in any simple way with land area, vegetation type, presence of migration barriers, or migration distance. When migrant faunas are subdivided to reflect taxonomic and ecological affinities, several patterns are clear. Nonpasserine groups are more diverse in "dry" than "wet" areas while the reverse is true for passerines. When smaller geographic areas are considered, the importance of habitat type in determining number of migrant species is reinforced except in Africa where migrants favor more open habitats as wintering grounds. Among geographic areas, overlap in species composition varies significantly among taxonomic-ecological groups. In general, nonpasserine species winter over a wider geographic area than do passerine species. The complexity of migration systems in the neotropics, demonstrated by many studies in this volume, is mirrored and expanded in other tropical areas.

Heterogeneity of Potential Food Abundance for Tropical Small Land Birds

No abstract.

There is no general all-purpose method of description of resources for small tropical terrestrial birds. To understand food resources for the birds in a habitat or for a particular species of bird, one has to determine what the bird(s) feed on and hand-tailor a census technique that collects data in a manner that correlates well with the actual resources taken by the bird. However, general statements about *potential* food may suggest detailed studies of birds and their resources that will produce informative close correlations. In this spirit, I offer a few brief stories about apparent severe heterogeneity of potential resources for birds in the tropics.

Rainy Season Insect Flush

In the lowland deciduous forest at Santa Rosa National Park (northwestern Guanacaste Province, Costa Rica), there is an abrupt and heavy production of new foliage at the beginning of the rainy season (May). Within two to four weeks of this flush of foliage, it is apparent that there is also a short-lived heavy peak in the biomass of moth and butterfly larvae feeding on this new foliage. Partly and entirely defoliated plants are common, and the ground is littered with caterpillar feces. A moment's inspection of vegetation produces numerous Lepidoptera larvae. Several months later, there is little trace of this event, other than the remnants of damaged leaves. A month earlier, there was no sign of caterpillars.

To quantify crudely this flush of caterpillars, four of us (P. DeVries, M. L. Higgins, G. Vega, D. H. Janzen) visually censused caterpillars on a 204-m trail-side transect through deciduous forest. The vegetation was examined closely for 2 m on each side of the trail and up to 2 m in height, on sunny clear days with scudding clouds, and between 800 and 1200 hr. All caterpillars were collected into alcohol, and later sorted by morphospecies and measured (table 1). The

vegetation is trail-edge and understory shrubs and saplings in old secondary deciduous forest; the trail was 1–2 m in width, and the canopy was irregularly closed overhead. The trail is the Nature Trail (Sendero Natural) from the first fork, and thence across the natural bridge to the second large rock in the trail in the guapinol grove. The following species of plants made up about half of the bulk of foliage examined: *Allophylus occidentalis*, *Casearia corymbosa*, *Hemiangium excelsum*, *Acacia collinsii*, *Maluaviscus arboreus*, *Hamelia patens*, *Psidium* spp., *Croton* spp., *Stemmadenia donnell-smithii*, *Hymenaea courbaril*, *Calycophyllum candidissimum*, *Cassia* spp., *Plumeria rubra*, *Luehea* spp., *Tabebuia neochrysantha*, *Tabebuia rosea*, *Ficus* spp., *Bursera simaruba*, *Bursera graveolens*, *Guazuma ulmifolia*, *Solanum* spp., *Myrospermum frutescens*, *Genipa caruto*, *Trichilia* spp., *Guettarda macrosperma*.

By the date of the August census, the abundance of caterpillars had fallen to the level that seems to persist through the remainder of the rainy season. There are a number of traits of the caterpillars that seem particularly relevant to their potential as bird food.

1) The average length of the caterpillars (2.0–2.5 cm) did not change over the six-month period. This suggests that a bird may be confronted with the same size distribution of caterpillars early in the season as later (and visual inspection of the caterpillars suggested that this was the case). However, with the absolute number of caterpillars much higher earlier than later in the season, the number of large caterpillars available would likewise be much greater earlier than later.

2) The caterpillars ranged from very cryptic to very aposematic, and there was no conspicuous trend in change in the proportions of these two extremes of life form over the six-month period.

3) Throughout the six-month period, birds feeding on this caterpillar peak were very inconspicuous if they

The Importance of Migrant Birds to the Advancement of Evolutionary Theory

Evolutionary Perspective

This volume brings together much descriptive information on what migrants do in the neotropics together with interpretation of ecological significance. Perhaps it is equally important to have begun a dialog over future directions for research, for the migration system as we know it may not have much time left. Ecology, as a field, has tended increasingly to assume that each species represents a fixed entity, all individuals alike, to be studied in relation to other such fixed entities. This emphasis on interspecific interactions has naturally produced a de-emphasis of evolutionary questions, since the major thrust is far from the level at which evolution operates. This vacuum has lately been filled by behavioral ecology, for only by studying intraspecific relationships can the selective forces acting upon individuals be discovered. Migrants provide perhaps the best system to illustrate the dichotomy that has grown between ecological and evolutionary approaches and also the synthesis provided by the behavioral-ecological approach.

The difficulty of applying an ecological approach to the goal of understanding evolutionary processes in migrant species is evident in this volume. One example is the so-called "plasticity" of migrants if their described roles change. Though not often explicit, this must mean that the individuals sampled have shown changes in the parameters studied, for example, between breeding and nonbreeding grounds, one part of a range from another, or perhaps even between the tropical seasons in one place. To achieve meaningfulness, "plasticity" must be discussed in relation to the sources of selection that produced the changes, for there are many migrant species that show little change and some that show great change—but both are equally adapted. Resident and migrant species show no real difference in "plasticity" anyway. The impor-

tant question is why: what are the proximate and ultimate factors that produced the change or lack of change between breeding and nonbreeding ecology?

The de-emphasis on evolution in ecology has caused some fairly obvious yet important phenomena to be overlooked. One may be the most important difference between North American or intratropical migrants and some tropical residents: the importance of pair bonds. Tropical-resident insectivores are characteristically permanently pair bonded, and they defend permanent territories. About 60 percent of tropical passerine species share these attributes. In contrast, migrant species show no indication of sexual recognition. Most of the resident species they join in flocks are pair bonded; their territories are defended jointly by the bonded pair (Powell, this volume). Why has selection not favored pair bonds in the many territorial migrant species? Even "psuedo" pair bonds, that might not remain through migration into the breeding season, would give an advantage over territorial defense by single birds. However, as several authors noted, territories are defended by both sexes against all other conspecifics—sex is not recognized. The answer is that there is apparently no way that this type of cooperation can be (genetically) favored unless reproduction takes place between the cooperators. (The Prothonotary Warbler may be an exception—they seem to maintain or assume pair bonds on the wintering grounds).

What are the ecological ramifications of this lone major difference between migrants and residents? Territorial migrants and residents alike show a tendency toward habitat restriction. They choose habitat structures that best predict insect availability relative to their specific morphological and behavioral specialties. But for nonterritorial migrants and residents, or those exhibiting facultative territoriality, movements in response to local or regional changes in food availability are possible. The absence of pair bonds promotes omnivory, the most ubiquitous tropical diet, together with a loosening of foraging zones. By not breeding in the tropics, and by assiduously avoiding the recognition of sex, the evolutionary background of "plasticity" for North American migrants becomes almost a syndrome.

There is probably strong selection *against* sexual recognition. Selection might favor females that look like males, if males are larger, if only because it gave them an advantage in social conflicts. This may be the process by which the sexes of territorial migrants have become identical or similar. For example, in most Red-winged Blackbirds (*Agelaius phoeniceus*), the sexes are readily distinguishable. The sexes also forage in somewhat different habitats and in separate flocks.

The Cuban redwing is an exception in which the sexes remain together when foraging, and conflicts are frequent (pers. obs.). Here the females are black, like the males. Selection has generally favored monochromatism when winter territories are defended but sexual dichromatism when quick pair formation is of paramount importance back in North America (plus lack of female participation in territorial defense).

The evolutionary perspective will give added interest to single species studies. As Karr (this volume) points out, each migrant species represents a unique adaptation within both temperate and tropical ranges. Many of these adaptations remain unidentified due to the "fixed entity" model necessary when ecological categories larger than the species are emphasized.

How Tropical Are Migrants?

The diets of migrants while in the tropics show a convergence toward those of resident species. There is a clear trend toward omnivory through the use of plant products, one of the major reasons why the tropics support a higher species diversity than temperate areas (Karr 1971; Morton 1973; Lovejoy 1975).

North American migrants, because of their abundance and mobility relative to resident species, must exert great influence on fruiting and flowering phenology of tropical plants. The timing of fruit production in *Phytolacca* species may be largely an adaptation for fruit dispersal by Swainson's Thrush (*Hylocichla ustulata*) in both temperate and tropical areas (Karr, this volume; Ramos pers. comm.; pers. obs.). The relationship between migratory orioles (*Icterus*) to flower timing and morphology in *Erythrina* species has been discussed by Cruden and Toledo (1977) and Morton (*in press*). The timing of fruit production in *Didymopanax morototoni* and the display of the fruit (sticking up through the treecrown to be visible to overflying birds) may be adapted for the Eastern Kingbirds' (*Tyrannus tyrannus*) tropical passage (Morton 1971). In Panama, *Combretum fruticosum* is pollinated almost exclusively by the Tennessee Warbler (*Vermivora peregrina*, Morton this volume).

The diversity in behavioral ecology exhibited by migrants in the tropics points to some unsuspected complications for their conservation. Except for sedentary, territorial species, habitat requirements are not easily assessed because these vary during a single season. Bay-breasted Warblers (*Dendroica castanea*), for example, utilize young forest, late shrub, and mature forest but require mature forest for a short but critical period between wet and dry seasons. Furthermore, food-rich habitats paradoxically may not be the only critical requirements. Food-rich habitats, young forest in the wet season for Bay-breasts, may produce low

social tolerance; certain sex and age classes could be forced into mature forest habitats. The destruction of these mature habitats may cause skewed sex ratios with a reduction in breeding potential. It is not realistic to study foraging, foods, or social behavior as separate entities, for they all act synergistically. We need much more information on intraspecific competition before we can either assess the impact of habitat changes in the neotropics on migrant populations or extract scientific generalizations about tropical adaptations that migrants have to tell us.

Literature Cited

- Cruden, R. W., and V. M. Toledo.
1977. Oriole pollination of *Erythrina breviflora* (Leguminosae): evidence for a polytypic view of ornithophily. *Plant Syst. Evol.* 126:393-403.
- Karr, J. R.
1971. Structure of avian communities in selected Panama and Illinois habitats. *Ecol. Monogr.* 41:207-33.
- Lovejoy, T. E.
1975. Bird diversity and abundance in Amazon forest communities. *Living Bird* 13:127-91.
- Morton, E. S.
1971. Food and migration habits of the Eastern Kingbird in Panama. *Auk* 88:925-26.
1973. On the evolutionary advantages and disadvantages of fruit-eating in tropical birds. *Amer. Nat.* 107:8-22.
1979. Effective pollination of *Erythrina fusca* by the Orchard Oriole (*Icterus spurius*): coevolved behavioral manipulation? *Ann. Mo. Bot. Garden.*

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Synthesis: Ecological Basis and Evolution of the Nearctic-Neotropical Bird Migration System

ABSTRACT

The original objectives of this volume were to define how nearctic-breeding species fit into the neotropical system, where the major species wintered, how their ecology compared with that of resident species, and how migrant and resident interacted. In the wider view, by bringing together a diversified team of experts in a range of areas, groups, and aspects of ecology, it was hoped to learn how northern Neotropica, a highly species-rich area presumably already "saturated" with species was able to "absorb" such vast hordes of seasonal intruders from outside. The conclusion has now come forward from many contributors that this way of looking at the situation is incorrect, that, by contrast, the migrants are part of the tropical ecosystem and that, though only present for some seven months, they retain "niches" there. Thus, Rappole and Warner hypothesize that most nearctic, long-distance migrants evolved from historically tropical species which were able to exploit niches common to many different forest types; that with low breeding success and intense competition for resources in tropical communities, individuals of these species took advantage of reduced competition in seasonal niches in temperate areas to increase reproductive success. Certainly, in the wintering grounds, there is no basis for the claim that migrants are competitively inferior to permanent resident species. Emlen, Stiles, and others find the striking degree of concordance between ecological distributions of permanent and winter residents as further evidence that they are really part of the tropical communities. Stiles sees the high degree of integration of winter

residents into tropical communities as demonstrating a long tropical history. Similar views are expressed by others.

In their wintering grounds, the migrant species separate out ecologically from each other and from residents, in a range of ways: geographically, on habitat, on feeding height and behavior, etc. The nature of these separations is the same as in bird communities elsewhere. While there is ample evidence of continuing species interaction and of species' influences on each other's ecology, it must be noted that the more closely related species (congeners) tend spatially to separate out fairly clearly. Since species composition in the wintering communities is quite different from that of the summer communities, it is obvious that the two communities have developed independently and by the assemblage of groups of species that are compatible within the adaptive capacity of the individual species.

Some 150 species of land and freshwater birds that breed in North America fly south annually to winter in Central and South America and in the West Indies. This ability to seasonally exploit two very different latitudes is a typically avian phenomenon. The migrants are able to utilize the spring flushes of insects and long days of the north to raise their young. Southward migration in the winter provides them with a supportive environment the rest of the year.

Thinking about the origins and ecological basis of migration has changed drastically over the last 150 years. Several writers in this symposium, for example, argue that migrants should not be looked upon as a northern assemblage that moves southward (reluctantly?) to escape winter, an alien element fitting as best it can into neotropical habitats. Rather, by contrast, migrants and residents should be viewed as part of a common co-evolving American avifauna. The concept of these migrants being, originally, tropical birds that go north to avail themselves of seasonal opportunities in the north is not new. It was the basis of the "southern ancestral" theory of bird migration. Either way, the interaction patterns of migrant and resident on the wintering grounds today are complex and dynamic, as many papers in this symposium testify.

Origins of the Basic Elements of the Nearctic Avifauna Relative to the Development of the Migratory Habit

The Nearctic Zoogeographic Region is defined as North America plus the Mexican Plateau; Neotropica, as South America attenuating northwards to the lowland rain forests of Guatemala and Chiapas. The division, while by no means absolute, delimits a temperate avifauna adapted to deciduous forest, pine-oak, and highlands, from an avifauna of tropical rain forest and savannah. The division is reinforced by many of the more distinctive southern families (Furnariidae, Formicariidae, Dendrocolaptidae) not presently entering the Mexican highlands or continental North America. The contemporary division of Nearctica from Neotropica, nevertheless, glosses over the fact that prior to the formation of the Panamanian land-bridge North America extended southwards as a peninsula as far south as Panama, evidenced by the presence of North American fossil mammals in the Miocene (Whitmore and Stewart 1965). Accordingly, there must formerly have been a North American tropical avifauna (Mayr 1946, 1964). There is evidence, however, that this peninsula was largely covered with savannah, not rain forest (Whitmore and Stewart 1965; Mayr 1964; and other sources).

Mayr (1946, 1964), stressing that the contemporary

North American avifauna are of multiple origins, has divided it into a series of elements based on the fossil record and centers of abundance. Mayr's recognition of six elements has received wide acceptance. These elements are: 1) Pantropical, 2) Panboreal, 3) Old World, 4) North American, 5) Pan-American, 6) South American, plus an aggregate element of avifauna of unanalyzed origin. This last element is made up of groups so evenly distributed between the Old and New Worlds that assessment of centers of origin is impossible. Included in this element are grebes, herons, ibises, ducks, and rallids.

The Panboreal element is small—only loons and phalaropes. The Old World element is large and, besides later colonizers, probably includes: the American quails within the Phasianidae; typical owls (Strigidae, because the related Tytonidae are clearly of Old World origin); the gnatcatchers (Poliophtilinae, now included within the Sylviinae); the pigeons (because their major radiation is in the Australian part of the Old World); the Crows (Corvidae); thrushes (Turdinae); cranes, kingfishers, cardueline finches, and titmice (Paridae). These groups probably entered Nearctica progressively during the Tertiary, and some have had a very long history here. Groups that are clearly late arrivals from the Old World include the barn owls (Tytonidae), larks (Alaudidae), nuthatches (Sittidae), creepers (Certhiidae), Old World warblers and kinglets (Sylviinae), and the shrikes (Laniidae).

The North American element (endemics that originated here) is considered by Mayr to include the New World vultures (Cathartidae), turkeys (Meleagrididae), grouse (Tetraonidae), dippers (Cinclidae), and the finch subfamily Emberizinae. Mayr agrees with Lonnberg (1927) that the thrashers and mockingbirds (Mimidae), vireos (Vireonidae), wood-warblers (Parulidae), waxwings (Bombycillidae), and wrens (Troglodytidae), are basically nearctic. He notes that the parulids have 16 genera in North America (many endemic), and only 6 in South America (none endemic).

The Pan-American element, prominent in both continents, includes the Icteridae and Tyrannidae. Today, both of these families are more diversified in South America than North America.

The term neotropical element applies to groups in which the overwhelming bulk of genera are South American or are confined to Neotropica, and few if any species penetrate northwards. Included in this element are the formicariids, furnariids, dendrocolaptids, cotingids, tanagers, and hummingbirds. Most of these are obviously closely linked to the specific attributes and habitats of multi-layered tropical forest with its abundant fruit and nectar resources.

From Mayr's framework, it is obvious (table 1) that migration has evolved in all groups irrespective of origin. Among the Panboreal element the phalaropes winter in the Southern Hemisphere, and within the Old World element quails, owls, gnatcatchers and thrushes are migrants. Migration is pronounced in the members of the nearctic and Pan-American elements, and the few true neotropical groups that penetrate well to the north are also migrants. Williams (1958) has developed a tabulation (table 2) in which he compares the wintering latitudes of species whose ancestors entered Nearctica from the north (i.e., species which apparently are of palaearctic origin) relative to those which entered Nearctica from the south. Half of the palaearctic species winter north of the U.S.-Mexican border, compared to 5 percent of the neotropicals. Only 1 percent of the palaearctic species penetrate into South America, compared to 36 percent of the Neotropicals.

Taxonomic Group and Ecological Category Relative to Migration Distance

Listed in table 1 are the various families of nearctic birds and the numbers of each species wintering in North America, Neotropica, or in both regions. The last category is, in part, made up of warm-temperate and subtropical forms centered in the southern United States and Central America.

The following avian families belong mainly or entirely to the group wintering in North America: loons, grebes, cormorants, grouse, quails, turkeys, cranes, woodpeckers, corvids, titmice, nuthatches, creepers and dippers, mimids, sylviids, pipits, bombycillids, and shrikes. Families in which most forms remain in Nearctica but in which there is also marked wintering in Central America include: herons, ibises, ducks, hawks, rails, pigeons and owls. Families in which wintering in Neotropica is predominant are: caprimulgids, swifts, swallows, tyrant flycatchers, vireos, parulids, and tanagers.

A number of the groups that winter both in North America and Central America, have small numbers of species that are long-distance migrants. These are: accipitres, falcons, plovers, cuckoos, hummingbirds, thrushes, orioles, and fringillids. The scolopacids have a significant proportion of very-long-distance migrants traveling to southern South America (Myers, this volume). Although only about 15 percent of icterid species winter in South America, they include one exceptionally long-distance migrant, the bobolink (*Dolichonyx oryzivorus*), that migrates to Brazil and northern Argentina. Among the 9 percent of the fringillids migrating to Neotropica are the Indigo Bunting (*Passerina cyanea*), the forest-dwelling Rose-breasted Grosbeak (*Pheucticus*

ludovicianus), and the grassland Dickcissel (*Spiza americana*).

Of the groups that are predominantly neotropical winterers, only 9 of the 30 species of tyrannids and only 14 of the 84 species of migratory parulid species winter in North America (Fitzpatrick, this volume).

The major groups that winter in Neotropica are the insect-eaters, the aerial-feeding swallows and swifts, caprimulgids, and tyrannids, and the woodland-dwelling and arboreal-feeding parulids, vireonids, and orioles. Their breeding in the north is obviously linked to the spring flushes of lepidopterous and other larvae. More data are needed, however, on the nature of the winter resource base in the south that supports the above neotropical winterers.

Where Do Migrants Winter in Neotropica?

A number of contributors to this volume provide data from north to south on the abundances of migrants relative to residents at various localities in Central America. These data are summarized by Terborgh (this volume). It shows a progressive southward drop-off in numbers of wintering species and individuals. Since the attenuation is matched by an increase in the numbers of *resident* species (as Slud [1976] and others, have noted), the impact of migrants on the system progressively diminishes southwardly.

In contrast, at the northern end of the wintering zone, *migrants* are dominant. Thus, Emlen finds that in Florida and the northern Bahamas, the number of species increases by 160–206 percent in winter; and the densities of individual birds fluctuates from about 900 per km² in April, after the migrants leave, to 1,600 per km² in mid-winter. In June with the acquisition of summer migrants, counts average 1,200 per km². An even more striking seasonal difference occurs in western Mexico where the tropical evergreen forest habitat that supports 67 small foliage gleaners per ha in winter supports only 1.7 per ha in summer (Hutto, this volume). The lowland sites averaged 25 times more warbler-guild birds in winter than in summer. Hutto in part ascribes the extreme difference to the fact that insect densities are 1.58 times higher in winter than in summer. In contrast with the southern nearctic localities is the situation in Ecuador, Peru and Bolivia at the southern extreme of the migrant wintering area. This area is "the most species-rich bird habitat in the world," with 420–480 species per 10 km². Here, wintering northern migrants make up only 5.2–7.3 percent of the species (Pearson 1975).

Terborgh tabulates the percentages of migrant individuals in the winter avifaunas of some 25 localities from Mexico through the West Indies and Central America to Bolivia. Although proportions vary with

Table 1. Seasonal migration in nearctic-breeding land and fresh-water species of birds: numbers wintering within Nearctica; Nearctica plus Neotropica; and entirely in Neotropica or the West Indies

<i>Family</i>	<i>Number of nearctic breeding species</i>	<i>Number wintering in Nearctica</i>	<i>Number wintering in both Nearctica and Neotropica</i>	<i>Number wintering in Neotropica</i>
Gaviidae (loons)	3	3	—	—
Podicipedidae (grebes)	6	5	1	—
Pelecanidae (pelicans)	2	1	1	—
Phalacrocoracidae (cormorants)	5	4	1	—
Anhingidae (darters)	1	—	1	—
Ardeidae (herons)	13	1	12	—
Ciconiidae (storks)	1	—	1	—
Threskiornithidae (ibises, spoonbills)	5	—	5	—
Phoenicopteridae (flamingos)	1	—	1	—
Anatidae (ducks)	42	30	11	1
Cathartidae (vultures)	4	1	3	—
Accipitridae (hawks)	24	10	11	3
Pandionidae (ospreys)	1	—	1	—
Falconidae (falcons)	7	2	4	1
Cracidae (curassows)	1	—	1	—
Tetraonidae (grouse)	9	9	—	—
Phasianidae (quails)	6	6	—	—
Meleagrididae (turkeys)	1	1	—	—
Gruidae (cranes)	2	2	—	—
Aramidae (limpkins)	1	1	—	—
Rallidae (rails)	9	5	4	—
Jacaniidae (jacanas)	1	—	1	—
Charadriidae (plovers)	10	3	5	2
Scolopacidae (sandpipers)	26	2	15	9
Recurvirostridae (stilts)	2	1	1	—
Columbidae (pigeons)	12	3	8	1
Psittacidae (parrots)	1	1	—	—
Cuculidae (cuckoos)	6	1	3	2
Tytonidae (Barn Owl)	17	11	6	—
Strigidae (owls)	—	—	—	—
Caprimulgidae (goatsuckers)	7	1	1	5
Apodidae (swifts)	4	—	1	3
Trochilidae (hummingbirds)	17	10	4	3
Trogonidae (trogons)	1	—	1	—
Alcedinidae (kingfishers)	2	—	2	—
Picidae (woodpeckers)	22	18	4	—
Cotingidae (cotingas)	1	—	1	—
Tyrannidae (tyrant flycatchers)	30	9	8	13
Alaudidae (larks)	1	—	1	—
Hirundinidae (swallows)	7	—	2	5
Corvidae (jays, crows)	15	13	2	—
Paridae (titmice)	14	14	—	—
Sittidae (nuthatches)	4	4	—	—
Certhiidae (creepers)	1	1	—	—

Table 1. (cont.)

<i>Family</i>	<i>Number of nearctic breeding species</i>	<i>Number wintering in Nearctica</i>	<i>Number wintering in both Nearctica and Neotropica</i>	<i>Number wintering in Neotropica</i>
Chamaeidae (wrentits)	1	1	—	—
Cinclidae (dippers)	1	1	—	—
Troglodytidae (wrens)	10	9	1	—
Mimidae (mockingbirds)	11	10	1	—
Muscicapidae Turdinae (thrushes)	12	9	—	3
Sylviinae (Old World warblers)	4	4	—	—
Motacillidae (pipits)	2	2	—	—
Bombycillidae (waxwings)	1	1	—	—
Ptilonotidae (silky flycatchers)	1	1	—	—
Laniidae (shrikes)	2	2	—	—
Vireonidae (vireos)	11	3	2	6
Coerebidae (honeycreepers)	1	1	—	—
Parulidae (wood warblers)	84	14	10	30
Icteridae (orioles, etc.)	21	11	7	3
Thraupidae (tanagers)	4	—	1	3
Fringillidae (finches, sparrows)	54	44	5	5

Table 2. Comparison of the southern extent of the wintering ranges for those birds thought to have originated either in North America (or most likely arrived from Eurasia via the Bering land bridge) to those birds which have invaded North America from southern tropical regions (from Williams, 1958)

<i>Southern limit of migration</i>	<i>Numbers of species</i>	
	<i>Pale- arctic origin</i>	<i>Neotropical origin</i>
Not south of U.S.	87	8
Central Mexico	44	30
Southern Mexico	7	16
Central America	13	56
Into South America	2	63
Totals	153	173

habitat, it is apparent that for most Mexican localities, migrants are in excess of 30 percent of the population. There is a precipitous drop-off in Costa Rica and Panama (typically less than 20 percent, but only 4–7 percent at some sites). (See figures of Willis, Stiles, Tramer and Kemp, this volume.) Colombian figures are high only for a mangrove site (46 percent of individuals), a disturbed oak forest habitat in the central Andean highlands (46 percent), and a couple dry forest sites (22–24 percent). For additional sets of figures, see Waide and Tramer (this volume) who, in addition, warn of the discrepancies that may result from counts made only by netting and strip-count methods.

In the West Indies, Terborgh and Faaborg (this volume) note that the fraction of North American migrants in winter bird populations shows a strong inverse dependence on distance from the mainland (Florida). The mean value for a large array of censuses in Hispaniola is about 35 percent but drops to 10 percent in Puerto Rico and to 1 percent (or less) in

more distant locations, such as the Lesser Antilles, Trinidad, and the Venezuelan mainland. This occurs even though the resident avifaunas become progressively impoverished.

Terborgh suggests that in winter half of all the migratory land birds are compressed into a segment of Mexico and the West Indies equal to 2 million km², compared to an area of 16 million km² in their North American breeding grounds. This obviously testifies to the high carrying capacity of these areas. In southern Argentina, however, Myers (this volume) records that in inland Pampas habitat, wintering migratory waders defend areas usually only one-tenth to one-hundredth the size of those defended during the breeding season, with up to 30 percent of the time being spent in territorial defense. That migrants are concentrated at such high densities is worrisome from the conservation viewpoint, suggesting that any deleterious change in these habitats will have disproportionate effects (Terborgh, this volume).

An interesting feature of winter habitat utilization by migrants is the differing abundances in the various habitats. Emlen, Hutto, Waide, Waide and Tramer, Keast, Hilty, Hespeneheide, Stiles, and others, document this. Thus, on Grand Bahama, winter migrants made up: 81 and 82 percent, respectively, of all birds in the coastal dunes and mangrove flat areas; 43 percent in pine forest; but only 33 percent in pine regrowth areas. The percentages of migratory species and individuals in a range of habitats in western Mexico is given by Hutto (this volume) as follows: gallery forest, 20–22 percent (64–69 percent of individuals); mangroves, 50–74 percent (75–83 percent); second growth, 51 percent (59–63 percent); thorn scrub, 36–43 percent (55–60 percent); tropical deciduous, 28–38 percent (17–24 percent); oak woodland, 33–41 percent (29–36 percent); pine-oak woodland, 29–40 percent (31–56 percent); and pine woodland, 24 percent (31 percent). In three Colombian forest sites studied by Orejuela et al (this volume), migrants made up 20 percent of all birds in an isolated lowland valley-floor site (Jamundí), and 14 percent in an intermediate site, but were absent from a tropical wet-forest site in the Pacific lowlands (Bajo Calima). In another Colombian study which emphasizes altitudinal effects, Hilty records that the number of migrants encountered per hour was 1.0 in the lowlands (elevation, 100 m), 1.8 at 1,000 m, and 2.6 at 1,900 m.

Karr (1976b) considers the use of lowland rain forests by migrants, noting that while these forests support species in Central America, the same kind of forest in Africa is avoided. Tramer and Kemp (this volume) find that the Monteverde forests of Costa Rica are relatively little used and suggest that this is

because the migrants, compared to residents, are poorly adapted for feeding on epiphytic growth. Stiles, however, suggests that the tendency for fewer migrants than residents to occupy the forest interior is merely a function of taxonomic affinities, even though the two distribution patterns are otherwise closely matched. In contrast, Rappole and Warner find that individuals of 14 migrant species were able to compete effectively in primary forest on a long-term basis. Morton (this volume) documents seasonal movements of some species to and from mature forests in Panama. Migrants occupy primary forests on Barro Colorado Island and along the Pipeline Road in the Canal Zone (Willis, Morton, this volume), and also along trails in primary forest in the Chiriqui Highlands. Regarding other forest habitats, Johnson (this volume) provides data on migrants in the subtropical lower montane forest of the Santa Marta Mountains, and Miller (1963) provides similar data relative to the Western Andes of Colombia.

In central and northern South America, some migrants are more numerous in the highlands than in the lowlands (Karr 1976; Smith 1975; and Keast, Hilty, both this volume). This does not, however, apply in Jamaica and Hispaniola (Lack and Lack 1972; Lack 1976; and Terborgh and Faaborg this volume). No author in this volume has set out to make a precise analysis of vertical abundance. Waide, however, reviews the available literature and concludes that the evidence is too conflicting to justify generalizations about the effect of elevation on the distribution of migrant birds. Altitudinal effects are difficult to separate from the effects of moisture and human disturbance. Stiles, studying migrants and residents at heights from 0 to 3,000 m in Costa Rica, finds that although the counts vary, there is no consistent relation between the migrants and residents vs elevation. Fitzpatrick (this volume) suggests that species segregation along the altitudinal gradient, while evident, is probably a byproduct of different habitats characterizing different elevations. Habitat quality, rather than altitude, may also be the major factor influencing migrant numbers.

Several authors (Terborgh, Waide, Pearson) discuss the assertion that migrants are concentrated at, or prefer, disturbed areas, second growth, marginal, patchy, and/or highly seasonal habitats (areas unused or underused by the residents) (Willis 1966; Leck 1972; Karr 1976). Alternatively, they concentrate on super-abundant and/or sporadically available resources (Karr 1976). Terborgh notes that data presented by Emlen from the Bahamas, Hutto from western Mexico, Pearson from Ecuador and Bolivia, Waide from southern Yucatán and Willis from Panama, provide

some support for the first assertion but that in other areas, such as the Bahamas (Emlen), Jamaica (Lack and Lack 1972), and northern Yucatán (Tramer 1974), migrants are equally common in primary and secondary vegetation. The generalization that migrants prefer second growth may also be misleading in that: 1) some migrants are actually successional stage species and 2) they may secondarily be forced to use this due to reduction of their natural habitat (Terborgh). Waide directs his study specifically to an analysis of three assertions: 1) migrants use patchy habitats (for example, mountaintops); 2) they concentrate on seasonal and unpredictable resources and, 3) they occupy new habitat types because resident species have not had time to adapt to these. The literature, he finds, provides little support for the first two hypotheses. His data fail to support the predictions of the third assertion. Thus, in the Campeche province of Mexico, while residents discriminate more strongly than migrants between forest and old fields, they nevertheless occupy old fields.

Finally, the earlier observation that the various taxonomic groups of North American birds winter in characteristic areas also applies regionally in Nearctica. The center of abundance of wintering tyrannids is southern Mexico (Fitzpatrick), and the greatest number of wintering warblers occur in the Guatemala-Costa Rica segment (Keast). No tyrannids winter in the West Indies, but good numbers of parulids do. Fitzpatrick shows that the high numbers of tyrannids in southern Mexico is due to the concentration of migrants from the western United States; eastern stocks mostly travel farther south, to southern Central America and northern South America. In a graph, Keast shows that the steep drop-off in numbers of wintering parulids from Guatemala into northern South America corresponds to an increase in numbers of such potential competitors as the small foliage-gleaning tyrannids.

Ecological Separation of Migrant-Migrant and Migrant-Resident Counterparts

The various authors of regional chapters deal comprehensively with the migrants in specific regions. Comparisons confirm that in migrant groups with many species, geographic (allopatric) replacement of species is marked. Three authors—Fitzpatrick dealing with tyrannids, Keast with parulids, and Barlow with vireos—develop species replacement in detail by the use of range maps. Keast points out that the species of the more common warbler genera such as *Dendroica*, *Oporornis*, and *Wilsonia*, show a marked degree of geographic separation. In *Dendroica*, for example, there are species that winter in northern Central America,

southern Central America, mainland South America, the West Indies, and the highlands relative to lowlands. Fitzpatrick notes that in the tyrannids geographic separation seems particularly pronounced among complexes of closely related species with similar wintering habitats. Thus, while tyrannid wintering patterns show only slight relationship to the resident community on a gross geographic scale, many wintering species sort out among themselves on a much finer scale. Ecologically dissimilar species show significant overlap on their wintering grounds. These remarks apply equally to the parulids.

Congeners also separate out on habitat. Fitzpatrick stresses that the winter habitat preferences of North American *Empidonax* flycatchers strongly resemble those of their breeding grounds. This certainly applies also to some of the parulid warblers such as *Dendroica petechia*, *Sciurus noveboracensis*, but the correlation is lacking in others.

Parulid warblers, with by far the greatest number of over-wintering migrant species, have attracted the most attention of ecologists (for example, Lack and Lack 1972; Bennett, Chipley, Rabenold, Tramer and Kemp, Keast, all this volume). Cohabiting species characteristically separate out ecologically from each other and from the resident parulids on feeding zone (Keast) and habitat, although there may be much overlap. They also differ in feeding habits, for example percentage of time spent gleaning as against hawking or fruit-eating, and several species show considerable flexibility in their feeding habits (Tramer and Kemp, this volume; Morton, this volume). This is further emphasized when feeding zones and habits in breeding and wintering grounds are compared. In fact, ecological plasticity is a basic feature of most migratory warblers (Keast).

Former workers (Lack and Lack 1972, writing of Jamaica), devoted much attention to cataloging how the various species of parulids differed ecologically from each other while in their wintering grounds. Emphasis was on habitat preferences, foraging height, and foraging habits. That each species was found to differ in one or more ways was regarded as confirmation of the competitive exclusion principle. Terborgh and Faaborg, dealing with the comparable Hispaniolan avifauna, and while also amply demonstrating these differences, have paid greater attention to evolutionary aspects. Ecological differences are considered relative to the alternative mechanisms of coadaptation (the species-developing ecological differences in response to the presence of each other) or selective screening (only species that are different can combine). They conclude that the latter is far more likely.

The papers of Feinsinger, and DesGranges and

Grant (this volume) consider the use of space and resources by migratory hummingbirds in tropical communities. Feinsinger investigates the implications of using patchily distributed resources, partial migration, and the alternative strategies of being a dominant or a fugitive species. DesGranges and Grant focus on the coexistence of resident and migrant species in four habitats in Colima, Mexico. They found that the migrants occur coincidentally with the season of superabundant nectar, food in excess of what the residents can consume. (This contrasts with the situation in the insectivorous birds.) Territorial behavior is widespread in both migrants and residents in wintertime; generally, however, the migrants are subordinate and display "fugitive" behavior. The authors conclude that the "dominant specialist," and the "interstitial specialist" hypotheses are not applicable. However, migrants and residents sometimes occupy niches that are fairly different. It is obvious, accordingly, that coexistence is achieved by several mechanisms operating simultaneously. These mechanisms are broadly similar to those operative in the insectivorous parulid warblers, although the resource base is quite different.

Migrant-resident coexistence patterns in the ecologically very different shorebirds in the Buenos Aires Province of Argentina are reviewed by Myers. Local breeding species prove to be taxonomically and ecologically distinct from the migrants. In Patagonia, there is less ecological similarity between the Argentine migrants and the Patagonian residents than there is between the Argentine migrants and the North American migrants which seasonally replace them. Distributions of several potential competitors among South American breeders and North American visitors resemble geographic replacement patterns. Patterns of resource use by the migrants do not support the generalization that they depend more than residents on ephemeral resources. Aggressive interactions between migrants and residents occur repeatedly (suggesting the presence of interspecific competition). Finally, Myers believes that the high densities of residents may prevent the northern scolopacids from establishing breeding territories. There is thus strong evidence that migratory and resident shorebirds in southern Neotropica have influenced each other's evolution.

In summary, nearctic migrants wintering in Neotropica must have evolved mechanisms that reduce both the effect of migrant upon migrant, and migrant upon resident (and vice versa). This might be achieved in a limited number of ways: allopatric separation, different feeding habits, and different feeding niches. Groups as diverse as insectivorous flycatchers, parulid warblers, hummingbirds, and shorebirds, all draw on these mechanisms. The extent to which such basic

separation mechanisms (and the other lesser ones) operate, varies with the group and its resource base.

Attributes of the Neotropics Relative to the Support of Winter Migrants

A consideration of how migrants use space and separate out ecologically is, of course, only part of the problem of interpreting the nearctic-neotropical bird migration system. An understanding of how the system is able to absorb so many additional birds is basic to the problem. Do the northern neotropics have special attributes?

The subject can be considered at various levels: general biotic richness, evidence from the resident breeders (species diversity), and special features of the tropics, such as habitat diversity, production of fruit, nectar, insects, and so on.

Avian Species Diversity in the Tropics

A gradient of increasing avian species diversity extends from cold temperate North America southwards to Central America. For this aspect, see papers on within-habitat (alpha) diversity by MacArthur *et al* (1966), and MacArthur (1969), and earlier papers listed therein; also see Orians (1969), Karr (1971), Karr and Roth (1971), Schoener (1971), and Tramer (1974). Diversity between wider geographic regions (gamma diversity) is treated by Simpson (1964) for mammals, and by Cook (1969) for birds. Tramer (1974), in his analysis of latitudinal changes in species numbers, found that alpha diversity remains stable southwards to 20°N (which ? represents a threshold of climatic stability), then increases to the tropics. Gamma diversity, calculated as occurrences in squares with sides of 500 km, showed a striking increase in species density in winter from 20 on Hudson Bay to 80 in Massachusetts, 103 in North Carolina, 371 in Vera Cruz, and 660 in Panama. However, in summer there is a decline in gamma diversity between 45° N and the Gulf of Mexico, a feature that also puzzled Cook (1969). The western United States has a higher summer gamma diversity than the east; this has been ascribed both to the greater altitudinal diversity in the West and to proximity of source areas in Central America.

Further evidence that the migrants from North America are entering an area phenomenally rich in bird species comes from the consideration of individual regions. Thus, Costa Rica, with a land area of only 32,000 km², has 189 genera and 330 species of passerine birds, "in relation to its small size . . . possibly the richest bird life of any country of comparable size" (Slud 1964:22). The large country of Colombia has 328 genera and 816 species of passerines (de Schau-

see, 1964). In the Amazon segments of Ecuador, Peru and Bolivia, studied by Pearson (this volume) 420 to 480 species of birds occur per 10 km². In his study area near Belem, Brazil, Lovejoy documented over 300 species—an avian species diversity exceeding that published for any other animal or plant community, although no northern migrants occur there (Lovejoy 1974).

Avian diversity indices are high for the northern neotropics: 5.31–5.55 for lowland rain forests in Veracruz (Davis and Moroney 1953; Davis 1955); 5.67 for Belem (Lovejoy 1974); 4.38 for Barro Colorado Island (Tramer 1969); figures are calculated to the base 2. For other figures, see Orians (1969), MacArthur et al (1966), Karr (1971). Diversity indices express evenness of spread of species numbers, as well as the total number of species. Hence, while they do provide an index to the nature of the avifauna, they play down rare species; the high figures for species numbers in the tropics are in part due to the presence of many rare species. Rare species, however, are unlikely to provide competition for migrants. Karr (1971) has found that in Panama 2 percent of the species netted, accounted for 36 percent of the individuals (comparable figures for Illinois were 3.0, 13.7, and 8.2 percent). In Belem, Lovejoy (1971) found that 29.9–42.4 percent of all species were below the 2 percent level of abundance.

Migrants from Nearctica thus enter areas that have an unusually high capacity to support a diversity of bird species, as demonstrated by the rich resident avifauna. The richness, on the other hand, argues for a high degree of species saturation, hence resistance to the establishment of more species. This problem faces only migrants that enter Neotropica proper; many avoid the problem by wintering in Mexico and the West Indies. The high proportion of rare species indicates, moreover, that the system lends itself to the absorption of species at low levels of abundance. Additional species of migrants could, theoretically, be absorbed provided their numbers in any area were low.

Avian Competitors in the Neotropics: the North-South Gradient of Increasing Species Numbers

Genera of migratory passerines with resident species in Central America include *Tyrannus*, *Contopus*, *Empidonax*, *Dendroica*, *Vireo* and *Piranga*. The number of species involved is, however, small and allopatric separations are fairly clear-cut. Of greater significance are the major, or potential competitor groups among the neotropical avifauna.

All the major neotropical passerine families become

increasingly diversified from Guatemala southwards. Thus, the furnariids have 13 genera and 17 species in Costa Rica compared to 26 and 68 in Colombia; the formicariids, 16 genera and 29 species to 42 and 123; the tanagers, 18 genera and 43 species to 40 and 123; the cotingids, 13 genera and 18 species to 23 and 48 (figures from Slud 1964, and de Schauensee 1964). Fitzpatrick (this volume) discusses the increasing diversity of tyrannid flycatchers from Central America southwards to the South American mainland. Keast (this volume) graphs the tapering off of numbers of wintering migratory parulids from Central America into mainland South America relative to the increase in the numbers of species of the small foliage-gleaning tyrannids, the parulids' ecological counterparts in South America. There is no significant difference in the numbers of genera and species of wrens (Troglodytidae), vireos and thrushes, between Costa Rica and Colombia.

It is a reasonable conclusion that 1) the increasing diversity of endemic groups from Central America southwards is a significant factor limiting the southward penetration of migratory nearctic passerines and, 2) in the longer term, furnariids, formicariids, and others have tended to restrict the morphological and ecological diversification of the parulids and others in South America.

Resource Base in Northern Neotropica during the Northern Winter

Seasonal cycles of productivity in the northern neotropics results in a heterogeneous resource base for migrants (Janzen). While the period of migrant residence is a time of peak nectar production in Mexico (DesGranges and Grant, this volume) and of insect production in Amazonian Ecuador, Peru, and Bolivia (Pearson), it is a time of reduced insect members in the Central American habitats (Janzen). Thus, in the lowland deciduous forests of Costa Rica (Santa Rosa National Park), there is a short-lived but heavy peak in biomass of moth and butterfly larvae in May, shortly after the migrants depart. These pupate, hatch within a few weeks, and depart as adults. There is no second generation, and by August caterpillar numbers are at a low level. The numbers remain low thereafter, throughout the duration of the migrants' stay. During the ensuing dry season (beginning in late September) many insects move from the drying hillsides into the riparian vegetation, resulting in relatively high numbers there during the dry season. The trend is not uniform, however; thus, while chrysomelid beetles are common in the riparian vegetation during the dry season, during this same period the bruchid beetles are

the most abundant on the hillsides. Numbers of species of insects, numbers of individuals, size frequencies, weight, and taxonomic category, vary from habitat to habitat during the dry season, as earlier documented (Janzen and Schoener 1968).

In the lower montane rain forests (Monteverde, Puntarenas Province) of Costa Rica, Buskirk and Buskirk (1976) record that forest understory insects were most abundant in the late dry season and early rainy season (April through June), and lowest during the cooler, windy months (November through January). Abundance fluctuated threefold during the year. Highest Coleoptera diversity coincided with peak abundance (April–June), and average body size in the entire fauna was largest in April. Predatory groups of arthropods lagged behind others in times of peak abundance: spider populations increased in November but peaked in June. The insect cycle may vary from year to year: populations were low in the rainy season of 1970 but were high during the late dry season and early rainy season in 1971.

Buskirk and Buskirk quote several works confirming that insect abundances in northern Neotropica tend to be highest during the wet season—see Bates (1945) for mosquitoes in Colombia, Dobzhansky and Pavan (1950) for *Drosophila* in Brazil, and Robinson and Robinson (1970) regarding spiders in Panama. The trend is not, however, uniformly applicable—note the findings of Janzen (1973) that insect populations were much higher in the dry season in abandoned bean and corn fields in Costa Rica. Moreover, at three undisturbed lowland sites, Hutto finds that insect abundances in the mid-winter dry season average 1.58 times the abundance of the mid-summer wet season; this relatively small seasonal difference is likely due to the higher (25–35 times higher) dry season population of insectivorous birds. The finding in Costa Rica that the migrants are present when insect numbers are lower, is repeated in Emlen's findings (this volume) in Grand Bahama Island.

Also, in the savannahs of West Africa, migrants are present during the dry season when food is least abundant (Moreau 1972). Morel (1973), however, has suggested that the dry season in Africa may not be as severe on migrants, inasmuch as they have the capacity to roam widely. By contrast, in the Serengeti savannahs of Tanzania, Sinclair (1978) records that there are two insect peaks—one in November–February when the migrants are present, and a smaller one in April–May after the migrants depart and when the resident birds breed. He also notes that during their stay, migrants tend to concentrate where there has been rain.

More elaborate studies still need to be done on the

seasonal aspects of the resource base in northern Neotropica, especially on the specific types of insects eaten by migrants.

Origin of Bird Migration Systems

This collection of papers the ecology of migrants in their wintering grounds is unique. Hitherto, writers have looked upon migration systems from a northern perspective, viewing southerly wintering grounds merely as alternative habitats during the season when conditions do not permit life in the north (Cooke 1888; Thomson 1936; Lincoln 1939; Wolfson 1948; Udvardy 1951; Salomonsen 1955; von Haartman 1968). But one should compare the writings of Mayr and Meise (1930), Lack (1954), and Cox (1968).

Recent years have seen a great amount of work on palaearctic migrants in their African wintering grounds, with research here proceeding faster than anything in Neotropica. This is largely due to the stimulus provided by Moreau (1952, 1966) and work begun in the Senegal (Morel and Bourlière, 1962).

Several contributors to the present Nearctica-Neotropica migrant symposium (Smith, Stiles) express indignation that we have so long looked at migration systems largely from the northern viewpoint. They note that migrants commonly spend seven months of their year in the south. (See the Keast paper that attempts to determine the actual fractions of the year spent by parulid warblers in the breeding grounds, on migration, and in the wintering grounds.) Of course, any migration system must be regarded in its entirety: its origins relative to past climatic changes, its maintenance, the ecology of species in the wintering grounds as well as breeding grounds, its energetic basic cost, and the varied adaptations of the migrants themselves.

In emphasizing ecology in wintering areas, this volume covers only part of this wider range of subjects. Fretwell reviews the evolution of migration relative to factors regulating bird numbers. He asks a series of questions (Why do some but not all birds migrate? What are the advantages of migration relative to residency?) and offers some explanatory hypotheses. Greenberg considers the demographic aspects of long-distance migration, time allocation by migrants, meaning of leapfrog migration, and other subjects. Morse considers whether population limitation in migrants occurs on the breeding or wintering grounds. Into this study, he brings habitat utilization, breeding densities over time (and evidence for population limitation both on breeding and wintering grounds), population losses during migration, and periodic disasters resulting in heavy die-offs. Buskirk considers the calendar of trans-Gulf migration relative to weather pat-

terns. He finds that the greatest frequency of high-magnitude autumnal flights coincides with recognizable improvement in flight conditions in mid-April and at the beginning of October. He reviews the literature on seasonal resource abundance in the wintering grounds relative to the timing of migration. He finds that although the insect standing crop varies with locality, it does not occur when the migrants are present; because of this, it appears that migration calendars are determined by temperate-zone phenomena.

Theories on the Origin and Ecological Basis of Birds Migration

A brief review of the literature on bird migration is appropriate. Earlier workers were impressed with the seeming mystique of the phenomenon and considered such things as "homing instinct patterns" to be the major basis of migration (Cooke 1888;). On the other hand, workers have long recognized the importance of climatic change, both long-term and short-term, in the evolution of migration.

Prominent in discussions are the "northern ancestral home" and "southern ancestral home" theories. The first of these saw migrants as former permanent residents of the north forced southward by increasing glaciation but which annually returned as closely as possible to their original home. By contrast, the alternative idea considered them as being originally southern forms, living in the general area of their original range and annually migrating northward to exploit the exceptional conditions temporarily available to the north. Most modern workers go along with this latter explanation, at least as far as American endemics are concerned (Mengel 1964; Rappole, Smith, Stiles, all this volume). The paper of Mayr (1946) on the origins of the nearctic avifauna set the stage for Williams (1958) to put the nearctic migration system into correct perspective. He noted that species of palaearctic origin ("northerners") reflect their cold-adapted ancestry by not going far south; 87 of these species remain within the United States, and only 2 enter South America. By contrast, species derived from neotropical stocks, for the most part, winter in South America (63 species compared to only 8 wintering north of the U.S.-Mexico border). Williams suggests that latitudinal bird migration is primarily the result of seasonal climatic change combined with land distribution patterns in the two hemispheres. He attempted to explain winter ranges by postulating that northern species do not winter farther south than they were driven during the last glaciation. The winter range of southern forms, by contrast, indicates the area for which the species originally developed a locality fixation so that they return

to this point annually, even though external conditions no longer force them to do so. Dorst (1962), however, correctly sees distributional changes in migratory birds as continuing (migratory populations in the Serin (*Serinus serinus*) have developed in the last hundred years), and suggests that these represented a "simple prolongation of immigration movements which followed the last glaciation" (page 190).

Some earlier workers (Mayr and Meise 1930), of course, viewed migration as not needing extreme climatic conditions but as a reaction to the existence of alternating favorable and unfavorable conditions. These authors also suggested that a biotic factor—intraspecific competition—and the need to avoid extreme crowding had had a reinforcing effect that might help explain "leapfrog" migration in which populations breeding farthest north winter farthest south. (See here the early paper by Swarth [1920] on wintering distribution in the fox sparrow, *Passerella*.)

That migration undoubtedly has a multiple origin has long been recognized (Kaleal 1954; Farner 1955). It also represented a balance between advantages and disadvantages to the bird. Thus, Lack (1954:244) wrote, "The resident habit has been evolved in those species in which, on the average, migration involves greater losses than winter residence"; thus, food shortages and low temperatures are a peril in the north, but residency has advantages—such as better opportunity to choose breeding territories. In a similar vein, Salomonsen (1955, 1970) saw migratory habits as demonstrating natural selection by the environment (with extrinsic factors operating similarly in breeding and on migration) and that selection in breeding and wintering areas may have a reinforcing effect or counteract each other. Salomonsen also states that spatial separation of bird populations in winter may ultimately lead to morphological differentiation.

Interspecific competition as a factor influencing migration patterns and winter ranges entered migration theory relatively late. Lack (1944), however, noted that each genus and species of migrant has its own wintering area and that, in many cases, the greatest differences are to be found in the most closely related species (*Anas*, *Larus*, *Anthus*, *Lanius*, *Emberiza*), and suggested that competition for food was the reason for wide dispersal. He also noted, however, that different populations commonly mixed freely in their wintering grounds. Subsequently, however, Udvardy (1951:113), reflecting the mood of the day about ecological competition as a selective force, wrote, "It has not been possible to prove in one single case that competition between species has any important influence upon the distribution ecology of European birdlife."

Later, Cox (1965) was able to develop a whole thesis

on the origins of migration relative to the need to avoid interspecific competition. Most of his ideas are still appropriate in the light of later knowledge. He postulates an evolutionary sequence of stages based on variation leading to incipient migratory movements into adjacent areas if the reduction in total competition (intraspecific and interspecific) allows greater survival or reproduction (the cost of migration being taken into consideration) than in the original range. Cox drew up a series of models illustrating sequences in the transition from resident to migrant. Possible ways in which competition between two partial migrants might be resolved include: 1) one migrant becoming a resident in an area from which it could eliminate the second, and the latter becoming a partial migrant; 2) both becoming fully migratory, and breeding and wintering in different areas, and; 3) partial competitive exclusion at one season only. Cox argued that some proof of the importance of interspecific competition in fixing different winter ranges comes from the small bill length differences between species in such nearctic migratory groups as the Parulidae and Emberizinae. Members of these groups have been less able to develop these differences as a means of ecological separation (Schoener 1965), hence must separate out allopatrically.

The kinds of sequences suggested by Cox may be invoked in the case of warblers and vireos, which have both migratory and resident populations. See Mengel (1964) for a discussion of post-glacial northward range extensions in parulid warblers. Cox's discussions of the role of interspecific competition as the factor determining winter ranges requires some modification in the light of later theoretical advances (Wiens 1977; and below).

Palearctic-Ethiopian Bird Migration System, A Parallel with the Nearctic One

In view of the detailed treatment accorded the nearctic neotropical system in this book, it is appropriate to review in some detail the parallel palaeartic-Ethiopian system. As will be seen, it involves many similarities, and also some striking contrasts with the former (Karr 1976a, this volume, and the next section).

Moreau, in his classic paper (1952), lays out the main features of the palaeartic-Ethiopian system, with much additional data being added subsequently by Morel and Bourlière (1962), Moreau (1972), and later workers. Migration out of the palaeartic follows three main streams: birds from Western Europe wintering mainly in West Africa, birds from Central Asia migrating to East Africa, and eastern palaeartic birds concentrating in Southeastern Asia. Of the 589 species of wholly or mainly palaeartic birds, 238 leave that

region in winter, with 183 species regularly migrating to sub-Saharan Africa. Of the western palaeartic species, 29 percent find their winter quarters wholly in Africa south of the Sahara. Africa provides winter quarters for 22 percent of the central palaeartic passerines against the 24 percent which enter India, although India is much nearer. Comparable figures are not available for the Far Eastern palaeartic birds, most of which winter on the Asian continent; some 8 species, however, winter in Africa. West Africa, with a land area of over one million square miles (excluding evergreen forest), supports 61 non-passerines and 37 passerines in winter; Kenya and Uganda with about half this land area support 70 nonpasserines and 43 passerines. The difference is due to the high number of Asian forms in East Africa. Migrants cross considerable areas of desert to reach the wintering ground where they typically spend the period October-March. Most of the area between the equator and the Sahara is already dry when the migrants arrive, and it becomes drier as the winter proceeds; on the other hand, in southern Africa, the rainy season begins soon after the arrival of the migrants. Evergreen forest and desert are not utilized by the migrants. Species utilize the same feeding zone as they do in Europe, for instance, nightingales (*Luscinia*) use dense thickets, as in Europe. Migrants occupy the same areas as residents but are generally fewer in number than the latter, except along waterways. However, a few species, such as the buzzard (*Buteo b. vulpinus*) and the swallow (*Hirundo rustica*), may greatly outnumber residents in some places. In the case of smaller species, migrants and residents commonly form mixed flocks. Moreau estimated that populations of palaeartic birds were only a fraction of their present numbers at the height of the glacial maxima when habitat was greatly reduced; at that time, a maximal area of Africa would have been available to wintering migrants. The clearing of the forests in Europe in post-Roman times must also have greatly reduced the numbers of migrants. It can be inferred, accordingly, that the palaeartic-Ethiopian bird migration system has been, and is, to some degree, in a state of flux.

Morel and Bourlière (1962), in a series of studies in the lower Senegal Valley, found that for eight months of the year palaeartic migrants, which include a spectrum embracing pipits, ducks, cuckoos, hawks, swallows, and warblers, form an appreciable part of the avifauna. Numbers of migrants and residents peak at the same time, although the two seldom belong to a common genus or a closely related one, and the migrants as a whole constitute a floating population. Also, most resident birds are themselves locally nomadic.

Nigerian studies (Elgood et al 1966, 1973) confirm the importance of the West African savannah zone to migrants. Here, one species in six is a palaearctic migrant. Endemic African migrants, furthermore, are also very common in the savannah zone: 120 migratory species comprise 28 percent of the avifauna here with 95 percent of the African migrants inhabiting the zone. By contrast, there are few migrants in the forests. The time of arrival of intra-African migrants corresponds with the onset of marked climatic changes elsewhere (beginning of rains, dry desert winds), and the movements would seem to be initiated by these factors.

The basis of seasonal movements in African and palaearctic migrants to West Africa have been compared for various groups: doves (Morel 1975), raptors (Thiollay 1975), and ducks (Roux et al 1978). Seven resident and one palaearctic dove species are present in the savannah only during the rainy season (June–July); three of these, however, retreat to the valley of the Senegal River when the dry season (December–February) begins.

The raptors fall into three groups: intra-tropical migrants, Palaearctic migrants, and erratically-occurring immatures of several species. Outside the vultures, half the raptors are migrants—40 percent of these raptors being palaearctics. Of the 54 species of hawks inhabiting the grasslands between the forest edge and the desert, 16 are sedentary, 6 perform regular migration (going north between March and August, and south from September to December); 14 are partial or erratic migrants; 14 are wintering palaearctic species; and the last 4 have one palaearctic and 1 Ethiopian race. Most of these hawks, which are medium to large in size, consume terrestrial vertebrates and insects in the open grasslands or along the rivers. In a subsequent paper concerned with the attributes of the migratory hawks, Thiollay (1978) records that they are morphologically adapted to feeding in open habitats, are very mobile (exploiting locally abundant but transient food sources), have high reproductive rates, are very sensitive to the dry heat of the Sahel, and, on the whole, overlap very little ecologically with resident birds of prey. The timing of migratory movements is closely correlated with the onset of the rains—the birds following the seasonal changes of the inter-tropical front, moving northward with the first rains in spring, and southward at the end of autumn. The seasonal shift in habitat is also correlated with an increase in the height of the grass cover and sometimes with flooding. There is good correlation between abundance of the migrants and that of grasshoppers, their major insect prey. The availability of drinking water is also important. African migrants generally stay in the southern savannahs

during the dry season when food is abundant, going north with the rains to utilize the food surplus left by the sparse populations of resident species. African migrants are the only ones to seasonally invade the northernmost grasslands. The southern Guinea savannahs are used by both palaearctic and African migrants during the breeding season of the resident species. However, the former, which have hunting methods and diets similar to those of the endemic migrants, never coexist with them during the dry season.

The ducks wintering in the lower Senegal (Roux et al 1978) consist of several Ethiopian species, reaching numbers of 35,000 in October when inundation is greatest, and about 120,000 palaearctic Garganey teal (*Anas querquedula*), and 100,000 pintail (*Anas acuta*). However, interspecific impact between resident and migrant is minimized by partly distinct periods of presence and habitat preference. It is suggested that the numbers of the Ethiopian species are limited by variable and adverse environmental pressures in summer; they are, in other words, underutilizing the habitat.

Studies of migrants in East Africa mainly concern a small number of passerine species. Pearson (1972) carried out a three-year trapping and banding program at Kampala, Uganda, and compiled data on 11 species, 3 of which were passage migrants en route south. Major species were: 4 species of sylviid warblers—2 *Acrocephalus*, plus *Sylvia borin* and *Phylloscopus trochilus*; the Spotted Flycatcher (*Muscicapa striata*); Yellow Wagtail (*Motacilla flava*); the Red-backed Shrike (*Lanius collurio*); and hirundines (*Hirundo rustica*, *Riparia riparia*). Most of the migrants arrived in October–November, and made their spring departure at the end of March, continuing throughout April. Half of the migrants trapped were warblers. Wet seasons were March–May and September–November, with the area tending to become parched in late winter. Migrant numbers varied greatly with habitat. In partly cultivated areas, they averaged only 1–2 per acre and were greatly outnumbered by locals. Near the lake, however, *Acrocephalus*, Yellow Wagtails and hirundines were much more numerous, and winter visitors comprised a large proportion of all birds present, averaging 10 or more per acre. In the vicinity of the lake, emergent chironomids and chaoborines were attended by equal numbers of migrant *Hirundo rustica*, *Riparia riparia*, and Ugandan swallows (*Hirundo angolensis*) in winter but, with the departure of the migrants in April and May, were dominated by sand martins (*Riparia*). Migratory warblers frequented various bush and forest-edge habitats where the principal resident species were a *Camaroptera*, a *Cisticola*, and 2 *Prinia*.

Here the migrants tended to be more unobtrusive than the locals.

Britton (1974), in a further consideration of which habitats are used by migrants in East Africa, arrived at a figure of 20 percent of individuals for overgrazed cultivation areas and 4 percent for papyrus swamp. Considering species only, however, papyrus had the greatest proportion of palaeartic birds—30 percent. Figures for introduced Lantana thickets were 25 percent of biomass for palaeartic species but only 1–11 percent for other habitats.

The review by Sinclair (1978) of the ecology of wintering palaeartic migrants in the woodlands of the Serengeti, Tanzania, provides interesting contrasts both with the West African situation and with Pearson's sites in Kenya. In contrast with West Africa where the migrants are present during the dry season (an interesting "paradox"—Moreau 1966) in the Serengeti, 14 northern migrants arrive about a month ahead of the wet season and remain through it, contemporaneous with the breeding residents. The winter visitors include 2 hawks, a stork, a roller, a bee-eater, a scolopacid, a plover, a chat, a wheatear, 2 shrikes, a flycatcher, a swallow, and a couple of sylviid warblers. The warblers keep largely to the streamside thickets. There is some obvious ecological separation of migratory and resident counterparts. Prior to the rains, both resident and migrant rollers inhabit the woodlands, but thereafter the migrants move on to the short-grass plains to feed on dung beetles. Migratory wheatears were somewhat nomadic, moving with the progress of the rains. The more abundant resident, capped wheatear (*Oenanthe pileata*) vigorously defended territories in December, presumably explaining why migrants were absent from areas of greatest resident density. The palaeartic warblers were rarely seen in the canopy frequented by residents. The migratory spotted flycatcher (*Muscicapa*) fed mainly on flying insects, while the resident species fed from the ground. The palaeartic bee-eater was larger than the endemic ones and possibly did not compete on that basis. Migrant and resident shrikes were of the same general size and occurred together; Sinclair suggests, however, that any competition was nullified by the increased food supplies following the rains.

Only a small number of palaeartic migrants penetrate to southern Africa (Moreau 1972; McLachlan and Liversidge 1978). Thus, the single warbler and flycatcher wintering in the Zambian *Brachystegia* woodland were in small numbers (Ulfstrand and Alerstam 1977), and were concentrated in disturbed habitats. In South Africa the migratory swallow, *Hirundo rustica*, occurs sometimes in very large flocks, greatly outnumbering the residents (McLachlan and Liversidge).

Palaeartic-Ethiopian and Nearctic-Neotropical Migration Systems Compared

Karr (this volume) in a comparison of the winter migrants in Africa, Neotropica, and the oriental region, gives figures of 118, 147, and 142 for the numbers of bird species wintering in each region. Thus, he concludes that available area clearly is not the main factor controlling species numbers. Rather, historical factors, geographic extent and diversity of habitats, topographic complexity, and patterns of seasonality must be invoked.

Karr tabulates the numbers of members of each family wintering in 4 major "migrant receptor" areas: Africa, the neotropics, Southeast Asia and the Indian sub-continent. Twice as many northern accipitrids and falcons migrate to Africa as to Neotropica (16 and 8 species, compared to 7 and 4). The same applies to thrushes (18 compared to 7), pipits (6 compared to 2), and swifts (4 compared to 2). However, the neotropics receive far more warblers (46 parulids compared to 29 sylviids entering Africa) and flycatchers (23 tyrannids compared to 3 muscicapids). As regards hummingbirds, vireos, and icterids, the several species of each entering the neotropics are confined to the Western Hemisphere.

Moreau (1972) outlines some of the problems facing migrants to sub-Saharan Africa: they must cross great sections of desert and in the east, must circumvent the high Himalayan Mountains. Long, direct flights are, therefore, common. No such problems face nearctic birds traveling to Neotropica, although many do make a long flight across the Caribbean. The long-distance flight of the Blackpoll Warbler (*Dendroica striata*) from Maine to South America (McClintock et al 1978) is exceptional for a nearctic breeding species. Linked to their long-distance flights, there is apparently a marked tendency for many palaeartic species to move southward in stages, pausing for weeks or even several months, before proceeding (Moreau and Dolp 1970; Pearson and Backhurst 1976). Slow migration, with intermediate stops is much less important in nearctic species, although it does occur. For example, Yellow-rumped Warblers (*Dendroica coronata*) do not arrive in Jamaica until January (Lack and Lack 1972), and some migrants going to South America apparently linger in Panama (Morton, this volume).

One of the more interesting differences in the two systems is in the habitats occupied by the migrants. As many have pointed out (Moreau 1952; Morel and Bourlière 1962; Elgood et al 1966; Brosset 1968; Morel 1968; Pearson 1971; Thiollay 1970a and b; Moreau 1972; and as reviewed by Karr 1976a) most migrant species in Africa winter in savannah and dry woodland

habitats. Mangroves may be much-used in West Africa (Cawkill 1964). On the other hand, besides desert areas, tropical evergreen forest is almost entirely neglected (Elgood et al 1966; Moreau 1966). Relatively few migrants use the limited highland areas (Karr 1976a). By contrast, in Nearctica the available range of habitats is basically different: highlands, pine woodlands, rain forests, and extensive areas of second growth occupy a position proximal to the northern migrant source. Grasslands are not an important wintering habitat for migrants (Karr 1976a); this may be because they are largely a secondary habitat in Central America. Just as availability determines what winter habitat is used by migrants, so do the dominant kinds of habitat and their seasons of productivity (in both north and south) determine the taxonomic kinds of birds that migrate, as noted above. Nevertheless, it is apparent that migrants forced southward by declining winter conditions must, in both areas, adapt to whatever habitat is available.

The species of passerines migrating to Africa show the same tendencies to separate out ecologically as do the nearctic ones in Neotropica. Moreau (1972) states that of 90 migrant species in six African habitats, 14 were without related native species as potential competitors, 19 were segregated by feeding site, and 32 differed significantly in size. Lack (1971) has given data for congeners in Africa as follows: 64 percent had non-overlapping ranges, 23 percent separated out on habitat, 2 percent separated out on foraging ecology, and only 10 percent had no obvious pattern of separation. Here, also see regional accounts of species separations in Pearson (1972) and Sinclair (1978).

As might be expected from the vast expanse of the Ethiopian wintering area and different regional climatic cycles, the seasonal conditions experienced by migrants in their wintering grounds vary greatly; in the Serengeti in East Africa they are present during the rainy season but in West Africa they are present during the dry season.

Interspecific Competition Relative to the Evolution of the Nearctic-Neotropical Bird Migration System

The development of species ecological specializations has long been recognized as an integral part of the speciation process (Mayr 1942). In typical systems, cohabiting species differ ecologically in one or more clearcut ways. The potential problem of interspecific competition is avoided by the occupation of different feeding zones, by differences in feeding habits, or by occupying distinct sub-habitats. A community thus consists of a group of species that either brought different adaptations with them into the system or

that have developed adjustments relative to each other.

A surprising finding that emerges from this volume is that migrants belong to quite different species associations or communities in the north and in the south. Their adjustments have, accordingly, been so much greater than in resident species. Can simple "interspecific competition" be invoked as the driving force behind these ecological separations?

Weins (1977) has recently reviewed the difficulties of trying to apply the competitive exclusion principle to avian communities:

1) Obviously, it must be related to species density yet densities undergo considerable annual variation, and the magnitude of such variation differs not only among species but also among local areas. That is to say, the impact of the species on each other is *not* in the form of a constant "pressure" such that might make it highly advantageous for them to acquire rigid "separation devices."

2) Virtually all mathematical treatments of competition are based on the assumption that the system is at equilibrium. Not only the populations but also their resource functions are assumed to be at equilibrium. Natural systems, however, are highly variable seasonally and from year to year. Hence, what is optimal at one time is not optimal at another.

3) In many systems, production is concentrated into a brief growing season. Hence, variations in resource-utilization in the course of the year may be profound. Conditions of shortage may affect cohabiting species very differently.

4) Most theories of optimal foraging predict that as resources become more abundant relative to demand, individuals should progressively restrict their diets, specializing on the optimal (most profitable) prey types, or most productive habitat patches. However, general and specialist strategies both have to be incorporated into the scheme. Competition theory predicts that under conditions of high resource availability, other species may successfully invade the community. Competition will then force resource specialization and separation. Alternatively, in the absence of an invader, the population should grow to resource-defined carrying capacities; this, however, will take time in the case of slow-producing animals such as birds. Thus, populations may frequently be below the carrying capacity, invalidating the competitive exclusion argument.

Many authors in the present symposium have considered the spatial and ecological relationships of migrants in terms of interspecific competition (Emlen, Myers, Faaborg and Terborgh, Fitzpatrick, Keast). Supporting evidence for its existence, it is suggested,

comes from various sources: the frequency of aggressive interactions between migrants and residents (for example, in shorebirds, Myers), habitat separation of congeners, feeding zone separations, presence of both dominant and fugitive species, and so on. At the broader evolutionary level, it is argued (Keast) that there is "resistance" by endemic groups to the southward penetration of nearctic groups like the parulid warblers. That migratory and resident species, and migrant and migrant, are interacting is undeniable. That the interaction system is a dynamic and evolving one is indicated by geographic variation in feeding ecology (compare, for example the observations of Tramer and Kemp on warbler feeding with those of Keast), such distributional anomalies as the bimodal distribution of the endemic ground warbler (*Microlegia palustris*) of Hispaniola (Terborgh and Faaborg), and varying species combinations from place to place. On the other hand, the consistency of ecological species differences, the failure of residents to expand into niches left vacant by returning migrants, and other factors, argue that there has been a long period of co-evolution of migrants and residents.

Literature Cited

- Bates, M.
1945. Observations on climate and seasonal distribution of mosquitos in Eastern Colombia. *J. Anim. Ecol.* 14: 17-25.
- Britton, P. L.
1974. Relative biomass of European and Palearctic passerines in West Kenya habitats. *Bull. Brit. Ornith. Club* 94:108-113.
- Brosset, A.
1968. Localisation écologique des oiseaux migrateurs dans la forêt équatoriale du Gabon. *Biologia Gabonica* 4: 211-26.
- Buskirk, R. E. and W. H. Buskirk
1976. Changes in arthropod abundance in a highland Costa Rican forest. *Am. Midl. Nat.* 95: 288-98.
- Cook, R. E.
1969. Variation in species density of North American birds. *Syst. Zool.* 18:63-84.
- Cooke, W. W.
1888. Report on bird migration in the Mississippi Valley. U.S. Nat. Museum, Washington.
- Cox, G. W.
1968. The role of competition in the evolution of migration. *Evolution* 22:180-92.
- Davis, L. I.
1955. Bird census 27. Audubon Field Notes 9:425-26
- Davis, L. I. and J. Moroney Jr.
1953. Bird census 31. Audubon Field Notes 7:352-53.
- De Schauensee, R. M.
1964. *The Birds of Colombia and Adjacent Areas of South and Central America*. Narberth, Pa.: Livingston, 430 pp
- Diamond, J. M.
1975. Distributional ecology and habits of some Bougainville birds. *Condor* 77:14-23.
- Dobzhansky, T. and C. Pavan.
1950. Local and seasonal variation in relative frequencies of species of *Drosophila* in Brazil. *J. Anim. Ecol.* 19: 1-14.
- Dorst, J.
1962. *The Migration of Birds*. Boston: Houghton Mifflin, 476 pp.
- Elgood, J. H., R. E. Sharland, and P. Ward.
1966. Palearctic migrants in Nigeria. *Ibis* 108:84-116.
- Elgood, J. H., C. H. Fry, and R. J. Dowsett.
1973. African migrants in Nigeria. *Ibis* 115:1-45, 375-409.
- Farner, D. S.
1955. *Recent Studies in Avian Biology*. Urbana: Univ. Illinois Press.
- Janzen, D. H.
1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity *Ecol.* 54:687-708.
- Janzen, D. H. and T. W. Schoener
1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecol.* 49:96-110.
- Kalela, O.
1954. Populations—ökologische Gesichtspunkte zur Entstehung des Vogelzuges. *Annales Zoologica Societis Zoologicae Botanicae Fennicae Vanama* 1:1-30.
- Karr, J. R.
1971. Structure of avian communities in selected Panama and Illinois habitats. *Ecol. Monogr.* 41:207-33.
- 1976a. Within- and between-habitat avian diversity in African and Neotropical lowland habitats. *Ecol. Monogr.* 46:457-81.
1976. On the relative abundance of migrants from the North Temperate Zone in tropical habitats. *Wils. Bull.* 88:433-58.
- Karr, J. R. and R. R. Roth
1971. Vegetation structure and avian diversity in several new world areas. *Amer. Nat.* 105:423-36.
- Keast, A.
1972. Ecological opportunities and dominant families, as illustrated by the Neotropical Tyrannidae (Aves). *Evolutionary Biology* 5:229-77.
- Lack, D. L.
1944. The problem of partial migration. *British Birds* 37: 122-30; 143-50.

1954. *The Natural Regulation of Animal Numbers*. London: Oxford.
1971. *Ecological isolation in birds*. Oxford, U.K.: Blackwells.
1976. *Island biology illustrated by the land birds of Jamaica*. Oxford U.K.: Blackwells, 445 pp.
- Lack, D. and P. Lack
1972. Wintering warblers in Jamaica. *Living Bird* 11:129-53.
- Leck, C. F.
1972. The impact of some North American migrants at fruiting trees in Panama. *Auk* 89:842-50.
- Lincoln, F. C.
1939. *The migration of American birds*. New York: Doubleday, Doran 189 pp.
- Lonnberg, E.
1927. Some speculations on the origin of the North American ornithic fauna. *Kungl. Svenska Vetenskapsakad. Handl. Ser. 3*, 4:1-24.
- Lovejoy, T. E.
1974. Bird diversity and abundance in Amazon forest communities. *Living Bird* 13:127-91.
- MacArthur, R. H.
1969. Patterns of communities in the tropics. *Biol. J. Linnaean Soc.* 1:19-30.
- MacArthur, R. H., J. W. MacArthur, and M. Cody
1966. On the relation between habitat selection and species diversity. *Amer. Nat.*, 100:319-32.
- McClintock, C. P., T. C. Williams, and J. M. Teal
1978. Autumnal bird migration observed from ships in the western north Atlantic Ocean. *Bird-Banding* 49:262-77.
- McLachlan, G. R. and R. Liversidge
1978. *Robert's Birds of South Africa*. Capetown, South Africa: Cape and Transvaal Printers
- Mayr, E.
1942. *Systematics and the origin of species*. New York: Colombia Univ. Press.
1964. Inferences concerning the Tertiary American bird faunas. *Proc. Nat. Acad. Sci.* 51:280-88.
1946. History of the North American bird fauna. *Wils. Bull.* 58:3-41.
- Mayr, E. and W. Meise
1930. Theoretisches zur Geschichte des vogelsuges. *Der Vogelzug* (Berlin) 1:149-72.
- Mayr, E. and W. H. Phelps, Jr.
1967. The origin of the bird fauna of the South Venezuelan Highlands. *Bull. Amer. Mus. Nat. Hist.* 136:269-328.
- Mengel, R. M.
1964. The probable history of species formation in some Northern Wood Warblers (Parulidae). *Living Bird* 3:9-43.
- Miller, A.
1963. Seasonal activity and ecology of the avifauna of American equatorial cloud forest. *Univ. Calif. Publ. Zool.* 68:1-78.
- Moreau, R. E.
1952. The place of Africa in the Palaearctic migration system. *J. Anim. Ecol.* 21:250-71.
1966. *The bird faunas of Africa and its islands*. New York: Academic Press.
1972. *The Palaearctic-African bird migration systems*. New York: Academic Press, 424 pp.
- Moreau, R. E. and R. M. Dolp
1970. Fat, water, weight and wing lengths of autumn migrants in transit on the northwest coast of Egypt. *Ibis* 112:209-28.
- Morel, G.
1968. Contribution à la synécologie des oiseaux du Sahel sénégalais *Mem. ORSTOM* 29, Paris.
1973. The Sahel zone as an environment for Palaearctic migrants. *Ibis* 115:413-17.
- Morel, G. and F. Bourlière
1952. Relations écologiques des avifaunes sédentaires et migratrices dans une savane sahélienne du bas Sénégal. *La Terre et la Vie*, 190:371:93.
- Morel, M. Y.
1975. Comportement de sept espèces de Tourterelles aux points d'eau naturel et artificiels dans une sauvage sahélienne du Ferlo Septentrional Sénégal. *L'Oiseau et R.F.O.* 45:97-126.
- Orians, G. H.
1969. The number of bird species in some tropical forests. *Ecol.* 50:783-801.
- Pearson, D. J.
1971. Weights of some Palaearctic migrants in southern Uganda. *Ibis* 111:173-84.
1972. The wintering and migration of Palaearctic passerines at Kampala, Uganda. *Ibis* 114:43-60.
- Pearson, D. J. and G. C. Backhurst
1976. The southward migration of Palaearctic birds over Ngulia, Kenya. *Ibis* 118:78-105.
- Pearson, D. L.
1975. The relation of foliage complexity to ecological diversity of three Amazonian bird communities. *Condor* 77:453-66.
1977. A pantropical comparison of bird community structure on six lowland forest sites. *Condor* 79:232-44.

- Robinson, M.H. and B. Robinson
1970. Prey caught by a sample population of the spider *Argiope argentata* (Araneae: Araneidae) in Panama: a year's census data. Zool. J. Linn. Soc. 4:345-57.
- Roux, F., R. Maheo, and A. Tamisier.
1978. L'exploitation de la Basse Vallée du Sénégal (Quartier d'Hiver Tropicale) par trois espèces de canards Paléarctiques et Ethiopien. La Terre et la Vie 32: 387-416.
- Salomonsen, F.
1955. The evolutionary significance of bird migration. Det Kongelige Danske Videnskabernes Selskat Biologiske Meddelelser 22:1-62.
1970. Zoogeographical and ecological problems in Arctic Birds. Pres. Add. Zoological Museum, Univ. Copenhagen, Denmark.
- Schoener, T. W.
1971. Large-billed insectivorous birds: a precipitous diversity gradient. Condor 73:154-61.
- Simpson, G. G.
1964. Species density of North American Mammals. Syst Zool. 12:57-73.
- Sinclair, A. E. R.
1978. Factors affecting the food supply and breeding season of resident birds and movements of Palaearctic migrants in a tropical African savannah. Ibis 120: 480-97.
- Slud, P.
1964. The birds of Costa Rica. Bull. Am. Mus. Nat. Hist. 128:1-430.
1976. Geographic and climatic relationships of avifaunas with special reference to comparative distribution in the Neotropics. Smith. Conf. Zoology 212:1-149.
- Smith, N.
1975. "Spshing noise": biological significance of its attraction and nonattraction by birds. Proc. Nat. Acad. Sci. 72:1411-14.
- Smith, V. M.
1966. Autumn and spring weights of some Palaearctic migrants in central Nigera. Ibis 108:492-512.
- Swarth, H. S.
1920. Revision of the avian genus *Passerella* with special reference to the distribution and migration of the races in California. Univ. California Pubs. Zoo. 21: 75-224.
- Terborgh, J. and J. S. Weske
1969. Colonization of secondary habitats by Peruvian birds. Ecol. 50:765-82.
- Thiollay, J. M.
1975. Les rapaces des Parcs Nationaux du Côte d'Ivoire, analyse du peuplement. L'Oiseau de la R.F. D'O. 45:241-57.
- 1977a. Le peuplement de Falconiformes d'une savane on-gandaïse L'Oiseau et la R.F. D'O 47:193-205.
1977b. Distribution saisonnière des rapaces diurnes en Afrique occidentale. L'Oiseau de la R.F. D'O. 47:253-94.
1978. Les migrations de rapaces en afrique occidentale: adaptations écologiques aux fluctuations saisonnières de production des écosystèmes. La Terre et la Vie 32:89-133.
- Thomson, A. L.
1936. Bird Migration: a Short Account. London: Witherby
- Tramer, E. J.
1974. On latitudinal gradients in avian diversity. Condor 76:123-130.
- Udvardy, M. D. F.
1951. The significance of interspecific competition in bird life. Oikos 3:98-123.
- Ulfstrand, S., and T. Alerstam
1977. Bird communities of Brachystegia and Acacia woodlands in Zambia. J. Ornith. 118:156-74.
- Von Haartman, L.
1968. The evolution of resident versus migratory habitat in birds: some considerations. Ornis Fennica 45:1-7.
- Vuilleumier, F. and D. Simberloff.
1980. Patchy distributions in birds of the high tropical Andes. Evol. Biol. 12.
- Wiens, J. A.
1977. On competition and variable environments Amer. Scientist 65:590-97.
- Whitmore, F. C. Jr. and R. H. Stewart
1965. Miocene mammals and Central American Pathways. Science 148:328-29.
- Williams, G. G.
1958. Evolutionary aspects of bird migration. Lida Scott Brown Lectures in Ornithology, University of California, Los Angeles.
- Willis, E. O.
1966. The role of migrant birds at swarms of army ants. Living Bird. 5:187-231.
- Wolfson, A.
1948. Bird migration and the concept of continental drift. D. Science 108:23-30.

