

DENSITY TRENDS AND RANGE BOUNDARY CONSTRAINTS OF FOREST BIRDS ALONG A LATITUDINAL GRADIENT

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ABSTRACT.—We plotted the density distributions of 41 land-bird species along a 1,200-km transect spanning 7°28' (865 km) of latitude through relatively uniform bottomland deciduous forest in middle North America. Standardized counts and observations at 12 survey stations, closely matched in habitat structure and widely distributed along the route, provided population data for all species and indices of total avian foraging pressure (consuming biomass) on each of six major foraging substrates.

Density curves for species fluctuated considerably from station to station but tended to be level across range centers and slope peripherally to north and south boundaries at rates of 3–30% per degree of latitude. Substrate foraging pressures declined northward on the aerial and midfoliage substrates and southward on the low-foliage substrate. Summed community densities showed no significant latitudinal trends.

We used the distinctive distribution patterns of climate (smooth latitudinal gradients), habitat structure (irregular mosaics of vegetation patches), and competition (reciprocally sloping density gradients) to identify and evaluate the role of these three constraints along the transect. Progressive latitudinal trends in species abundance thus were attributed to climatic factors, irregular station-to-station fluctuations to habitat factors, and inversely sloping density trends in paired profiles to competition. On this basis all species apparently responded to both climatic and habitat factors, and about half of the species showed suggestions of competition. In a correlation analysis across the 12 stations, latitude per se most closely matched density distribution in 12 species, one or another of the habitat parameters in 25 species. We proposed that season length (days available for breeding activity) was the principal constraining attribute of latitude at northern range boundaries, day length (hours available for feeding and provisioning young) at southern boundaries.

Boundaries have been essentially stable during the past 50–100 yr in most species, but the northern boundary expanded northward in one species following human-induced habitat enhancement, and temporarily receded southward in another following a winter of severe stress. We attribute this general stability of range boundaries over time to within-population gene flow and the associated peripherally declining mean fitness of phenotypes adapted to central range conditions along radially diverging environmental gradients.

We suggest that two boundary lines should be recognized for each species, an inner functional boundary at the line where birth rates drop below death rates, and an outer empirical boundary at the limit of recorded occurrences. *Received 21 June 1985, accepted 20 April 1986.*

RECENT developments in estimating bird densities (Ralph and Scott 1981) have made it

possible to plot species distributions quantitatively on maps showing contours of relative abundance as well as the locations of range boundaries (Bystrak 1981). These developments have also created opportunities to evaluate the effects of habitat structure (primarily vegetation), climate (ambient physical conditions), and competition on population growth and dispersion. Habitat factors, often changing extensively over short distances, have been examined intensively with relation to bird den-

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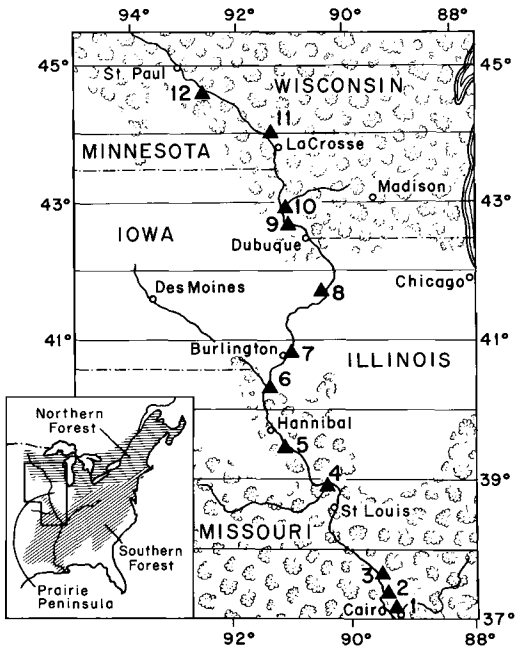


Fig. 1. Location of the 12 survey stations along the Mississippi bottomland transect. Inset shows setting in relation to northern and southern forests and the intervening "prairie peninsula."

sity distributions in many regional community studies. But climatic factors (where conditions change gradually over long distances) and competition (where distributional responses reflect direct or indirect interactions between taxa in the community) present problems that can be approached only on a broad geographic scale.

The direct effects of climate on bird distributions and densities can be separated from the effects of habitat structure by recognizing the distinctive distributional patterns of the two categories: smooth latitudinal (or altitudinal) gradients for climate, patchy mosaics for habitat structure. We attempted to separate climatic and habitat effects empirically by collecting population density data at a series of survey sites selected to minimize habitat variance (stations were similar in vegetation structure) and maximize climatic variance (stations were widely spaced along an extended latitudinal transect). Competition, the third constraint category, could, we suggest, be revealed along the transect by reciprocally sloping density gradients in ecologically similar species pairs.

STUDY AREA AND METHODS

We studied the elm-ash-maple bottomland forest of the central Mississippi River Valley, an area supporting one of the longest north-south stretches of relatively uniform vegetation on the North American continent. We laid out a transect of 12 survey stations between Cairo, Illinois, and St. Paul, Minnesota, a distance of 1,200 km covering $7^{\circ}28'$ (865 km) of latitude (Fig. 1). The southern third of this transect lies in the southern deciduous forest biome of eastern North America, the central third forms a narrow habitat corridor bridging the 9,000-yr-old (Webb 1981) prairie peninsula of the central plains, and the northern third lies in the northern deciduous forest biome.

Although continuously wooded until 150 yr ago, this strip is now fragmented into a series of forest patches. Many of the bird species that occupy these patches as breeding residents appear to have originated in the south, others in the north. Their present distributions presumably reflect varying range expansions along the extended strip between the Gulf of Mexico and Hudson Bay.

The Mississippi River flows southward (Fig. 1) through the middle of a broad and gently sloping basin bounded by steep bluffs. The floodplain averages 2-4 km in width at the northern end of our transect, gradually widens to 5-10 km at midpoint, and spreads to 10-20 km as the bluffs become lower at the southern end. The river itself, varying from 300 to 2,000 m in width, meanders through the floodplain between scattered sloughs and oxbows, interrupted every 15-40 km by long artificial lakes created by navigation dams built in the 1930's.

The climate of the area is midtemperate continental. Mean annual precipitation ranges from 1,000 mm in the south to 700 mm in the north. Actual evapotranspiration (AE) rates, indicators of local primary productivity (Rosenzweig 1968), also decline northward (Table 1). Mean daily temperatures at the northern end of the transect average about 5°C colder in summer and 9°C colder in winter. Stressful summer heat is slightly less frequent in the north than in the south, but stressful winter cold is considerably more frequent in the north. Summer season length, a measure of the period of insect availability, is two months shorter in the north; day length, a measure of hours available for foraging and provisioning young, is 1.2 h longer (Table 1).

The high, closed-canopy, mesic forest of elm, ash, silver maple, and oak that originally covered this floodplain has been cleared extensively for agriculture, industry, and urban development and persists only as a broken chain of forest patches, connected along river and slough banks by narrow strips of willow and cottonwood. Vegetation structure varied only slightly from station to station and showed no significant latitudinal trends in any of our measured dimensions (Table 2). Forest composition and extent

TABLE 1. Locations of and climatic data for survey stations along the Mississippi bottomland transect.

Survey station		Location		Temperature (1975-1979)							
				Mean daily ^a		No. stress days		Pro- duc- tivity (AE) ^b	Breed- ing season length ^c	Day length (June) ^d	
						Sum- mer (No. >35°)	Win- ter (No. <-20°)				
Station	Nearest city	Lat. (°N)	Long. (°W)	Summer	Winter						
1 Cache	Cairo, Illinois	37°07'	89°17'	26.7°	-1.7°	7.0	0	805	237	14.4	
2 Jones- boro	Cape Girardeau, Missouri	37°25'	89°22'	25.4°	0°	4.6	1.2		234	14.5	
3 Oak- wood	Carbondale, Illinois	37°40'	89°26'	24.2°	-1.3°	2.8	4.0		230	14.5	
4 Grafton	St. Louis, Missouri	38°56'	90°25'	25.1°	-1.8°	5.0	2.8	756	219	14.7	
5 Ash- burn	Hannibal, Missouri	39°30'	91°05'	23.9°	-4.2°	4.0	8.6	713	210	14.8	
6 War- saw	Keokuk, Iowa	40°22'	91°25'	24.3°	-3.6°	2.6	6.8		204	14.9	
7 Burling- ton	Burlington, Iowa	40°51'	91°03'	22.4°	-5.5°	2.2	10.2	716	200	15.0	
8 Wapsi- pini- con	Clinton, Iowa	41°44'	90°20'	22.4°	-6.2°	1.6	14.0		193	15.1	
9 Cass- ville	Dubuque, Iowa	42°44'	91°03'	22.0°	-6.8°	0.6	15.8	656	185	15.1	
10 Wyalu- sing	Prairie du Chien, Wisconsin	43°00'	91°20'	21.7°	-7.6°	3.0	22.2		182	15.2	
11 Black River	LaCrosse, Wisconsin	43°59'	91°20'	21.1°	-8.9°	0.6	25.4	640	173	15.4	
12 Cannon River	St. Paul, Minnesota	44°35'	92°38'	21.6°	-9.9°	1.4	26.8	621	164	15.6	

^a Mean daily temperature (°C) for June-July (summer) and December-February (winter) at nearest city (U.S. Environ. Data and Info. Serv. 1975-1979). The deviations from a smooth latitudinal gradient are attributed largely to differences in altitude and exposure of the nearest meteorological stations, which are located up to 25 km from the survey station sites.

^b Actual evapotranspiration rates in millimeters (Thorntwaite Assocs. 1964).

^c Number of days in which the daytime mean temperature was above 10°C (computed from Smithsonian Meteorol. Tables 1964).

^d Number of hours between sunrise and sunset during June.

were less uniform because of the patchy and uneven distribution of soil types and human disturbance areas, but again we found no consistent latitudinal trends.

Along its margins the floodplain changes abruptly at the foot of the bordering bluffs to strips or blocks of upland forest dominated by oak. Beyond the bluff tops lie broad expanses of farmland with scattered woodlots on terrain that formerly was covered with hardwood forests in the north and south, and open prairie in the central portion (Fig. 1, inset).

The 43 bird species (15 permanent residents and 28 summer migrants) that we recorded along this transect (Table 3) are midlatitude representatives of a breeding fauna that extends from the Gulf of Mexico at 29°N to Hudson Bay at 57°N (Fig. 2). All of the species are found beyond the 7° span of our transect,

but the southern boundaries of 6 northern species and the northern boundaries of 12 southern species fall within this area.

Observations were made at 12 survey stations along the transect in areas with extensive and minimally disturbed natural stands of large trees. To obtain phenologically comparable data we (1) restricted all observations to a 30-day period at the height of the breeding season (June) in a single year (1979), (2) made two 10-12-day traverses of the route, one in early June (odd-numbered stations), the other in late June (even-numbered stations), and (3) traversed the route from south to north both times, roughly keeping pace with the advancing season of ca. 120 km per day. One observer (JE) participated in and coordinated both traverses; three additional observers participated on each traverse, each of them experienced

TABLE 2. Habitat measurements and assessments at the 12 transect stations.

Habitat parameter	Transect station												CV	Slope ^a	r ²	
	1	2	3	4	5	6	7	8	9	10	11	12				
Canopy quality ^b	36	41	32	35	35	35	30	35	39	34	35	37	8.13	N 1.32	0.000	
Forest extent ^c	50	30	70	20	40	20	20	50	40	50	60	40	39.70	S 2.03	0.009	
Forest profile ^d																
Upper trees (>15 m)	8.0	8.3	6.7	7.1	6.9	6.7	5.4	7.2	8.4	7.6	7.4	7.6	11.29	S 0.20	0.002	
Lower trees (7-15 m)	5.8	8.0	6.6	6.7	6.9	7.3	6.8	6.6	6.7	5.6	6.9	7.0	9.22	N 0.39	0.012	
Upper shrubs (2-7 m)	4.0	6.3	5.8	6.2	4.7	4.0	5.4	5.2	3.3	3.0	4.9	3.6	23.87	N 4.45	0.326	
Lower shrubs (0.8-2 m)	2.6	3.8	4.7	4.8	4.3	2.5	3.9	3.1	1.4	1.1	4.3	1.2	43.51	N 6.84	0.289	
Herbs (0.1-0.8 m)	6.2	6.6	6.5	8.3	5.8	7.6	6.6	9.4	4.1	7.0	8.8	8.3	20.67	S 2.13	0.085	
Ground cover (<0.1 m)	7.0	9.9	5.8	10.0	9.5	9.9	7.7	9.4	6.6	7.9	8.0	8.3	8.33	N 0.37	0.003	
Forest structure																
Mean DBH (cm)	24.3	35.3	23.7	36.3	24.5	32.7	26.6	30.6	25.4	32.1	27.1	23.7	16.27	N 1.03	0.029	
Density (trees/ha)	635	417	613	403	650	531	739	514	860	613	714	578	21.62	S 3.01	0.168	
Basal area (m ² /ha)	32.6	40.7	27.0	41.5	30.3	44.7	41.0	37.8	43.6	49.5	41.1	26.0	19.45	S 1.55	0.048	
Dead trees (no./ha)	56.1	36.5	72.6	49.6	109.1	23.2	71.4	66.2	78.6	142.2	132.2	49.6	49.71	S 6.37	0.196	
Saplings (no./100 m ²)	7.9	5.4	13.1	4.6	3.9	3.6	12.5	7.3	4.3	2.5	4.0	4.3	56.70	N 7.10	0.188	
Lianas (no./100 m ²)	0.5	1.3	0.5	0.2	0.1	0.7	1.0	1.0	0.1	0.2	0.3	1.8	83.65	S 3.42	0.015	

^a Regression slope in percentage decrease northward (N) or southward (S) per degree of latitude.

^b A relative evaluation of tree canopy volume derived by summing 3 × the canopy cover estimate of large trees (>15 m), and 2 × the canopy cover estimate of small trees (7-15 m).

^c Proportion of a 28-km² (3-km radius) area surrounding each station that was forested.

^d Direct subjective evaluations of vegetative cover in tenths of complete cover for six forest levels from treetop to ground. Values are the means of observations at the 60 bird counting points at each survey station.

field ornithologists familiar with the census procedure and with all species resident in the area.

Census methods.—At each station we selected the four least disturbed and most extensive forest stands and assigned one observer to each. Each observer plotted his own course, following essentially straight segments through the forest, staying at least 100 m from edges, avoiding slashed, grazed, and otherwise disturbed areas, and making counts only where the tree canopy was closed (estimated >70% cover).

Because of the difficulty of following straight courses through the trackless and sometimes difficult understory, we adopted a point-count census method similar to that of Reynolds et al. (1980), in which the observer stopped every 100 m or more along a transect to stand and listen for 7 min. All birds detected by sight or sound (>90% were by sound) were recorded at each point. Fifteen points were sampled by each observer on nonrainy, nonwindy mornings within 3 h of sunrise. We thus collected data at $15 \times 4 = 60$ points at each of the 12 stations.

All diurnal land birds, except raptors and nonforest species passing overhead, were tallied as detected, and the records of each observer totaled for each station. Tallies based on song detections were doubled to give a total population estimate (assuming equal numbers of males and females). Tallies based on call notes and visual detections were not doubled, and juvenile birds (recorded in only a few late June surveys) were omitted. For each species we adjusted the count for changes in total detection frequency between the early and late June traverses on the assumption that such differences reflected seasonal changes in vocal activity and hence conspicuousness rather than changes in actual population density. Counts were higher in the late traverse for some species and in the early traverse for others, and, again assuming that the lower of the two reflected seasonally depressed song activity, we applied the adjustment to the lower of the two values in each case.

We summed the densities for the entire community and for each of six trophic categories (Table 3) after converting the adjusted counts for each species at each station to absolute density estimates. For this conversion we applied species-specific areal denominators derived from field measurements of detection threshold distances (Emlen and DeJong 1981, DeJong and Emlen 1985) (Table 3). Threshold values not available from the Emlen and DeJong studies were estimated by subjective interpolation from values for species with similar vocal and behavioral characteristics.

Foraging observations.—We made foraging observations for all species at all stations as opportunity permitted. For each observed or apparent prey capture we recorded the bird's position in the vegetation, height above the ground, foraging substrate, and foraging method. To minimize sampling bias we recorded no more than five observations on any single

bird. Our first objective was to quantify the distribution of foraging activity for each species across the six primary substrates of the forest (air, bark, ground, upper tree foliage, lower tree foliage, and shrub foliage). Our second objective was to estimate the total avian activity and foraging pressure on each substrate (F_s) in terms of summed density and consuming biomass (all species) per unit of forest area [$F_s = \sum Psi(D_i M_i^{0.74})$, where Psi is the proportion of total foraging activity on substrate s by species i , D_i is the density, and $M_i^{0.74}$ is the mean body mass of the species adjusted for metabolic efficiency related to body size (Lasiewski and Dawson 1967)].

Habitat assessment.—We used two procedures to assess the forest structure and composition at each of the 12 survey stations along the transect: (1) a quick visual appraisal of the forest profile within approximately 30 m of the observer at each of the 60 census points at each station, and (2) a partially randomized sampling of major vegetation parameters at points located by random numbers in 30 successive 100-m intervals through representative portions of the forest.

The profile analyses were made on the census route immediately following each 7-min bird count and before moving to the next census points. We scored cover density from 0 (no cover) to 10 (full cover) at each of six levels in the forest: upper tree canopy (>15 m), lower tree canopy (7–15 m), upper shrub canopy (2–7 m), lower shrub canopy (0.8–2.0 m), herb cover (0.1–0.8 m), and ground cover (<0.1 m).

The partially randomized vegetation sampling was done by two members of the party experienced in habitat measurement. Circular plots of 0.01 ha were located at each of the 30 sampling sites at each station, and within each plot each tree (>10 cm diameter at breast height) was identified and measured (basal area). Saplings and lianas (2.5–10 cm DBH) within each plot also were identified and counted.

RESULTS

Species density pattern and profiles.—Densities decreased northward in all of the 12 southern species at rates between 2.6% and 29.8% per degree of latitude (Fig. 3A). They decreased southward in all 6 northern species at rates between 2.5% and 27.7% per degree of latitude (Fig. 3B). Profiles for the 23 wide-ranging species in which our transect spanned only a middle segment of the total latitudinal range (Fig. 3C) sloped variously from 14.1% south to 13.3% north and averaged essentially level (0.06% south).

Community density patterns.—Significant latitudinal gradients were found in 3 of the 6 foraging substrate categories. Aerial sallying and midfoliage gleaning declined northward at rates

TABLE 3. Bird species recorded along the Mississippi bottomland transect with pertinent distributional, seasonal, foraging, and census data.

Species ^a	Re- gion of sub- ori- gin ^b	No. of spe- cies ^c	Sea- son- al sta- tus ^d	Foraging distribution ^e						Dete- ction dis- tance ^f	Body mass ^g	
				Gd	Tr	A	Fl	Fm	Fh			
Yellow-billed Cuckoo (<i>Coccyzus ameri- canus</i>) ^h		(1)	S						10	190	58	
Black-billed Cuckoo (<i>C. erythrophthalmus</i>) ^h												
Northern Flicker (<i>Colaptes auratus</i>)	?	3	P	4	6					160	133	
Red-bellied Woodpecker (<i>Melanerpes caro- linus</i>)	S	1	P		9			1		130	64	
Red-headed Woodpecker (<i>M. erythro- cephalus</i>)	?	1	P		8	2				130	67	
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	N	1	S		9			1		100	50	
Hairy Woodpecker (<i>Picoides villosus</i>)	?	3	P		10					120	66	
Downy Woodpecker (<i>P. pubescens</i>)	?	3	P		8			2		110	27	
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	?	2	P		10					190	314	
Eastern Wood-Pewee (<i>Contopus virens</i>)	?	1	S				9			1	120	14
Acadian Flycatcher (<i>Empidonax virescens</i>)	S	1	S				6		2	2	90	13
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	?	1	S				6			4	130	34
Blue Jay (<i>Cyanocitta cristata</i>)	?	2	P	6	2					2	130	87
Black-capped Chickadee (<i>Parus atricapil- lus</i>)	N	1	P		1				9		80	10.8
Carolina Chickadee (<i>P. carolinensis</i>)	S	2	P		1				9		80	9.2
Tufted Titmouse (<i>P. bicolor</i>)	S	1	P		2				8		150	22
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	?	2	P		9			1			110	21
Brown Creeper (<i>Certhia americana</i>)	N	1	P		10						80	8.4
Carolina Wren (<i>Thryothorus ludovicianus</i>)	S	1	P	2	3		5				150	21
House Wren (<i>Troglodytes aedon</i>)	N	1	S	2	3		5				140	11
Blue-gray Gnatcatcher (<i>Poliopitila caerulea</i>)	S	1	S		1	1					70	6.0
Wood Thrush (<i>Hylocichla mustelina</i>)	S	1	S	8			1	1			180	47
American Robin (<i>Turdus migratorius</i>)	?	2	S	7	1		1			1	150	77
Gray Catbird (<i>Dumetella carolinensis</i>)	?	1	S	2	3		5				110	37
White-eyed Vireo (<i>Vireo griseus</i>)	S	1	S				10				110	11
Yellow-throated Vireo (<i>V. flavifrons</i>)	?	1	S							10	130	19
Warbling Vireo (<i>V. gilvus</i>)	?	1	S							10	110	12
Red-eyed Vireo (<i>V. olivaceus</i>)	?	1	S							10	130	17
Northern Parula (<i>Parula americana</i>)	S	1	S							10	90	9
Cerulean Warbler (<i>Dendroica caerulea</i>)	?	1	S							10	90	9
Yellow-throated Warbler (<i>D. dominica</i>)	S	1	S		2					8	100	9
American Redstart (<i>Setophaga ruticilla</i>)	N	2	S		1	2			5	2	100	8
Prothonotary Warbler (<i>Protonotaria citrea</i>)	S	1	S		4				1	3	130	17
Kentucky Warbler (<i>Oporornis formosus</i>)	S	1	S	4			6				130	14
Common Yellowthroat (<i>Geothlypis trichas</i>)	?	2	S	8			2				120	10
Summer Tanager (<i>Piranga rubra</i>)	S	1	S							10	140	30
Scarlet Tanager (<i>P. olivacea</i>)	N	1	S							10	140	29
Northern Cardinal (<i>Cardinalis cardinalis</i>)	S	1	P	7			2	1			180	45
Rose-breasted Grosbeak (<i>Pheucticus ludo- vicianus</i>)	N	1	S						8	2	140	46
Indigo Bunting (<i>Passerina cyanea</i>)	?	1	S	6			4				140	15
Song Sparrow (<i>Melospiza melodia</i>)	N	1	P	5			5				120	21
Brown-headed Cowbird (<i>Molothrus ater</i>)	?	1	S	8					1	1	100	39
Northern Oriole (<i>Icterus galbula</i>)	?	1	S	1						9	140	34

^a Nomenclature follows A.O.U. 1983. Waterbirds, birds of prey, nocturnal birds, and land birds recorded fewer than 5 times in the study are not included in this list.

^b Presumed derivation of the bottomland corridor populations from southern deciduous forests (S) or northern mixed conifer-hardwood forests (N). A question mark indicates indeterminate origin.

^c Number of subspecies (A.O.U. 1957) along the extended north-south axis of the Mississippi River Valley between the Gulf of Mexico and Hudson Bay.

of 12.79% and 7.73% per degree of latitude, respectively, while low-foliage gleaning declined southward at rates of 12.4% per degree of latitude (Fig. 4). Thus, total avian foraging pressures on the air and midfoliage substrates were less than half as high at the northern as at the southern end of the transect, while in the low foliage they were twice as high. Whole communities (the sum of all species populations) showed no significant density trends along the transect (Fig. 3C, block 24).

BOUNDARY CONSTRAINTS

We recognize three primary environmental factors potentially restricting range dispersal along our transect: climate, habitat structure, and interspecies competition. Climate and habitat structure are both direct functions of latitude, but while the relationship of latitude with climate is essentially uncomplicated in our topographically uniform study area, its relationship with habitat structure is strongly complicated by irregular edaphic patterns and human-created mosaics of agriculture and urbanization along the route. On this basis we interpret the underlying directional trends in most of the distributional profiles (Fig. 3) as reflecting climatic factors, and the irregular, station-to-station fluctuations superimposed on the profile slopes as reflecting the complex patterns of habitat distribution along the transect. Competition is not related directly to latitude but may be revealed in reciprocally sloping latitudinal slopes where species ranges overlap.

Climatic factors.—We recognize three climate-related factors as constraints on latitudinal range expansion: temperature, season length, and day length. While range boundaries often coincide neatly with isotherms, little progress has been made in distinguishing whether temperature acts on avian distributions directly or secondarily through its effects on vegetation

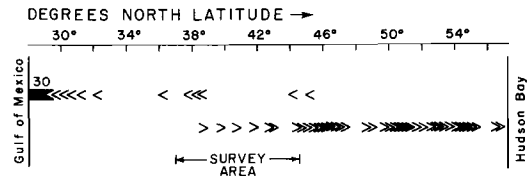


Fig. 2. Distribution of the southern and northern range boundaries of the 41 forest bird species of this study along the 90°W meridian of longitude between the Gulf of Mexico (at left) and Hudson Bay (at right). (Thirty species extend south to within 2° of the Gulf coast.) Data from Peterson (1980).

and resources. Although the close correlation of periodic advances and retreats of northern range boundaries with temperature cycles (e.g. von Haartman 1973, Järvinen and Väisänen 1979) suggests direct temperature responses, the proximal factors in these cases may be food and substrate changes rather than temperature per se.

While the direct effects of temperature are difficult to demonstrate under stable or relatively stable conditions, episodes of climatic extremes, such as floods, storms, and droughts, may decimate local populations of vulnerable species, periodically producing temporary boundary retractions or population extirpations. The Carolina Wren (*Thryothorus ludovicianus*), a nonmigratory terrestrial insectivore, is such a species. Normally an abundant member of southeastern hardwood forest communities as far north as 42° (transect station 8), we never detected this species along our transect in 1979. This scarcity was attributed to a two-week period of extreme cold and deep snow in the winter of 1976–1977 when the species was essentially extirpated from the northern third of its geographic range (Graber and Graber 1979).

Food availability, commonly invoked as the prime determiner of a species' presence and abundance in an area (Lack 1954, Newton 1980),

^d P = permanent resident, S = summer resident (migrant).

^e Proportion of foraging activity (in tenths) on six forest substrates: ground, tree trunks, air, low foliage (shrub level), medium-height foliage (subcanopy level), and high foliage (upper canopy). (Data from on-site observations supplemented as necessary by literature.)

^f Threshold distance (m) for detecting songs of each species as described in text. Used as the radius of detection areas for density calculations.

^g Body mass in grams (from tabulations of Dunning 1984).

^h The difficulty of distinguishing these species by call necessitated a pooling of all cuckoo records. Detection distances and body masses here are means for the two species.

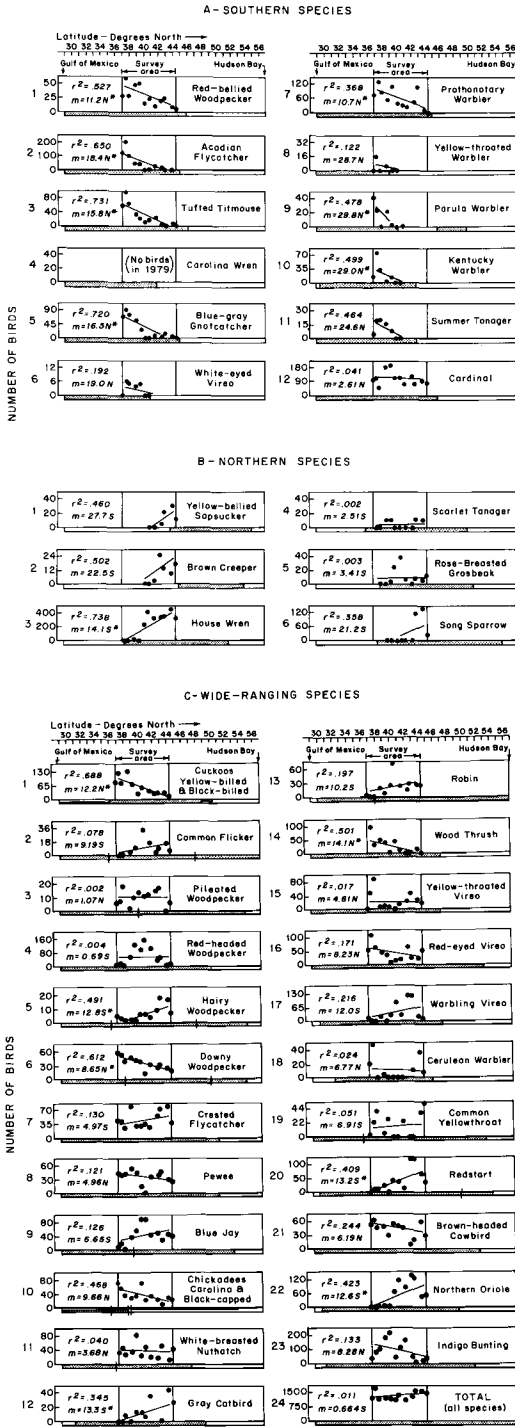


Fig. 3. Abundance profiles for 41 forest bird species along the Mississippi bottomland transect; (A) southern species, (B) northern species, and (C) species with extensive north-south ranges. Shaded bars at

depends on the time available for foraging as well as on prey abundance (see Austin 1978, Zammuto et al. 1981). Thus, in species adapted for the long summers of southern latitudes, a northward range expansion may be suppressed by progressive northerly reductions in the number of days in which vegetation, food, and foraging conditions are favorable for breeding and raising young. Similarly, species adapted for the long summer days of northern latitudes may be constrained from southward range expansion by the shorter daylight hours available for foraging and provisioning their young.

The season of favorable conditions for breeding is determined by many factors and cannot be measured definitively. We arbitrarily selected 10°C as a temperature threshold for high insect activity and used the number of days when the mean daily temperature curve for each locality was above threshold level as our indicator of breeding season length. The constraints of season length on northward range expansion are obvious and well documented for subarctic species where the potential season in these terms is less than 50 days (cf. Morton 1976, Järvinen 1980). Constraints are less obvious but potentially considerable in the middle latitudes where differences in season length between southern and northern range boundaries ranged between about 100 and 180 days

the base of each block indicate the extent of the range of each species along a north-south axis between the Gulf of Mexico and Hudson Bay (data from Peterson 1980). Dots and sloping lines in the middle sections indicate the number of birds detected at 60 observation points at each of the 12 stations, and the calculated linear slope of population trends [m = percentage decrease per degree of latitude northward (N) or southward (S) within the transect area]. An asterisk indicates significance at the 0.05 level. Short vertical bars along the baseline (e.g. C-2) indicate the boundaries between recognized subspecies; the double bar on graph C-10 indicates a species boundary.

Three species recorded fewer than 10 times are omitted because of small sample sizes. One species, the Carolina Wren, is included although none were recorded (see text). Records for the two cuckoos were combined and the pair treated as a single species because of our inability to consistently distinguish between their vocalizations in the field. Records for the two chickadees are profiled together to show their distributional relationship.

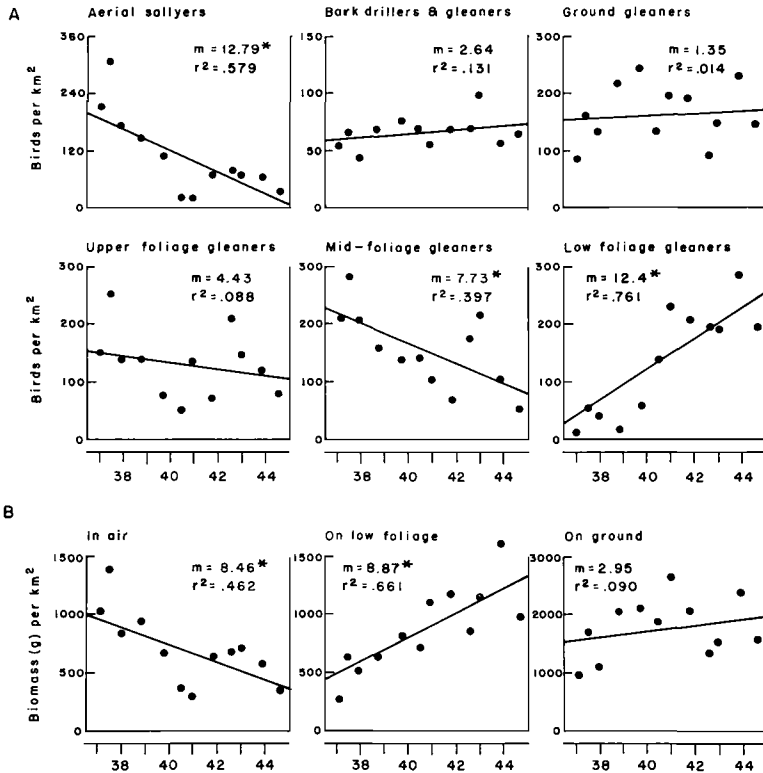


Fig. 4. (A) Latitudinal density trends for 6 trophic categories along the transect, and (B) latitudinal trends of summed foraging pressure (total foraging activity) on the air, low-foliage, and ground substrates. Density and biomass values (ordinate) are reduced to a common areal denominator to permit the grouping of species with different detectability values. Slope values (m) represent percentage decrease northward (to right) or southward (to left) per degree of latitude. Asterisks indicate significance at the 0.05 level.

for the various species (see Fig. 3 baselines for species range boundaries and Table 1, column 8 for season length indicators).

The number of daylight hours available for foraging and provisioning nestlings or fledglings (defined here as the time between sunrise and sunset at summer solstice) decreases southward from about 18 h at Hudson Bay to 14 h at the Gulf of Mexico. We know very little about the effect of available foraging time on reproductive success, but where small variations in reproductive output are critical for the survival of a population, even a slight reduction in parental provisioning time could constitute a barrier to southward range expansion.

Habitat factors.—Although ostensibly minimized in our study, considerable latitude-unrelated density variation was evident in the station-to-station fluctuations in the density profiles (Fig. 3). We attributed many of these

fluctuations to variations in vegetation structure and composition associated particularly with patchy soil distribution and human interference.

While habitats and their associated food supplies have changed extensively over the past century, range boundaries apparently have been relatively stable in most species. A conspicuous exception is the Northern Cardinal (*Cardinalis cardinalis*), whose populations have increased and expanded in the past century, particularly in the northern portions of the transect area. This expansion has coincided with a recent increase in winter feeding and ornamental shrub planting around human habitations (Mayfield 1962). Food offered at suburban feeding stations also may have affected population densities in the Tufted Titmouse (*Parus bicolor*) in New England (Kricher 1981). Direct evidence for the role of food abundance in bird

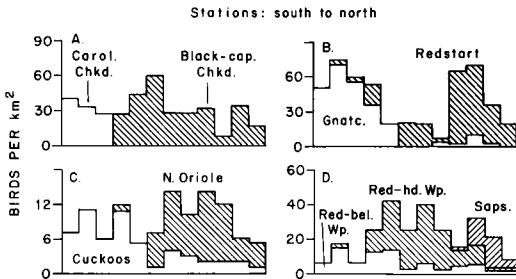


Fig. 5. Density distribution patterns along the latitudinal gradient for selected pairs of phylogenetically or ecologically related species.

abundance and distribution is difficult to obtain except in such unplanned natural experiments.

Evidence for a direct link between population density and nest substrate abundance can be seen in the Prothonotary Warbler (*Protonotaria citrea*), a species closely associated with hollow tree stubs over standing or running water (Bent 1953). Prothonotaries were more numerous where these conditions prevailed at our southern stations, and at station 10 in the north (Fig. 3A, block 7). House Wrens (*Troglodytes aedon*) have increased markedly in southern Illinois with the provision of artificial nest boxes around human habitations, but this numerical increase apparently has not been reflected in a southward range expansion in the species' natural bottomland habitat (R. Graber pers. comm.).

Increases in summed foraging activity northward on the air and midfoliage substrates and southward on low-foliage substrates (Fig. 4) suggest corresponding latitudinal trends in insect prey densities. Time constraints did not allow us to test these possibilities.

Competition.—Prevailing theory predicts that the joint exploitation of a limiting resource by two or more sympatric species will lead to a reduction in the available supply and precipitate either a behavioral or a population adjustment in one or the other population. If there is no behavioral adjustment, a geographic adjustment would be expected, with one of the species disappearing from the zone of overlap. Thus, disjunct ranges in congeneric pairs or broken strings of segregated ranges in congeneric groups have been interpreted as evidence of competition (Terborgh 1971, Diamond 1973).

We adopt this rationale, but found no reason to restrict this search procedure to congenetics or to expect complete withdrawal of either competing species from the area of range overlap (Pielou 1975).

Among the 29 species in the Mississippi bottomland bird community for which we have sufficient data on density slopes, 14 faced potential or real competitors as identified by congeneric status or appreciable overlap in food requirements and foraging substrate preferences. Geographic displacement was complete and abrupt in two of these (one pair), partial and graduated in the others. The two segregated species, the Black-capped (*Parus atricapillus*) and Carolina chickadees (*P. carolinensis*) (Figs. 3C, block 10; and 5A), resemble each other closely in morphology, behavior, and ecology. Boundaries overlap slightly in winter, but the two populations withdraw to the appropriate side of the line each spring before the onset of breeding (Tanner 1952, Merritt 1981). A third member of the genus, the Tufted Titmouse, is a considerably larger bird with little ecological overlap with the two chickadees and no evidence of distributional interaction (Fig. 3A, block 3).

The remaining congeneric pairs in the community showed various degrees of overlap. The Downy (*Picoides pubescens*) and Hairy woodpeckers (*P. villosus*) had broadly overlapping distributions with densities sloping reciprocally in the surveyed middle section of their ranges (Fig. 3C, blocks 5 and 6). The two tanagers (genus *Piranga*), apparently very similar in foraging and nesting requirements, overlapped over about half of their respective geographic ranges (Fig. 3A, block 11, and 3B, block 4); the Summer Tanager (*P. rubra*) decreased northward rather steeply to its northern boundary; the Scarlet Tanager's (*P. olivacea*) sample was small and showed no clear density trend. Opposing density slopes in 2 of the 3 arboreal vireos (genus *Vireo*), although not significantly different from zero in this small sample, suggest a possible competitive interaction in their broad area of range overlap (Fig. 3C, blocks 15–17). The mid-transect increase of the Warbling Vireo (*V. gilvus*), however, may simply reflect a response of a characteristically open woodland species to subtle habitat variations in the area of the prairie peninsula at stations 6–10. The fourth vireo in the community, the shrub-foraging White-

eyed Vireo (*V. griseus*), showed no evidence of geographic interaction with its arboreal congeners (Fig. 3A, block 6). The northward slopes of warblers of the genus *Dendroica* showed no suggestions of geographical displacement; the Cerulean Warbler (*D. caerulea*) (Fig. 3C, block 18) reached its highest densities in the area of overlap with the southern Yellow-throated Warbler (*D. dominica*) (Fig. 3A, block 8).

The most striking examples of reciprocal density trends along our transect occurred between noncongeneric species. Reciprocal trends were predicted in these cases on the basis of strong trophic and ecological similarities in each of the matched pairs. Blue-gray Gnatcatchers (*Poliophtila caerulea*) (Sylviidae) decreased in density northward as Redstarts (*Setophaga ruticilla*) (Parulidae) increased (Fig. 5B); both are arboreal insect gleaners of the middle canopy that indulge in considerable aerial sallying (Table 3). Cuckoos (*Coccyzus* spp.) (Cuculiformes) decreased northward as Northern Orioles (*Icterus galbula*) (Passeriformes) increased (Fig. 5C); both are large arboreal insect gleaners of the upper canopy that specialize on hairy lepidopteran larvae, prey items avoided by most birds (Bent 1958). The Yellow-bellied Sapsucker (*Sphyrapicus varius*) occurred only in the northern third of the transect where Red-bellied Woodpeckers (*Melanerpes carolinus*) were scarce (Fig. 5D). These two woodpeckers are similar in size and overlap considerably in their trophic specializations, but belong to remotely related genera. A third species, the Red-headed Woodpecker (*M. erythrocephalus*), which frequents taller trees in more open situations, reached its highest densities in the central stations, suggesting a possible compensatory interaction between these three middle-size woodpeckers. The reason for the steep density attenuation of House Wrens south of latitude 40° (Fig. 3B, block 3) is unclear, but the boundary roughly coincides with the northern range boundary of the normally common Carolina Wren (Fig. 3A, block 4), another insect gleaner of the forest understory. This could reflect a compensatory interaction prior to the abrupt disappearance of Carolina Wrens two years before our survey.

For situations in which more than two species may be competing for a common resource (i.e. diffuse competition), we compared the density distribution of single, abundant species with

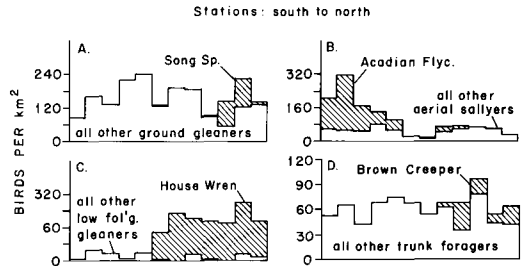


Fig. 6. Density distribution patterns for dominant guild members and their guild associates.

the summed density of the other (secondary) members of the same trophic guild (Fig. 6). Evidence for the predicted suppression of the secondary species by the numerically dominant species is lacking in two of these tests (Fig. 6B, C) and equivocal in the other two (Fig. 6A, D). In the air sallyers a sharp reduction in the abundant Acadian Flycatcher (*Empidonax virens*) north of station 5 was not matched with a compensatory increase in the numbers of other flycatchers (Fig. 6B). A similar absence of competitive replacement was seen in the low-foliage gleaners, where the sudden appearance of abundant House Wrens north of station 6 had no apparent suppressive effect on the other low-foliage gleaners (Fig. 6C). The previously noted scarcity of Carolina Wrens in the southern forests in the year of our survey may have contributed to the striking summed density contrast. The pattern of species replacement predicted by competition theory was potentially detectable in the ground-gleaner guild (Fig. 6A) and the bark-gleaner guild (Fig. 6D), but in neither case was it adequate to be considered evidence for competitive displacement.

Relative importance of the constraining factors.—The factors discussed above may combine in various ways to suppress a population along a species' latitudinal range. Certain factors undoubtedly dominate in each species, and we have attempted to identify through correlation analyses the single environmental factor or category that most closely paralleled the density changes of each species across the 12 stations. Latitude, interpreted as operating through season length or day length, was most closely correlated in 12 species; one or another dimension of habitat structure was most closely correlated in 25 (Table 4). Competition, not accessible for this analysis, presumably played a prominent

TABLE 4. Principal environmental constraints on range expansion for Mississippi bottomland birds as indicated by correlations of density patterns with habitat factors (Table 2) and latitude across the survey stations of the transect. A question mark indicates that no environmental factors were significantly correlated.

Species ^a	Principal constraint	r ²
Cuckoos (2 spp.)	Latitude	0.688
Northern Flicker	Sparse tall trees	0.529
Red-bellied Woodpecker	Latitude	0.527
Red-headed Woodpecker	Sparse tall trees	0.492
Yellow-bellied Sapsucker	Many dead trees	0.666
Hairy Woodpecker	Many dead trees	0.494
Downy Woodpecker	Latitude	0.612
Pileated Woodpecker	?	
Eastern Wood-Pewee	Dense tall trees	0.319
Acadian Flycatcher	Latitude	0.650
Great Crested Flycatcher	?	
Blue Jay	Small forest extent	0.420
Chickadees (2 spp.)	Latitude	0.468
Tufted Titmouse	Latitude	0.731
White-breasted Nuthatch	?	
Brown Creeper	Dense tall trees	0.732
Carolina Wren	?	
House Wren	Latitude	0.738
Blue-gray Gnatcatcher	Latitude	0.720
Wood Thrush	Dense low trees	0.656
American Robin	Sparse tall trees	0.486
Gray Catbird	Dense herbs	0.410
White-eyed Vireo	Dense low shrubs	0.519
Yellow-throated Vireo	Large forest extent	0.384
Warbling Vireo	Large basal area	0.475
Red-eyed Vireo	Good canopy quality	0.475
Northern Parula	Dense tall trees	0.590
Cerulean Warbler	?	
Yellow-throated Warbler	Good canopy quality	0.722
American Redstart	Large basal area	0.418
Prothonotary Warbler	Latitude	0.368
Kentucky Warbler	Latitude	0.499
Common Yellowthroat	Small basal area	0.515
Summer Tanager	Dense high shrubs	0.569
Scarlet Tanager	Many dead trees	0.418
Northern Cardinal	Small forest extent	0.446
Rose-breasted Grosbeak	Sparse tall trees	0.527
Indigo Bunting	Dense low shrubs	0.375
Song Sparrow	Many dead trees	0.592
Brown-headed Cowbird	Many high shrubs	0.485
Northern Oriole	Latitude	0.423

^a For scientific names and other data on species, see Table 2.

role in the 2 species (1 pair) that showed abrupt geographic replacement, and may have featured in 12 others (6 pairs) where densities declined reciprocally over the zones of range overlap.

BOUNDARY DYNAMICS

In our study we concentrated on ecological constraint systems and did not consider why many populations in the peripheral zones of their geographic ranges do not, over evolutionary time, adapt to peripheral constraining factors and expand their ranges until they encounter a physical or steep environmental barrier. To explain this phenomenon we favor the model that visualizes species populations as constrained adaptationally and hence geographically by the neutralizing effects of within-range gene flow on adaptive selection in peripheral zones (Miller 1947, Haldane 1956, Mayr 1970). On this basis we attribute the observed centrifugally declining densities to declining fitness of relatively uniform phenotypes along radially diverging environmental gradients.

Peripherally attenuating densities complicate the problem of designating range boundary lines. Two lines should be recognized for most continental land-bird ranges: a functional boundary beyond which reproduction, on average, falls below mortality, and an empirical boundary enclosing an outer submarginal zone within which the species occurs and may occasionally breed though, on average, unsuccessfully. The boundaries that appear in most current field reference books and distribution maps are empirically determined outer boundaries.

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