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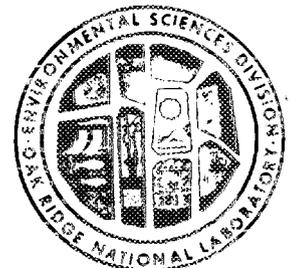
MARTIN MARIETTA

**Forest Bird Demography
in a Landscape Mosaic**

D. L. Urban
H. H. Shugart, Jr.
D. L. DeAngelis
R. V. O'Neill

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ENVIRONMENTAL SCIENCES DIVISION

FOREST BIRD DEMOGRAPHY IN A LANDSCAPE MOSAIC¹

D. L. Urban,² H. H. Shugart, Jr.,² D. L. DeAngelis, and R. V. O'Neill

Environmental Sciences Division
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¹Submitted as a thesis by D. L. Urban to the Graduate Council of the University of Tennessee in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

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A tandem approach of field studies and simulation modeling was used to examine avian demography in a landscape mosaic of habitat patches. A particular goal was to attempt to account for the regional decline in abundance of a subset of bird species sensitive to forest fragmentation. Species abundance patterns in forest patches were framed as the consequence of individual birds' demographics, constrained by their landscape context; this context was partitioned to emphasize habitat availability (or area), accessibility (or isolation), and localized factors affecting reproductive success (nest predation and brood parasitism). Each of these constraints was examined in turn, to assess their relative contribution to species abundance patterns observed in landscape mosaics.

A forest simulation model was used to develop a theoretical basis for the importance of microhabitat pattern in forest bird communities. Simulated patterns in microhabitat availability could provide for successional trends in bird species diversity, a relation between niche position and species abundance, the occurrence of more rare species than common ones, and a species/area effect. Hypotheses about microhabitat variety and bird species distribution in landscapes were not supported by data from woodlots in Cadiz Township, southern Wisconsin. But a mechanistic understanding of the agents affecting

microhabitat pattern suggested scenarios under which empirical estimates of microhabitat diversity might contribute substantially to predictions of birds species abundance patterns.

Habitat accessibility did not seem to be an effective constraint on species distribution in the Cadiz mosaic. Neither patterns of spatial dispersion of common species, nor species tallies per woodlot offered compelling evidence that any woodlots were so isolated as to affect avian vagility. Simulation experiments suggested that patch isolation becomes increasingly important as the mean distance between patches increases, until this distance is similar to the dispersal range of the bird species; in mosaics with still greater distances between patches, isolation decreases in importance as an explanatory variable.

Sensitivity analysis of natality terms in the simulation model implicated factors affecting reproductive success as potentially powerful constraints on the distribution of species susceptible to nest predation and brood parasitism. Analysis of model uncertainty suggested that predictions of population trends at the landscape scale cannot rely on detailed demographic mechanisms, but should proceed instead to derive coarser-resolution models that might be implemented at the landscape scale. The hierarchical conceptual model developed in this study represents a synthetic general model, a framework that can be simplified under specified scenarios to provide predictions about bird species abundance patterns in landscape mosaics.

CHAPTER 1

AVIAN DEMOGRAPHY IN MOSAIC LANDSCAPES

Introduction

A terrestrial landscape is a mosaic of heterogeneous landforms, vegetation types, and human land uses. The study of landscapes is currently emerging as a new discipline in ecology (Forman 1981, 1983; Forman and Godron 1981, 1986; Naveh and Lieberman 1984). One concern of landscape ecology is to account for species abundance patterns in the mosaic of habitats that landscapes provide (Risser et al. 1984).

Many studies in landscape ecology have their roots in island biogeographic theory (MacArthur and Wilson 1967). In particular, many studies pursued the relationship between habitat (island) area and species richness. A number of these studies have focused on forest birds in woodlots (e.g., Ambuel and Temple 1983, Forman et al. 1976, Galli et al. 1976, Moore and Hooper 1975, MacClintock et al. 1977). In fact, the species/area relationship was a rather uninteresting result. Larger woodlots support more species. A more interesting result was the identification of a subset of species that are symptomatically rare in small and/or isolated woodlots (Figure 1.1) (Whitcomb et al. 1981; see also Forman et al. 1976, Lynch and Whigham 1984, Lynch and Whitcomb 1978, Robbins 1979, Whitcomb et al. 1976). For study sites with sufficient historical data to record a trend, these "area-sensitive" species have shown a gradual but steady decline in abundance over the past several decades (Figure 1.2). To the

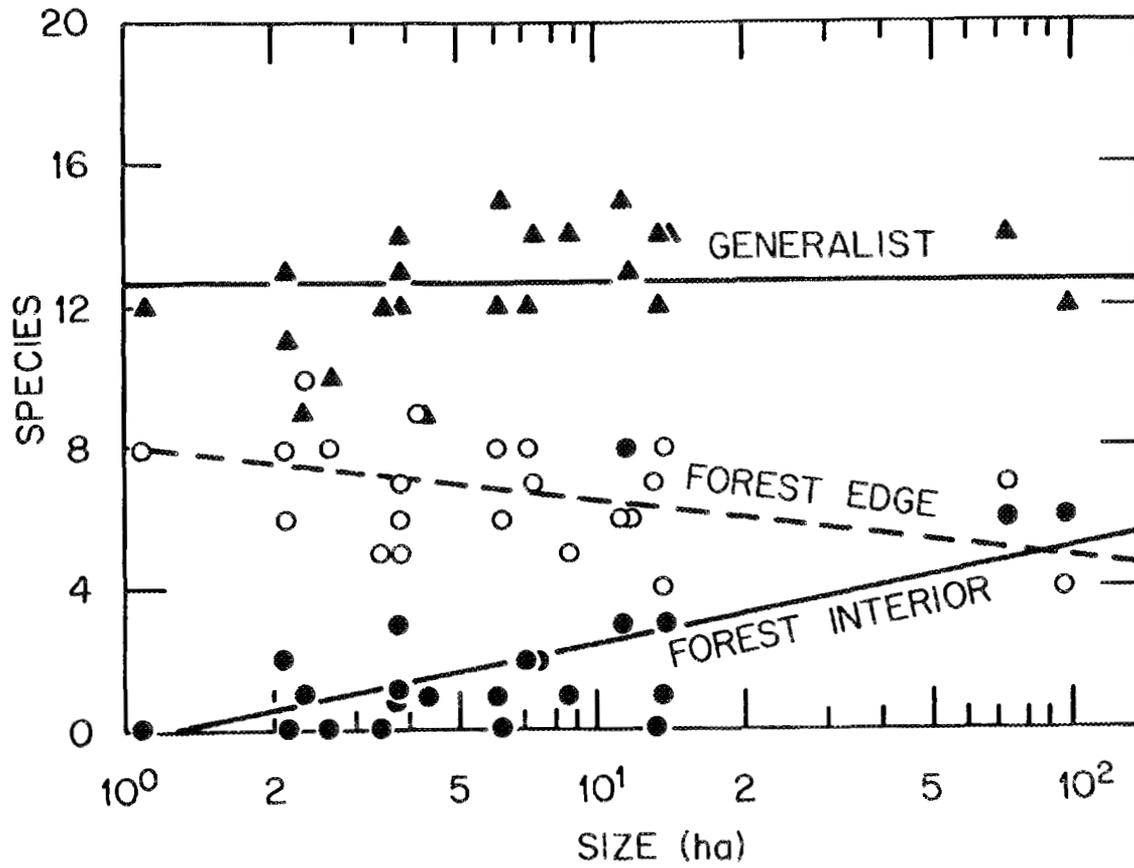


Figure 1.1. Incidence of generalist, edge, and forest interior bird species in surveys of forest tracts ranging 1-100 ha in area (redrawn from Whitcomb et al. 1981).

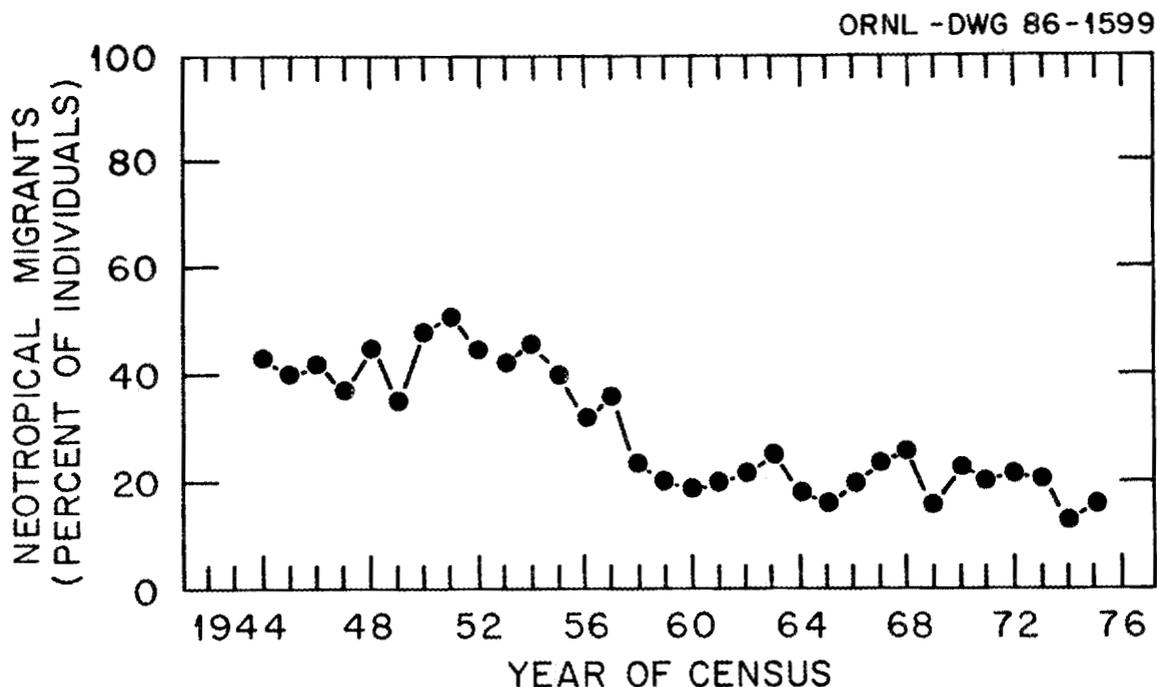


Figure 1.2. Incidence of neotropical migrants in censuses of Trelease Woods, an isolated 22-ha tract in central Illinois (redrawn from Lynch and Whitcomb 1978).

extent that this same general trend could be witnessed over much of the eastern deciduous forest, this decline has achieved the status of a phenomenon.

A Hierarchical Perspective

A useful perspective on a variety of natural phenomena derives from hierarchy theory (Allen and Starr 1982; O'Neill et al. 1986; Pattee 1973; Whyte et al. 1969). Hierarchy theory asserts that a natural event witnessed as a phenomenon is the consequence of mechanisms acting in a constraining context. That is, the full potential of the mechanisms is restricted by their environmental

context so that their realized behavior is different from their potential. Hierarchy explicitly invokes three levels of reference in modeling a phenomenon: lower-level mechanisms, the event itself, and higher-level context.

For bird species abundance patterns in a habitat mosaic, the mechanisms of concern are the demographics of individual birds: their natality, dispersal, and mortality. The context is provided by the landscape itself: the variety and relative abundance of habitats, and their spatial configuration. Because the mosaic metapopulation (the sum of the populations of a species in all the patches) can provide for qualitatively different population dynamics in patches for large versus small metapopulations, it is appropriate to consider the metapopulation as context as well (Figure 1.3).

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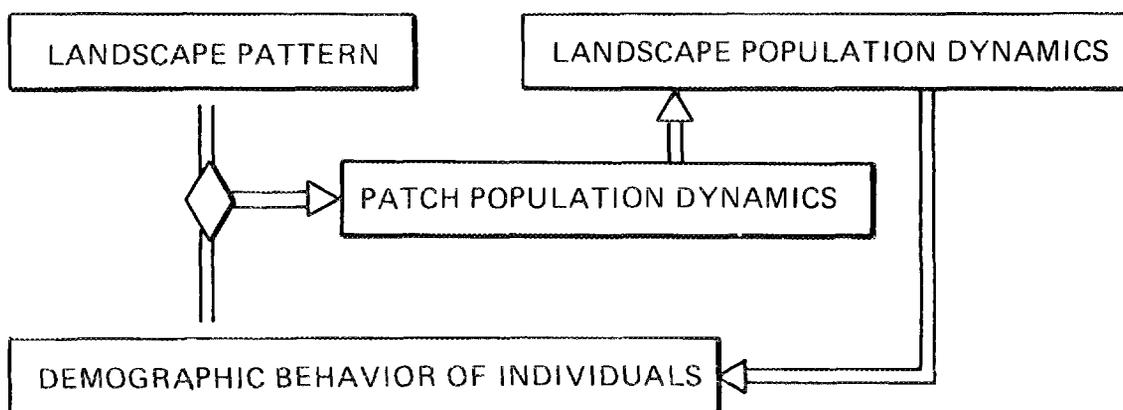


Figure 1.3. Conceptual model of avian population dynamics in forest patches as the consequence of individuals' demographics in a constraining context.

Mechanisms of Avian Demography

Avian ecologists have gone a long way toward explaining species' sensitivity to forest fragmentation by focusing on suites of life-history tactics (Lynch and Whitcomb 1978, Robbins 1979, Whitcomb et al. 1981). Clearly certain life-history tactics are disadvantageous in a fragmented-forest mosaic (Figure 1.4) (Whitcomb et al. 1981). The Ovenbird (common names follow AOU 1982; see Appendix), an archetypal area-sensitive species, is a neotropical migrant warbler with rigid habitat preferences for mature, interior forest, where it builds an open nest on the ground. Consequently, the Ovenbird may be subject to high rates of brood parasitism and nest depredation in small woodlots, it may be restricted by its rigid requirements for preferred microhabitat, and may have difficulty locating available but spatially isolated patches of breeding habitat. The Ovenbird is a good example of a bad strategy on being a bird in a fragmented-forest landscape.

The Landscape Context

Consider the three conditions a bird population must meet to persist regionally: (1) potential breeding habitat must be available (it must exist); (2) habitats must be accessible to the birds; and (3) net recruitment, on average, must be nonnegative. Potential breeding habitat is defined relative to the habitat selection criteria of particular bird species, but habitat availability is not a function of bird biology. Rather, habitat availability depends on the dynamic interplay between disturbances (including forest management) and

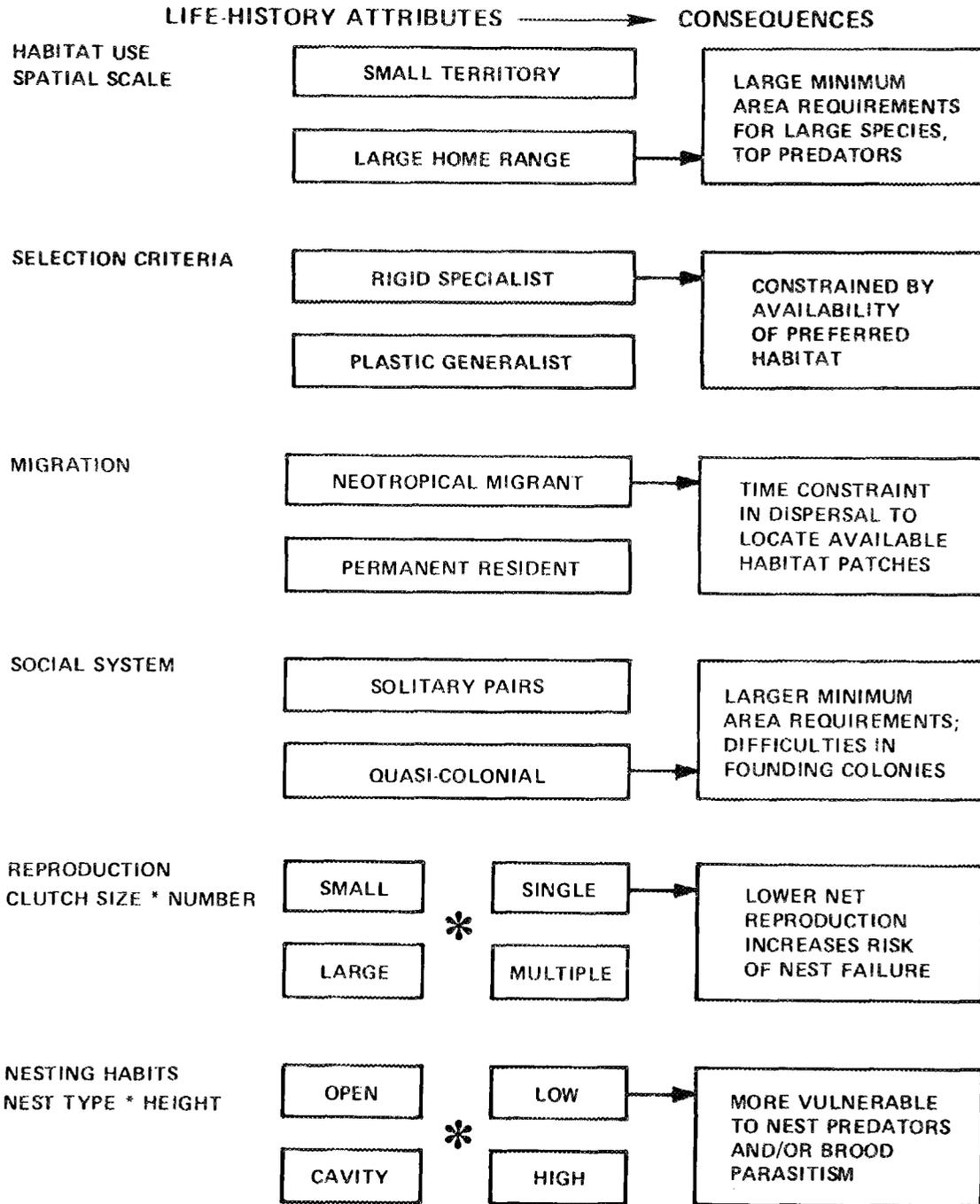


Figure 1.4. Summary of avian life-history tactics sensitive to forest fragmentation (modified from Whitcomb et al. 1981).

succession. Habitat accessibility and net recruitment, however, are functions of bird biology. Accessibility depends on the dispersal abilities of bird species. Net recruitment is simply natality minus mortality, hence reflects factors affecting these. For birds in forest fragments, two very important factors are brood parasitism (Brittingham and Temple 1983) and nest depredation (Gates and Gysel 1978, Wilcove 1985). Both of these are primarily edge effects.

Now consider the changes in these three conditions attendant with forest fragmentation over the past several decades. As forests were cleared for human land uses, the total amount of forest decreased dramatically; forest management has likely influenced microhabitat diversity within remnant forests as well. As fragmentation proceeded, the distance between remnant patches increased, rescaling habitat accessibility relative to birds' dispersal abilities. Finally, as patch size decreased, the proportion of edge habitat per unit area increased, locally intensifying edge effects on net reproduction. These three conditions are thus interrelated, and have changed dramatically over the past several decades (Figure 1.5).

Rationale and Overview

It is instructive to reconsider avian life-history tactics relative to the landscape-scale constraint system: each of the sensitive tactics reflects species response to habitat availability, accessibility, or net recruitment. As the bird species pool for the eastern deciduous forest has remained essentially unchanged over the past century while the constraints on bird demography have changed

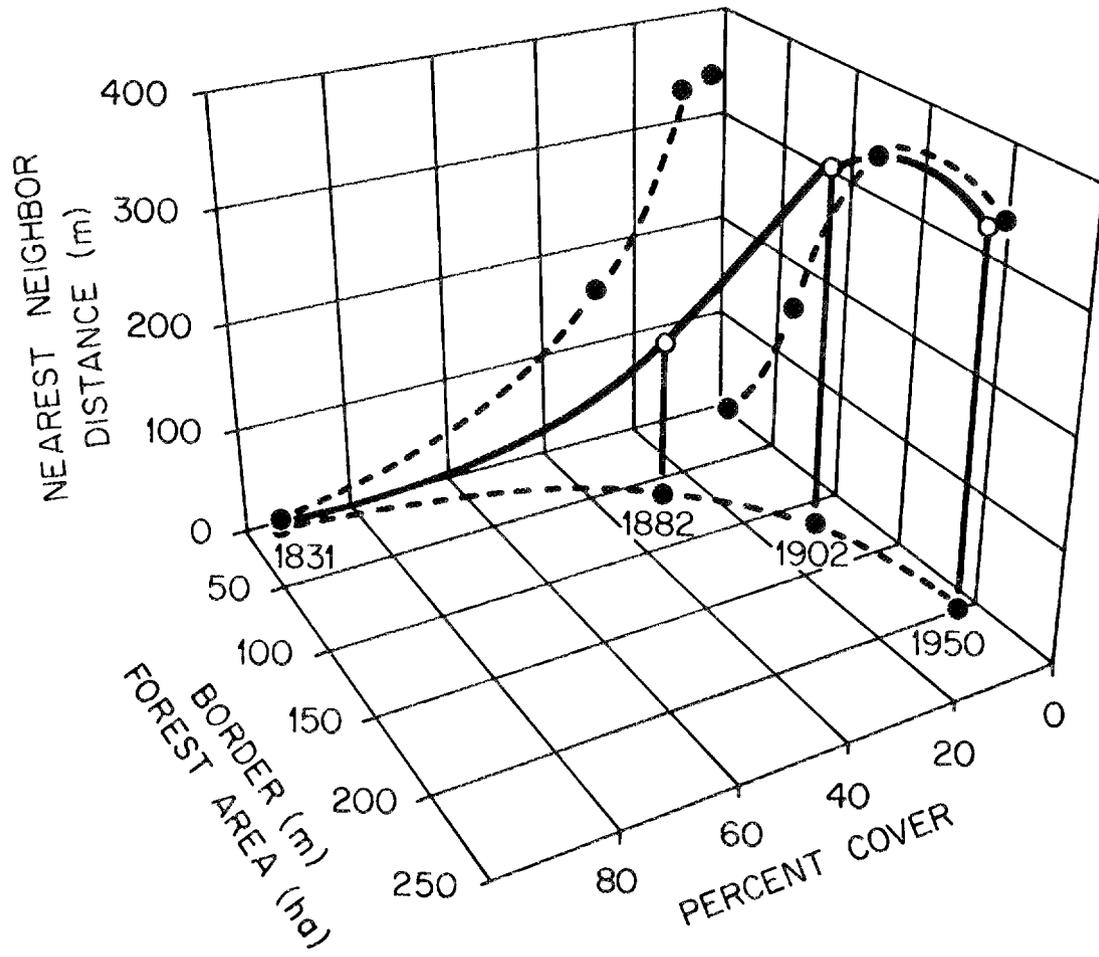


Figure 1.5. Trajectory of change in total forest area, edge area, and mean distance between patches in Cadiz Township, southern Wisconsin (redrawn from Sharpe et al. 1981).

dramatically, it seems plausible to adopt the working hypothesis that the phenomenological decline in abundance of area-sensitive species can be attributed to the altered constraint system. Subsequent chapters attend each of these constraints in turn.

The focus in this dissertation is on bird demography during the breeding season. For neotropical migrants, this focus ignores the likelihood that events on the wintering grounds may have an important effect on breeding bird populations (e.g., Keast and Morton 1980). The distribution of permanent residents may likewise be constrained by the rigors of overwintering, e.g., by limiting food resources. While some aspects of these are clearly related to the three constraints considered here (especially habitat availability), an in-depth treatment of them is beyond the scope of this dissertation.

Note that because the three constraints are interrelated (just as birds life-history tactics are intercorrelated), the goal is not so much to determine whether an effect exists, but rather, to gauge the relative magnitude of the effect of each constraint on bird demography. To this end, a tandem approach of field studies and simulation modeling provides a means of partitioning the effects of several contributing factors. Chapter 2 introduces the study area in southern Wisconsin; the simulation model is developed in the following chapter. The model, an implementation of the "mechanism in context" conceptualization, makes predictions that are tested against data from southern Wisconsin woodlots. Reciprocally, the Wisconsin data suggest further model explorations. The model is also useful in extrapolating

Wisconsin-based conclusions to mosaic landscapes of other spatial configurations.

The final chapter attempts to synthesize a general model of avian demography in mosaic landscapes. The model derives from the hierarchical conceptualization outlined in this chapter (Figure 1.3), but is tempered by two further considerations. First, in situations where one or more of the constraints is not an effective control on demographics, appropriate simplifications can be made in the model. Secondly, where actual mechanisms of importance cannot be resolved empirically for logistical reasons, the model suggests the proper surrogate, the higher-level integration of the mechanisms. Because the model is general it can explain a variety of demographic phenomena; because it is hierarchical, it provides for simplification in its own terms. As such, the general hierarchical model provides a powerful framework with which to explain and predict bird species abundance patterns in mosaic landscapes.

CHAPTER 2

CADIZ TOWNSHIP, REVISITED

Introduction

In 1904 Shriner and Copeland introduced Cadiz Township to an ecological audience, documenting the extent of forest fragmentation in this southern Wisconsin township and speculating about consequent soil erosion and degradation of water quality in farmland streams. Curtis (1956) highlighted Cadiz Township in a classic paper on the effects of forest fragmentation on tree species abundance patterns in woodlots (Figure 2.1).

Southern Wisconsin has hosted a number of classic studies in ecology. The general area contributed study sites to the monumental "Vegetation of Wisconsin" (Curtis 1959), as well as to Bond's classic study of bird species abundance patterns in woodlots (Bond 1957). Bond's monograph was among the first extensive studies of bird species abundance patterns in woodlots of the eastern deciduous forest. He documented differential bird species response to forest area as well as to a synthetic forest moisture gradient (the continuum index). More recent studies in southern Wisconsin have taken advantage of the area's well documented history. Ambuel and Temple (1982) compared current bird populations in southern Wisconsin woodlots to data from Bond (1957), and found that several bird species continue to decline in local abundance. Temple and coworkers continue to study factors effecting bird species distribution in southcentral Wisconsin

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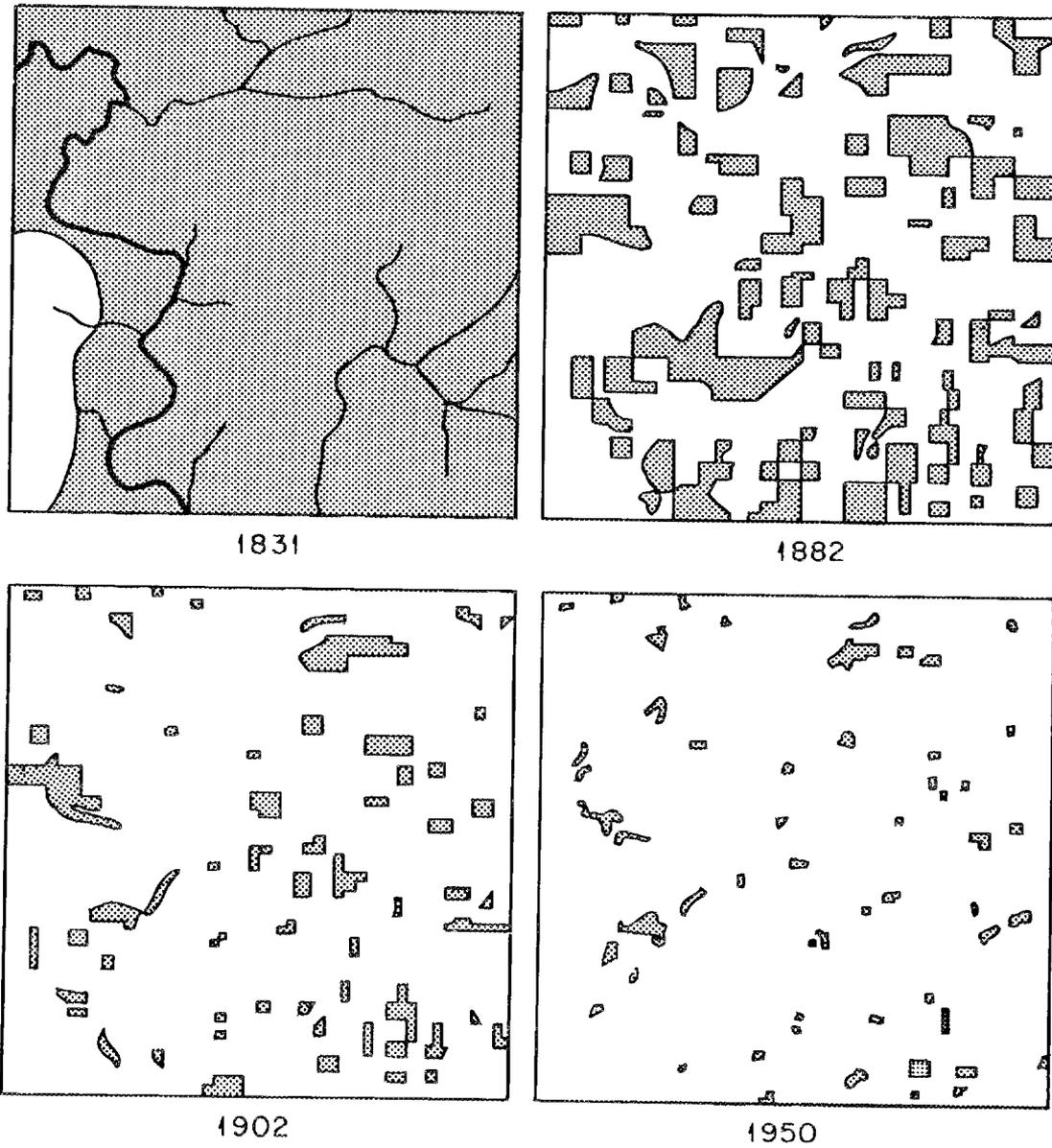


Figure 2.1. History of forest fragmentation in Cadiz Township, southern Wisconsin, as area remaining in forest at settlement, 1882, 1902, and 1950 (from Curtis 1956).

woodlots (Brittingham and Temple 1983, Ambuel and Temple 1983, Temple 1986).

A new Cadiz project was initiated in 1983, funded by the National Science Foundation and directed by F. Stearns (University of Wisconsin-Milwaukee) and D. Sharpe (Southern Illinois University-Carbondale). One goal of this Cadiz project has been to extensively characterize forest patches in the township so that plant species distributions could be related to patterns of land use and other site factors. This goal motivated the collection of a vegetation data base that is perhaps unique: the data are simultaneously detailed (represented by samples of ground cover, shrub, and tree strata), extensive (all of Cadiz Township plus part of adjoining Clarno Township), exhaustive (essentially every upland woodlot larger than 1 ha in area), and spatially explicit. Because a concern to account for bird species distribution on a landscape requires habitat data of similar scope and resolution (Allen et al. 1984), fieldwork for this dissertation was conducted in collaboration with the Sharpe-Stearns Cadiz project.

The remainder of this chapter summarizes the Cadiz Township landscape, the vegetation data base, and bird census data collected in woodlots in this study area. This data base will be referenced repeatedly but selectively in subsequent chapters, so it is appropriate to begin with a general overview of the forest patches and avifauna. Because some conclusions will ultimately be generalized to landscape mosaics of different spatial configurations, it will also be helpful

to characterize the Cadiz landscape relative to other documented landscapes in the eastern United States.

The Cadiz Landscape

Cadiz Township lies on the Illinois border in Green County, southcentral Wisconsin (89°54' W., 43°30' N.). The township includes two physiographic landforms. West of the Pecatonica River and north of U.S. Highway 11 lies the driftless area, a region not overrun by the Wisconsin glaciation. The region west of the river historically supported prairie-oak savannah under a regime of frequent fires (Figure 2.2). Since fires were suppressed after European settlement, this area now supports closed canopy forest dominated by oaks (especially Quercus macrocarpa and Q. alba) (Sharpe et al., in press). The northern region of the township, east of the river, was apparently spared the frequent fires that occurred to the west; this area now supports oak forest dominated by Q. alba. South and east of the driftless area the landscape is more gently rolling; this area currently supports more mesic forest dominated by sugar maple (Acer saccharum) and other northern hardwoods. On the east, in a broad band extending from the northeast to the southcentral border of the township, was a sward of prairie. This area is still essentially devoid of forest. Thus, topography and native vegetation delineate a natural, internally consistent landscape unit in the southeastern and southcentral part of the township (Sharpe et al., in press). This area, approximately 50 km², was selected as a study area.

CADIZ TOWNSHIP

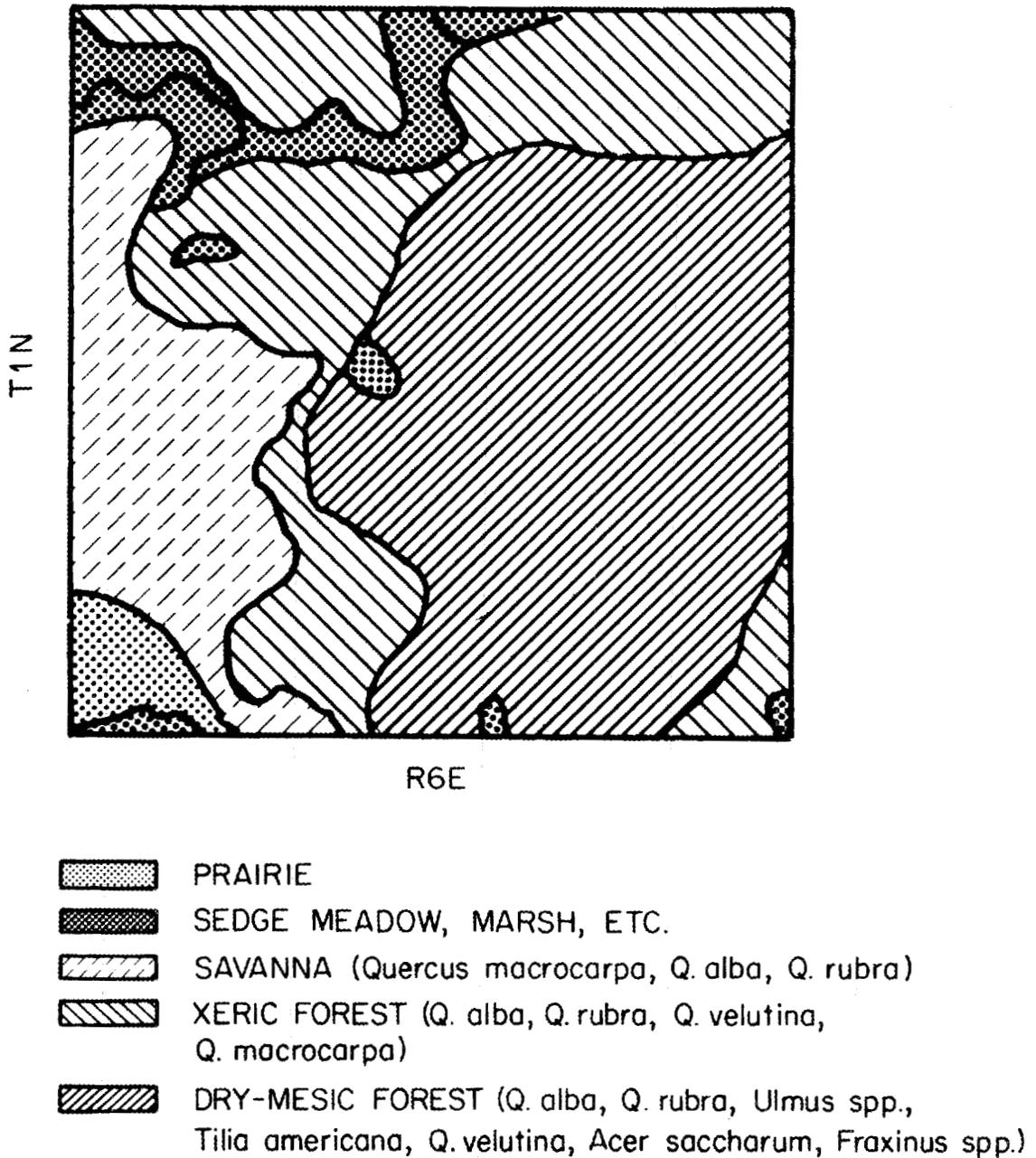


Figure 2.2. Presettlement vegetation in Cadiz Township, southern Wisconsin (from map by Finley 1976).

Field Methods

Vegetation Sampling

In 1983 Cadiz Township was gridded, on U.S.G.S. topographic quadrangles (map scale 1:24000), to a resolution of 100 m. The 1-ha grid cells coincide conveniently with conventional survey measures. Upland woodlots at least 1 ha in area were selected for study; smaller patches and wooded corridors less than 100 m wide were not included. In each woodlot, trees, shrubs, and ground cover were sampled using nested quadrats. For present purposes, further attention is restricted to the tree stratum. In general, each wooded grid cell contained 2 10x100-m transects (at 30- and 70-m positions in the cell); each transect comprised 4 10x25-m quadrats (Figure 2.3). An effort was made to sample all cells that were entirely forested, but this was not always feasible. Fractional cells (less than 50% wooded) were not sampled if they were vegetationally similar to adjacent sampled cells. In large woodlots where it was impractical to sample every cell, sampled cells were stratified throughout the woodlot. In some cases a single transect per cell was used so that more cells in a given woodlot could be represented. The total sample analyzed within the study area included 690 quadrats in 201 cells in 45 woodlots (Figure 2.4).

Bird Censuses

Breeding bird censuses were conducted in 42 woodlots from 25 May-7 July 1984 and in 45 woodlots from 2 June-3 July 1985. In

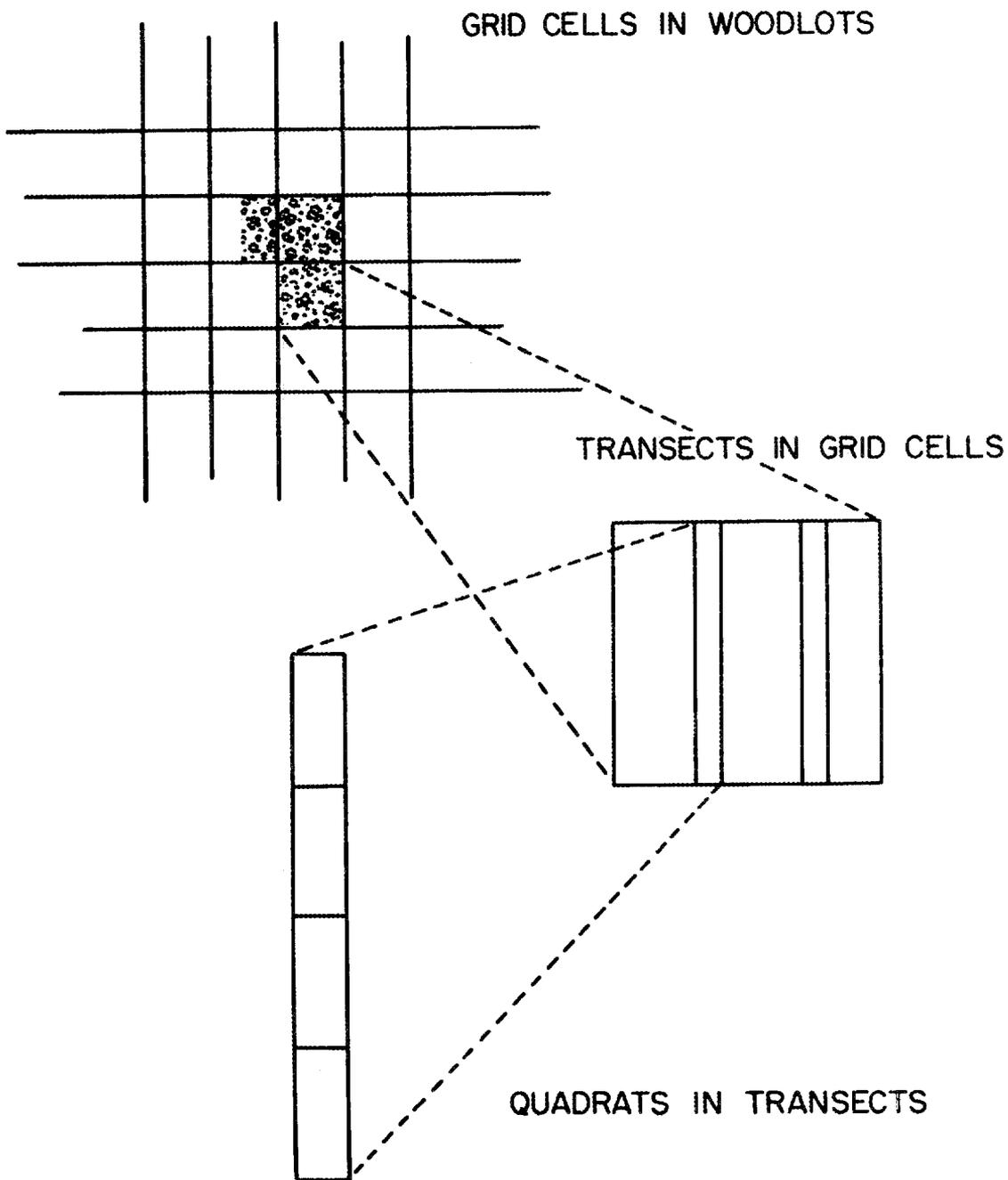


Figure 2.3. Scheme of nested 0.025-ha quadrats in transects in 1-ha grid cells, used to sample woodlots in Cadiz Township.

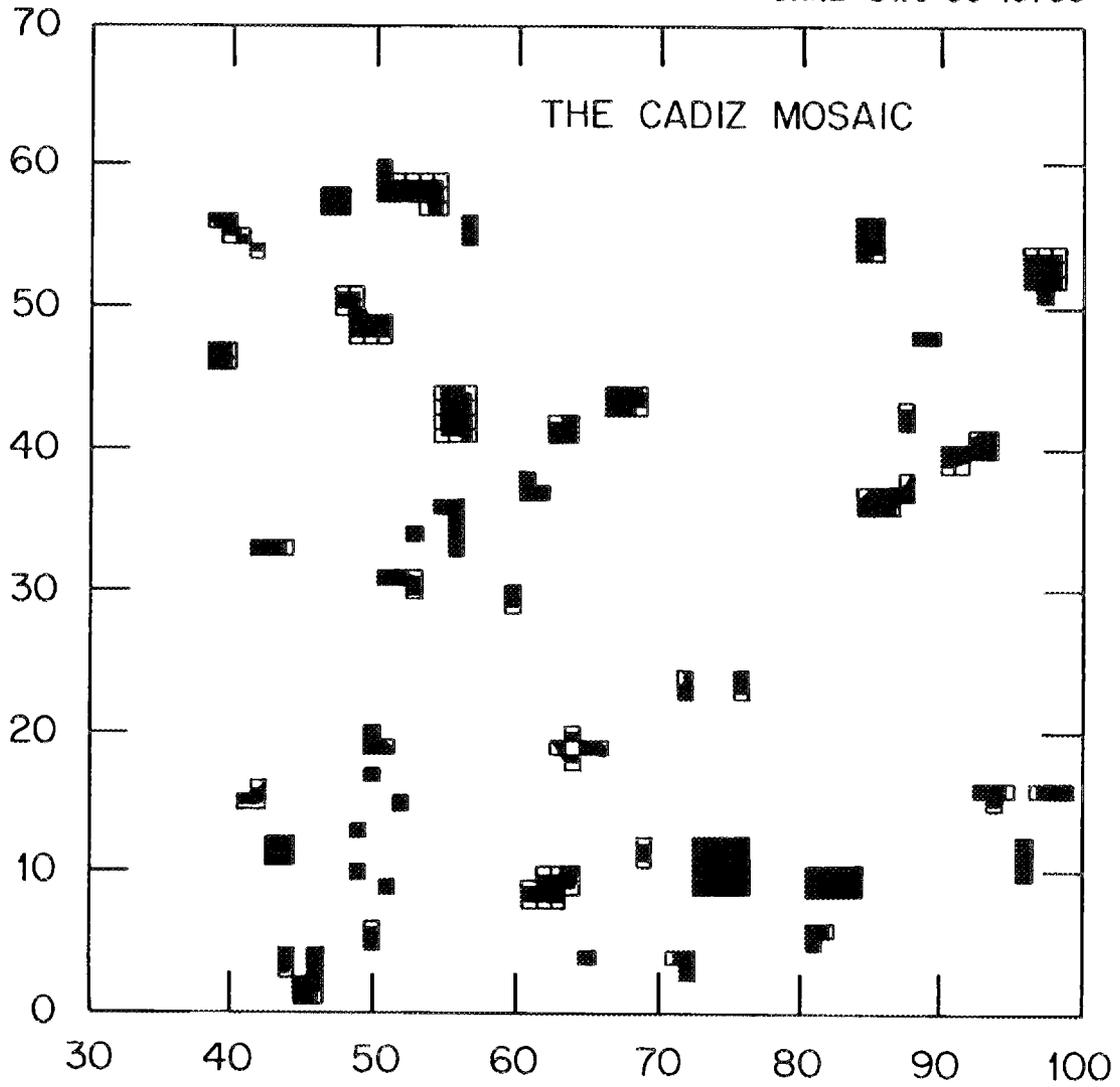


Figure 2.4. The Cadiz Township study area of 45 woodlots, overlain by 201 1-ha grid cells (grid coordinates originate in southwest corner of the township).

each year, a subset of woodlots was monitored daily during spring migration, and breeding censuses were deferred until the incidence of nonresident migrants had decreased to a level such that censused birds could be safely assumed to be breeding residents. The ending date in July was arbitrary, but after these dates the increasing incidence of fledged juveniles in censuses, decreased vocalization by breeders, and relaxed territoriality combined to degrade censuses. Visits to woodlots after early July were used to verify earlier census records but were not used for density estimates or territory maps.

Birds were censused using a lagged-cruise census that was developed during preliminary censuses in May 1984. This method is a hybrid of conventional cruise censuses and the point-survey method described by Whitcomb et al. (1981). Woodlots were cruised along transects aligned at midpoints of grid cells (i.e., at 100-m intervals); 15-minute lags (point surveys) were added at the beginning and end of each transect, as well as at any additional points that were difficult to census due to topography or structural heterogeneity. A minimum of 60 minutes was spent in each census, with additional effort proportional to woodlot area and/or heterogeneity. In censuses, all birds were recorded except nocturnal species, strictly nonforest species, and raptors. Woodlots were visited between from 0530-1030 hr in fair weather.

The lagged-cruise method represents yet another nonstandard census technique, but offered the advantage that census records were essentially complete after one visit. In verification tests, subsequent visits did not substantially improve censuses; nonetheless

each woodlot was visited at least twice. Moreover, the combination of point surveys with stratified cruises provided reasonable estimates not only of bird abundances but also their spatial locations within the woodlot (generally recorded to the nearest quarter-cell).

One prediction of the conceptual model of avian demography in a habitat mosaic is that species abundance patterns should vary somewhat from year to year, especially for uncommon species. Species turnover rates in woodlots support this prediction (Lynch and Whitcomb 1978). Consequently, it seemed appropriate to consider each year's census results independently. Because 1985 censuses represented more woodlots and were recorded with better spatial resolution than in 1984, this dissertation focuses on 1985 census data.

Forest Habitats in Cadiz Woodlots

The study area includes approximately 171 ha of upland forest in the 45 study woodlots (recall that this excludes riparian corridors and numerous very small patches). The median woodlot is 3.0 ha in size, with sizes strongly skewed toward smaller woodlots (Figure 2.5). Woodlots tend to be rectangular and their spatial configuration tends to reflect original land survey boundaries. The original parceling of land (ca. 1830, Curtis 1956) mandated that each parcel retain and preserve a proportionate area in forest (to provide fuelwood and fence posts). Consequently, remnant forest patches are small but abundant, and their spatial distribution over the landscape is largely irrespective of topography or soil type (Sharpe et al., in press). Relative to other landscapes that have been the focus of bird

The Cadiz Mosaic

Number of Woodlots: 45

Area in Upland Forest Patches:	Total	Core	Edge
Area (ha):	170.8	31.5	139.3
Percent of Total:		18.5	81.6

Patch Size Distribution:

Area:	1-2 ha	2-4 ha	4-8 ha	8-16 ha	16+ ha
N =	12	18	9	5	1
Median Patch Size:	3.0 ha				

Mean Nearest-Neighbor Distance Between Patches: 307 m

Figure 2.5. Spatial configuration of the Cadiz mosaic.

studies (Wisconsin: Ambuel and Temple 1983, Bond 1957, Brittingham and Temple 1983); New Jersey: Galli et al. 1976; Maryland: Lynch and Whigham 1984, Whitcomb et al. 1981), woodlots in Cadiz Township are smaller, more numerous, and closer together. Especially, the largest woodlot in the study area is only 16 ha, while most previous studies have included very large forest remnants (>100 ha).

Microhabitat Pattern

Major sources of microhabitat variation in the study area were identified by performing principal components analysis on 3 data sets collated to the quadrat level (.025-ha samples). The first data set consisted of structural variables, as stem tallies in 5 diameter classes (2.5-10, 10-20, 20-30, 30-60, and >60 cm). The second set consisted of species importance values for 21 major tree species, with

importance defined as the average of relative basal area and relative density for all stems larger than 10 cm. The third set included the structural as well as the compositional variables.

Most of the systematic variation in microhabitats at the quadrat scale was structural. Principal components of forest structure were readily interpretable in terms of the relative density of subcanopy, overstory, and understory trees; these 3 components accounted for 71% of the total variance in forest structure. In comparison, species composition showed no major patterns at this scale. Compositional components corresponded to each of the dominant tree species in the study area, but the first principal component accounted for less than 10% of the total compositional variance, and it required 18 components to account for 90% of the total compositional variance. When structural as well as compositional variables were included in the analysis (and standardized to weight the different variables equitably), the structural variables loaded heavily on each of the first 5 principal components.

The importance of microhabitat structure in these samples, of course, stems from the criterion of species-compositional homogeneity inherent in the delineation of the study area. This selection criterion has the further consequence of focusing subsequent analyses on forest structure, which is an important basis of microhabitat selection by forest birds (Hilden 1965; James 1971; see Chapter 4).

Bird Species Abundance Patterns

Censuses recorded 31 species that maintained residency in woodlots during the breeding season (Table 2.1). For future reference, this table also includes other forest species in the local species pool that were not recorded in woodlot censuses. This determination of the pool is rather subjective, as southern Wisconsin represents the edge of the geographical range of some species (e.g., Veery). Species composition was strongly biased toward edge species and habitat generalists (14 species of each). Reciprocally, forest interior species were especially rare: 3 species (Table 2.2). In particular, edge species accounted for 55% of total censused individuals, and generalists, 40%. Only 4% of total censused individuals were interior species. The scarcity of interior species is hardly surprising: if "interior" is defined as being more than 50 m from a forest edge, only 31.5 ha (18% of total forest area) qualifies as interior; if interior is defined as being more than 100 m from an edge, only 4 ha qualify. No forest habitat in the study area is more than 200 m from an edge. Importantly, the interior species recorded in Cadiz woodlots (Hairy Woodpecker, White-breasted Nuthatch, and Scarlet Tanager) are species that are relatively insensitive to forest fragmentation (Whitcomb et al. 1981). These species seem to prefer interior-like microhabitats, but these habitats need not be inside a very large forest tract.

Neotropical migrants comprised 9 of the species recorded in the study area, versus 11 permanent residents (Table 2.2). These totals

Table 2.1. Bird species censused in 45 woodlots in Cadiz Township, southern Wisconsin, in 1985, and the regional species pool.

BIRD SPECIES		HABITAT	MIGRATORY	NUMBER OF RECORDED	
CODE	AOU Common Name ¹	AFFINITY ²	STRATEGY ³	WOODLOTS	PAIRS
YBCu	Yellow-billed Cuckoo	G	NTM	2	2
RHWp	Red-headed Woodpecker	G	PR	31	34
RBWp	Red-bellied Woodpecker	G	PR	10	11
DWp	Downy Woodpecker	G	PR	25	30
HWp	Hairy Woodpecker	I	PR	7	8
Flik	Northern Flicker	E	SDM	31	38
PWp	Pileated Woodpecker	I	PR	0	0
Pewe	Eastern Wood-Pewee	G	NTM	36	44
AFly	Acadian Flycatcher	I	NTM	0	0
CFly	Great Crested Flycatcher	G	NTM	29	31
BJay	Blue Jay	G	PR	40	54
BCC	Black-capped Chickadee	G	PR	27	31
TTm	Tufted Titmouse	G	PR	0	0
WBN	White-breasted Nuthatch	I	PR	33	37
BGG	Blue-gray Gnatcatcher	G	NTM	0	0
Veer	Veery	I	NTM	0	0
WoTh	Wood Thrush	G	NTM	10	17
GCat	Gray Catbird	G	SDM	32	87
YTVi	Yellow-throated Vireo	G	NTM	1	1
REVi	Red-eyed Vireo	G	NTM	21	45
CerW	Cerulean Warbler	I	NTM	0	0
B&WW	Black and White Warbler	I	NTM	0	0
ARed	American Redstart	I	NTM	0	0
Oven	Ovenbird	I	NTM	0	0
CYt	Common Yellowthroat	E	SDM	9	9
ScTa	Scarlet Tanager	I	NTM	7	7
Card	Northern Cardinal	G	PR	37	56
RBG	Rose-Breasted Grosbeak	G	NTM	28	42
RST	Rufous-sided Towhee	G	SDM	1	1
wren	House Wren	E	SDM	39	178
BrTh	Brown Thrasher	E	SDM	18	24
YeW	Yellow Warbler	E	NTM	0	0
Bunt	Indigo Bunting	E	NTM	36	75
FSp	Field Sparrow	E	SDM	1	2
SSp	Song Sparrow	E	SDM	20	29
NOri	Northern Oriole	E	NTM	19	19
Dove	Mourning Dove	E	SDM	20	29
Robn	American Robin	E	PR	35	90
Star	European Starling	E	PR	32	114
CSp	Chipping Sparrow	E	SDM	1	1
Grak	Common Grackle	E	SDM	7	9
BHC	Brown-headed Cowbird	E	SDM	38	51

¹Common names according to AOU (1982); scientific names in appendix

²Habitat affinities are generalist (G), edge (E), or interior (I).

³Neotropical migrant (NTM), short-distance migrant (SDM), or permanent resident (PR).

Table 2.2. Bird species abundances in Cadiz woodlots, 1985, sorted according to habitat affinity and migratory strategy.

CATEGORY	SPECIES		INDIVIDUALS	
	POOL	CADIZ	NUMBER	PERCENT
HABITAT AFFINITY				
Habitat Generalist	17	14	486	40.3
Forest Interior	10	3	52	4.3
Forest Edge	15	14	668	55.4
MIGRATORY STRATEGY				
Permanent Resident	13	11	503	41.7
Short-distance Migrant	11	11	420	34.8
Neotropical Migrant	18	9	283	23.5

represent 50% of the local pool of migrants, versus 85% of the permanent residents. Note that migratory strategy and habitat affinities are not independent. Seven neotropical migrants are also interior species; of these, only the Scarlet Tanager was recorded in Cadiz woodlots. Nine of the 11 short-distance migrants recorded in censuses are edge species. The other short-distance migrants (Gray Catbird and Rufous-sided Towhee) are classified as generalists but prefer edge-like conditions (e.g., canopy gaps) within forests.

Of those species marked as sensitive to forest fragmentation (Ambuel and Temple 1983, Forman et al. 1976, Whitcomb et al. 1981), which include 10 species in the southern Wisconsin species pool, only 3 species, comprising 1% of total individuals, were recorded.

Restructuring of the Regional Avifauna

Relative to the avifauna of other mosaic landscapes, Cadiz probably represents an extreme example of the effects of forest fragmentation on a regional avifauna. A simple exercise will serve to illustrate the power of the constraints of habitat availability, accessibility, and factors affecting net reproduction to restructure the avifauna of a severely fragmented forest mosaic.

Consider three levels of response for each of the three constraints: positive, neutral, and negative. For habitat availability, these levels correspond to edge species, generalists, and interior habitat specialists. For habitat accessibility, far-ranging permanent residents, species of intermediate dispersal potential, and small neotropical migrants form three convenient response categories. Similarly, three crude categories of reproductive potential can be defined according to total reproductive effort and vulnerability to nest predation and parasitism (after Whitcomb et al. 1981). These three responses to the three constraints comprise 27 functional types of species, 20 of which are represented by at least one species in the pool of species inhabiting eastern deciduous forests.

The number of species and individuals were tallied for each of these types as censused in the Cadiz woodlots. For comparison, similar tallies were compiled and averaged over six extensive forest tracts throughout the eastern deciduous forest (census data compiled by Whitcomb et al. 1981). This composite served as a crude estimate

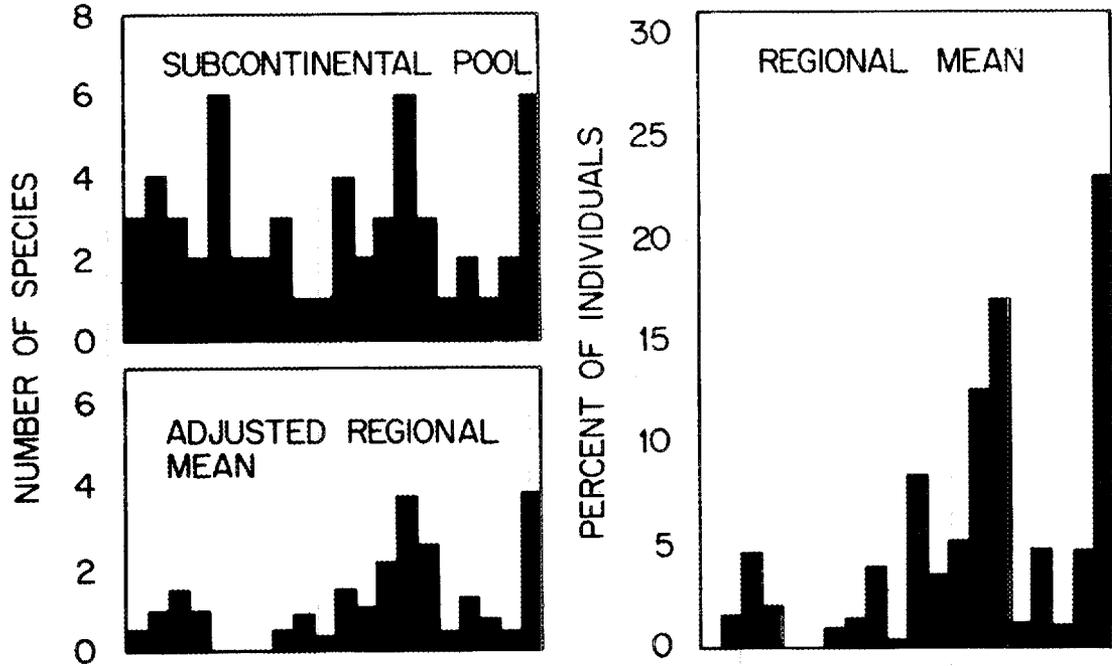
of the species composition of presettlement forest. The frequency distributions of species and individuals were arrayed to emphasize the change in species composition attendant with forest fragmentation: area-sensitive species at one extreme, edge species and disturbed-site species at the other extreme. The change from presettlement forest to the Cadiz landscape is quite striking (Figure 2.6).

Beyond being a rather telling illustration of the potential of the landscape context to act as shaping force on a regional avifauna, this figure suggests an important caveat for this study. It may emerge that the Cadiz avifauna is so degraded by the combined effects of forest fragmentation that the particular effects of the three constraints may not be detectable. In such cases, it would be helpful to have a means by which these effects could be assessed in landscapes intermediate in configuration to either the Cadiz or extensive forest landscapes. Simulation modeling provides a means to this end, as is developed in the following chapter.

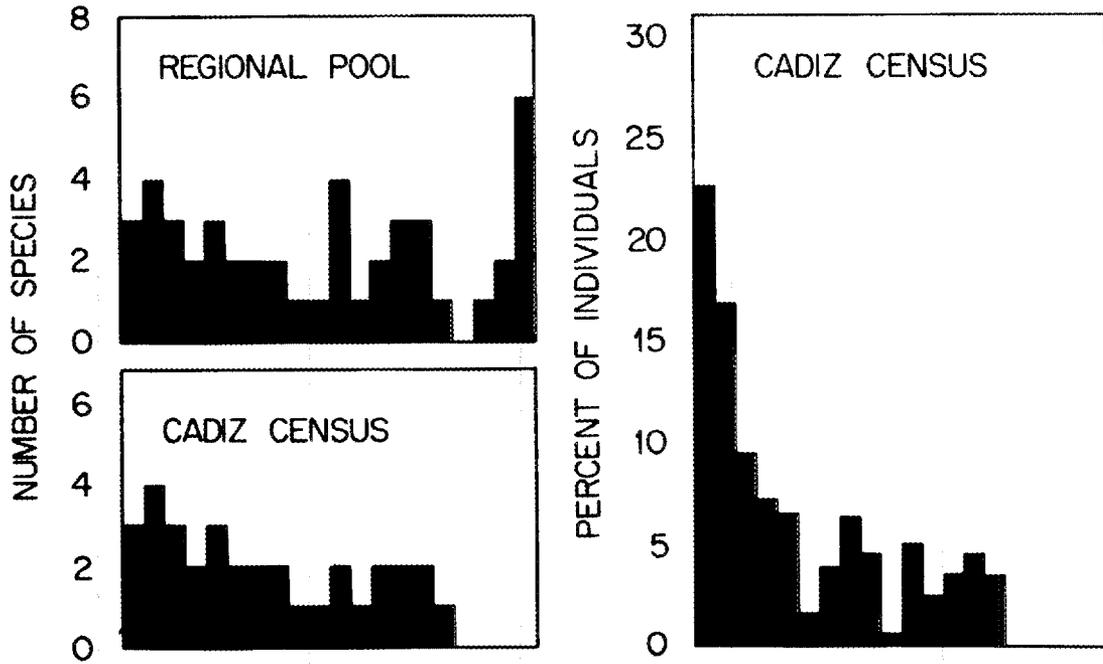
Figure 2.6. Restructuring of the Cadiz avifauna via forest fragmentation.

Categories are defined according to species response to habitat availability, accessibility, and net reproduction constraints (see text), arrayed from insensitive to sensitive (left to right). Top: extensive eastern deciduous forests, a composite from census data compiled by Whitcomb et al. (1981). Bottom: the Cadiz avifauna as censused in 1985.

EASTERN DECIDUOUS FOREST



SOUTHERN WISCONSIN



CHAPTER 3

DEVELOPMENT OF AN AVIAN DEMOGRAPHY SIMULATOR

Introduction

In this chapter the conceptual model of avian demography becomes a working hypothesis in the dynamical sense of the term: a computerized simulator. Use of the simulation model is motivated by several troublesome aspects of empirical approaches to landscape ecology. To account for species abundance patterns in a habitat mosaic requires data that are simultaneously detailed (censuses tally individual birds); extensive (for birds, "landscapes" are measured at least in km); and, if spatial pattern is to be considered, exhaustive (without gaps in the data base). Further, if temporal trends are of interest, the data records must be long-term. Obviously, such data are logistically difficult to collect. Models offer a means of extending or extrapolating beyond a data base.

Even given an extensive and detailed data base, data from a particular landscape are by definition artifactual: each landscape has its own geographic peculiarities and history. This makes it difficult to compare different landscapes because study areas of different spatial configuration should, in fact, support different bird species abundance patterns. The question is, how different? If all avian ecologists collected data that were strictly comparable (e.g., using the same census techniques and sampling design), generalizations would be easier--but the situation is not so idyllic.

A simulation model can generate census data that, while not real, resemble real data and are strictly comparable for different landscapes or different bird species.

Ideally, the importance of particular factors in determining bird species abundance patterns could be evaluated experimentally by manipulating the factor of interest while holding other potentially confounding factors constant. Unfortunately, direct manipulations either of birds' life-history tactics or of a landscape's spatial configuration are not really feasible. Even if one were so fortunate as to gather experimental evidence directly, or clever enough to control confounding factors indirectly (Wilcove 1985), the resultant data would still be subject to the first limitation: they would represent just one case. With the simulation approach it is possible to create new species as experimentally controlled combinations of life-history tactics. It is also possible to define experimental landscapes of any desired configuration. Thus, model experiments can be structured and replicated to satisfy the conditions of valid statistical inference. Again, the model-generated data may not be strictly realistic, but the degree of control and standardization of such data make the simulation approach appealingly useful.

It would be remiss not to acknowledge the myriad other approaches to modeling populations in patchy environments (see Levin 1976, Okubo 1980). These models can be partitioned into formulations that model the frequency of patches occupied by species (e.g., Cohen 1970, Levins and Culver 1971, Slatkin 1974), as compared to those that model population numbers explicitly (Levin 1974, DeAngelis et al. 1986),

with the latter typically featuring diffusion-reaction equations (Okubo 1980; Skellum 1951, 1973). These approaches have been concerned especially with the role of patchiness in stabilizing predator-prey systems (e.g., Caswell 1978, Hastings 1977, Hilborn 1975, Zeigler 1977) or competitor systems (e.g., Cohen 1970, Horn and MacArthur 1972, Levin 1974, Levins and Culver 1971). DeAngelis et al. (1979) likened a single species in a mosaic of habitat patches to a set of mutualistic populations (because the patches assist one another through dispersal), and used M-matrix analyses to derive criteria for persistence and stability for populations in habitat mosaics (see also DeAngelis et al. 1986). Fahrig et al. (1983; see also Lefkovitch and Fahrig 1985) used transition matrices to model within- and among-patch dynamics for mouse populations in constellations of woodlots. The avian demographics simulator described in this chapter is loosely based on Fahrig's model.

Any model is a simplification of reality, and the simplifying assumptions explicit in the model specify its domain of applicability. There is, of course, no single best modeling approach for the general problem of population dynamics in a patchy environment. The avian demographics simulator described here was developed to strictly parallel the conceptual model illustrated in Figure 1.3 (page 4). Because of its hierarchical structure, the model can be applied to a wide variety of situations without altering its basic assumptions or formulations.

The avian demographics simulator was developed to meet a number of objectives. Immediate research goals specified two essential

features of the model: it must provide a means to assess (1) different combinations of life-history tactics under the same set of landscape-scale constraints, as well as (2) the same set of life-history tactics under different constraints. Attendant with the former need is the further consideration that a given life-history tactic could be implemented independently of other tactics, so that the confounding intercorrelations among avian traits (Whitcomb et al. 1981) might be partitioned. It was especially desirable to implement life-history tactics via parameters that could be easily estimated with comparable accuracy for a large number of species.

The second essential feature of the model, that different landscapes provide for potentially different model behaviors, follows directly from the "mechanism in context" conceptualization illustrated in the first chapter. Because life-history tactics are implemented in the model as maximum potential behaviors (e.g., potential fecundity, potential dispersal), and then constrained (reduced) according to their spatial context, landscapes of different configuration can provide different constraints and thus elicit different demographic phenomena.

The salient feature of the model is that patch-level population dynamics can be investigated with the model by specifying various mechanisms (life-history parameters) or various contexts (landscape configurations), and that these factors can be manipulated experimentally. The remainder of this chapter details the development and implementation of the simulator, and illustrates typical model behaviors for a variety of bird species and landscape configurations.

The model is used to explore specific hypotheses in the following chapters.

Model Development

The computerized simulator is a rather detailed implementation that perhaps can be envisioned most appropriately as the translation of Figures 1.3 (page 4) and 1.4 (page 6) into FORTRAN. Fortunately, the details of implementation are not strictly necessary to appreciate the uses of the model presented here. What follows is an overview of the salient features of the simulator; the model is more completely documented in the appendices.

Model Structure

The model simulates annual natality, mortality, and dispersal for each individual bird, of each species, in each patch of a habitat mosaic. The essential biology simulated by the model is contained in three demographics subroutines; the bulk of the program performs bookkeeping tasks and generates summary statistics (Figure 3.1).

A bird species is defined by a suite of life-history parameters that reflect its habitat use, natality, dispersal, and mortality (Table 3.1). These parameters define the demographic mechanisms for a simulation. Parameter estimates for 42 bird species found in forests in the study area were collated primarily from Whitcomb et al. (1981) (Table 3.2). Longevity records were updated according to Clapp et al. (1983), Klimkiewicz et al. (1983), and M. K. Klimkiewicz (personal communication of Bird Banding Laboratory records). No attempt is made

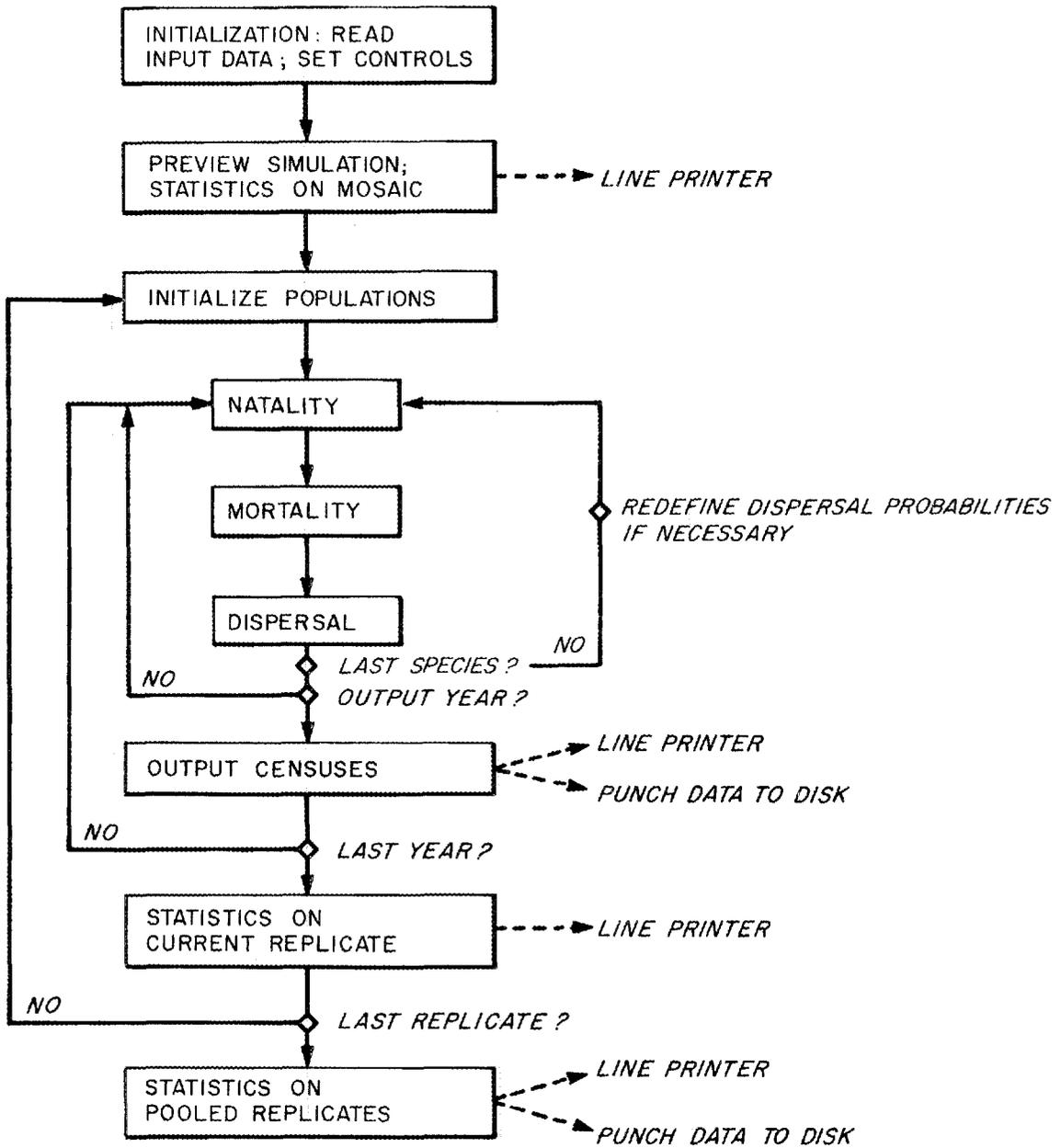


Figure 3.1. Schematic flow diagram for the avian demographics simulator.

Table 3.1. Definition of bird life-history parameters.

PARAMETER	DEFINITION
H Habitat Affinity	=0 if habitat generalist, =1 if forest interior, =2 if forest edge, =3 if field edge
TS Territory Size	Defended breeding territory, to nearest larger 0.5 ha
MBD Breeding Density	maximum density in intact forest, in males per 100 ha
XCS Mean Clutch Size	Eggs per clutch; in implementation, net clutch is .5 male x % successful
NB Number of Broods	Mean number of broods per season
P Predation	Sensitivity to nest depredation; =0 if canopy/cavity nester, =1 if canopy/open nester or low/cavity nester, =2 if understory/open, =3 if ground/open nester
BP Brood Parasitism	=0 if not a cowbird host, =1 if an occasional host, =2 if common host, =3 if preferred host
AGE Longevity	Maximum age (years) recorded for wild birds (excluding exceptional cases)
R Dispersal Range	Distance (m) a bird will disperse in a single move; increases with body size
M Mobility	Number of dispersal episodes before breeding begins; varies according to migratory strategy (=3 if neotropical migrant, =6 if short-distance migrant, =9 if permanent resident)

Table 3.2. Life-history parameters as estimated for 42 bird species found in southern Wisconsin forests.

SPECIES ¹	H	TS	MBD	XCS	NB	P	B	AGE	R	M
YBCu	0	2.0	17	2.55	1.0	1	0	10	5000	3
RHwp	0	1.5	56	4.50	1.0	0	0	9	7500	9
RBwp	0	1.5	29	4.50	1.0	0	0	9	7500	9
Dwp	0	1.5	21	4.06	1.0	0	0	9	2500	9
Hwp	1	2.0	10	4.08	1.0	0	0	10	7500	9
Flik	2	1.5	27	6.30	1.0	0	0	7	10000	9
PWp	1	4.0	1	2.00	1.0	0	0	15	15000	9
Pewe	0	1.5	24	2.75	1.0	1	2	11	5000	3
AFly	1	1.0	68	3.33	1.0	2	2	10	2500	3
CFly	0	2.0	17	4.80	1.0	1	0	12	5000	3
BJay	0	1.0	40	4.55	1.0	0	0	9	7500	9
BCC	0	1.0	39	5.95	1.0	1	0	6	2500	9
TTm	0	1.0	56	5.10	1.0	0	0	7	2500	9
WBN	1	1.5	20	6.22	1.0	0	0	7	2500	9
BGG	0	1.5	28	4.75	1.5	1	1	7	2500	3
Veer	1	1.0	42	3.33	1.0	3	2	9	5000	3
Woth	0	0.5	125	3.80	2.0	2	2	7	5000	3
GCat	0	0.5	198	3.80	2.5	2	0	6	5000	6
YTVi	0	1.5	25	3.12	1.5	1	3	8	2500	3
REVi	0	0.5	138	3.25	2.0	2	3	8	2500	3
CerW	1	0.5	83	3.33	1.0	1	1	9	2500	3
B&WW	1	1.5	27	6.17	1.0	3	1	10	2500	3
ARed	1	1.0	71	3.56	1.0	1	3	9	2500	3
Oven	1	0.5	114	4.67	1.0	3	3	8	2500	3
CYT	2	0.5	111	3.75	2.0	3	3	9	2500	6
ScTa	1	1.5	27	3.12	1.5	1	2	10	5000	3
Card	0	0.5	96	3.30	3.0	2	1	8	5000	9
RBG	0	1.0	75	4.00	1.0	2	1	9	5000	3
RST	0	1.0	68	3.75	2.0	3	3	8	5000	6
Wren	2	0.5	100	5.59	2.0	1	0	5	2500	6
BrTh	2	1.5	34	3.88	2.0	3	0	8	7500	6
YeIW	2	1.0	63	4.00	1.0	2	3	9	2500	3
Bunt	2	1.0	52	3.23	2.0	3	3	9	2500	3
FSp	2	0.5	80	3.67	3.0	3	2	5	2500	6
SSp	2	0.5	109	4.32	3.0	3	3	6	2500	6
NOri	2	1.5	10	4.59	1.0	0	0	8	5000	3
Dove	3	1.5	20	2.00	3.5	2	0	8	10000	6
Robn	3	0.5	122	3.80	2.5	2	0	7	7500	9
Star	3	0.5	200	5.30	2.5	0	0	7	7500	9
CSp	3	0.5	90	3.06	2.0	2	3	7	2500	6
Grak	3	1.5	10	4.45	1.0	0	0	10	10000	6
BHC	3	1.0	42	3.68	1.5	2	0	8	5000	6

¹See species codes in Table 2.1, page 24;
parameter codes in Table 3.1, page 36.

to justify these estimates as being definitive values for these species. Indeed, given the natural variability in these traits (geographically as well as among local individuals), there probably can be no definitive values for these parameters. For purposes of this dissertation, it is sufficient that the parameters assume biologically reasonable values.

A landscape mosaic is specified as an array of habitat patches, each described by its total area, edge area (a 50-m perimeter), and core (interior) area. Patch locations are provided as an array of inter-patch distances. Specifying these sets of parameters defines the constraining context for the simulation.

For each species, each patch has a carrying capacity determined by its habitat area and the average territory size of the species. Total patch area may be specified as usable habitat. Optionally, (1) species may be designated generalists (using total patch area) or edge species (using only a 50-m wide perimeter area); (2) species may be defined as generalists, edge species, or interior species (using only core habitat at least 50-m from an edge); or (3) area of potential breeding habitat per species per patch may be provided as input data, such as might be generated by a habitat simulation model (e.g., Smith et al. 1981). This last option is not used in this study.

Two territory sizes are used for each species: (1) minimum defended territory and (2) territory size estimated from maximum reported densities in intact forest. Defended territory size defines the minimum patch size that a species can occupy, which is proportional to but smaller than the area that maximum breeding densities would

suggest (e.g., Morse 1977). In the model, the smaller territory size allows a species to use small patches, while the larger territory size prevents the species from packing large woodlots at extraordinary densities. Birds are territorial "breeders" until carrying capacity is reached. Birds in excess of carrying capacity are nonterritorial nonbreeders ("floaters"). The model tracks males only (nested pairs), which is compatible with conventional census data records of territorial males. The state variables in the model are the numbers of breeders and floaters of each species, in each patch, as updated for each simulation year.

Model Demographics

In the course of a simulation year, (1) natality is computed for each breeder, (2) birds suffer "overwinter" mortality, and (3) survivors disperse in search of available territories. After dispersal, breeding and floating subpopulations are redefined, and the cycle repeats.

Potential fecundity is based on the average clutch size for a species and the average number of broods produced per breeding season. It is assumed that, as a rule, 60% of a typical clutch is successfully fledged by an open-nesting bird; this is a conventional estimate of the best an open-nester could do in the absence of undue nest depredation or brood parasitism (after Hann 1937). Fledging success is set at 66% for hole-nesting birds (Nice 1957). It is further assumed that half of a clutch is male, so base fledging success is 30% or 33% of a typical clutch for open- and hole-nesting

species, respectively. Breeding success may also vary according to the nesting habits of each species. Species that are hosts to brood parasitism may suffer reduced fledging success in edge habitats, and species subject to nest depredation (especially low, open-nesting species) may suffer total nest failures. Both brood parasitism and predation are implemented stochastically on a per-nest, per-bird basis (Figure 3.2a). Ambient intensities of brood parasitism and nest depredation are specified as model parameters.

Annual mortality is based on the assumptions that mortality is age-independent after the first year and that only 1% of the individuals of a species live to reach the maximum age for the species. The assumptions specify the annual survivorship expected on average for the species, and each bird lives or dies each year according to this probability (Figure 3.2b). First-year (juvenile) survivorship is set at 50% of the adult rate (Ricklefs 1969, 1972). Floaters may be subject to a proportionately higher rate of mortality, to reflect their displacement to "marginal habitat" (nonterritories). The relative survivorship of floaters as compared to breeders is specified as a model parameter, and as a default value is set at 50%.

Dispersal is stochastic, with the probability of dispersal between two patches defined by the distance between the patches relative to the maximum range of the species, and by the site fidelity of the subpopulation. Breeders have high site fidelity; floaters, low fidelity (Greenwood 1980, Greenwood and Harvey 1982). Thus, breeders tend to return to the same patch year after year, while juveniles (and other floaters) disperse away from their natal patch, within a radius

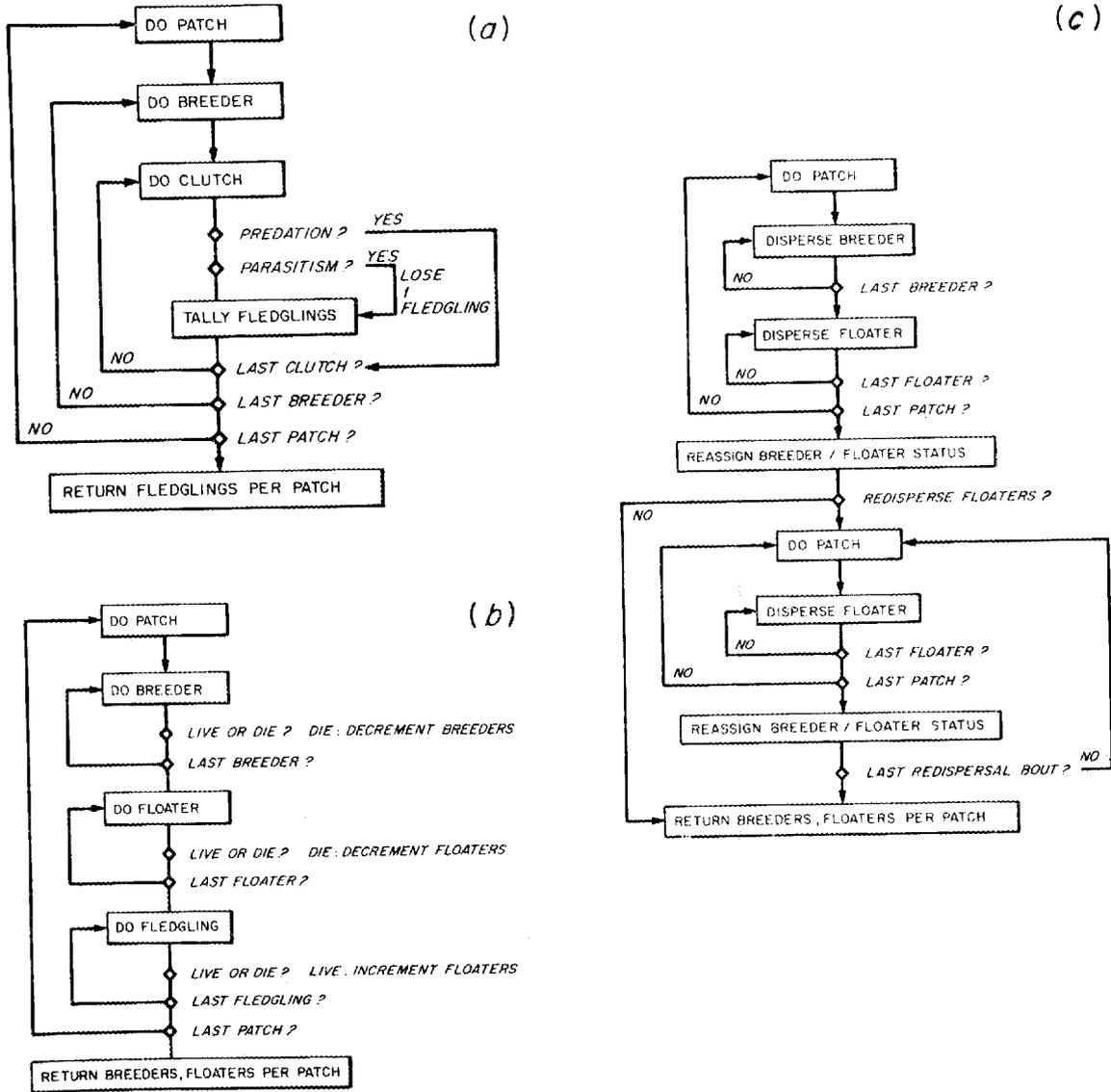


Figure 3.2. Flow diagrams for (a) natality, (b) mortality, and (c) dispersal routines in the avian demographics simulator.

defined by the range of the species. Each year, juveniles attempt to reoccupy their natal patch first, which is successful only if there are territories available. This effectively permits within-patch dispersal for large patches (which frequently have available territories), but forces between-patch dispersal for small patches (which typically have available territories only if a parent dies). Birds disperse according to two life-history parameters: range and mobility. Range indexes the maximum distance a bird is likely to fly in a single move, and generally increases with body size. Mobility defines the number of discrete moves a bird may make, and varies with migratory strategy (permanent residents have greater mobility). Thus, dispersal is modeled as a series of stochastic moves, as across stepping stones (Figure 3.2c).

Implementation

The simulator is written to be as general and versatile possible, so that a variety of hypotheses can be explored without making major changes in the model. To this end, the model includes a block of control parameters that collectively configure the simulator for specific applications. In its simplest structure the model is equivalent to a first-order difference equation in which base natality, mortality, and carrying capacity of the mosaic determine bird abundance. In more elaborate cases, the spatial complexity of the mosaic, edge effects, and other mechanistic details (specified as options) can provide for much more complex model configurations. Most of these optional details are automatically invoked by certain species

parameters (e.g., only cowbird hosts are subject to brood parasitism). Other control parameters are user defined (e.g., ambient intensity of brood parasitism). Applications use the simplest possible model configuration (combination of options) that will address a specific hypothesis.

There are two separate versions of the simulator: a "focal species" and a "multi-species" version. The former provides a vehicle to take advantage of the richness of natural history data available for some species, and generates greater detail in model output. The multi-species version sacrifices detail for generality; this version currently simulates the demographics of a 42-species pool.

Simulation Landscapes

A variety of artificial habitat mosaics were generated for use with the simulator. Each mosaic comprised a random number of circular patches in a 10-km square landscape. The number of patches varied normally between 15 and 65 (mean=40). Patches were of 8 discrete sizes on a doubling scale: 1, 2, 4, 8, 16, 32, 64, and 128 ha. The discrete sizes made it easier to analyze model results categorically by size. The size distribution was subjectively skewed (log-normally) so that most patches were small (1-8 ha), while very large patches were rare (some mosaics did not include any very large patches). Patch locations were determined by uniformly random grid coordinates. A total of 33 habitat mosaics were generated.

A habitat mosaic can be characterized by a number of measures that summarize its spatial configuration. Here, mosaics were indexed

according to the number of patches, total habitat area, the percent of this area in edge habitat, the percent in large refugia (patches larger than 40 ha), and the mean nearest-neighbor distance between patches. Most of the simulations focused on a subset of the available mosaics that represented the range of variation in these characters (Table 3.3). Some simulations were also based on the Cadiz Township study area (characterized in Figure 2.5, page 21).

Table 3.3. Spatial configuration of artificial landscape mosaics generated for use with the demographics simulator.

MOSAIC	PATCHES	AREA ¹ (ha)	% EDGE ²	% REFUGE ³	NND (m) ⁴
ML #4	20	374	32.8	51.3	977
ML #7	25	149	59.7	0.0	956
ML #9	30	379	38.8	33.8	741
ML #19	44	469	41.7	40.9	522
ML #26	51	379	55.3	0.0	567

¹Total area of habitat patches

²Based on 50-m wide perimeter

³Area in patches larger than 40 ha

⁴Mean nearest-neighbor distance

Simulations

Because the model is stochastic, each simulation realizes a possible, but not necessarily an average result. To assess average model behavior under a specified scenario, 10 replicates were run for each scenario. The first replicate was saved as a representative result (hereafter, "exemplar"). Averages of 10 runs were used to

describe general trends. Each replicate simulated 30 years, which was sufficient time for any population trends to be clearly established.

Simulations were initiated with populations at 50% of the total carrying capacity of the mosaic. These initials were located randomly within available habitat patches, with only breeders in the population (no floaters). New initial populations were used for each replicate simulation.

Illustrative Simulation Results

The simulator is applied to specific hypotheses about avian demography in subsequent chapters, but it will be helpful to first demonstrate the range of behaviors that can be simulated by the model. These simulations are not meant to be inferential about any particular hypotheses. The first examples are focal-species simulations, and depict (1) consequent population dynamics for different species in the same landscape context, (2) dynamics for the same species in different landscape contexts, and (3) population dynamics as witnessed at the scale of the habitat patch and at the scale of the entire mosaic (the metapopulation).

In multi-species applications the simulator generates "censuses" of breeding birds, per species, per habitat patch, per simulation year. This represents a potentially overwhelming volume of model-generated data, which generally must be subsampled or otherwise edited before analysis. Where specific hypotheses are evaluated, model-generated data are filtered according to the criterion in question. Here, summary examples illustrate two trends in

multi-species assemblages: (4) trends in the relative abundance of neotropical migrants, and (5) the relationship between patch area and the number of resident bird species.

Different Species in the Same Context

Each bird species is specified by a unique set of life-history parameters, which define its mechanistic demographics in the model. Because each species responds individually to the constraints provided by a particular landscape, different species in the same landscape may exhibit qualitatively different dynamics. Two extreme examples are the Red-headed Woodpecker and the Ovenbird. (It should be emphasized again at this point that the simulated species may not correspond exactly to their nominal counterparts, so the following examples should not be overinterpreted.)

The woodpecker is a habitat generalist, a hole nester, and a permanent resident; as such it is relatively immune to the effects of forest fragmentation. The warbler, conversely, is perhaps an archetypal example of a sensitive species. These two species exhibit markedly different dynamics in the same mosaic landscape (Figure 3.3, in which metapopulations are averages of 10 replicates; mosaic labels refer to Table 3.3). The woodpecker increases slightly over 30 years, with a great deal of variation among replicates (reflecting the small population size). The Ovenbird population declines rapidly toward zero.

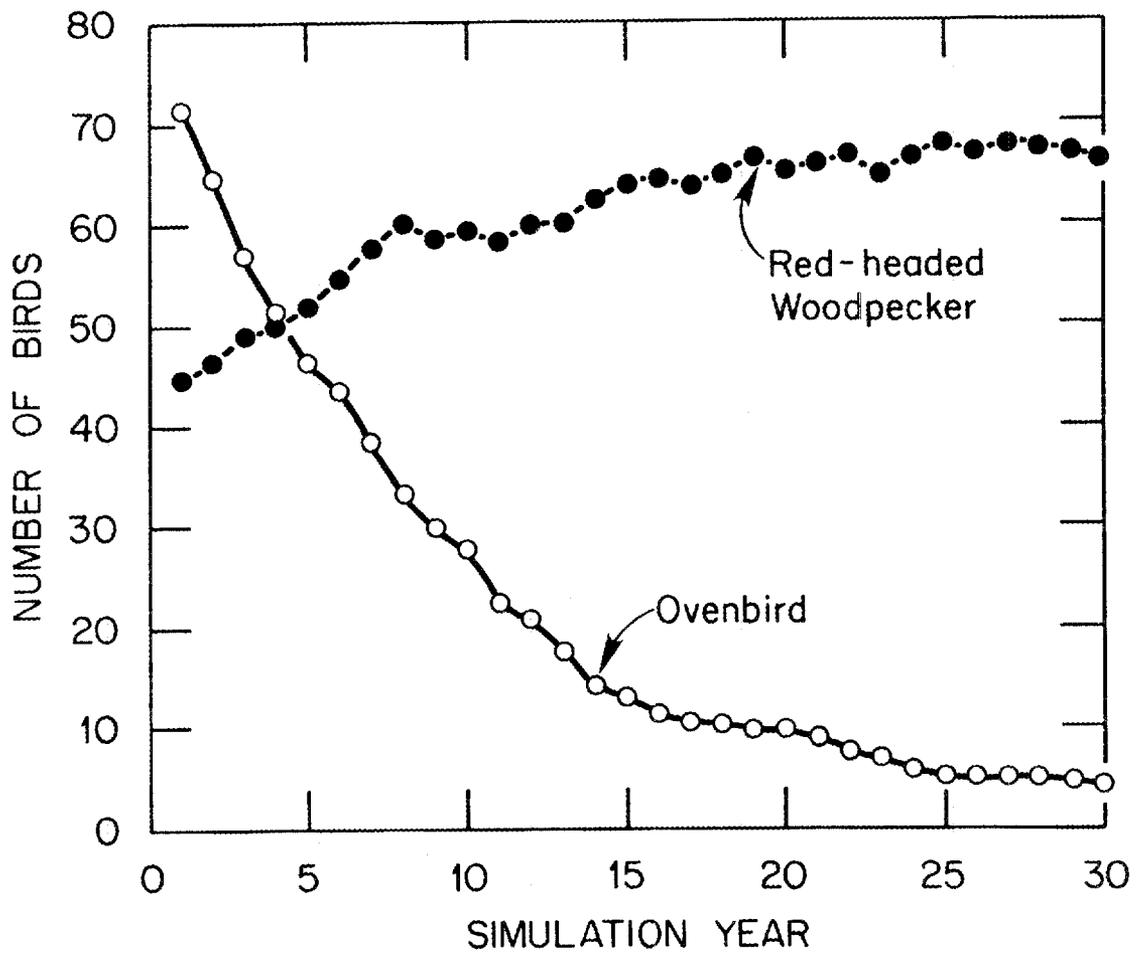


Figure 3.3. Simulated metapopulation dynamics of 2 species in a mosaic of 25 habitat patches.

The Red-headed Woodpecker is tolerant of forest fragmentation; the Ovenbird is a sensitive species.

The Same Species in Different Contexts

A given mosaic landscape provides a potentially unique context for avian demography. Edge effects on natality, for example, would be much more pronounced in a mosaic of many small patches than in one with a few larger patches. Isolation effects in dispersal would be more likely to develop in a sparse mosaic than in one with high patch density. For a species sensitive to the effects of forest fragmentation, the spatial configuration of a landscape can determine species abundance patterns observed in the mosaic. This result is illustrated for the Red-eyed Vireo as parameterized in Table 3.2. The 2 mosaics are equivalent in total habitat area (374 and 379 ha, see Table 3.3), but mosaic #4 includes 2 large patches while mosaic #26 has a larger number of small patches. The simulated species shows qualitatively different dynamics in the 2 landscapes (Figure 3.4). This evokes the idea of the "ecological trap" of Gates and Gysel (1978): a species attempts to nest in small patches of apparently usable habitat, but cannot successfully breed; the small patches are a drain on the local metapopulation. This notion is pursued in Chapter 6.

Patch-Level Populations and the Metapopulation

Population dynamics can be examined at the scale of the individual patch or for the entire habitat mosaic. In most cases, populations in patches fluctuate considerably through time, while

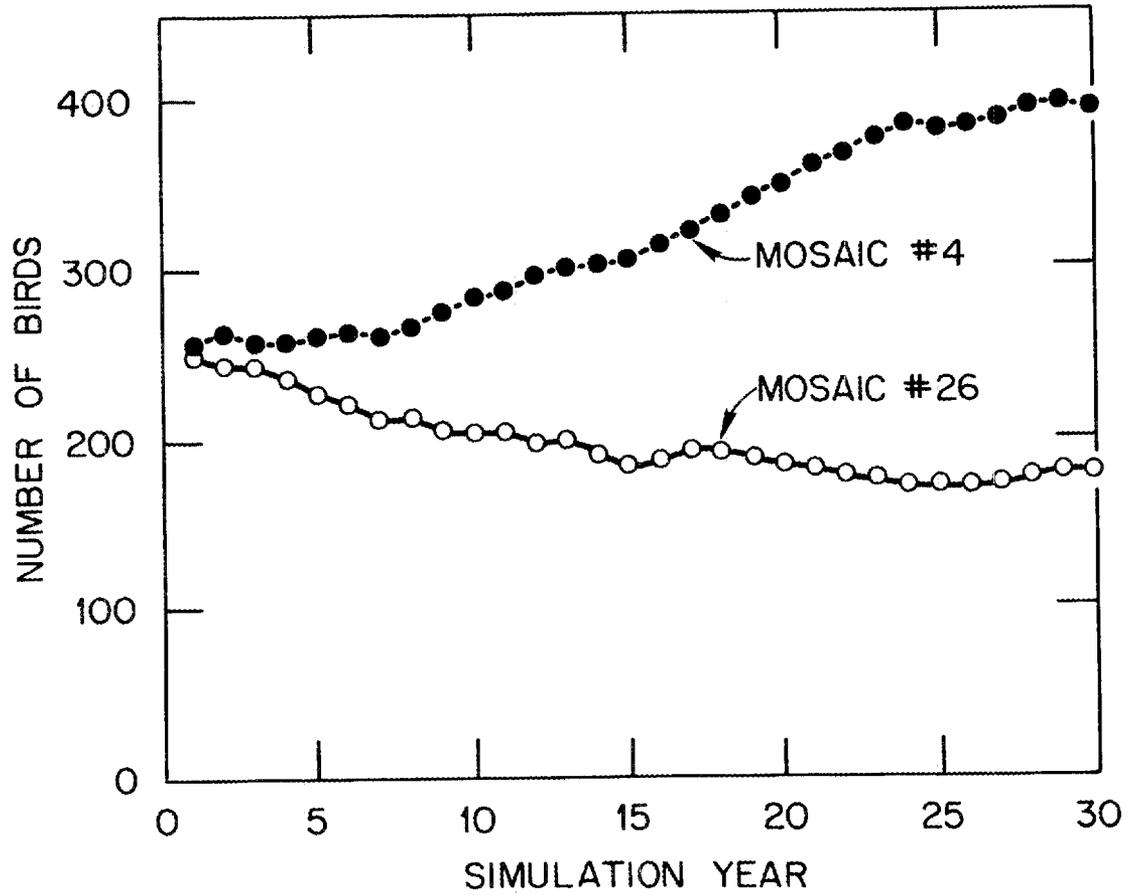


Figure 3.4. Simulated metapopulation dynamics for a species moderately sensitive to forest fragmentation, in 2 different landscape contexts.

Mosaic #4 includes 2 large reserves and is 33% edge, mosaic #26 has no reserves and is 55% edge.

metapopulation dynamics are comparatively damped (Figure 3.5, an exemplary result for the Red-headed Woodpecker). This largely reflects the averaging effect of numbers: smaller populations fluctuate more than larger populations. In some cases, population dynamics may be qualitatively different in patches as compared to the metapopulation. For a species undergoing a general decline in abundance, many patches quickly lose their populations (especially small patches), while a few patches remain self-sustaining; the metapopulation integrates these patch-level dynamics as a slow, asymptotic decline (Figure 3.6, an exemplar for the Red-eyed Vireo).

Incidence of Neotropical Migrants

Neotropical migrants are an appropriate summary focus because migratory strategy is correlated with a number of other life-history tactics that seem to confer sensitivity to forest fragmentation (Whitcomb et al. 1981). In model simulations, a general decline in abundance of migrants (as percent of total individuals) is generally evident (Figure 3.7, an exemplar). A mosaic with proportionately more area in very large patches retains a higher percentage of migrant birds in simulations, but the qualitative decline is similar.

Species/Area Relationships

The relationship between habitat area and bird species richness is central to this study, so it is appropriate here to illustrate the species/area relationship as generated by the simulator. As an example, demographics were simulated for 42 species in a mosaic of

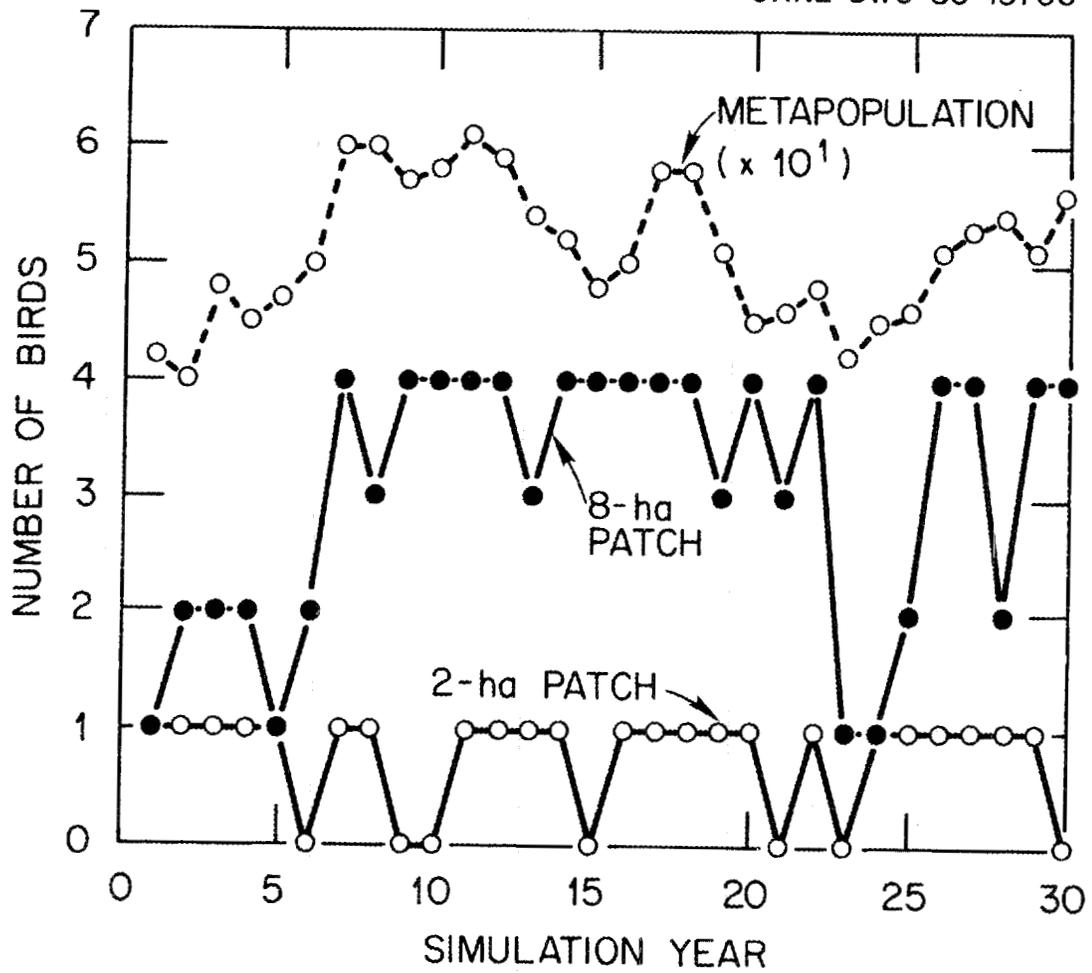


Figure 3.5. Simulated population dynamics for a species insensitive to forest fragmentation, as witnessed at the scale of individual 2-ha and 8-ha patches, and the metapopulation.

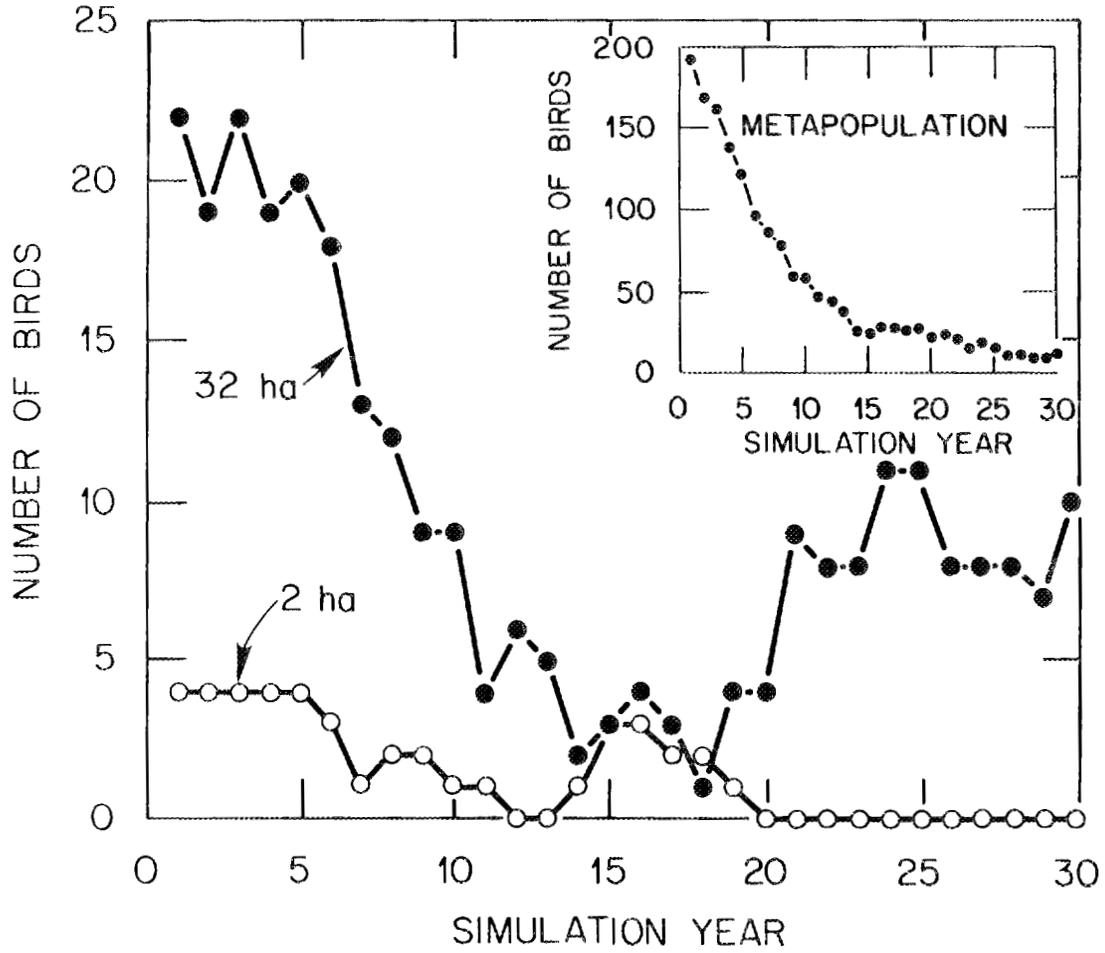


Figure 3.6. Simulated population dynamics for a species undergoing a gradual decline in abundance, as witnessed at the scale of individual 2-ha and 32-ha patches, and the metapopulation (inset).

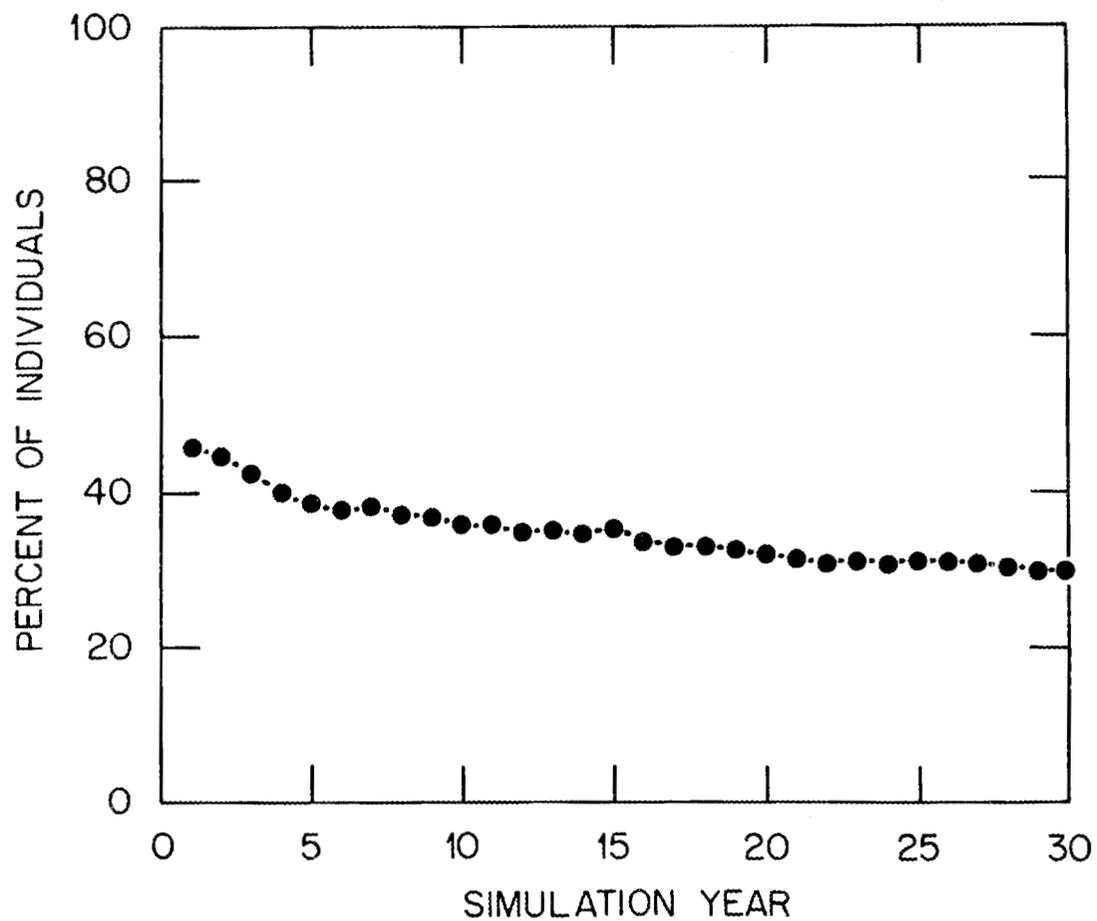


Figure 3.7. Incidence of neotropical migrants in metapopulations supported by a mosaic of 25 patches.

44 habitat patches ranging in size from 1 to 128 ha (mosaic #19, Table 3.3). Species richness was tallied in the final year of a 30-year simulation, and these tallies were averaged over 10 replicates. The species/area relationship is quite apparent (Figure 3.8). In real forest patches, this areal dependency reflects (at least) microhabitat variety, edge effects and biotic interactions, dispersal effects, and the size and persistence of the breeding population. The model incorporates each of these factors except microhabitat variety. In the following chapters, the relative contribution of each of the factors in the model is assessed directly, via model experiments. The importance of microhabitat variety is inferred indirectly by noting the extent to which the factors in the model fail to generate realistic results.

Model Adequacy and Reliability

The simulation results presented in this chapter were selected to illustrate model capabilities, and while these examples are appealingly realistic, it is important to address the limitations of the model. The applicability of a model can be assessed in terms of (1) behaviors that are shared by the model and the system being modeled, (2) behaviors the system exhibits but the model does not reproduce, and (3) behaviors produced by the model but not exhibited by the real system (Cale et al. 1983, Mankin et al. 1975). For present purposes these might be loosely translated as (1) things the model does correctly, (2) real things the model cannot do, and (3) unrealistic things the model does. Model "adequacy" increases as

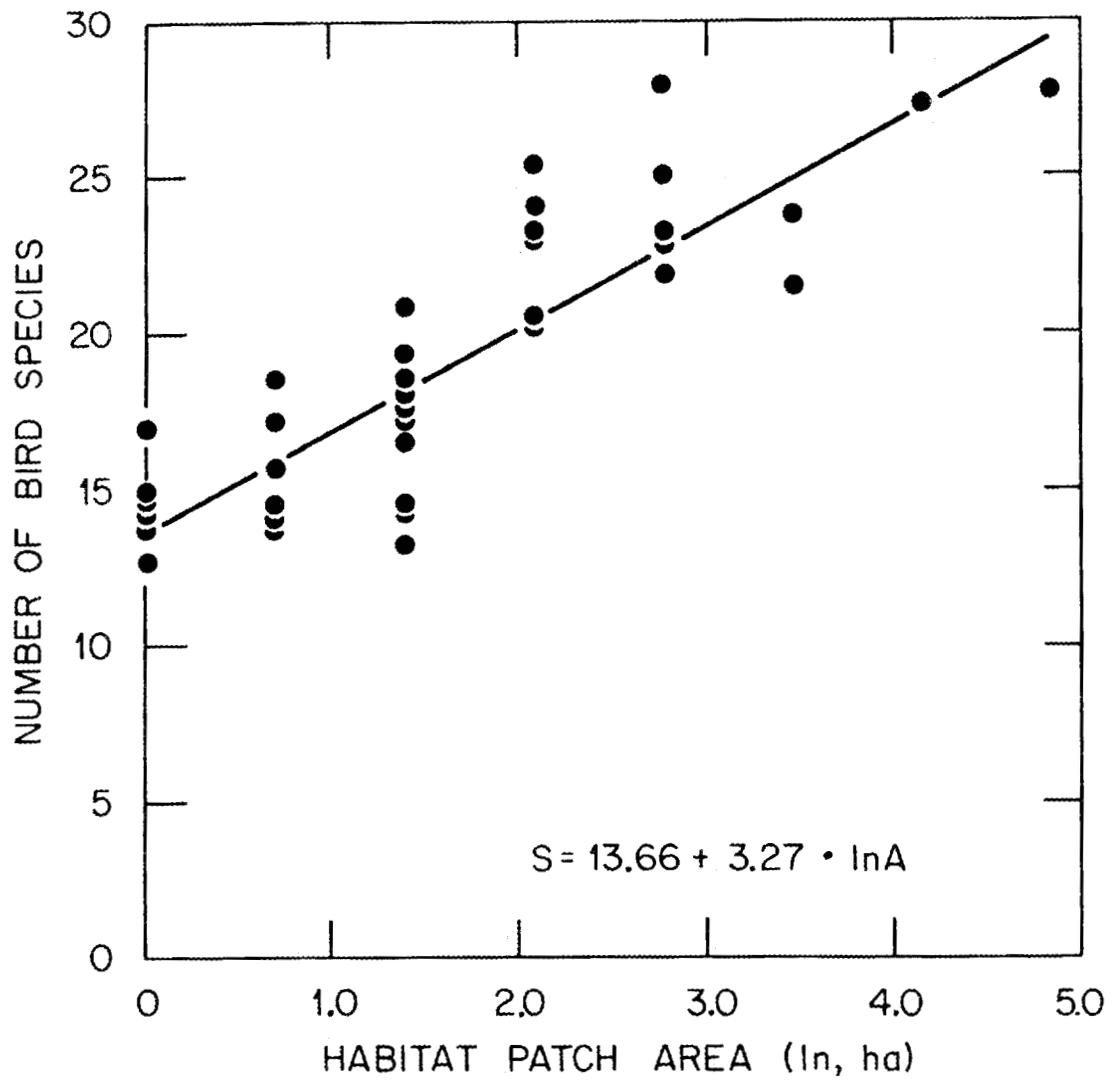


Figure 3.8. Simulated species/area relationship for a mosaic of 44 habitat patches ranging 1-128 ha in size.

(1) increases relative to (2); model "reliability" increases as (3) decreases relative to (1) (Cale et al. 1983, Mankin et al. 1975). Obviously, the ideal model would be very adequate as well as reliable, but a model can be useful even if it is not ideal. It is important, however, to determine the domain of applicability of the model so it is not used beyond its limitations.

Unfortunately, the adequacy and reliability of a model can only be established by using the model. In application, the more trials a model meets successfully, the better its adequacy and reliability are established. Even casual consideration of the demographics simulator reveals a wealth of biological detail that has not been included. The model is clearly not adequate for every purpose. Still, the simulator was written to be versatile, and results illustrated in this chapter suggest that the model is adequate for the variety of applications considered in this dissertation.

Of greater concern here is model reliability, whether model output is sufficiently realistic. It is instructive to partition unrealistic model behaviors into random errors and systematic bias. Random errors arise from such sources as uncertainties in parameter estimates. Certainly, estimates of avian life-history parameters are subject to this sort of error. Importantly, if these errors are random with respect to species (no taxa is systematically overestimated or underestimated), then consequent error in model output can be statistically controlled. In evaluating specific hypotheses, this control is effected by testing model output against other model output. Such applications are examples of model

experiments, in which one parameter is varied while controlling other parameters. Random errors in the model are thus incorporated into the statistical design and assessed accordingly. This approach is used in Chapters 5 and 6.

Systematic bias in model behavior may arise if the conceptualization (model structure) or formulations (state equations) are insufficient or simply incorrect. Clearly, the demographics simulator is insufficient in that the details of microhabitat utilization and breeding behavior of forest birds are not included. Systematic bias, while somewhat frustrating to the modeler, can be of great heuristic value because it provides strong inference about the importance of aspects that were not included in the model. We learn from our mistakes. This approach is used in Chapters 6 and 7.

CHAPTER 4

HABITAT AVAILABILITY AND BIRD SPECIES DISTRIBUTION

Introduction

Microhabitat has long been a focus of avian autecology and community ecology (Anderson and Shugart 1974; Cody 1968, 1981, 1985; Hilden 1965; James 1971; Wiens 1969, 1974; Willson 1974). Such studies, particularly when couched in terms of resource partitioning (Schoener 1974), have been successful in large measure because of the fundamental importance of microhabitat to bird ecology. In this chapter this importance is translated upscale, from the microhabitat encompassed by the breeding territory of an individual bird, to the bird community supported by a forest stand, and finally to the role of microhabitat availability in effecting bird species abundance patterns at the landscape scale.

Microhabitat Selection in Avian Autecology

A typical forest bird defends a breeding territory that provides the basic requirements for nesting and feeding. Thus, "habitat" encompasses other niche dimensions (e.g., trophic dimensions), and can be considered a fundamental resource base for forest birds, sensu Grinnell (1917) or Hutchinson (1957) (see Cody 1985).

In general, forest birds select breeding habitat on the basis of proximate cues reflecting gross vegetation structure (Hilden 1965, James 1971, Klopfer 1965; but see Robinson and Holmes 1982).

James (1971) coined the term "niche gestalt" to refer to the characteristic vegetation profile associated with the breeding territory of a particular species (Figure 4.1). The niche gestalt has been a useful construct in avian ecology because it can be readily quantified with simple measures of vegetation structure and multivariate statistical techniques (James 1971).

Several studies have demonstrated that microhabitat affinities of birds are fine-grained (resolved on a spatial scale of about 0.1 ha or less), and when not over-interpreted statistically (see Capen 1981), both useful and real. Here, "real" means that different studies of the same species usually produce comparable microhabitat descriptions (Noon et al. 1980). "Useful" implies that measures of vegetation structure are often sufficient to account for the distribution of bird species in heterogeneous habitats (Cody 1968, 1981, 1985; James 1971; Wiens 1969, 1974).

Territory size generally is inversely related to resource availability, in that rich habitats support smaller territories than less productive habitats (Stenger and Falls 1959). However, Smith et al. (1982) found that measures of vegetation structure were better predictors of Ovenbird territory size than were actual estimates of food resource availability. They suggested that, because the abundance of prey items varies considerably both within and between breeding seasons, vegetation structure might serve as a more consistent index of site quality. Thus, birds fare better in the long run by relying on proximate cues to habitat quality. This is

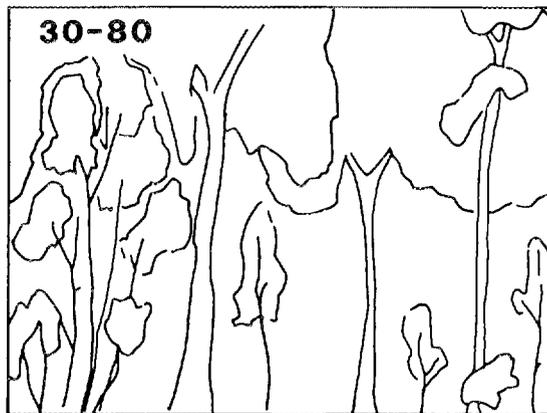
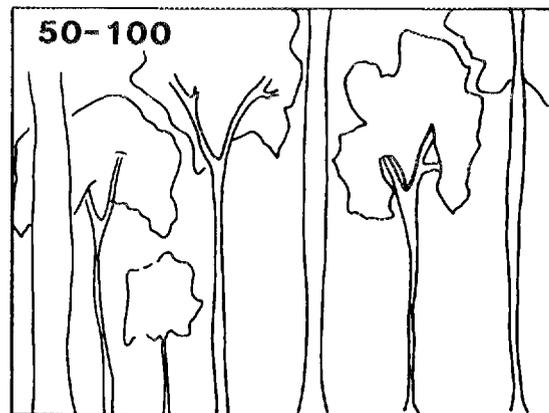
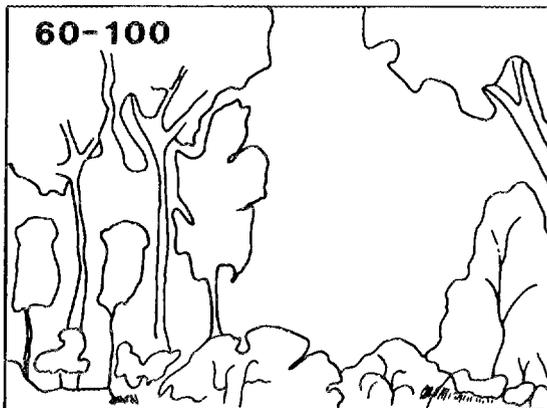
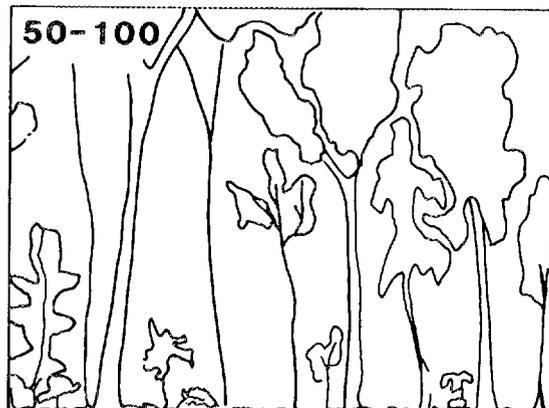
THE NICHE GESTALT**RED-EYE VIREO****BLACK-AND-WHITE WARBLER****HOODED WARBLER****OVENBIRD**

Figure 4.1. Niche gestalts for 4 forest bird species, representing the characteristic vegetation profiles of their breeding territories (redrawn from James 1971).

consistent with Hilden's (1965) discussion of proximate cues, and further underscores the importance of microhabitat structure in avian autecology.

Microhabitat Pattern and Bird Community Structure

At the level of the forest stand, bird species diversity is strongly related to the variety and relative abundance of microhabitats encompassed by the stand. This relationship was established empirically by MacArthur, who found bird species diversity to be linearly related to an index of foliage height diversity (MacArthur and MacArthur 1961, MacArthur et al. 1962). Roth (1976) has provided an insightful discussion of the relative role of horizontal and vertical components of patchiness in effecting bird species diversity.

Urban and Smith (in review) used a forest simulation model to assess the relationship between forest microhabitat pattern and bird community structure at scales not directly accessible empirically. This study analyzed assemblages of randomly generated, hypothetical bird species, so that community-level patterns obtained were a consequence solely of microhabitat availability rather than of bird biology. Because this emphasis on microhabitat availability is especially pertinent here--it motivates much of the remainder of this chapter--it is appropriate to discuss these results in some detail.

Smith developed a gridded version of a forest simulation model (Shugart and West 1977) that is capable of simulating large tracts of forest while retaining the fine-scale details of forest structural

dynamics (Smith and Urban, in prep.). Urban and Smith (in review) used the model to simulate a 9-ha stand of east Tennessee forest, as a 30 x 30 grid of 0.01-ha cells. The modeled stand was spatially explicit to a scale of 0.01 ha, and was sampled exhaustively with 0.04-ha quadrats (4 grid cells square). Each quadrat was analyzed as a microhabitat sample. The stand was simulated for 750 years and was sampled at 50-year intervals, generating a microhabitat sample of 225 quadrats over 15 sample periods, or 3375 total quadrats.

Principal components analysis summarized the major patterns in forest structure, in terms of stem densities in 5 diameter classes. The first two principal components reflected trends in understory versus overstory tree density. These two axes were used as a framework in which to illustrate patterns in forest bird communities.

The "bird species" in this study were randomly generated ellipses in a 2-dimensional "habitat space" defined by understory and overstory tree density (the first two principal components of habitat structure). Bird species abundance patterns were analyzed by tallying, in each sampling period, the number of microhabitat quadrats that satisfied the simulated habitat preferences of the various species (i.e., by falling within the habitat ellipse of a species in principal component space). For an illustrative analysis of real forest bird niches in principal component space, see Sherry and Holmes (1985).

Successional Patterns

The forest simulation emphasized the increase in microhabitat diversity in secondary succession, and the steady-state pattern of microhabitats maintained in mature forest (Figure 4.2). In succession, microhabitats become increasingly dissimilar to one another because of differences in species composition, growth rates, and the stochastic in-seeding and mortality of individual trees. As the microhabitats become more dissimilar, they collectively satisfy the habitat selection criteria of more and more bird species. This seral increase in microhabitat diversity accounts for the characteristic increase in species richness through time (Figure 4.3).

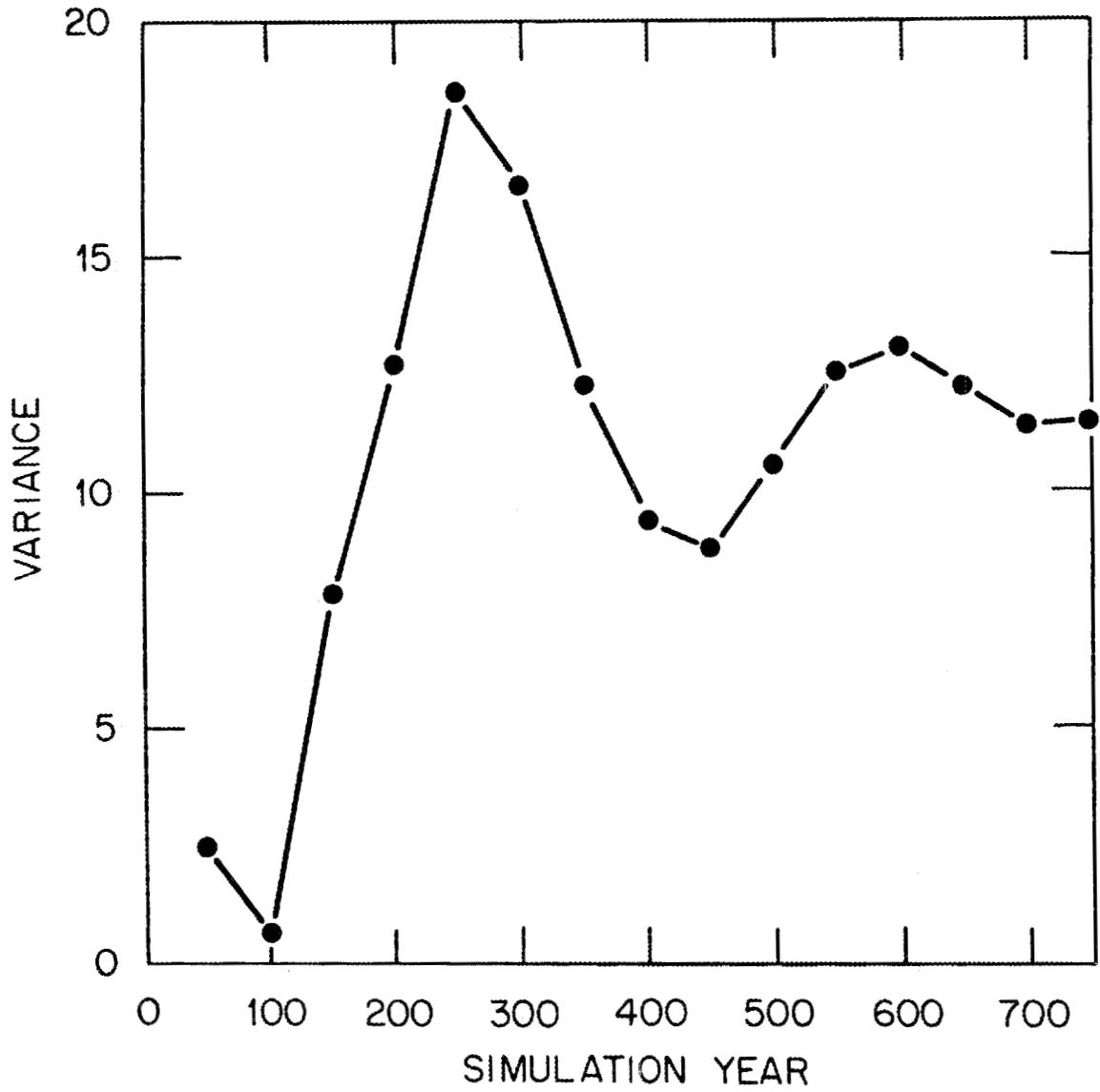
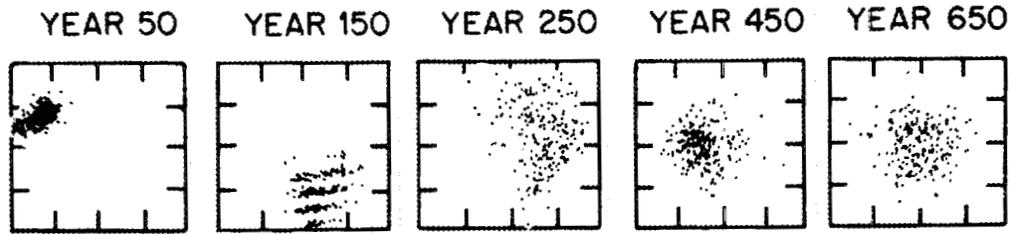
Because microhabitat variety is low in early succession, species whose preferred habitat is represented at all are generally represented abundantly. Thus, there is high numerical dominance by a few species initially. As microhabitat variety increases later in succession, species dominance decreases and equitability increases accordingly (Figure 4.4).

Microhabitats change rapidly in early succession because saplings and small trees change more quickly in stature than do large trees, so the rate of change in forest structure decreases with successional age (Smith and Urban, in review). Bird species turnover rates reflect this, with high turnover early in succession. In mature forests approaching steady-state, fine-scale microhabitat dynamics continue to elicit an appreciable turnover in species occurrence (Figure 4.5).

Figure 4.2. Temporal patterns in variation in forest microhabitats, as simulated for 750 years of succession.

Insets: statistical distributions of 225 sample quadrats at 5 sampling periods, in principal component space defined by understory density (PC I) and overstory density (PC II). Variance is indexed as area of 95% confidence ellipses about these distributions, for each of 15 sampling periods (from Urban and Smith, in review).

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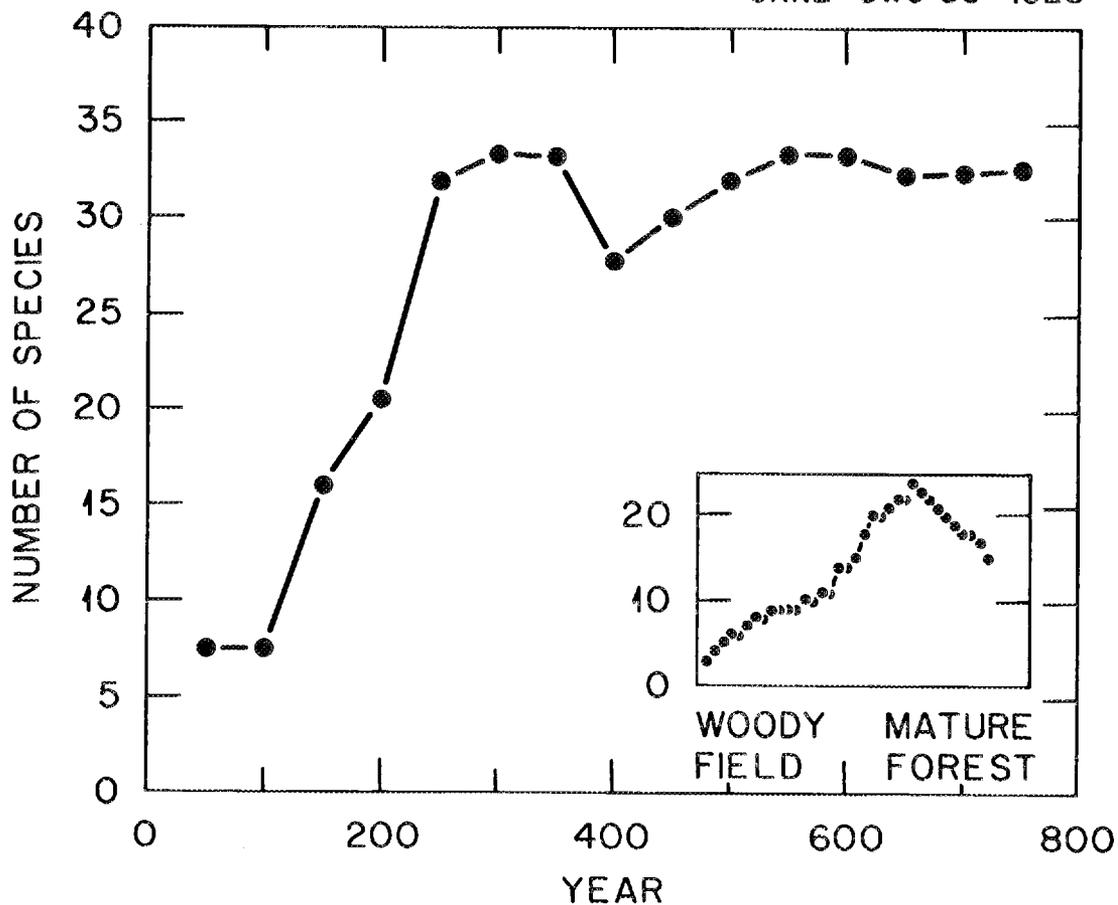


Figure 4.3. Increase in bird species richness through succession to mature, steady-state forest (as simulated by Urban and Smith, in review).

Inset: bird species richness along an ordinated successional gradient for southern Illinois forests (mature forest on ordination axis corresponds to 400-year simulated forest; unpublished data from Urban 1981).

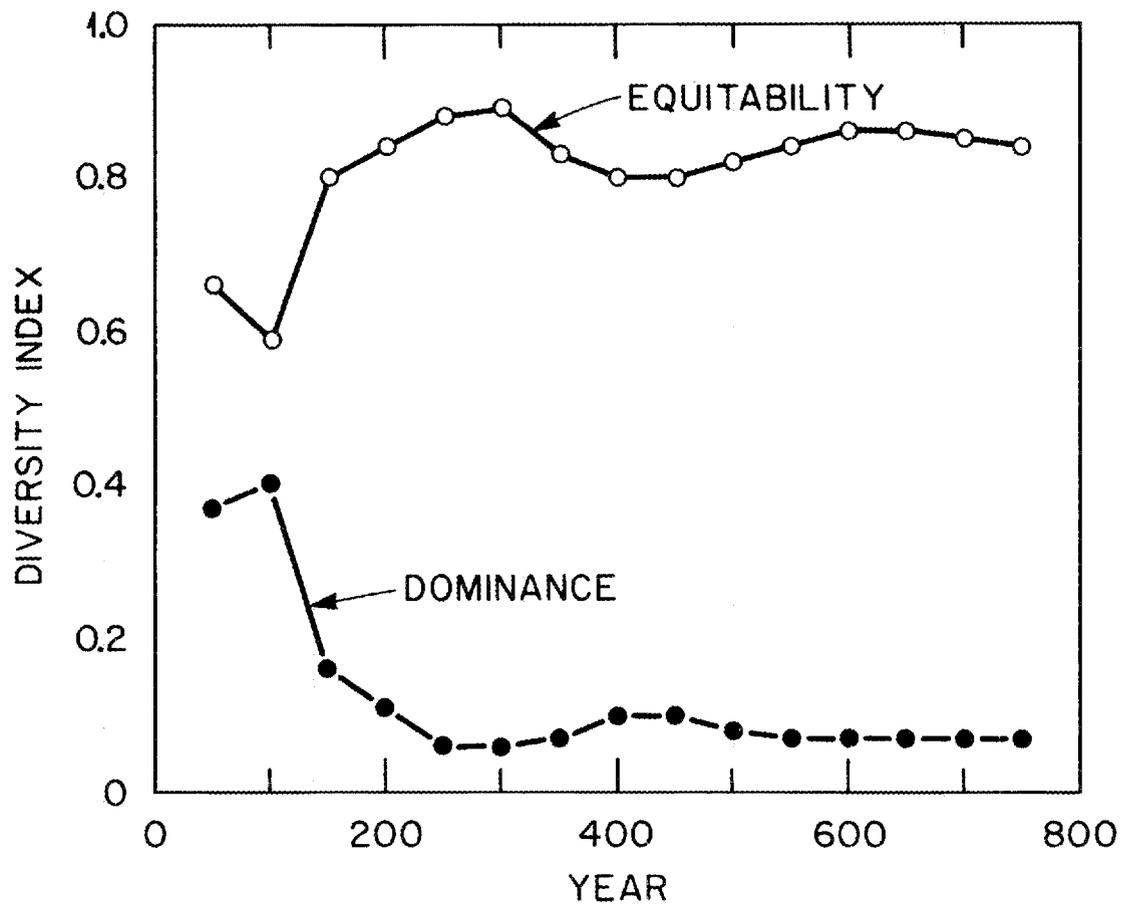


Figure 4.4. Trends in numerical dominance and equitability among bird species through succession to mature, steady-state forest (as simulated by Urban and Smith, in review).

Dominance is $\sum p(i)^2$, where $p(i)$ is the relative abundance of species i . Equitability is $H/\ln S$, where $H = -\sum p(i)\ln p(i)$, $p(i)$ is as defined as above, and S is the number of species present.

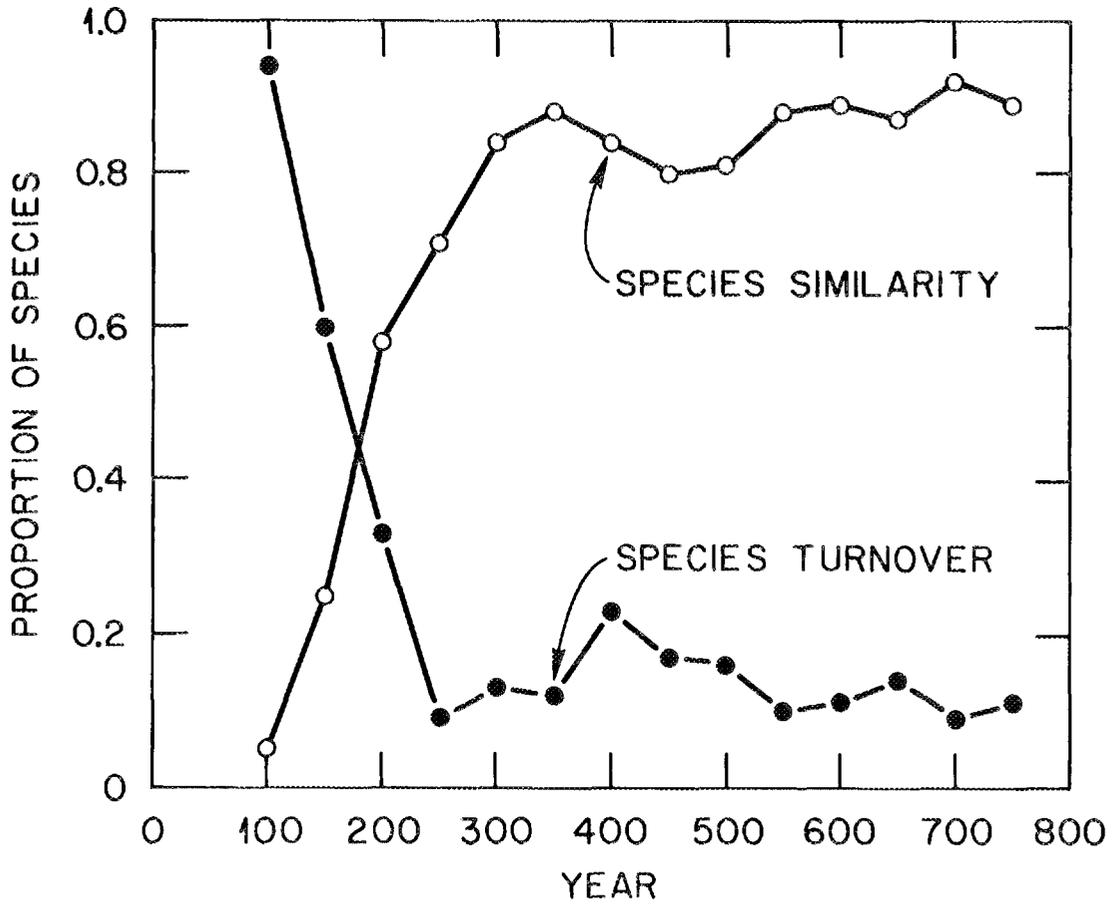


Figure 4.5. Bird species turnover and similarity through succession to mature, steady-state forest (as simulated by Urban and Smith, in review).

Turnover is defined as the percentage of species present at time t that are no longer present at time $t+1$. Similarity is $200C/(A+B)$, where A is the number of species present at time t , B is the number of species at time $t+1$, and C is the number of species present at both times.

Patterns in Mature Forest

The steady-state pattern of microhabitats maintained by mature forests (sensu Bormann and Likens 1979; Shugart 1984; Watt 1925, 1947) accounts for three common patterns in animal communities. Because common microhabitats are centrally located in multivariate niche space while unusual microhabitats are peripherally located (Carnes and Slade 1982, Shugart and Patten 1972, Dueser and Shugart 1979, Seagle et al. 1984, Seagle and McCracken 1986), there is an inverse relationship between species abundance and niche position (here, niche position indexes a species' habitat affinities: species utilizing common microhabitats have low niche position; species that prefer unusual microhabitats have high niche position) (Figure 4.6).

The sample distribution of microhabitats is such that species with affinities for unusual microhabitats will always be rare at the scale of the forest stand. Because there is no reason for species to evolve affinities for common microhabitats more often than for rare microhabitats (which would require something akin to divine guidance), the sample distribution of microhabitats provides for more rare species than common species (Figure 4.7; see also MacArthur 1971; Preston 1962; Seagle et al. 1984; Seagle and McCracken 1986).

The spatial pattern of microhabitats, which in the simulated forest is generated by gap dynamics, provides for an increase in microhabitat diversity for increasingly large subsamples of the forest stand. This horizontal heterogeneity reflects the juxtaposition of

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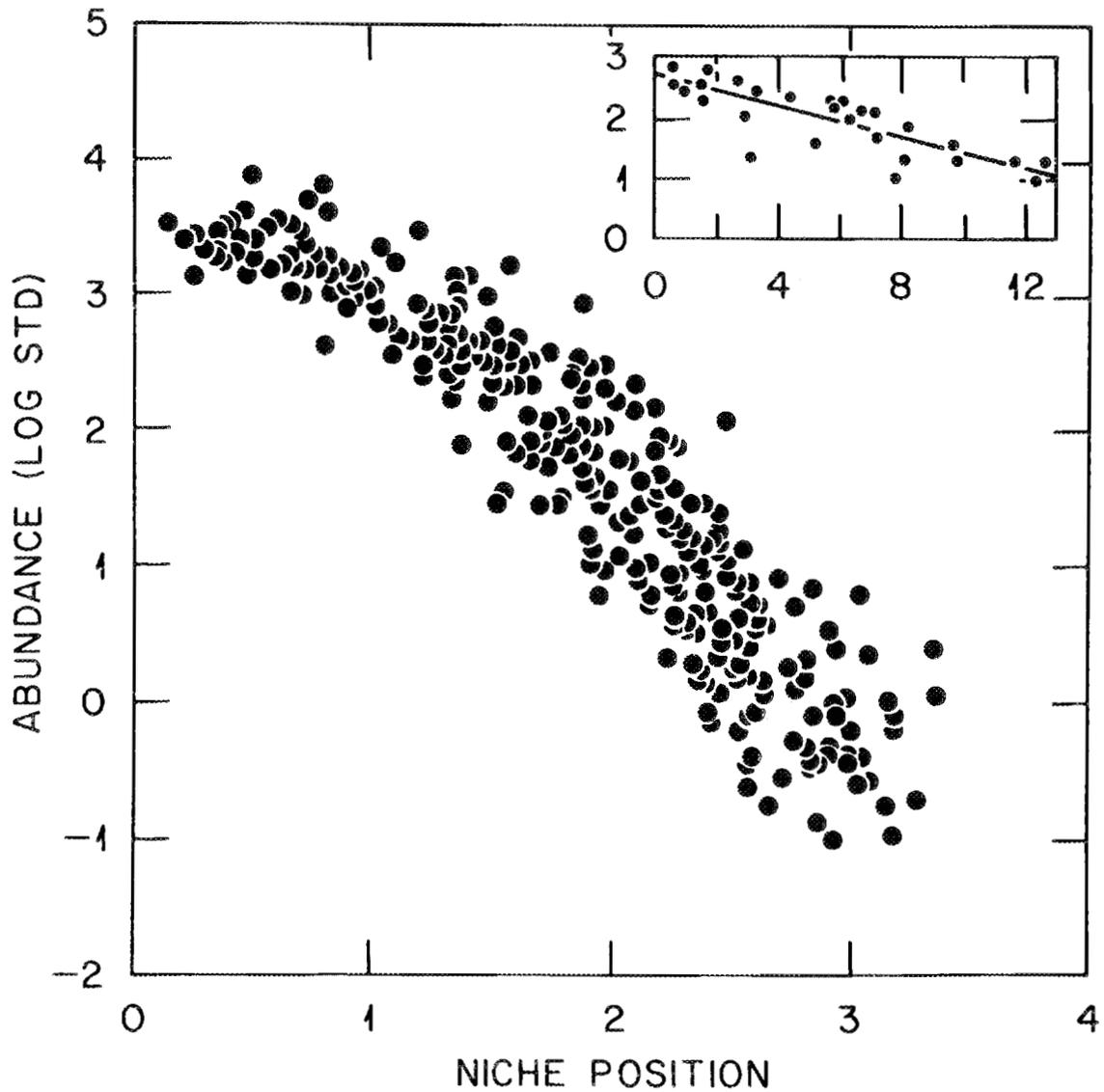


Figure 4.6. Relationship between bird species abundance and niche position for bird communities in mature, steady-state forest (as simulated by Urban and Smith, in review).

Niche position is the Euclidean distance from a species' niche centroid in the statistical habitat space, to the pooled-sample habitat centroid. Species with affinities for unusual habitats have high niche position. Inset: abundance and niche position for birds in southern Illinois forests (units on axes are not standardized; unpublished data from Urban 1981).

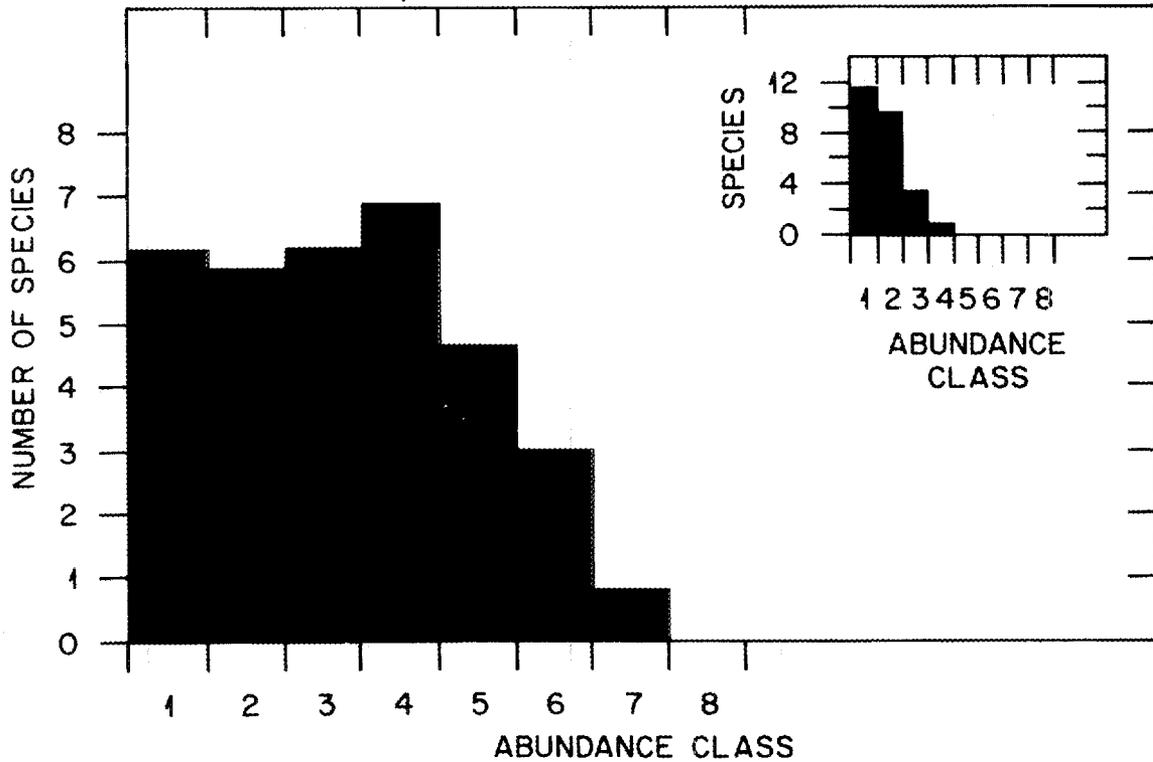


Figure 4.7. Distribution of abundance classes for bird species in mature, steady-state forest (as simulated by Urban and Smith, in review).

Inset: abundance classes for birds in Cadiz woodlots (averaged for 6 woodlots 6-10 ha in size). Correcting the simulated classes (0.04-ha quadrats) for avian territory size (circa 1 ha) would shift the simulated distribution to roughly match the empirical classes.

vertical profiles (here indexed by the relative importance of understory and overstory trees) that are locally out of phase with one another (Roth 1976). This spatial pattern thus provides for a species/area relationship mediated by microhabitat diversity (Figure 4.8).

Other factors, of course, contribute to observed species abundance patterns for forest birds (Sherry and Holmes 1985). But the important conclusion here is that many characteristic patterns in bird community structure can be attributed, in large part at least, to the dynamic pattern of microhabitat availability within a forest stand.

Bird Species Distribution in Landscapes

Results of the simulation study suggest that statistical indices of habitat variety, estimated at the level of the forest stand, would be useful in predicting bird species diversity at the landscape scale, i.e., for a mosaic of forest patches. It follows that habitat variety should be correlated with bird species richness in woodlots. Surprisingly, this has been difficult to demonstrate empirically. Galli et al. (1976) indexed habitat diversity in several woodlots as a Shannon-Weaver function of foliage density in 5 strata, measured at several sample points per woodlot. This index did not increase with increasing forest area for woodlots larger than about 2 ha. The index was not related to bird species diversity. In Wisconsin, Ambuel and Temple (1983) defined 20 different foliage profile types, and indexed habitat diversity as a Shannon-Weaver function of the relative abundance of each of these profile types found within a woodlot. This

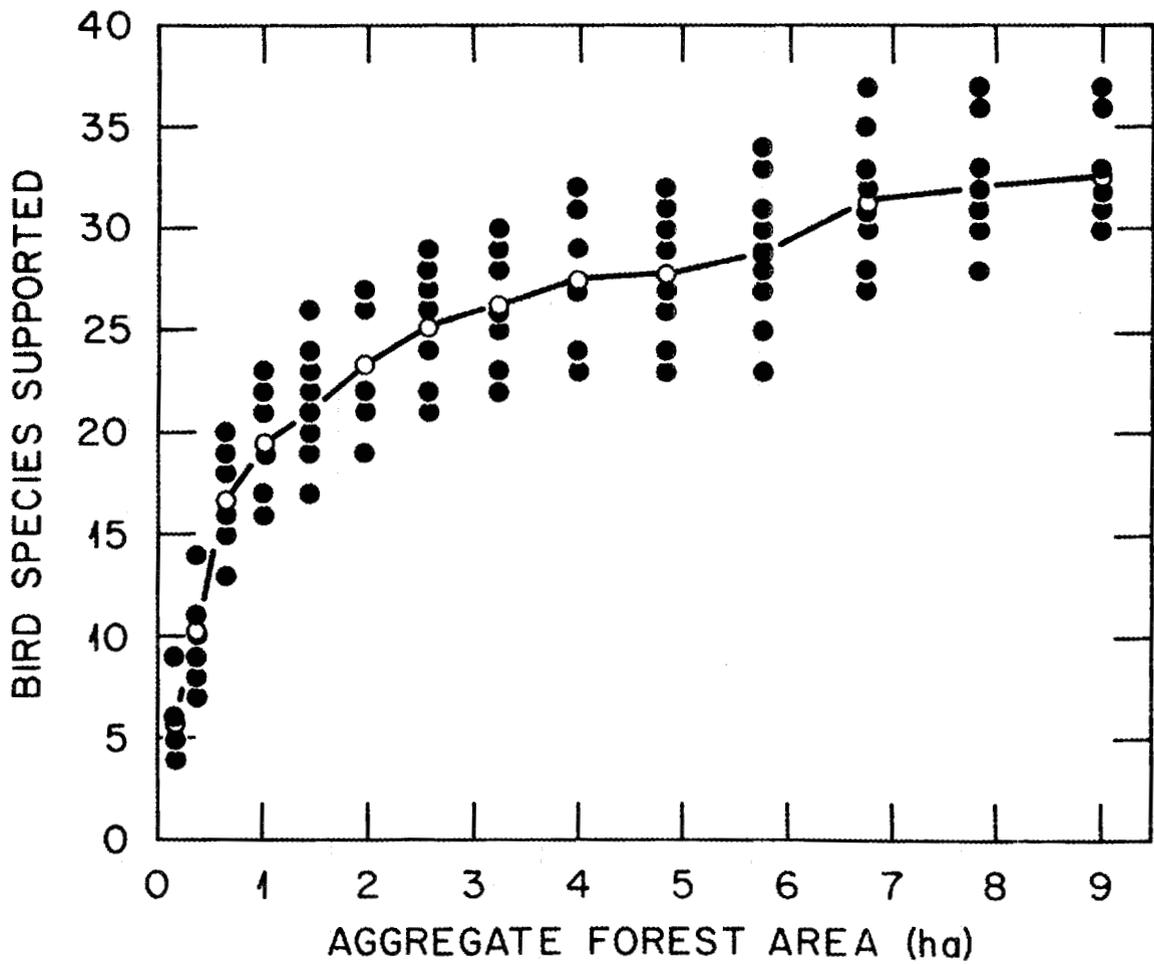


Figure 4.8. Species/area relationship for subsamples of a 9-ha stand of mature, steady-state forest (as simulated by Urban and Smith, in review).

index was uncorrelated with forest area, leading Ambuel and Temple to conclude that habitat variety in itself did not contribute substantially to a species/area relationship observed in their data.

Microhabitats and Birds in the Cadiz Mosaic

Forewarned that the relationship between habitat variety and bird species diversity in woodlots is, at best, not necessarily straightforward, an exploratory approach was adopted for the Cadiz woodlots. Microhabitat variety was indexed as habitat richness, the number of different structural microhabitats represented within a woodlot. Richness is perhaps the least elegant of myriad diversity indices, but it is also the least ambiguous in interpretation.

Discrete structural microhabitats were identified via cluster analysis (FASTCLUS procedure, SAS 1982). Discriminant functions were then calculated to assess the validity of the typical microhabitats at several levels of resolution (i.e., for different numbers of clusters). At each level, back-classification of the input samples according to the calculated functions indicated the proportion of samples that could be classified correctly. With 20 typical microhabitats clustered, samples could be back-classified with 93% accuracy. The selection of this level of resolution was, of course, arbitrary; but any ecologically significant relationship between habitat variety and bird species richness should be somewhat robust to subtle distinctions about "habitats."

At the least, microhabitat richness should increase with woodlot area. Because bird species richness also increases with woodlot area,

microhabitat richness and bird species richness should be positively correlated. Such a result would be consistent with the postulated importance of microhabitat pattern to bird communities, but would not distinguish habitat effects from any effects of woodlot area in itself. A more rigorous test of the importance of habitat availability would require a relationship between microhabitat richness and bird species richness, once the effect of area has been accounted; that is, a relationship between habitat richness and residual variation in bird species richness. This relationship was tested via partial regression analysis.

Microhabitat richness and woodlot area were positively correlated for the Cadiz woodlots ($r=0.64$, $p>0.0001$). Area was more strongly correlated with bird species richness ($r=0.71$), and this relationship was still stronger when area is log-transformed ($r=0.79$). Microhabitat richness was more weakly correlated with bird species richness ($r=0.62$). These correlations suggest that the relationship between habitat richness and bird species richness may be coincidental to the area effect. Indeed, in partial regression, habitat richness did not contribute significantly to predicting bird species richness ($p>0.14$).

Area as a Surrogate for Microhabitat Pattern

The failure to relate bird species diversity to patterns in microhabitat variety and abundance in woodlots, when there is strong theoretical support for such a relationship, warrants some discussion. It remains, of course, that the postulated dependency

between bird species richness and habitat variety might emerge from further analyses of habitats defined by other means, or at different levels of resolution, or for some other index of diversity. But it might also be argued that such a relationship, if finally demonstrated, is too dearly purchased. It is certainly difficult to recommend relentless statistical analysis as a general approach; in most cases this approach would be logistically prohibitive.

A mechanistic understanding of the factors that generate microhabitat pattern in forests suggests the conditions under which empirical estimates of microhabitat pattern should prove useful, as well as those cases when such estimates might fail to account for bird species abundance patterns. In general, if the processes generating forest microhabitat pattern are similar for all forest patches in a landscape, then the area of a stand or woodlot should be a sufficient surrogate variable for the distribution of finer-scale microhabitats. In such cases, bird species diversity should be correlated with habitat diversity, but there should be so little residual variation in habitat diversity (beyond that accounted by area itself) that empirical habitat measures might be superfluous. Further, if there is considerable difficulty in defining "habitat" in terms that are relevant to birds, or if the distribution of these habitats is difficult to estimate accurately in the field, then area might serve as a better estimator of habitat diversity than actual measurements.

Conversely, if the factors generating microhabitat pattern vary considerably among woodlots, then empirical estimates of the distribution of microhabitats should be useful predictors of bird

species abundance patterns. There are three factors that might contribute to variation among woodlots in man-dominated landscapes. (1) Disturbances that are similar in spatial scale to the size of woodlots (such as fires or catastrophic windstorms) will affect entire or large parts of woodlots, overriding the spatial patterning of microhabitats. This category includes management practices of sufficient intensity as to be considered disturbances (e.g., logging). Urban and Smith (in review) simulated the effects of two timber management practices (selective logging and thinning), and showed that the resultant microhabitat distributions supported very different bird communities. In agricultural landscapes of the midwestern United States, timber management units often correspond to patterns of ownership; small woodlots have a single owner and are managed as entire units, while large woodlots may have several owners with each parcel managed independently.

(2) Forest management practices that are not so intense as to be considered disturbances may still homogenize microhabitat pattern within a woodlot, reducing the overall variety of microhabitats. Chronic light grazing or removal of firewood are examples of timber uses that might homogenize the internal patterning of microhabitats. Related to this case are woodlots that are of such irregular shape or small size that they include only edge habitat (Levenson 1981).

(3) Historical patterns of forest clearing and current land use may result in forest remnants that are small relative to the scale of environmental gradients (e.g., topographic pattern). Consequently, small woodlots may represent only local samples of larger patterns.

A small bottomland woodlot might support very different microhabitats than an upland woodlot of the same size. These differences can be compounded by disturbances that occur differentially with respect to topographic gradients, such as fire or windthrow. Conversely, if remnant forest patches themselves are restricted to only certain kinds of sites (e.g., topographically rugged sites, Bowen and Burgess 1981), then differences among woodlots might be reduced in some instances.

In each of these three cases, woodlots that are similar in size may be very different in habitat diversity, and actual estimates of habitat diversity might improve predictions of species abundance in habitat mosaics. It does seem likely, however, that these empirical estimates would prove most useful in explaining residual variation in microhabitat or bird species diversity not accounted by area itself. Thus, empirical estimates of habitat variety would augment but not replace area itself as a predictive variable. Again, if there are logistical problems in adequately characterizing microhabitat distributions in the field, then area might serve as a better estimate than empirical measures.

The disturbance history of Cadiz Township involved widespread grazing and logging of woodlots, as well as occasional fires on some sites. This history is reflected in current forest habitats (Sharpe et al., in press); the effects of disturbance are frequently obvious in the structural patterns of particular woodlots. This again suggests that measures of microhabitat diversity should be related to patterns in bird species richness in Cadiz woodlots. That this expected relationship did not emerge from the foregoing analyses

evokes a further speculation about bird species response to microhabitat pattern. In the Cadiz avifauna, 90% of the species and 95% of the individuals are either edge species or habitat generalists (Table 2.2, page 25). It seems likely that the lack of statistical association between bird species and microhabitats may reflect the lack of species with pronounced affinities for particular microhabitats. This implies that the relationship between bird species diversity and microhabitat pattern may be more interpretable with reference to the trajectory of avifaunal reorganization illustrated in Figure 2.6 (page 28). Specifically, the association of higher bird species diversity with increased microhabitat diversity and heterogeneity should be more pronounced (statistically stronger) in primeval forest (extensively forested landscapes) than in sparse mosaics that have been fragmented for a long time.

In retrospect, it is worth remarking that many extensive studies of forest stands have selected study sites subject to a criterion of similarity or homogeneity (omitting sites with obvious evidence of disturbance or unusual topographic features). This conventional sampling scheme is appropriate for studies of forest stands (or their supported animal communities) because the nearly similar replicates increase sample sizes and strengthen the inferences drawn from them. But this approach obscures the very source of variation that becomes interesting at the landscape scale: among-stand variation. Landscape-scale studies must redefine their sampling schemes and analytic methods to emphasize new sources of variation that contribute to landscape patterns.

AVIAN VAGILITY AND HABITAT ACCESSIBILITY

Introduction

This chapter focuses on the role of avian dispersal in determining the relative accessibility and utilization of discrete habitat patches. In part, this concern is motivated by predictions of island-biogeographic theory (MacArthur and Wilson 1967). According to island theory, the number of species supported by an island depends on a dynamic equilibrium between species immigrations and local extinctions. Other factors being equal, immigration rates are higher for islands near a species-rich source area (e.g., a mainland) as compared to more distant islands. So "near" islands support more species than "far" islands (Figure 5.1).

Although island theory has fallen from favor as a paradigm for studies of terrestrial habitat mosaics (Gilbert 1980; Middleton and Merriam 1981, 1983; Whitcomb et al. 1981), the prediction of an isolation effect is still interesting. The mechanism of interest here is avian dispersal, especially the dispersal of fledglings. Available data illustrate that dispersal patterns of juvenile birds are qualitatively similar to the immigration curves of island theory. Nice (1937) banded nestling song sparrows, and then mapped the positions of birds relocated the next year. Her data illustrate that juveniles tend to return nearby, but not exactly to where they were born, with a dispersal-distance relationship that suggests negative

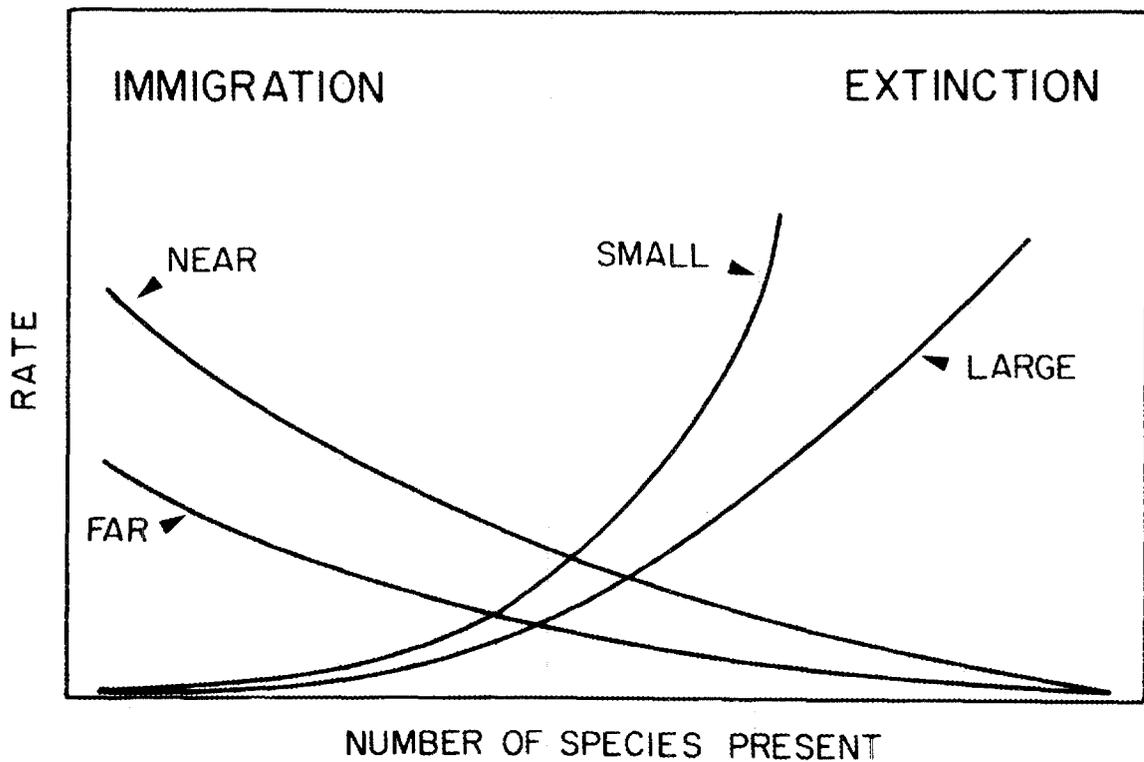


Figure 5.1. Species richness on islands as a dynamic equilibrium between immigration and local extinction (redrawn from MacArthur and Wilson 1967).

Near islands have higher immigration rates than far islands; large islands have lower extinction rates than small islands.

exponential decay (Figure 5.2). Data for several other bird species show the same general relationship, although apparent dispersal ranges vary considerably among species (Weise and Meyer 1979, Whitcomb et al. 1981).

This dispersal/distance relationship predicts that an isolation effect should be observed in a habitat mosaic. Isolated patches should be species-poor and patches near rich source areas should be species-rich. Indeed, MacClintock et al. (1977) found unusually high species richness in a small woodlot near a larger forest tract, suggesting that the satellite woodlot was heavily subsidized by birds dispersing from the larger forest.

This chapter examines three hypotheses about avian dispersal and habitat accessibility. (1) In the case of a single species that is limited by its dispersal range, individuals of the mosaic metapopulation should be contagiously distributed within available habitats. (2) If dispersal limitations reflect not the dispersal range of a species, but rather, the time spent searching for available habitats (its mobility), then spatial distributions of neotropical migrants should differ from the distributions of permanent residents, because permanent residents presumably have more time to disperse. Specifically, migrants should be more contagiously distributed than permanent residents. (3) For species assemblages in which some species tend to be limited by their dispersal range and/or mobility, the number of species supported by a woodlot should be related to the woodlot's isolation with respect to other woodlots. Again, isolated

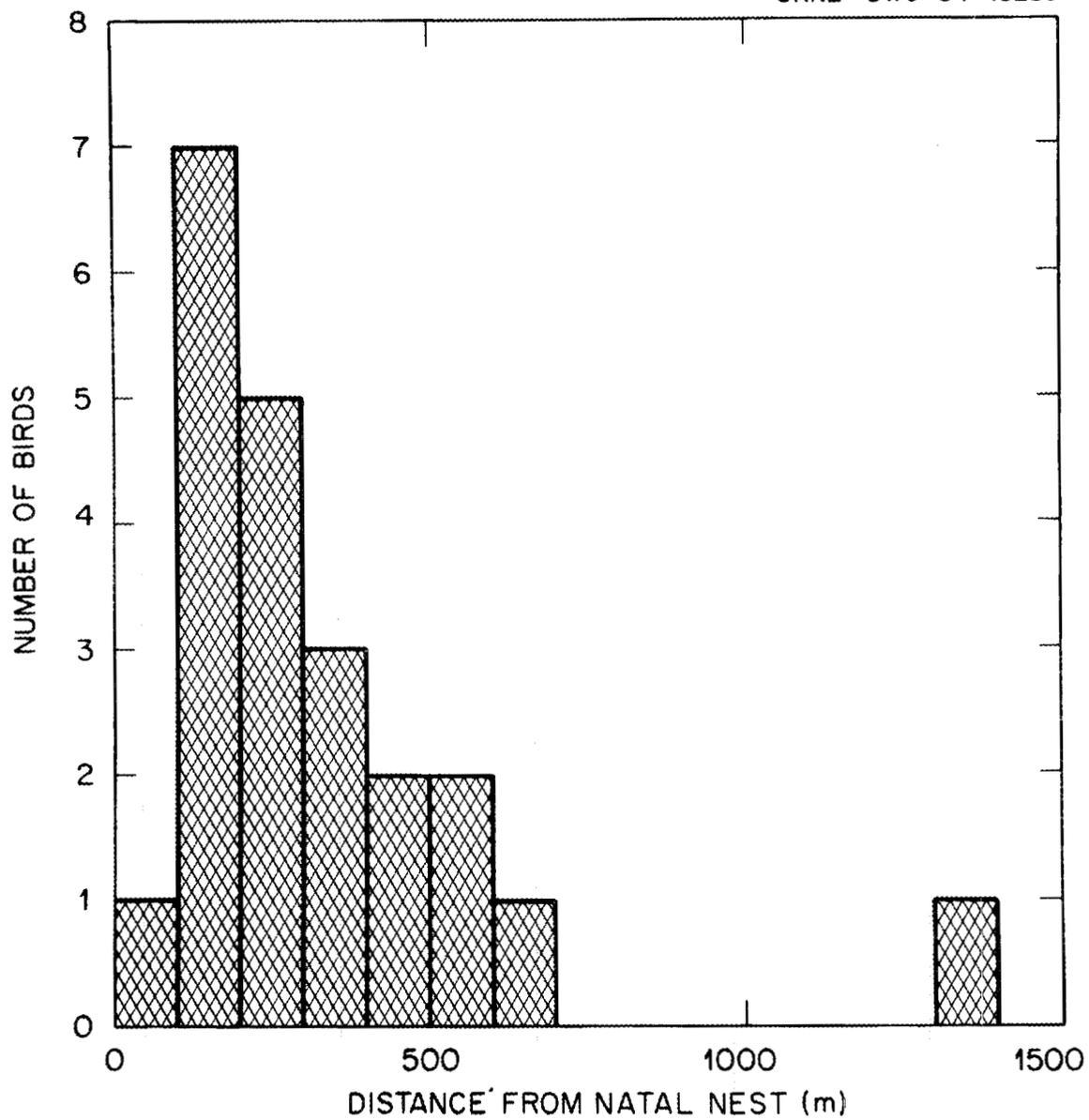


Figure 5.2. Dispersal distance patterns for yearling Song Sparrows banded as nestlings (data from Nice 1937).

woodlots should be comparatively species-poor. In the following sections each of these hypotheses is tested in turn.

Spatial Pattern of Birds in the Cadiz Mosaic

Dispersion of Common Species

In conventional pattern analysis the spatial distribution expected under the null hypothesis of randomness is given by the Poisson distribution (e.g., Pielou 1977). In the case of bird distribution in a habitat mosaic, this null distribution is not correct because the only possible locations for birds are in woodlots, and the woodlots have a spatial pattern of their own. Here the concern is to examine the spatial pattern of birds relative to the pattern of available habitats: an analysis of one pattern superimposed on another. The analysis proceeds in three steps: (1) index the spatial pattern of individual birds of a given species; (2) characterize the probability density function of indices calculated from random distributions of the same sample size; and (3) compare the observed species pattern index to the expected values, to see if it differs significantly from a random pattern.

Species dispersion was indexed as mean nearest-neighbor distance, by finding the minimum Euclidean distance from a given individual to another conspecific, and then averaging these distances for all individuals of that species. This calculation relied on census maps in which each bird was recorded to a particular grid cell. The Red-headed Woodpecker is a typical illustration (Figure 5.3).

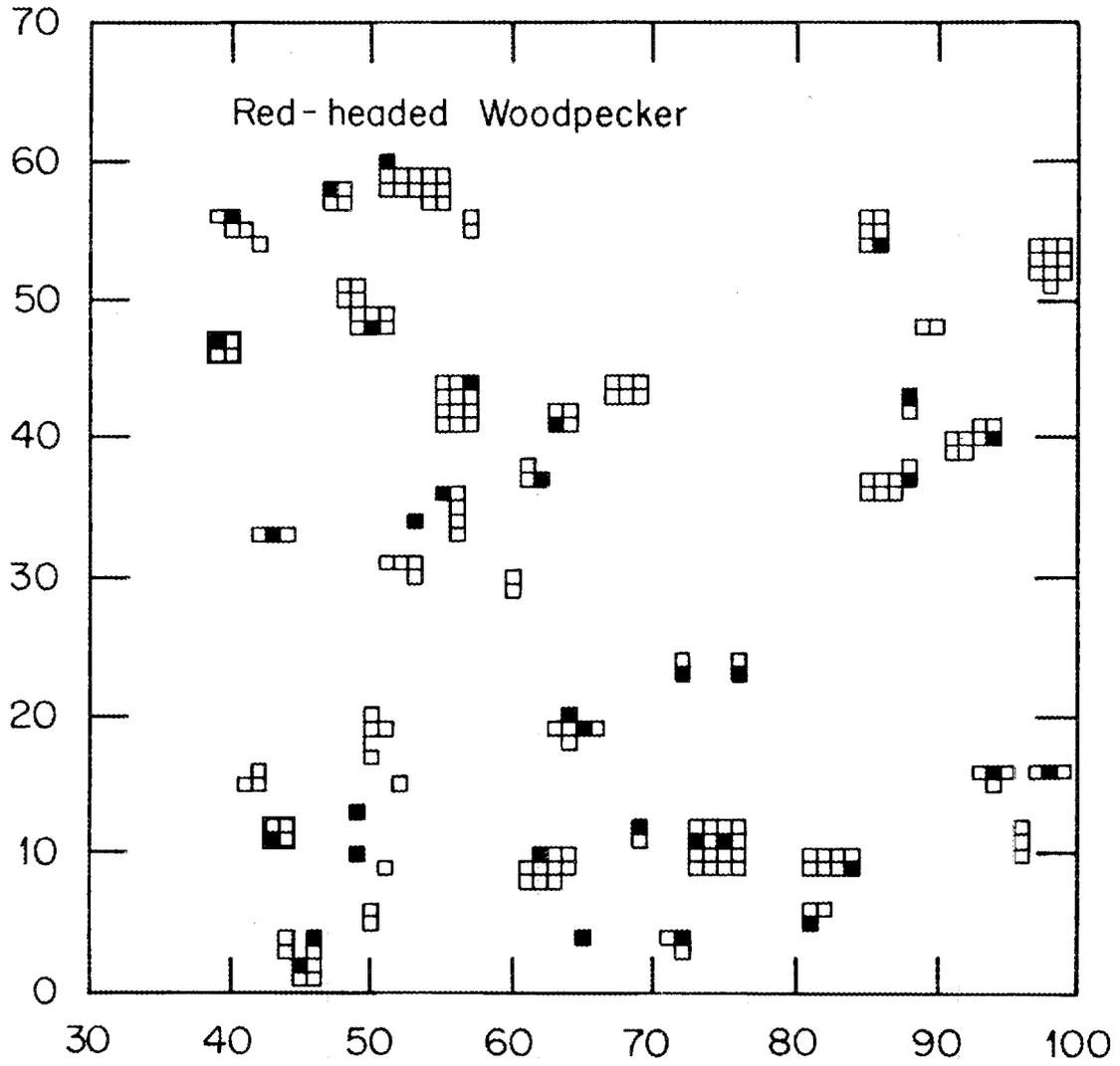


Figure 5.3. Spatial distribution of Red-headed Woodpeckers in the Cadiz mosaic in 1985.

Random distributions were generated by drawing random grid cells--the same number as the observed sample size for the species of interest--and calculating the mean nearest-neighbor distance for these. The eligibility of each cell drawn was determined by the forest area of the grid cell and the territory size of the species: cells smaller than half a territory were disqualified from random draws, as were larger cells when they were saturated (e.g., a 1-ha cell could support 2 birds of a species with a 0.5-ha territory, so that cell would be sampled with replacement until it was drawn twice, then disqualified). A second territory-size constraint was invoked at the woodlot scale, in that no woodlot was permitted to contain more random birds than empirically observed maximum breeding densities. Thus, the random positions of birds were constrained toward realism at both the cell and woodlot scale. This process was repeated for 1000 random draws.

From the pool of 1000 random indices, nonparametric (quantile) and parametric descriptive statistics were calculated. The 1st, 5th, and 10th percentiles indexed degrees of contagion (underdispersion) that would be expected with probabilities $p=0.01$, 0.05 , and 0.10 , respectively. Similarly, the 99th, 95th, and 90th percentiles signified overdispersion at $p=0.01$, 0.05 , and 0.10 , respectively. To generate corresponding parametric tests of significance, the mean and standard deviation of the random indices were computed. The observed index for a given species was then standardized to a z-score, and compared to tabled values of the normal distribution. Pooled samples were tested for normality, and dispersion was assessed according to the percentile or z-score, as appropriate.

This analysis was conducted for 22 species with more than 10 observations. Interpretation of nearest-neighbor distances was confounded by species abundance relative to the number of woodlots. Particularly, for species with more individuals than there were woodlots (i.e., $N > 45$), the average distance to 2 nearest neighbors better characterized species dispersion at the woodlot scale. Similarly, for species with more than twice as many individuals as woodlots ($N > 90$), the average distance to 3 nearest neighbors was used. These higher-order indices allow the statistic to reflect the dispersions of species that did not occur in every woodlot but were abundant where they did occur. Thus, the nearest-neighbor statistic used for subsequent analyses was selected according to species abundance. Because nearest-neighbor distances decrease with increasing species abundance, further comparisons among species utilized nearest-neighbor indices that were standardized relative to the pooled sample for each species (z-scores). While the pooled samples for a few species were not strictly normal ($p > 0.05$), z-scores were very similar in magnitude to nonparametric (percentile) scores, so use of z-scores probably did not bias these comparisons.

Of the 22 species tested, 12 were randomly distributed ($p > 0.10$), 4 were statistically overdispersed ($p < 0.10$), and 6 were contagiously distributed ($p < 0.10$) (Table 5.1). Those species that were overdispersed included 3 large omnivores and the Brown-headed Cowbird; each of these species might in fact regularly use more space than their apparent territory sizes would indicate. Contagiously distributed species included 3 comparatively small neotropical

Table 5.1. Spatial pattern of common bird species in Cadiz woodlots, 1985, as mean nearest-neighbor distance between individuals.

SPECIES ¹	NO ²	NND ³	PERCENTILE ⁴	Z	N	p >Z	D ⁵
RHWp	34	494		1.85	y	0.06	+
RBWp	11	968		-0.04	y	0.97	0
DWp	30	606	.75<p<.90	1.23	n	0.22	0
Flik	38	486		1.49	y	0.14	0
Pewe	44	424	.75<p<.90	0.83	n	0.41	0
CFly	31	488		-1.94	y	0.05	-
BJay	54	457 (2)		2.14	y	0.03	+
BCC	31	525		1.33	y	0.18	0
WBN	37	537		1.55	y	0.12	0
Wren	178	125 (3)		-3.38	y	0.01	-
WoTh	17	426		-1.90	y	0.06	-
Robn	90	271 (3)		-2.16	y	0.03	-
GCat	87	207 (2)		-0.73	y	0.47	0
BrTh	24	489		-0.80	y	0.42	0
Star	114	187 (3)		-3.03	y	0.01	-
REVi	45	363 (2)	.05<p<.10	-1.67	n	0.10	-
Card	56	411 (2)		1.82	y	0.07	+
RBG	42	383		1.19	y	0.23	0
Bunt	75	293 (2)		-0.01	y	0.99	0
SSp	29	506		1.07	y	0.28	0
BHC	51	488 (2)		2.41	y	0.02	+
NOri	19	775		0.27	y	0.79	0

¹See species codes in Table 3.3, page 44.

²Number of observations

³Mean nearest-neighbor distance (m). If (2), distance is to 2 nearest neighbors (for $N \geq 45$); (3), for 3 nearest neighbors ($N \geq 90$).

⁴Percentile scores for species not normally distributed (y/n); z-scores for all species, with probability of a greater absolute value of z.

⁵Spatial pattern is overdispersed (+), random (0), or contagious (=).

migrants, but also included 3 other species typical of disturbed habitats (House Wren, Robin, and Starling). These latter species tended to be either abundant or absent at the woodlot scale, hence contagiously distributed.

If spatial dispersion is related to the dispersal range of a species, then the nearest-neighbor statistic should be correlated with species range. But the nearest-neighbor index was uncorrelated with this parameter ($p > 0.50$), implying that dispersion is not systematically related to apparent dispersal range.

Spatial Pattern and Migratory Strategy

The mean standardized distance for neotropical migrants was -0.74 ($n=6$). For short-distance migrants this distance was -0.29 ($n=5$); for permanent residents, 0.67 ($n=11$). There is an apparent difference in dispersion relative to migratory strategy, but these means are not statistically different ($F=1.43$, $p > 0.26$). This lack of significance reflects the variability in dispersion among species (standard deviations in these scores were 1.24, 2.19, and 1.72 for neotropical migrants, short-distance migrants, and permanent residents, respectively). Thus, there is no compelling evidence that neotropical migrants as a group are dispersal-limited, as would be evidenced by more contagiously distributed populations.

This conclusion is also supported by simulation experiments with the demographics model. In exploring a preliminary version of the model, Urban and Shugart (1986) found that a very small number of redispersal episodes (e.g., 3) were sufficient to meet the constraint

of habitat accessibility in a habitat mosaic. This does not rule out isolation effects for patches that are very remote, but it does suggest that dispersal limitation is the exception rather than the rule in habitat mosaics.

Species Richness and Woodlot Isolation

The hypothesis that isolated woodlots should be comparatively species-poor was tested via linear regression. Woodlot isolation was indexed by finding the minimum nearest-neighbor distance for each woodlot. Bird species richness was then regressed against the natural log of woodlot area, and the expected number of species per woodlot was calculated. The deviation in species richness from the number predicted from patch area was then regressed against the index of patch isolation. A significant regression on these residuals would confirm a relationship between bird species richness and woodlot isolation.

The regression equation relating bird species richness to woodlot area (log-transformed) was

$$\hat{S} = 8.91 + 5.711\ln(A), \quad (5.1)$$

where \hat{S} is predicted species richness and A is woodlot area. This regression was highly significant ($p < 0.0001$) but accounted for only 62% of the variance in species richness. Thus, there were appreciable residuals to warrant further analysis. These residuals, however, were not correlated with any of 3 indices of woodlot isolation calculated as distances to the nearest, 2 nearest, and 3 nearest neighbors

($p > 0.15$ in each case). Thus, there is no evidence that any woodlot in the Cadiz landscape is so isolated as to affect its bird species richness.

Habitat Accessibility in Other Landscapes

Overall, it seems obvious that species dispersal does not limit avian access to and utilization of woodlots in the Cadiz landscape. But as noted, Cadiz Township includes comparatively many woodlots that are very close together. Consequently, it may be that the lack of evidence of an isolation effect in species distributions may be somewhat misleading, and may not be typical of landscape mosaics in general. In Maryland landscapes, where the forest patches are more dispersed, Lynch and Whigham (1984) found 16 of 31 forest bird species showed differential response to indices of patch isolation (some species showed positive correlations with isolation; some, negative). In particular, of 12 migrant species that showed significant correlations with the isolation index, 9 correlations were negative. This suggests that isolation effects might emerge in mosaics that have more sparsely distributed woodlots than the Cadiz landscape.

One way to assess the importance of habitat isolation in comparatively sparse mosaics is to take advantage of the structure of the simulation model. In the model, patch locations are specified as an array of Euclidean distances between patches. If every element of this array is multiplied by a constant, the mosaic expands to a sparser configuration while retaining the relative positions of the patches. Of course, all other features of the mosaic (patch sizes and edge/area

ratios) remain unchanged. By choosing appropriate multipliers, a single mosaic can be manipulated experimentally to test the effect of habitat isolation as the mean inter-patch distance increases.

This approach was used with mosaic #9, a mosaic of 30 patches with a mean nearest-neighbor distance between patches of 741 m (Table 3.3, page 44). The mosaic has a single 128-ha reserve. This mosaic was expanded by factors of 1.35, 2.70, 4.05, and 5.40 to yield an experimental series of mosaics with mean nearest-neighbor distances of 1, 2, 3, and 4 km, respectively.

Demographics of 42 species were simulated in a series of 40 replicates, 10 for each of the experimental mosaics. Each replicate simulated 30 years. The number of species present in each patch in the final year was tallied and retained for analysis. Patch isolation was indexed in 2 ways: (1) nearest-neighbor distance to any other patch, and (2) distance to the 128-ha reserve.

For each simulation, species richness was regressed against patch area (log-transformed) and the nearest-neighbor distance. The partial sum-of-squares associated with the isolation index, divided by the total (corrected) sum-of-squares in the model, indexed the proportion of variance in species number explained by isolation. Partial coefficients of determination were then compared for the 4 experimental mosaics, to determine whether patch isolation was more important in the sparser mosaics.

Regressions were highly significant statistically for each of the mosaics ($p < 0.0001$), and in every case the isolation index contributed significantly to the regression (Table 5.2). Mean partial

regression coefficients for the nearest-neighbor index were 0.28, 0.35, 0.33, and 0.27, for mosaics with mean dispersions of 1, 2, 3, and 4 km, respectively.

In a separate series of regressions, distance-to-the-reserve also contributed significantly to every regression, but its relative contribution as a predictor was usually negligible. While the relative influence of this index showed the same pattern in importance in the 4 mosaics as did the nearest-neighbor index, distance-to-the-reserve explained at most only 12% of the variance in species number. This was because the reserve was functionally connected to only a few of the patches, so its effect, while significant, was rather local.

Table 5.2. The relative contribution of woodlot isolation in predicting bird species richness, for mosaics with mean inter-patch distances of 1, 2, 3, and 4 km.

MOSAIC	TOTAL	AREA	ISOLATION	SPECIES ²
1	0.67 ¹ (0.06)	0.39 (0.10)	0.28 (0.11)	16.52 (0.61)
2	0.70 (0.09)	0.35 (0.05)	0.35 (0.10)	12.32 (0.51)
3	0.68 (0.03)	0.36 (0.06)	0.33 (0.06)	9.71 (0.33)
4	0.67 (0.04)	0.40 (0.05)	0.27 (0.05)	8.61 (0.31)

¹Tabled values are partial sum-of-squares divided by corrected total sum-of-squares, for total model, area (log-transformed), and nearest-neighbor distance; means are for 10 replicates (std. dev. in parentheses).

²Mean number of species per patch.

The relative importance of the nearest-neighbor index as a predictor forms an interesting pattern in increasingly sparser mosaics. The importance of isolation increases and then decreases monotonically in relation to the mean dispersion of the mosaic (Figure 5.4). In simulations, this was because most dispersal-limited species were lost before the final simulation year, so these species did not contribute any variance in species richness. The maximum importance of the isolation index as a predictor of species number coincides with the modeled dispersal range of a large number of species in the simulations.

This scheme is not incompatible with classical island-biogeographic theory (MacArthur and Wilson 1967). For a set of islands very near a rich source of colonists, immigration rates would be similarly high for all islands; thus variation in species number would be attributed either to random chance or to area (habitat) effects. At the other extreme, very isolated islands are so little subsidized by immigration from distant sources that, again, distance effects would explain little of the variation in species richness. The relative importance of isolation would be maximized in intermediate cases where area and distance effects could each contribute substantially to variation in species number.

It is perhaps worth emphasizing that the regressions based on patch area and isolation accounted for only about 70% of the total variance in species number. This is notable because area and isolation are the only factors contributing to this variation as generated by the demographics simulator. Thus, the residual variation

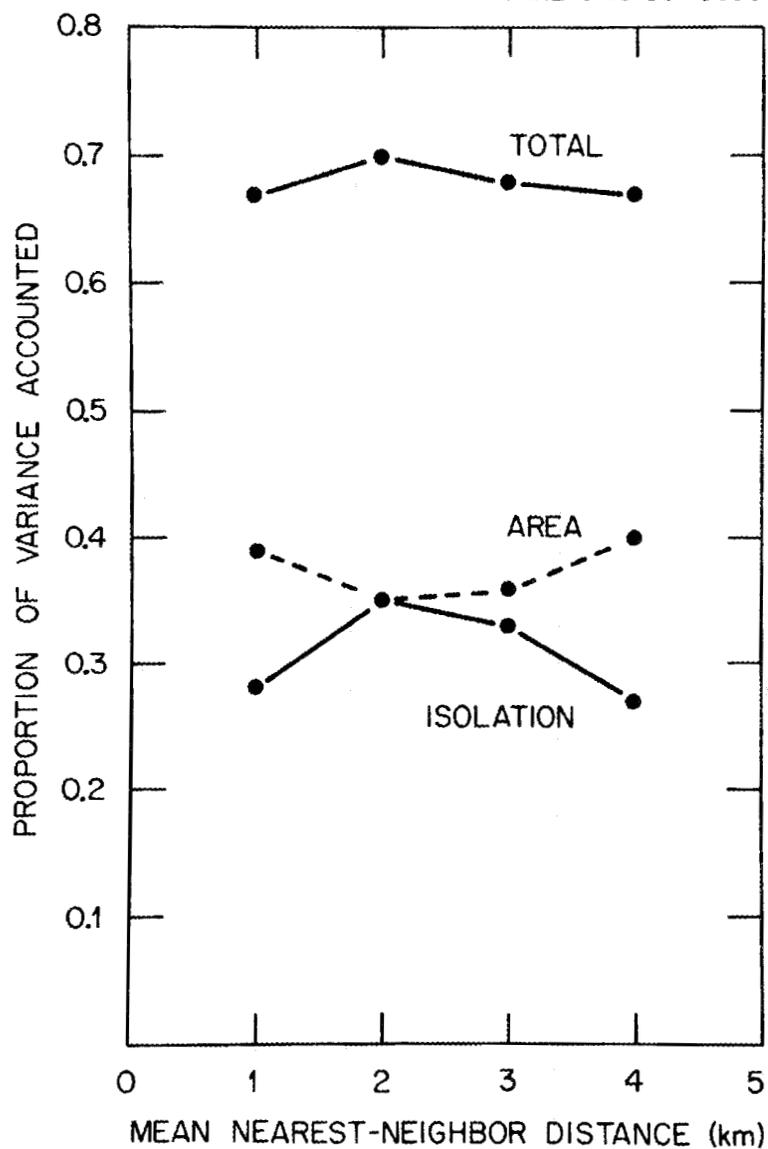


Figure 5.4. Relative importance of patch isolation in predicting bird species richness in increasingly sparse mosaics.

Predictive power is indexed as relative partial regression sum-of-squares; mosaic dispersions are mean nearest-neighbor distances between patches (km).

may be an accurate reflection of the amount of variation introduced by the stochastic dispersal of individual birds among patches. If this is true, it suggests that the degree of precision conventionally sought in predictions should be relaxed somewhat for predictions about habitat mosaics: great precision is probably unattainable.

A Further Consideration

An important consideration remains. Model simulations thus far have assumed that birds would readily disperse to the fullest of their abilities, that is, that there are no behavioral limits on dispersal. It remains to be demonstrated empirically that birds will freely disperse across alien habitats (e.g., cropland) to access remote forest patches. Observations of edge species and mobile generalists suggest that these species fly readily among woodlots in agricultural mosaics (Urban, personal observation; Middleton and Merriam 1981). However, intuition suggests that species with preferences for interior forest habitats might not disperse so freely in a mosaic landscape. Finding species to be contagiously distributed in habitat mosaics where inter-patch distances are small relative to the presumed dispersal abilities of the species (as with the Wood Thrush and Red-eyed Vireo in the Cadiz mosaic) certainly suggests that actual dispersal behavior is less than presumed possible for these species. Characterizing realized patterns of dispersal in habitat mosaics thus assumes a high priority in field studies of avian demography.

Another aspect of dispersal that warrants attention is the realized dispersal range of species relative to the size of a

particular patch, especially for large patches. This relative difference might effect the qualitative pattern of dispersal, from within-patch to among-patch. If large patches tend to release juvenile birds through dispersal to small, isolated patches (which likely produce proportionately fewer offspring per breeder than larger patches), then the large patches might actually act as net sources in a landscape. This would accelerate the decline of sensitive metapopulations. Conversely, if large patches tend to retain their juveniles through within-patch dispersal, then the large patch would not serve as a net source. The critical patch size at which realized dispersal becomes a within- as compared to an among-patch phenomenon is currently unknown, and represents a second data criticality.

Finally, if site fidelity decreases after failed nesting attempts (as it likely does, Greenwood 1980), and nesting fails more often in small, isolated patches than in large refugia, then large patches might function as net sinks, accumulating proportionately more birds through time. If this could be demonstrated, it would be compelling evidence in support of a conservation strategy emphasizing large reserves. For these reasons, empirical verification of dispersal patterns by forest species in mosaic landscapes should be a high priority in landscape-scale studies of avian demography.

CHAPTER 6

NET REPRODUCTION IN A HABITAT MOSAIC

Introduction

Net recruitment is demographic gains minus losses. For the most part, gains represent natality and losses are due to mortality. Immigration and emigration may also be important fluxes in net recruitment, either at the scale of the individual habitat patch or for an entire mosaic. For present purposes it has been assumed that there is no net flux at the mosaic level, because the central question is whether a given mosaic can support a self-sustaining population of a given species. Thus, cases where a population persists because it is subsidized by another population are not considered here. Patch-level consequences of dispersal were discussed in the preceding chapter. This chapter focuses on natality and mortality, and factors affecting these in a landscape mosaic of forest patches.

There is ample evidence that factors affecting nesting success can contribute substantially to species abundance patterns in woodlots. It is generally agreed that predation is a primary factor controlling nest success in open-nesting birds (Best and Stauffer 1980, Kendeigh 1942, Nice 1957, Nolan 1963, Ricklefs 1969). Brood parasitism may also be an important regulator of fledging success in host species (Hann 1937, May and Robinson 1985, Ricklefs 1972). Because these effects are locally intensified in forest edges (Figure 6.1, Gates and Gysel 1978; see also Brittingham and Temple

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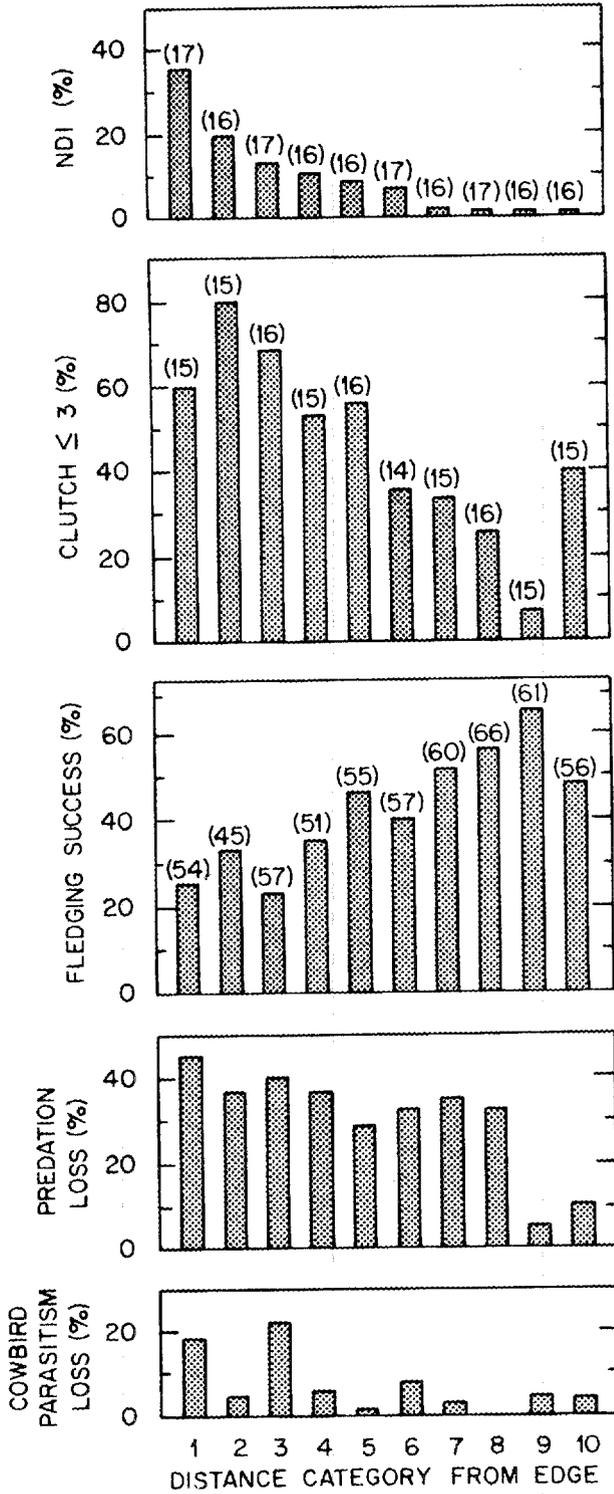


Figure 6.1. Incidence of (a) nest density, (b) clutch size, (c) total fledging success, (d) predation, and (e) brood parasitism, at increasing distances from the forest edge (redrawn from Gates and Gysel 1978).

Distance categories are: (1) 0.0-0.8, (2) 0.8-2.2, (3) 2.2-4.3, (4) 4.3-6.9, (5) 6.9-10.1, (6) 10.1-14.2, (7) 14.2-26.7, (8) 26.7-46.2, (9) 46.2-65.6, and (10) 65.6-123 m (based on sample sizes).

1983, Wilcove 1985), this chapter focuses primarily on the role of edge effects on realized natality in influencing metapopulation dynamics.

The approach is exploratory rather than definitive. The chapter begins by defining a simple, mechanistic model of net recruitment, so that the parameters contributing to net recruitment can be related to one another. A cursory analysis of this model suggests the relative sensitivity of these parameters, which indicates their potential to effect an appreciable change in population dynamics. Factors that vary considerably and systematically relative to their sensitivity are implicated as effective constraints on species abundance patterns in a mosaic of forest patches.

The second concern is to translate model sensitivity into terms of population response. Bird populations have an inherent temporal variability due to stochastic aspects of natality, dispersal, and mortality. Given this natural variability, what is the critical change in factors affecting recruitment that will produce appreciable differences in observed population dynamics? This domain of uncertainty indicates a scale of resolution at which the parameters can be used to make reliable predictions of population dynamics.

To anticipate, it will emerge that model parameters related to net reproduction are very sensitive, in that small changes in these parameters elicit pronounced population responses. Further, the stochastic nature of population dynamics makes it difficult to predict population response to these parameters, over the time scales at which these dynamics are typically observed (e.g., a few years). Finally,

the mechanistic details of factors affecting net recruitment are logistically difficult to account directly in field situations. Indeed, such an effort at the landscape scale would be overwhelming. But the pattern of local intensity of these factors as edge effects provides a possible means of accounting these effects indirectly. This chapter concludes by considering a protocol that would use edge area to predict species abundance patterns in forest patches.

A Mechanistic Model of Net Recruitment

Consider the minimum set of parameters needed to describe net recruitment mechanistically for a single population. For simplicity, assume that all habitats are identical and that there is no net flux due to immigration or emigration. Neither assumption, of course, is entirely realistic but the consequences of these are deferred until later. At the least, recruitment depends on:

- (1) Clutch size, the number of potential breeders produced by a breeder in a single season. Assuming a 1:1 sex ratio, this equals half the product of eggs per brood times broods per season. Denote clutch size c .
- (2) Fledging success rate (f), the proportion of potential breeders that are successfully reared to independence. Note that f can be decomposed further into any number of factors that contribute to realized fledging success. In particular, nest predation and brood parasitism can be emphasized by specifying each independently (p and b , respectively). To be consistent with other parameters, p and b specify the proportion of

potential breeders that survive each factor. Each of these can be further decomposed into an incidence term (the frequency of the event) and a severity term (the proportion of young lost per incidence). Thus, p (or b) equals 1.0 minus the product of severity and incidence.

(3) Post-fledging survivorship (s), the proportion of fledged young that live until they join the breeding population. Since most forest passerines breed their second year, post-fledging survivorship refers to the first (hatching-year) winter.

(4) Mortality (m), the average, annual per-capita death rate for breeders.

Let N_t represent the number of breeders at time t . The number of new breeders at time $t+1 = cfsN_t$, and those breeders lost to mortality equals mN_t . Then the breeding population at time $t+1$ is the new recruits minus adult mortality:

$$N_{t+1} = cfsN_t - mN_t \quad (6.1)$$

and the net recruitment rate (r) is

$$r = cfs - m \quad (6.2)$$

Since the net recruitment rate is the difference of the natality product and the mortality rate, commensurate changes in either of these have the same effect. For present purposes, a constant mortality rate is assumed, and the following discussion focuses on the natality terms. Note that because the terms are multiplicative, net recruitment changes if any of the terms in the product change.

Further, substantial net changes can accrue from small changes in several of the parameters. Also, because the terms are defined in equivalent units they are equally sensitive. That is, a 5% reduction in clutch size has the same effect as a 5% increase in predation pressure, or a 5% decrease in post-fledging survival, or any combination of factors whose product is equivalent to a 5% change. (Note that these percentages refer to incremental changes of 0.05, not to 5% of the mean value of each parameter.) The practical consequence of this is that it is sufficient to determine the sensitivity of only one natality parameter, and the sensitivity of other parameters can be inferred from this. This assessment of parameter sensitivity is provided by the demographics simulator.

Modeling Population Response to Net Recruitment

Metapopulation-level response to changes in net recruitment rate was assessed by simulating the demographics of a single species in a mosaic of 25 patches (mosaic #7, Table 3.3, page 44). The simulated species was a hypothetical habitat generalist, with adequate dispersal abilities; reproductive parameters were subsumed into a single experimental parameter, realized clutch size (Table 6.1).

Simulations and Analysis

The simulation series implemented 12 values (levels) for the experimental parameter, with 30 replicate simulations per level. The total number of breeding birds was tallied over all patches at the end of each simulation (year 30) and retained for analysis.

Table 6.1. Demographic parameters for a hypothetical bird species simulated to assess model sensitivity and uncertainty of population response to variation in realized clutch size.

PARAMETER ¹	VALUE
Habitat Affinity	0 (generalist)
Territory Size	1.0 ha
Maximum Breeding Density	50 territorial males/100 ha
Dispersal Range	5000 m
Mobility	9 redispersal bouts
Annual survivorship	0.588 (maximum age=8.675 years)
Realized Clutch Size	Base: 1.40 female fledglings/ female/year Increment: 0.07 (5% of base) Range: 1.05-1.82

¹See parameter definitions in Table 3.1, page 36.

Analyses focused on two aspects of population response to variation in clutch size: sensitivity and uncertainty (Gardner et al. 1981). A parameter is sensitive if small changes in its value elicit pronounced changes in model behavior. Model response is uncertain if knowledge of the parameter value does not provide for very reliable predictions of model behavior. Here, sensitivity refers to the magnitude of population response, on average, to changes in clutch size. Uncertainty refers to the ability to predict final-year population levels, in particular cases, using clutch size as a predictor.

Sensitivity and uncertainty can be inferred from a regression of final-year population size for a series of clutch sizes. The slope of

the regression line indicates the average response of the population to variation in clutch size, and indexes sensitivity (Gardner et al. 1981). A sensitive parameter has a comparatively steep regression slope. The variation about the regression line (as illustrated by confidence intervals) indicates the uncertainty of the predicted population levels for each clutch size. If there is very little variation about this line, then the parameter can be used to make predictions at a fine scale of resolution in the parameter; conversely, if there is considerable variation about the regression line, fine-scale predictions are not possible.

Sensitivity and Uncertainty of Net Natality

Because population size is bounded at 0 and 77 (carrying capacity for the mosaic), observations near these boundaries were deleted from the regression analysis. A regression based on clutch sizes 1.26-1.68 (210 observations) provided the best regression in terms of constancy of residuals. The regression analysis indicates that clutch size is a very good predictor of final-year population size (Figure 6.2). The regression equation,

$$\hat{P} = 139.39 C - 165.02 \quad (6.2)$$

(where \hat{P} is predicted population size and C is clutch size) accounted for 73% of the variation in population size (model $F=575.31$, $p<0.0001$). The regression slope is steep over the relevant range of population sizes (0 to carrying capacity), illustrating the importance

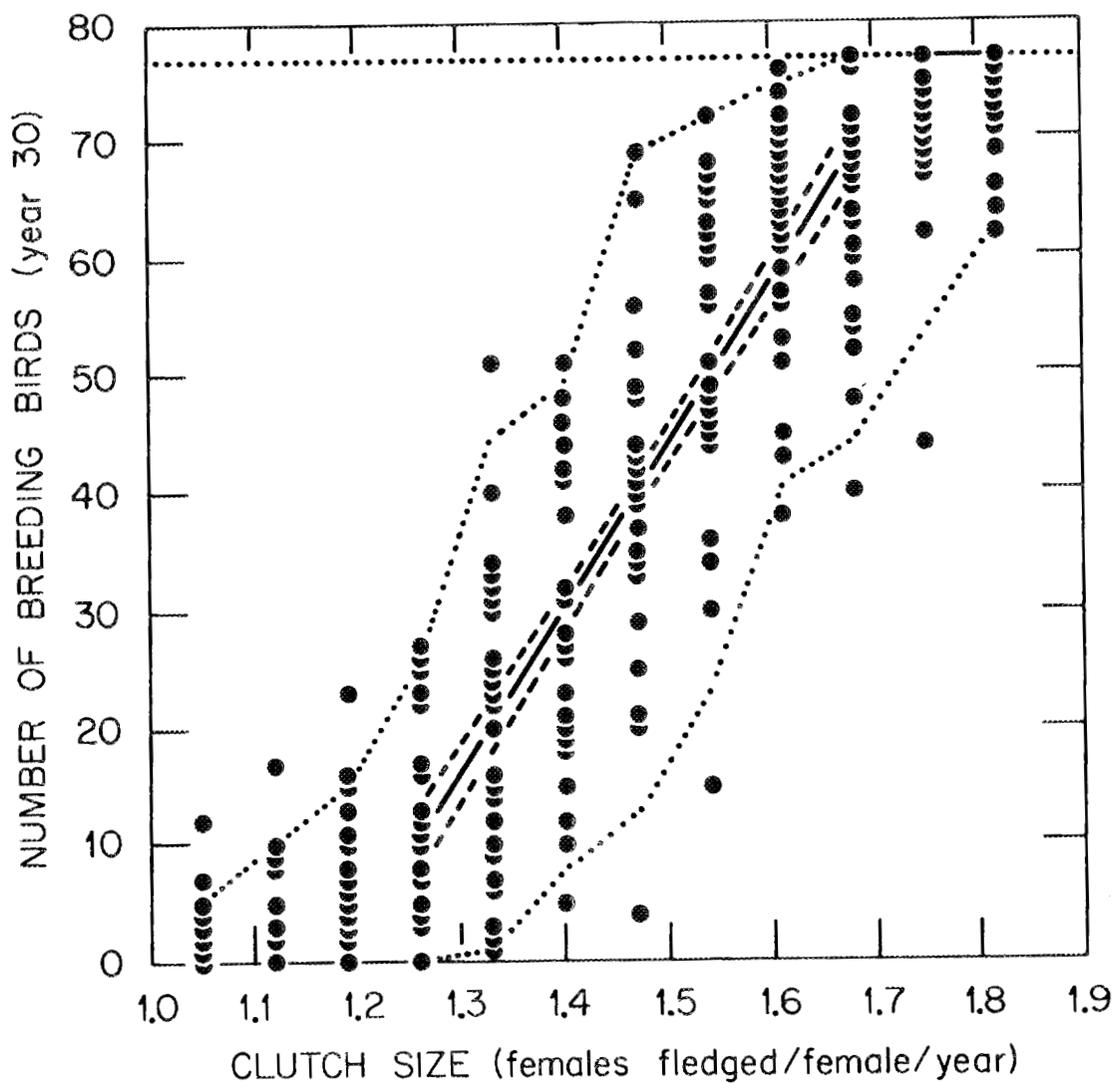


Figure 6.2. Regression of simulated population size (year 30) for clutch sizes in the domain 1.26-1.68 female fledglings/female/year.

Dashed lines: 95% confidence intervals for the regression slope.
 Dotted lines: confidence intervals for simulated population size.
 Carrying capacity for the mosaic is 77 birds (dotted line at top).

of clutch size to population dynamics. The 95% confidence intervals on the regression slope (dashed line in Figure 6.2) imply that changes in clutch size on the order of 0.02 female fledglings/female/year (roughly 1% of the base value) result in appreciably different predictions of population size (i.e., predictions with nonoverlapping confidence intervals).

More interesting, for present purposes, is the variation about the regression line. A graphical example will serve to illustrate how the uncertainty of modeled population response can be inferred from this variation. Consider a horizontal line drawn through the graph at a population size of 40. This line intersects the confidence intervals for observed population sizes (dotted lines) at points corresponding to clutch sizes of roughly 1.3 and 1.6. Thus, the observed population size might be the result of clutch sizes varying on the order of 0.3. This domain indexes the uncertainty of population response.

These domains of sensitivity and uncertainty can be determined for any values of clutch size or population size, and for any degree of confidence (confidence intervals are arbitrary). In this example, estimates of clutch size resolved on the order of 0.02 result in appreciably different population sizes; in the limit (over longer time spans), populations would respond to such small changes in clutch size. But given the uncertainty of population response, clutch size is not a particularly reliable predictor of population size in the short term. Stating this obversely underscores this point: given an observed population size, it is not possible to infer the effective

clutch size to a resolution finer than about 0.3. The uncertainty associated with clutch size is roughly an order of magnitude greater than its sensitivity.

The uncertainty of population response to clutch size in the simulations warrants further discussion. Replicate simulations are quite variable (Figure 6.3). This stems from the stochastic implementation of natality, dispersal, and mortality in the model, but this inherent variability is propagated and amplified in the mosaic metapopulation by positive feedback (DeAngelis et al. 1986). Because individual patches in the mosaic are functionally linked by juvenile dispersal, a stochastic nesting failure in one patch in a given year represents a loss of a breeding bird in an adjacent patch in the next year, which reduces the number of juveniles for that year, and so on. Conversely, population increases tend to be self-propagating because the number of juveniles increases proportionately. In either case, the variability in population dynamics is more pronounced in small metapopulations that cannot effectively buffer the stochastic demographics of individuals.

Other Natality Parameters

Model sensitivity applies to other recruitment parameters as follows. Because clutch size is usually measured in eggs rather than in potential breeders, the sensitivity of measured clutch size would be twice the critical increment (assuming a 1:1 sex ratio). The parameter sensitivity for factors effecting fledging success corresponds to incremental changes of the same magnitude as realized

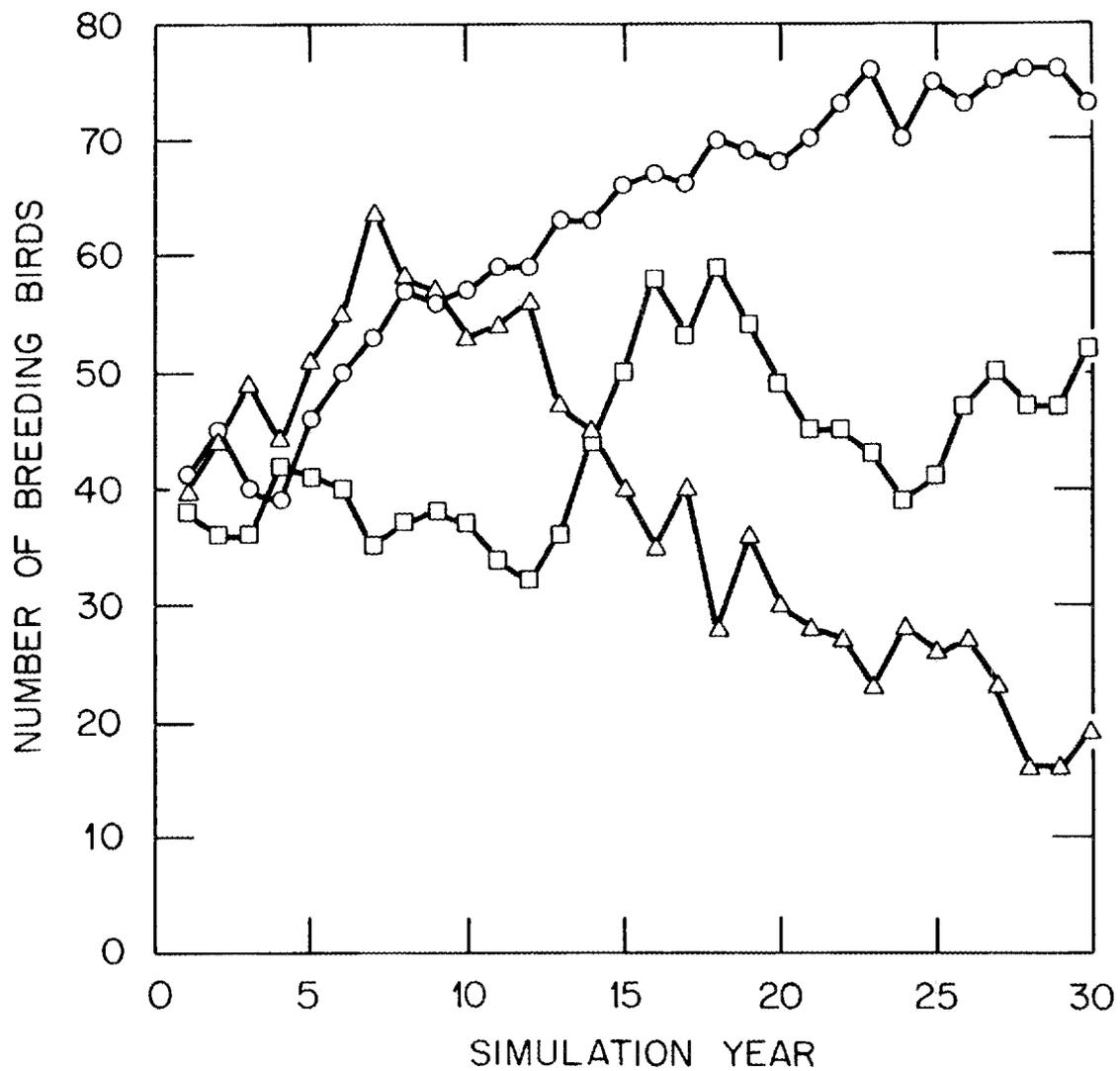


Figure 6.3. Typical metapopulation trajectories for a species with a realized clutch size of 1.54 fledglings/pair/year.

clutch size. For predation and brood parasitism, the effective sensitivity of incidence (frequency of the event) depends on the severity of the event (proportion of young surviving an event). If predation results in the loss of the entire clutch, parameter sensitivity applies to incidence alone. Because parasitism often does not result in total nest failure, sensitivity applies to the product of incidence and severity, so the apparent sensitivity of incidence decreases as the severity of parasitism decreases. Because nest predation and brood parasitism are stochastic events, the uncertainty of population response to these factors is likely greater than for clutch size.

Net Reproduction in Forest Patches

The simulation results indicated a degree of variation in recruitment parameters to which modeled populations were responsive. The interpretative value of this stems from three further considerations: (1) the distribution of actual values of each parameter relative to its sensitivity; (2) the inherent error in estimating a parameter empirically, relative to its sensitivity and the uncertainty of population response; and (3) the sources of natural variation in these parameters, especially if a forest mosaic presents new sources of variation. These considerations apply differently to some of the recruitment parameters, so it is appropriate to consider these categorically.

Clutch Size

Clutch size varies considerably in natural bird populations. Given the apparent sensitivity of this parameter, it goes almost without saying that natural populations must be responsive to this variation. Indeed, this is generally regarded as being a primary mechanism by which density-dependent regulation of populations is effected (Lack 1947, 1954, 1966, 1968; Ricklefs 1972). As a generalization, clutch size increases at low population densities and decreases at high densities. Because the minimum realizable increment in clutch size (1 egg) is large relative to its sensitivity, natural populations can be effectively governed by variations in clutch size.

Also germane to the present discussion is the inherent difficulty in estimating clutch size with acceptable resolution. Consider a species that lays a clutch of "3 to 5 eggs, usually 4." This resolution, typical of natural history accounts, yields a parameter estimate of 1.2 fledged females per female, plus or minus 0.3. Even this variation, which ignores extremes, is still well beyond the sensitive increment for this parameter. Assuming an annual mortality rate the same as for the simulations illustrated in Figure 6.2, this estimate of clutch size would predict a year-30 population size of roughly 10 birds; but the model uncertainty might result in populations ranging from extinction to near carrying capacity. This suggests that it may be very difficult to make predictions of population responses from empirical estimates of clutch size. Further, it seems that such estimates reported out of their context

(food availability, time of year, population density, spatial location) may not be particularly meaningful.

It is interesting to consider the sources of variation in clutch size, particularly patterns of variation in a mosaic of forest patches. While clutch size is ultimately related to the quality of the resource base (food supply), the pattern of nesting density in forest patches (Figure 6.1a) seems to elicit a strong edge effect in clutch size (Figure 6.1b). Presumably this is mediated by scramble competition among the many individuals that utilize forest edges. To date, studies of nesting success in woodlots have usually focused on the obvious impacts of nest predation and brood parasitism. But edge effects on clutch size would be at least as consequential to population dynamics, and warrant further attention.

Fledging Success, Predation, and Parasitism

The effects of nest predation and brood parasitism in woodlots have now been sufficiently documented as to require little amplification. While losses to these factors may vary around 10-20% or less in intact forest, these values may approach 80-100% in forest edges (Brittingham and Temple 1983, Gates and Gysel 1978, Wilcove 1985). These latter values are large relative to the sensitivity and uncertainty associated with these parameters, so that detecting the results of these factors is not really a problem. The problem is that these factors vary spatially as well as temporally in terms of their frequency, severity, and demographic consequences. Nest depredation and brood parasitism occur more frequently near forest edges.

Temporally, the frequency of these events coincides with the peak in nesting activity in early summer. Thus, the open-nesting Eastern Wood-Pewee, a prime candidate for brood parasitism, seems nonetheless to escape intense parasitism pressure by nesting late in the season (Bent 1942). The ultimate consequences of predation or parasitism to an individual breeding bird depend on the timing of the event relative to the bird's nesting cycle. Early in the laying cycle, egg losses can often be replaced by a bird that is still in laying condition. Later in the nesting cycle, a bird may be physiologically incapable of replacing lost eggs or nestlings. Of course, if nesting fails late in the season, there may not be sufficient time left to renest successfully, even if a bird were physiologically able.

Clearly, it would be difficult if not impossible to predict the population-level consequences of factors affecting fledging success on an individual, casewise basis. The net result of this spatial and temporal variation in fledging success is to make real population demographics considerably more uncertain than in the simulation model.

Concerning the spatial distribution of these factors, it must be emphasized that these are novel pressures on net recruitment for some forest interior species, pressures to which they are ill adapted (Gates and Gysel 1978). For example, the Ovenbird (as parameterized in Table 3.2, page 37) can persist in the absence of intense predation or parasitism pressure, but more intense values for these pressures in edges (predation frequency=0.45; parasitism=0.30) effect a dramatic population decline (Figure 6.4). As a further speculation, note that the range in variation in these factors is sufficient that even

species that are adapted to these pressures (through habits of multiple brooding or nest defense) may be affected by edge effects of abnormal intensity.

Mortality

Post-fledging survivorship and adult breeder survivorship are plagued by an inherent difficulty of estimation. A long-term study of the Tufted Titmouse is an illustrative example of this problem. Edler (1985) monitored a local population of titmice for 15 years, recording observations on 258 marked individuals. His estimate of annual survivorship, based on life-table methods, was 0.62. Banding data from the archives of the Bird Banding Laboratory (Clapp et al. 1983), also analysed by Edler, yielded an estimate of 0.51. The method used to parameterize the simulation model assumed that survivorship is constant (age-independent) and that 1% of individuals reach maximum age in years. Using 10 years as maximum age for titmice (from Edler's data), estimated survivorship is

$$s^{10} = 0.01, \quad (6.3a)$$

or,

$$10 \ln(s) = \ln(0.01), \quad (6.3b)$$

or,

$$s = \exp(-4.605/10), \quad (6.3c)$$

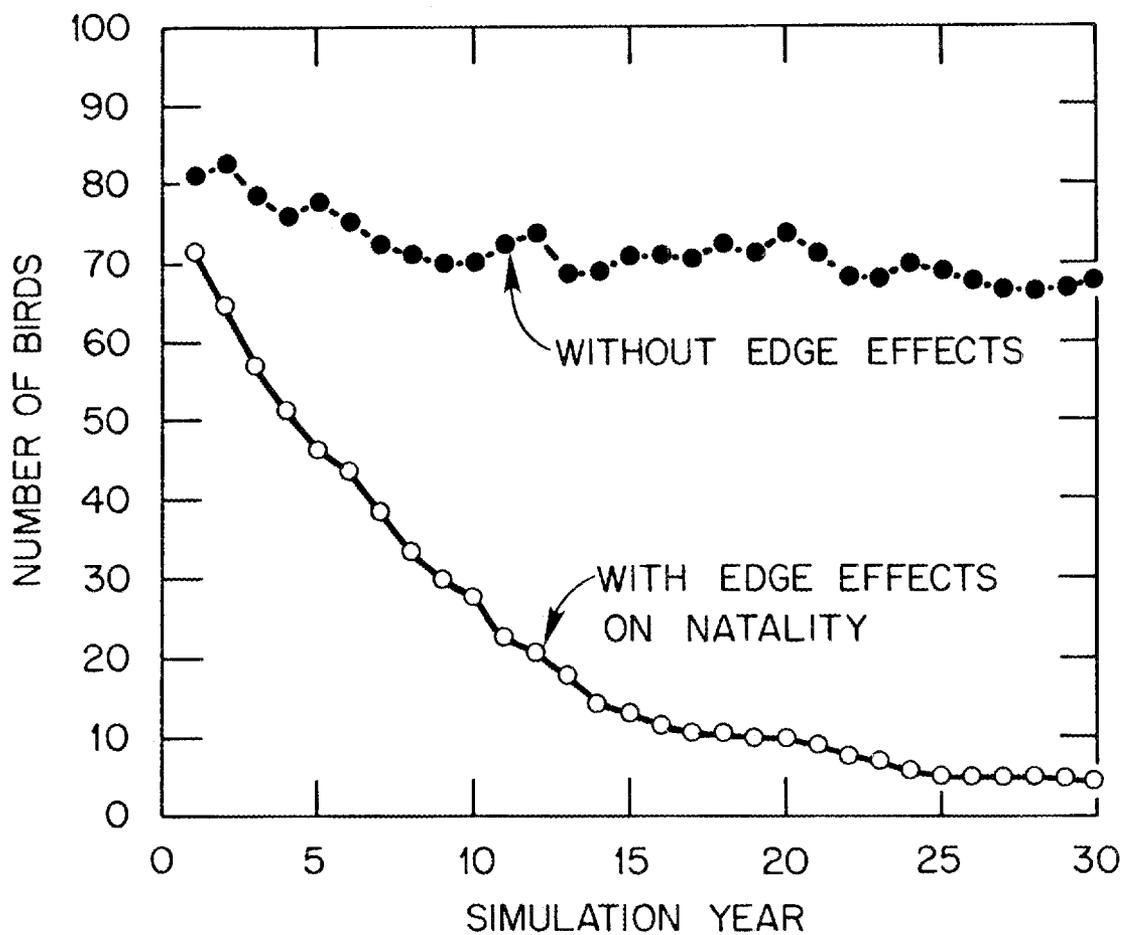


Figure 6.4. Simulated metapopulation dynamics for the Ovenbird, with and without edge effects on net reproduction.

which equals 0.63. This is not a bad estimate of Edler's calculated value. But from Edler's data, only 1 in 258 birds reached the age of 10 years, which leads to an estimated survivorship of 0.57 (by substituting $1/258$ for 0.01 above). The point is, these parameter estimates are 8% (0.57) and 18% (0.51) different from Edler's estimate. The exponential model provided an adequate estimate (within the sensitivity), but unfortunately, the percentage of individuals reaching the reported maximum age for a species is hardly ever known. It seems likely that errors of estimation are often greater than the sensitivity of this parameter. In any case, natural variation in mortality (e.g., associated with vagaries of the weather) is likely of sufficient magnitude, relative to the sensitivity of the mortality parameter, as to render average annual mortality a very uncertain predictor of population trends.

Post-fledging survivorship is subject to the same sort of difficulty of estimation as adult survivorship, but the situation is worse because juvenile dispersal makes it virtually impossible to track individuals with sufficient resolution to record their survivorship. Compounding this problem is a new potential source of variation in post-fledging mortality: mortality occurring during dispersal among forest patches in an open matrix of nonforest land uses. It seems likely that birds dispersing in an agricultural landscape might be subject to greater mortality than in intact forest, but this would be difficult to demonstrate empirically. Given the low frequency with which actual mortality events are witnessed in nature,

it seems unlikely that this source of mortality could be quantified with acceptable accuracy.

A Lesson for Mechanistic Modelers

There is an important conclusion to be drawn from this discussion. Accept as premises that (1) a mechanistic model of net recruitment requires several parameters; (2) these parameters are of equivalent sensitivity, so that populations will respond to changes in any of them; (3) this sensitivity is often beyond the limits of normal errors of parameter estimation; and (4) population response to these factors is often so uncertain as to preclude reliable prediction of population trends over the time scales of interest (a few years). Even these limitations might be overcome, through diligence, in a small-scale study of one or a few species. But at the landscape scale, spatial and temporal variation in these factors is consequential, so the distribution of these parameters must be estimated as well. If a large number of species is of interest, parameterization becomes logistically overwhelming. The important conclusion is that landscape-scale studies of species abundance patterns cannot rely on detailed mechanistic models of net recruitment in forest bird demography. Landscape-scale studies of recruitment must integrate the details of smaller-scale studies of reproductive success; they must rely on data resolved at a larger scale.

Predicting Recruitment Effects in a Forest Mosaic

Thus far the tone of this discussion has been rather pessimistic. But the prospectus is not so bleak, if certain priorities are established. The primary concern here is to account for species abundance patterns in a mosaic of forest patches, as these are influenced by changes in factors effecting net recruitment. One general and simplifying assumption that can be made is that, for every persistent member of the regional species pool, net natality and mortality were roughly in balance in presettlement forests. The immediate concern is with species for which this balance has been disrupted, those species declining in abundance in forest patches. So far as has been demonstrated, recruitment factors effecting this decline are overwhelmingly edge effects: nest predation, brood parasitism, and potentially, clutch size.

The pattern of local intensity of these factors suggests that they can be subsumed by a single parameter relating net recruitment near forest edges to that realized in interior forest habitats. For this approach to be justified, it must be demonstrated that (1) it is simpler and (2) it can account for observed species abundance patterns.

It seems intuitively obvious that such an approach would be simpler. It should be much easier to measure a pattern resulting from several interacting processes than to measure the processes themselves. In this case, the necessary data would be estimates of overall reproductive success in edges as compared to interior habitats, or a simple function relating reproductive success

to distance-to-an-edge. In fact, this is the sort of summary data that is most often reported from empirical studies of nesting success.

More importantly, can this approach work? Unfortunately, the Cadiz data are moot on this point; nearly all of the forest area is edge habitat, and most species that are potentially very vulnerable to edge effects on natality are no longer found in these woodlots. But a study by Temple (1986) is encouraging. Temple (1986) compared two regression models in terms of their power to predict species presence or absence in Wisconsin woodlots. The first model, a conventional approach, used total forest area as a predictor. The second model used core area, defined by Temple as forest habitat at least 200 m from an edge. The core area model consistently provided better predictions. Here, core area as a predictor subsumes edge effects, and also incorporates the shape complexity of forest patches, distinguishing between compact and irregular patches of the same total area.

In summary, several points should be emphasized. Factors affecting net recruitment represent a very effective constraint on bird species abundance patterns in a mosaic of forest patches. Species vulnerable to nest predation and brood parasitism are especially sensitive, but if clutch size is reduced systematically in forest edges then other species may be affected as well. The mechanistic details of these factors are probably beyond the grasp of empirical studies at the landscape scale. These effects, however, might be predicted by subsuming the detailed mechanisms into a parameter describing net reproductive success in edges as compared to interior

habitats. Net recruitment for a mosaic metapopulation can then be integrated from the relative productivity of edges and the relative proportion of edge habitat. This approach provides an useful direction for further studies of avian demography in mosaic landscapes.

SYNTHESIS AND PROSPECTUS

Introduction

The preceding three chapters considered the roles of the constraints of habitat availability, accessibility, and productivity in effecting bird species abundance patterns in a forest mosaic. A hierarchical framework invoked three levels of reference: territories (or individual breeding birds), forest patches (or woodlot bird assemblages), and the landscape mosaic (metapopulations) (Figure 7.1). In considering the three constraints, each of these levels was accessed as appropriate. The focal level emphasized individual habitat patches, and related habitat diversity, isolation, or edge effects to the number and variety of birds a patch could support. In each case, these constraints governed the demographics of individual birds, to generate patch-level population dynamics. These patch-level dynamics, integrated over the entire mosaic, generated species abundance patterns for the mosaic.

An important lesson that emerges from this study is that a mechanistic understanding of a complex system does not necessarily imply any ability to predict its behavior in a simple manner. Each of the three constraints considered in the preceding chapters effect avian demographics via mechanisms that are difficult if not impossible to account directly at the landscape scale. This concluding chapter attempts to synthesize a general model of avian demography in mosaic

FOREST	→	BIRDS
Landscape Mosaic	→	Metapopulation
Forest Stand (Woodlot)	→	Population
Territory	→	Nested Pair

Figure 7.1. Hierarchy of microhabitats, forest stands (woodlots), and the landscape mosaic, as a framework for studying individuals, patch-level populations (species assemblages), and metapopulations (landscape avifauna).

landscapes, and to reconcile the tandem goal of understanding as well as predicting bird species abundance patterns in habitat patches.

Because the constraints of habitat availability, accessibility, and reproductive success were assessed separately in preceding chapters, it will be helpful first to recapitulate the important results of these analyses. The focus in this synthesis is the familiar species/area relationship (Figure 7.2).

The Relative Influence of the Three Constraints

The species/area relationship is a useful focus in this synthesis because the increase in species number with increasing habitat area is a truly general phenomenon in nature. The present concern is to try to determine the relative contribution of habitat effects, dispersal effects, and patterns of reproductive success to this relationship as

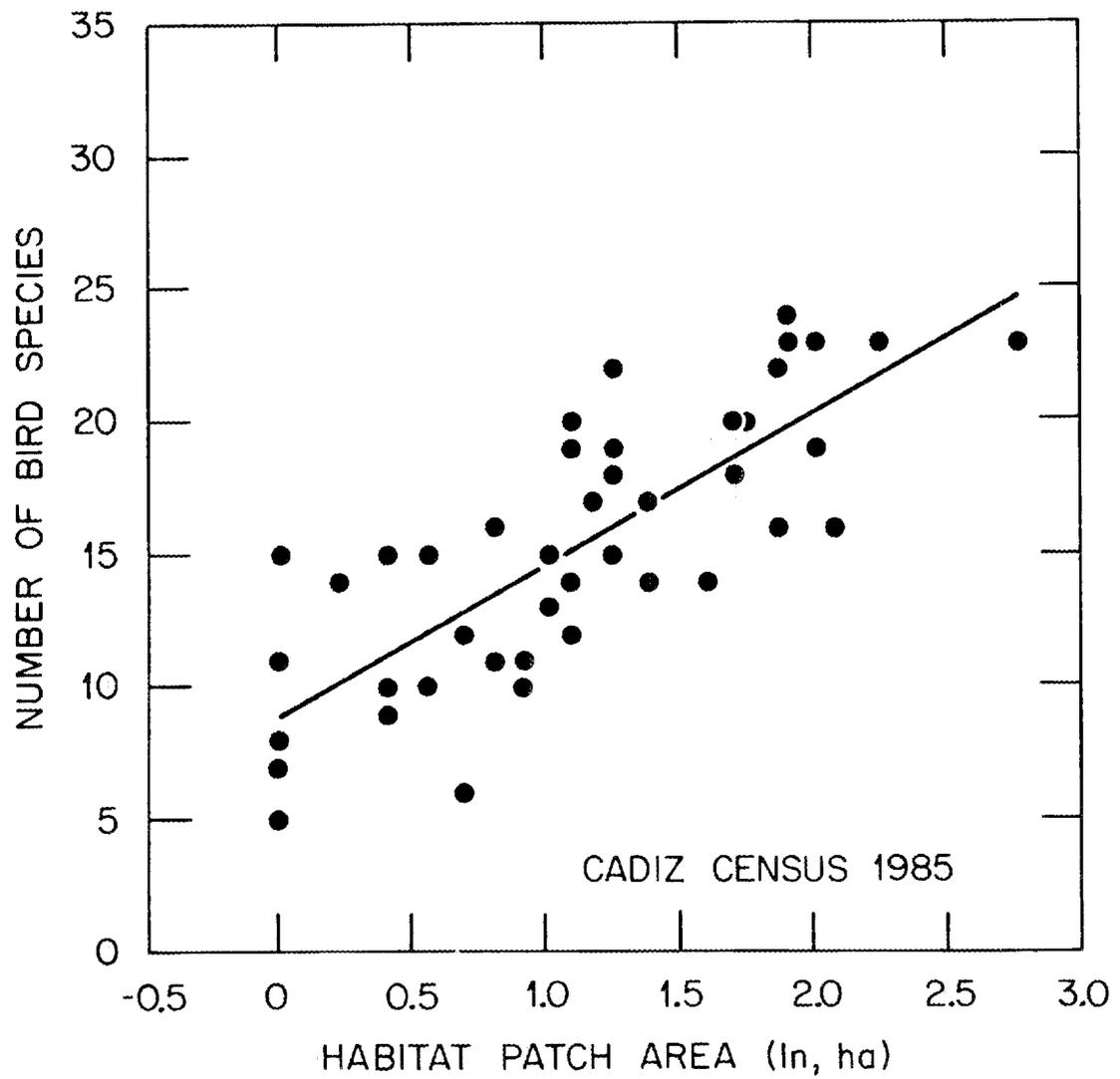


Figure 7.2. Species/area relationship for birds in Cadiz woodlots, as censused in 1985.

observed for forest birds. Direct effects of habitat area are a convenient starting point, which leads to a consideration of why area serves as such a powerful predictive variable. Later, the discussion will turn to factors that modify the basic area effect; that is, to residual variation in species abundance patterns.

Microhabitat Effects and Habitat Area

In Chapter 4 a tandem argument was developed for the utility of area as a proper surrogate for various aspects of habitat diversity. It was argued that within-stand patterns of microhabitat dynamics could generate a strong area dependency in microhabitat diversity. The forest simulation study of Urban and Smith (in review), detailed in Chapter 4, generated an area-dependency in structural microhabitat variety with approximately the same strength (regression slope) as the species/area relation found for bird species in Cadiz woodlots. While this coincidence should not be overinterpreted, it is worth noting because (to anticipate) none of the other constraints considered in this study can elicit an area effect of similar magnitude.

Edge effects on forest dynamics reduce habitat variety in very small patches (or those of irregular shape) by effectively removing these habitats from normal successional dynamics, imposing a large minimum area requirement for interior-like microhabitats. At larger scales, microhabitat turnover and beta-diversity can continue to contribute to predictable area effects even for very large forest tracts.

A second line of argument was advanced to suggest that area itself might often be a better predictor of habitat diversity than actual empirical estimates. This reflects the conceptual difficulty in defining "habitat" in terms that are relevant to birds, and the logistical difficulty of exhaustively measuring habitat diversity in field situations.

A mechanistic understanding of the factors that generate microhabitat pattern in forests suggests the conditions under which area should suffice as a surrogate variable. This in turn suggests when estimates of actual habitat diversity might prove useful in explaining residual variation in species abundance that is not accounted by area. Three factors that might contribute to such effects in man-dominated landscapes are: (1) natural or anthropogenic disturbances that are similar in spatial scale to the size of woodlots; (2) forest management practices that homogenize microhabitat pattern within management units; and (3) land use patterns that have resulted in forest remnants that are small relative to the scale of environmental gradients, so that small woodlots represent only local samples of larger patterns. In each case, woodlots that are similar in size may be very different in habitat diversity, and actual estimates of habitat diversity might improve predictions of species abundance. Even so, it seems likely that area would serve as the first estimate of habitat diversity, and empirical habitat measures might serve to account for residual variation in species abundance.

Dispersal and Isolation Effects

The dynamics of avian dispersal among habitat patches of different sizes can result in more species being supported by larger patches. In the absence of habitat variation or edge effects on net reproduction, this would result from "target" effects in dispersal and, more importantly, area effects in the persistence of founder populations. Larger patches can support more individuals, and larger populations tend to persist longer. In simulations, this species/area relation is not nearly as pronounced as in actual census data, and grossly overpredicts species abundance in small patches (Figure 7.3).

A more noteworthy contribution of dispersal is to explain isolation effects as residual variation in species abundance not attributable to habitat area. In Chapter 5 it emerged that this contribution, as relative explanatory power, bears a simple (if rather noisy) relationship to the mean dispersion of patches in a mosaic relative to the dispersal range of the local species. The explanatory power of isolation (indexed as nearest-neighbor distance) is maximized when patch dispersion is very similar to species dispersal range. For mosaics of much less dispersion (dense mosaics), isolation effects do not develop; likewise, in very sparse mosaics all of the patches are isolated so isolation has little predictive value.

Edge Effects on Net Reproduction

Biotic pressures on net natality clearly can act as an effective constraint on the distribution of at least some bird species in a

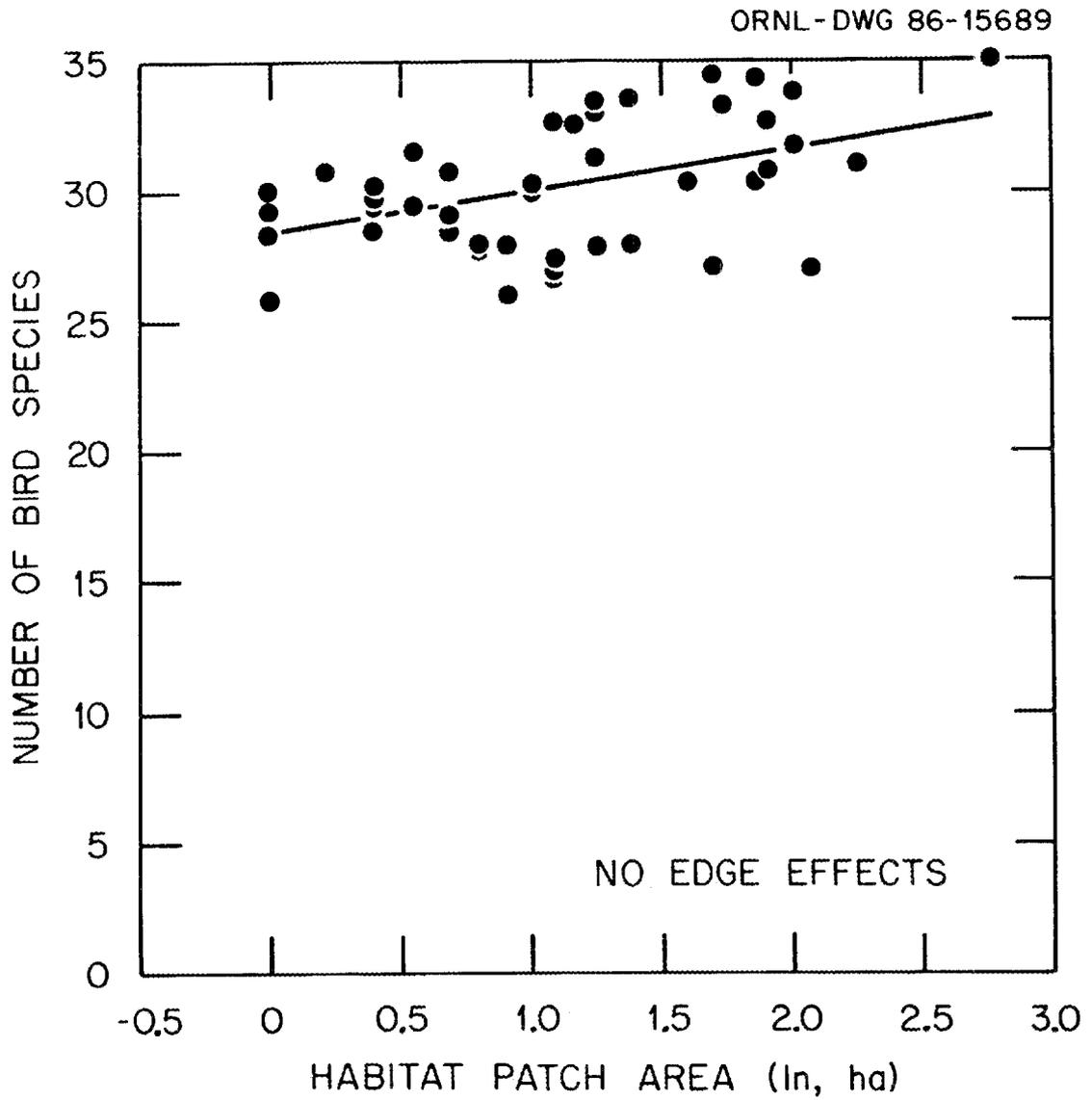


Figure 7.3. Species/area relationship for birds in Cadiz woodlots, as simulated subject to dispersal and area effects only.

forest mosaic. Because these pressures are locally intensified in forest edges, patterns of reproductive success contribute to a weak species/area relationship (Figure 7.4). This area dependency itself is not as pronounced as empirical species/area relationships for forest birds. Changes in the modeled frequency or extent (i.e., the width of the edge in which the events occur) of predation or brood parasitism do not alter this species/area relationship substantially. More intense edge effects depress the entire line but do not change the slope of this relationship.

Again, the more important contribution of edge effects on natality is to explain residual variation in species abundance not accounted by area. In particular, reduced reproductive success can explain why some species do not occur regularly in forest patches that include potential breeding habitat, but are not so large or compact as to be buffered from intense biotic pressures on nesting success.

A Prospectus from Hierarchy

The original goal of this study was to discover what has effected the regional decline of bird species sensitive to forest fragmentation. A multifactorial model invoked three constraints as likely candidates, and the question was rephrased to consider the relative contribution of each of the constraints. It has emerged, not surprisingly, that each of the constraints can contribute substantially to species abundance patterns in a forest mosaic, and that the relative importance of each constraint depends on the bird species of interest and the configuration of the habitat mosaic.

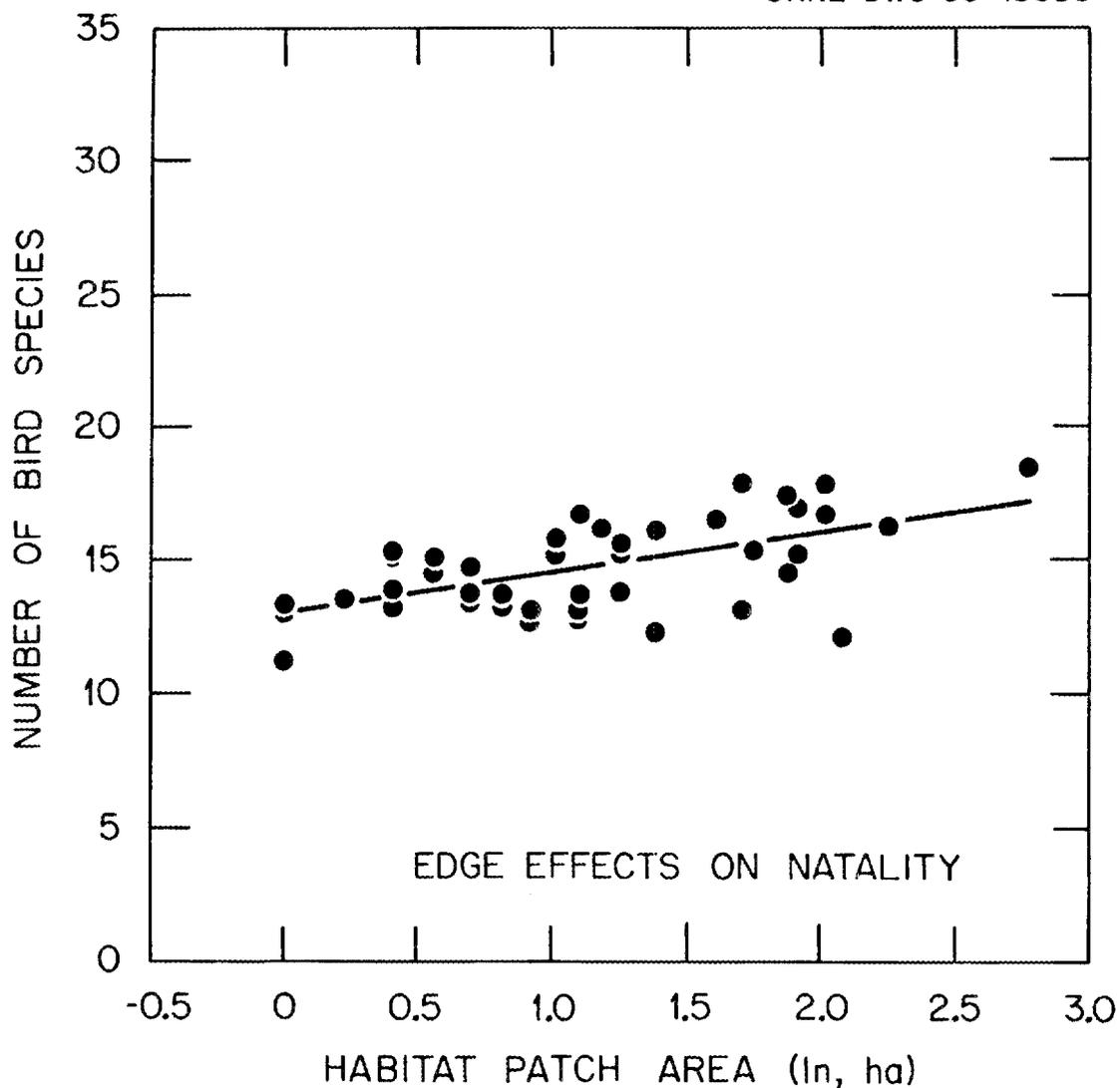


Figure 7.4. Species/area relationship for birds in Cadiz woodlots, as simulated subject to dispersal, area, and edge effects on net reproduction.

This is not a particularly satisfying answer. After all, it was apparent at the outset that the situation was complicated. But importantly, it has been possible to specify the conditions under which each of the constraints is most effective, or conversely, when each is relatively unimportant and can be ignored. Overall, the situation is complicated but specific scenarios often can be simplified considerably. Guidelines on how to simplify complex systems come from general systems theory, and from hierarchy theory in particular.

General systems theory recognizes three kinds of systems (Weinberg 1975). A large-number system is one in which the individual elements are so numerous and so similar that a description of the average element suffices to describe total system behavior. In comparison, a small-number system is one in which the elements are so few that the behavior of each can be described individually. In physics, these two approaches are exemplified by statistical and Newtonian mechanics, respectively. Between these two extremes are middle-number systems, in which the elements are too many to be described individually, but too few or too different to be averaged. Most ecological systems are middle-number systems.

When a middle-number system can be described as a multileveled hierarchy, much of its complexity can be resolved (Allen and Starr 1982, O'Neill et al. 1986). In the present case, the hierarchy of territories, woodlots, and landscape mosaic has proven to be a profitable framework in which to study birds at the level of individuals, woodlot assemblages, and metapopulations, respectively.

In this final section, hierarchy provides a prospective means of further simplifying this fundamental framework, to derive parsimonious predictive models for specific applications.

Predicting Bird Species Abundance in a Mosaic

In predictive applications the approach is to respecify the system for each case, retaining only those features of the original hierarchy that are necessary to describe and predict system behavior under the given set of conditions. The conditions vary in different landscapes or for different species of interest. The results summarized in the preceding section suggest the conditions under which each simplification can be made. There are three simplifications of the fundamental model.

Habitat Availability Limiting

The situation in which habitat availability is the principal constraint limiting a population is perhaps the simplest case. This case assumes that the constraints of accessibility and net reproduction are not important controls on the species of interest; that is, the species is neither dispersal-limited nor subject to reduced reproductive success in some habitats. In this case, the hierarchical model can be respecified as a large-number system. Describing a landscape as a large-number system deletes the patch (woodlot) level of reference, effectively divorcing microhabitats (territories) from their spatial context within woodlots. The average territory then suffices to predict species abundance at the landscape

scale (Figure 7.5a). For a habitat generalist, species abundance in the landscape is simply a function of total forest area. For a microhabitat specialist, total area of preferred breeding habitat replaces forest area as the predictive variable. As a point of reference, this seems to be--implicitly or explicitly--the working model in most traditional studies of wildlife/habitat relationships. In fact, this is probably the appropriate model for the majority of bird species in the eastern deciduous forest pool.

Habitat Accessibility Limiting

In cases where habitat is sufficiently available and all patches are similarly productive, but patches are very isolated, the effective control on demographics may be the relative accessibility of

Habitat Availability Limiting: Predicted birds = f(area)	(a)
Habitat Accessibility Limiting: Predicted birds = f(area, isolation)	(b)
Net Reproduction Limiting: Predicted birds = f(core area, edge area)	(c)

Figure 7.5. Schematic models for predicting bird species abundance in a landscape mosaic, as simplifications of a more complex model: (a) habitat availability limiting; (b) habitat accessibility limiting; (c) net reproduction limiting.

individual patches. The appropriate simplification is then to redefine the system as a small-number system. Specifying a landscape as a small-number system emphasizes the patch level of description, effectively ignoring finer-scale details. In this case, the relative frequencies (probabilities) of dispersal among patches serve to make predictions at the patch level (Figure 7.5b). It should be apparent that this is the model of island-biogeographic theory. In this perspective, a difficulty with the island-theoretic model is that the phenomenological colonization and extinction curves cannot be reduced easily to the underlying demographic mechanisms. Consequently, it is difficult to specify these curves for complex habitat mosaics. Still, it seems that the failure of island-theoretic models to consistently provide accurate predictions of bird species assemblages in woodlots may not stem from the inadequacy of the model itself. Rather, these failures may reflect the limited number of cases in which habitat accessibility is a principal determinant of bird species abundance patterns in forest mosaics. The hierarchical conceptual model, on the other hand, suggests the conditions under which the island model is appropriate.

Net Reproduction Limiting

In cases where habitats are available and accessible but they differ markedly in terms of reproductive success, it is appropriate to respecify the system to emphasize the effective factors controlling net reproduction. If all edge habitats are equally unproductive and all core habitats similarly productive, then the simplification is to

a large-number system in which the total areas of edge and core habitat are the predictor variables (Figure 7.5c). Operationally, this approach would consider territories and woodlots in summing core and edge area for the mosaic, but would not use these lower levels in making predictions. This model might have to be redefined (reparameterized) for each species of interest, depending on its particular vulnerability to factors affecting reproductive success. Such a model might also vary for different landscapes. This approach represents a potentially data-intensive task in formulating and verifying the model, but still is far simpler than dealing with myriad patches individually.

Note that the constraint of differential reproductive success can be defined more generally, to incorporate other effects on net reproduction beyond edge effects such as predation and parasitism. If habitat productivity varies in terms of food supply or some other factor that contributes to net reproduction, the model can still be partitioned in terms of productive and unproductive habitats. The general model predicts total species abundance as the integration of relative habitat productivity over the distribution of habitats of each productivity class.

This model intersects the "habitat area" model at two points. The habitat model uses the average habitat as the basis for prediction. In fact, it is only true as a special case that the expected species abundance for a mosaic (a distribution of habitats) is equal to the value predicted from the average habitat. The special case is when the integral of the distribution is equal to the mean of

the distribution, and the predictive function is linear. As a general case, the expected value for a function is the integral of the values expected from each element of the distribution (that is, the function integrated over the distribution). Thus, the general case of the first model is the general case of the third model, if productivity is the criterion. The important point is, given a habitat mosaic and an estimate of the relative productivity of the habitat patches, either model can provide a useful simplification.

The second point of intersection in the two models occurs in cases where the relative reproductive success of a species in some habitats is so low as to be nonexistent. In the limit, potential breeding habitat that is wholly unproductive is not really "habitat" at all. In this case, the "productivity" model can refine the "habitat area" model by excluding some habitats from further consideration. This intersection of the two models results in a hybrid that is simpler than either of its parent models.

The "habitat area" and "productivity" models are also similar in that each can make predictions at the mosaic scale without including woodlots explicitly. The "isolation" model can only predict at the landscape scale by summing predictions from individual patches. Of course, either of the two former models can also make predictions about individual woodlots.

A General Model

These three simplifications are special cases of a more general model that incorporates all of the cases. The general model is

consequently more complex, but not unmanageably so. In effect, each of the above simplifications is incorporated into the general model, so even this model is simpler than multifarious nature, in which each landscape is a unique integration of interacting patches, each of which is itself an integration of finer-scale microhabitat patterns and demographic processes.

The general model is a hierarchical system in which each level is isolated as a small-number subsystem of lower-level elements (Figure 7.6). Thus, each patch is an admixture of productive and unproductive (here, core and edge) territories of potential breeding habitat. Net reproductive potential is integrated to the patch level, subsuming finer-level, mechanistic descriptions of within-patch events. Patch-level interactions are specified in terms of distances between patches, reflecting but subsuming the actual mechanisms of birds flying among patches. At the level of the landscape mosaic, the behavior of the metapopulation is the integration of net recruitment in individual habitat patches, as constrained by patch accessibility.

The model is simple in that the description of the system at any level is minimalist; it is complex in that there are three levels invoked in the description. The model is general in that changes in the mechanisms or the constraints at any level will elicit different behavior for the system as a whole; obversely, a wide range of mosaic-level behaviors can be reduced to mechanisms and constraints at different levels. The model is rich because it incorporates three simpler, but more limited models. It is useful because it specifies the conditions under which each of the simpler models can provide

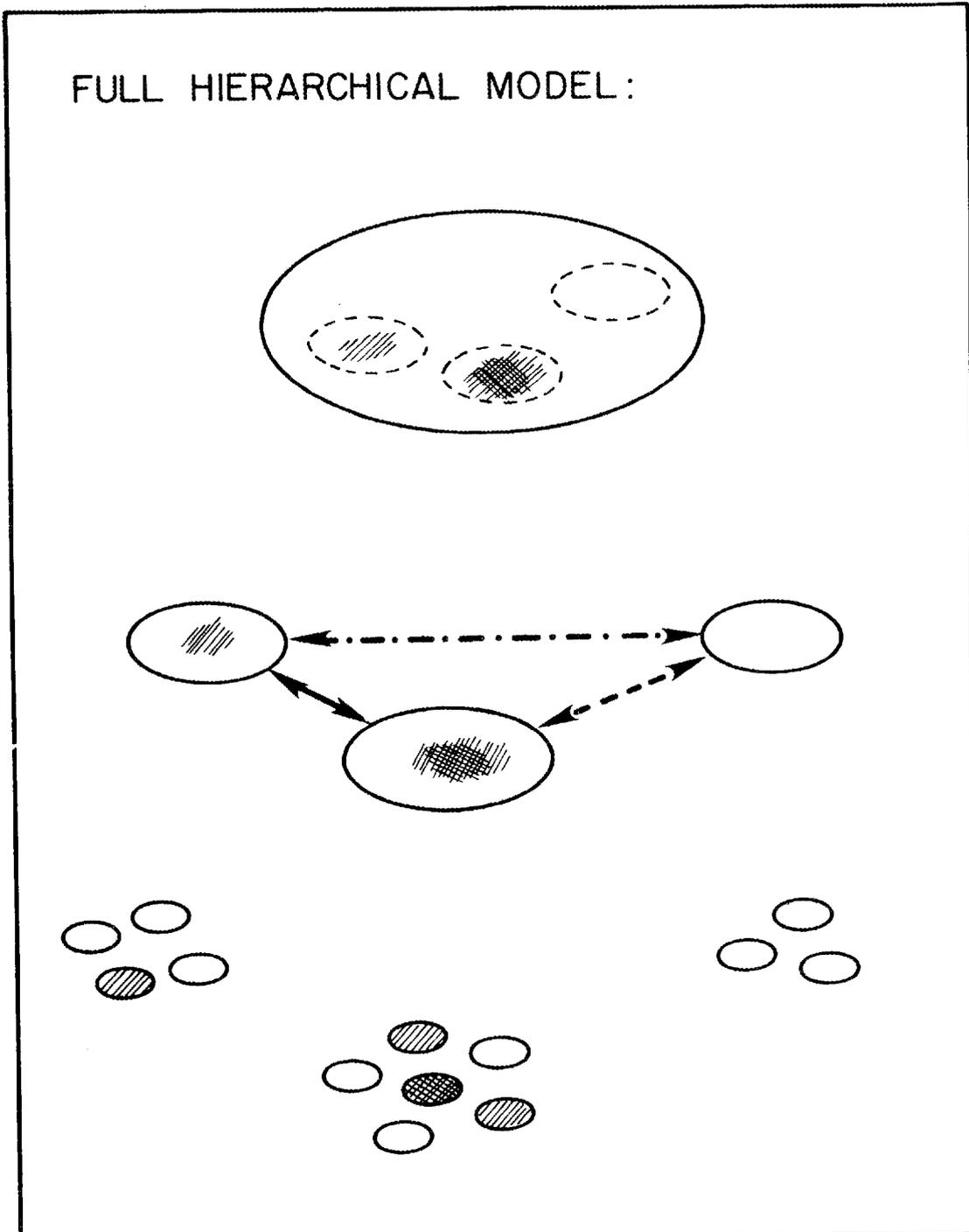


Figure 7.6. A generalized hierarchical model for predicting bird species abundance in a landscape mosaic.

valid predictions of total system behavior. As such, the general hierarchical model represents a powerful conceptual framework that can be used to extrapolate our current knowledge of avian autecology and community ecology to understand and predict bird species abundance patterns at the landscape scale.

LIST OF REFERENCES

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- Allen, T.F.H., and T.B. Starr. 1982. Hierarchy: perspectives for ecological complexity. Univ. Chicago Press, Chicago.
- Allen, T.F.H., R.V. O'Neill, and T.W. Hoekstra. 1984. Interlevel relations in ecological research and management: some working principles from hierarchy theory. USDA/FS Gen. Tech. Rep. RM-110. Rocky Mtn. For. and Range Exp. Sta., Ft. Collins, Col.
- Ambuel, B., and S.A. Temple. 1982. Songbird populations in southern Wisconsin: 1954 and 1979. *J. Field Ornithol.* 53:149-158.
- Ambuel, B., and S.A. Temple. 1983. Area-dependent changes in bird communities and vegetation of southern Wisconsin woodlots. *Ecology* 64:1057-1068.
- American Ornithologists' Union (AOU). 1982. Check-list of North American birds. *Auk* 99:1cc-16cc (supplement).
- Anderson, S.H., and H.H. Shugart, Jr. 1974. Avian community analysis of Walker Branch watershed. ORNL/TM-4700. Oak Ridge National Laboratory, Oak Ridge, Tenn.
- Bent, A.C. 1942 (1963 reprint). Life histories of North American flycatchers, larks, swallows, and their allies. Dover, New York.
- Best, L.B., and D.F. Stauffer. 1980. Factors affecting nesting success in riparian bird communities. *Condor* 82:149-158.
- Bond, R.R. 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. *Ecol. Monogr.* 27:351-384.
- Bormann, F.H., and G.E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York.
- Bowen, G.W., and R.L. Burgess. 1981. A quantitative analysis of forest island pattern in selected Ohio landscapes. ORNL/TM-7759. Oak Ridge National Laboratory, Oak Ridge, Tenn.
- Brittingham, M., and S.A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33:31-35.
- Cale, W.G., Jr., R.V. O'Neill, and H.H. Shugart, Jr. 1983. Development and application of desirable ecological models. *Ecol. Modelling* 18:171-186.
- Capen, D.E. (ed.). 1981. The use of multivariate statistics in studies of wildlife habitat. USDA For. Serv. Gen. Tech. Rep. RM-87. Rocky Mtn. For. and Range Exp. Sta., Ft. Collins, Col.

- Carnes, B.A., and N.A. Slade. 1982. Some comments on niche analysis in canonical space. *Ecology* 63:888-893.
- Caswell, H. 1978. Predator-mediated coexistence: a non-equilibrium model. *Am. Nat.* 112:127-154.
- Clapp, R.B., M.K. Klimkiewicz, and A.G. Futcher. 1983. Longevity records of North American birds: Columbidae through Paridae. *J. Field Ornithol.* 54:123-137.
- Cody, M.L. 1968. On the methods of resource division in grassland bird communities. *Am. Nat.* 102:107-147.
- Cody, M.L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and productivity. *BioScience* 31:107-113.
- Cody, M.L. (ed.). 1985. *Habitat selection in birds*. Academic Press, Orlando, Fla.
- Cohen, J.E. 1970. A Markov contingency table model for replicated Lotka-Volterra systems near equilibrium. *Am. Nat.* 104:547-559.
- Curtis, J.T. 1956. The modification of mid-latitude grasslands and forests by man. Pages 721-736 in W.L. Thomas (ed.), *Man's role in changing the face of the earth*. Univ. Chicago Press, Chicago.
- Curtis, J.T. 1959. *The vegetation of Wisconsin: an ordination of plant communities*. Univ. Wisconsin Press, Madison.
- DeAngelis, D.L., W.M. Post, and C.C. Travis. 1986. *Positive feedback in natural systems*. Springer-Verlag, Berlin.
- DeAngelis, D.L., C.C. Travis, and W.M. Post. 1979. Persistence and stability of seed-dispersed species in a patchy environment. *Theor. Pop. Biol.* 6:107-125.
- Dueser, R.D., and H.H. Shugart, Jr. 1979. Niche pattern in a forest-floor small mammal fauna. *Ecology* 60:108-118.
- Edler, W.H. 1985. Survivorship in the tufted titmouse. *Wilson Bull.* 97:517-524.
- Fahrig, L., L.P. Lefkovitch, and H.G. Merriam. 1983. Population stability in patchy environment. Pages 61-67 in W.K. Lauenroth, G.V. Skogerboe, and M. Flug (eds.), *Analysis of ecological systems: state-of-the-art in ecological modelling*. *Developments in Environmental Modelling*, No. 5. Elsevier, Amsterdam.

- Finley, R.W. 1976. Original vegetation cover of Wisconsin from United States General Land Office notes. (map) USDA For. Serv., Northcentral For. Exp. Sta., St. Paul, Minn.
- Forman, R.T.T. 1981. Interactions among landscape elements: a core of landscape ecology. Pages 35-48 in S.P. Tjallingii and A.A. de Veer (eds.), *Perspectives in landscape ecology*, Pudoc, Wageningen.
- Forman, R.T.T. 1983. An ecology of the landscape. *BioScience* 33:535.
- Forman, R.T.T., and M. Godron. 1981. Patches and structural components for a landscape ecology. *BioScience* 31:733-740.
- Forman, R.T.T., and M. Godron. 1986. *Landscape ecology*. Wiley, New York.
- Forman, R.T.T., A.E. Galli, and C.F. Leck. 1976. Forest size and avian diversity in New Jersey woodlots with some land use implications. *Oecologia* 26:1-8.
- Galli, A.E., C.F. Leck, and R.T.T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. *Auk* 93:356-364.
- Gardner, R.H., R.V. O'Neill, and J.H. Carney. 1981. A comparison of sensitivity analysis and error analysis based on a stream ecosystem model. *Ecol. Modelling* 12:173-190.
- Gates, J.E., and L.W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871-883.
- Gilbert, L.E. 1980. The equilibrium theory of island biogeography: fact or fiction? *J. Biogeogr.* 7:209-235.
- Greenwood, P.J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.* 28:1140-1162.
- Greenwood, P.J., and P.H. Harvey. 1982. The natal and breeding dispersal of birds. *Ann. Rev. Ecol. Syst.* 13:1-21.
- Grinnell, J. 1917. The niche-relationships of the California thrasher. *Auk* 34:427-433.
- Hann, H.W. 1937. Life history of the ovenbird in southern Michigan. *Wilson Bull.* 49:145-237.
- Hastings, A. 1977. Spatial heterogeneity and the stability of predator-prey systems. *Theor. Pop. Biol.* 12:37-48.

- Hilborn, R. 1975. The effect of spatial heterogeneity on the persistence of predator-prey interactions. *Theor. Pop. Biol.* 8:346-355.
- Hilden, O. 1965. Habitat selection in birds. *Ann. Zool. Fenn.* 2:53-75.
- Horn, H.S., and R.H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. *Ecology* 53:749-752.
- Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harbor Symp. on Quant. Biol.* 22:415-427.
- James, F.C. 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bull.* 83:215-236.
- Keast, A., and E.S. Morton (eds.). 1980. *Migrant birds in the neotropics: ecology, behavior, distribution, and conservation.* Smithsonian Inst. Press, Washington, D.C.
- Kendeigh, S.C. 1942. Analysis of losses in the nesting of birds. *J. Wildl. Manage.* 6:19-26.
- Klimkiewicz, M.K., R.B. Clapp, and A.G. Futcher. 1983. Longevity records of North American birds: Remizidae through Parulinae. *J. Field Ornithol.* 54:287-294.
- Klopfer, P. 1965. Behavioral aspects of habitat selection: a preliminary report on stereotypy in foliage preferences of birds. *Wilson Bull.* 77:376-381.
- Lack, D. 1947. The significance of clutch size. *Ibis* 89:302-352.
- Lack, D. 1954. *The natural regulation of animal numbers.* Clarendon, Oxford.
- Lack, D. 1966. *Population studies of birds.* Clarendon, Oxford.
- Lack, D. 1968. *Ecological adaptations for breeding in birds.* Methuen, London.
- Lefkovitch, L.P., and L. Fahrig. 1985. Spatial characteristics of habitat patches and population survival. *Ecol. Modelling* 30:297-308.
- Levenson, J.B. 1981. Woodlots as biogeographic islands in southeastern Wisconsin. Pages 13-39 in R.L. Burgess and D.M. Sharpe (eds.), *Forest island dynamics in man-dominated landscapes.* Springer-Verlag, New York.

- Levin, S.A. 1974. Dispersion and population interactions. *Am. Nat.* 108:207-228.
- Levin, S.A. 1976. Population dynamic models in heterogeneous environments. *Ann. Rev. Ecol. Syst.* 7:287-310.
- Levins, R., and D. Culver. 1971. Regional co-existence of species and competition between rare species. *Proc. Nat. Acad. Sci.* 68:1246-1248.
- Lynch, J.F., and D.F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biol. Conserv.* 28:287-324.
- Lynch, J.F., and R.F. Whitcomb. 1978. Effects of the insularization of the eastern deciduous forest on avifaunal diversity and turnover. Pages 461-489 in A. Marmelstein (ed.), *Classification, inventory, and analysis of fish and wildlife habitat*. USDI Fish and Wildlife Service, Washington, D.C.
- MacArthur, R.H. 1971. Patterns in terrestrial bird communities. Pages 189-221 in D.S. Farner and J.R. King (eds.), *Avian biology*. Vol. 1. Academic Press, New York.
- MacArthur, R.H., and J.W. MacArthur. 1961. On bird species diversity. *Ecology* 42:494-498.
- MacArthur, R.H., and E.O. Wilson. 1967. *The theory of island biogeography*. Princeton Univ. Press, Princeton, N.J.
- MacArthur, R.H., J.W. MacArthur, and J. Preer. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. *Am. Nat.* 96:167-174.
- MacClintock, R.F. Whitcomb, and B.L. Whitcomb. 1977. Island biogeography and "habitat islands" of eastern forest. II. Evidence for the value of corridors and minimization of isolation in preservation of biotic diversity. *Am. Birds* 31:6-16.
- Mankin, J.B., R.V. O'Neill, H.H. Shugart, Jr., and B.W. Rust. 1975. The importance of validation in ecosystems analysis. In G.S. Innis (ed.), *New directions in the analysis of ecological systems, part 1*. Simulation Councils Proceedings Series, vol. 5, Simulation Councils, LaJolla, Cal.
- May, R.M., and S.K. Robinson. 1985. Population dynamics of avian brood parasitism. *Am. Nat.* 126:475-494.
- Middleton, J.D., and G. Merriam. 1981. Woodland mice in a farmland mosaic. *J. Appl. Ecol.* 18:703-710.

- Middleton, J.D., and G. Merriam. 1983. Distribution of woodland species in farmland woods. *J. Appl. Ecol.* 20:625-644.
- Moore, N.W., and M.D. Hooper. 1975. On the number of bird species in British woods. *Biol. Conserv.* 8:239-250.
- Morse, D.H. 1977. The occupation of small islands by passerine birds. *Condor* 79:399-412.
- Naveh, Z., and A.S. Liebermann. 1984. *Landscape ecology: theory and application.* Springer-Verlag, New York.
- Nice, M.M. 1937 (1964 reprint). *Studies in the life history of the song sparrow.* Dover Press, New York.
- Nice, M.M. 1957. Nesting success in altricial birds. *Auk* 74:305-321.
- Nolan, V. 1963. Reproductive success of birds in a deciduous scrub habitat. *Ecology* 44:305-313.
- Noon, B.R., D.K. Dawson, D.B. Inkley, C.S. Robbins, and S.H. Anderson. 1980. Consistency in habitat preference of forest birds. *Trans. North Am. Wildl. and Nat. Resource Conf.* 45:226-244.
- Okubo, A. 1980. *Diffusion and ecological problems: mathematical models.* Springer-Verlag, New York.
- O'Neill, R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen. 1986. *A hierarchical concept of the ecosystem.* Princeton Univ. Press, Princeton, N.J.
- Pattee, H. 1973. *Hierarchy theory.* Braziller, New York.
- Pielou, E.C. 1977. *Mathematical ecology.* Wiley, New York.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity. I. *Ecology* 43:185-215. II. *Ecology* 43:410-432.
- Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contrib. Zool.* 9:1-48.
- Ricklefs, R.E. 1972. Fecundity, mortality, and avian demography. Pages 366-435 in D.S. Farner (ed.), *Breeding biology of birds.* Nat. Acad. Sci., Washington, D.C.
- Risser, P.G., J.R. Karr, and R.T.T. Forman. 1984. *Landscape ecology: directions and approaches.* Special Publ. No. 2, Ill. Nat. Hist. Surv., Champaign, Ill.

- Robbins, C.S. 1979. Effect of forest fragmentation on bird populations. Pages 198-212 in R.M. DeGraaf and K.E. Evans (eds.), Management of northcentral and northeastern forests for nongame birds. USDA For. Serv. Gen. Tech. Rep. NC-51. Northcentral For. Exp. Sta., St. Paul, Minn.
- Robinson, S.K., and R.T. Holmes. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology* 63:1918-1931.
- Roth, R.R. 1976. Spatial heterogeneity and bird species diversity. *Ecology* 57:773-782.
- SAS (Statistical Analysis System). 1982. SAS user's guide: statistics. SAS Institute, Cary, N.C.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science* 185:27-39.
- Seagle, S.W., and G.F. McCracken. 1986. Species abundance, niche position, and niche breadth for five terrestrial animal assemblages. *Ecology* 67:816-818.
- Seagle, S.W., H.H. Shugart, Jr., and D.C. West. 1984. Habitat availability and animal community characteristics. ORNL/TM-8864. Oak Ridge National Laboratory, Oak Ridge, Tenn.
- Sharpe, D.M., F.W. Stearns, R.L. Burgess, and W.C. Johnson. 1981. Spatio-temporal patterns of forest ecosystems in man-dominated landscapes. Pages 109-116 in S.P. Tjallingii and A.A. de Veer (eds.), Perspectives in landscape ecology. Pudoc, Wageningen.
- Sharpe, D.M., G.R. Gunterspergen, C.P. Dunn, L. Leitner, and F. Stearns. Vegetation dynamics of a southern Wisconsin agricultural landscape. In M.L. Turner (ed.), Landscape heterogeneity and disturbance. Springer-Verlag, New York. (in press)
- Sherry, T.W., and R.T. Holmes. 1985. Dispersion patterns and habitat responses of birds in northern hardwood forests. Pages 283-309 in M.L. Cody (ed.), Habitat selection in birds. Academic Press, Orlando, Fla.
- Shriner, F.A., and E.B. Copeland. 1904. Deforestation and creek flow about Monroe, Wisconsin. *Bot. Gazette* 37:139-143.
- Shugart, H.H., Jr. 1984. A theory of forest dynamics. Springer-Verlag, New York.

- Shugart, H.H., Jr., and B.C. Patten. 1972. Niche quantification and the concept of niche pattern. Pages 283-327 in B.C. Patten (ed.), Systems analysis and simulation in ecology, vol. II. Academic Press, New York.
- Shugart, H.H., Jr., and D.C. West. 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. J. Environ. Manage. 5:161-179.
- Skellam, J.G. 1951. Random dispersal in theoretical populations. Biometrika 38:196-218.
- Skellam, J.G. 1973. The formulation and interpretation of mathematical models of diffusory processes in population biology. Pages 63-85 in M.S. Bartlett and R.W. Hiorns (eds.), The mathematical theory of the dynamics of biological populations. Academic Press, New York.
- Slatkin, M. 1974. Competition and regional coexistence. Ecology 55:128-134.
- Smith, T.M., and D.L. Urban. Scale and resolution of forest structural pattern. (manuscript in review)
- Smith, T.M., and D.L. Urban. ZELIG: a spatially interactive forest simulator. ORNL/TM-_____, Oak Ridge National Laboratory, Oak Ridge, Tenn. (in prep.)
- Smith, T.M., H.H. Shugart, Jr., and D.C. West. 1981. FORHAB: a forest simulation model to predict habitat structure. Pages 104-113 in D.E. Capen (ed.), The use of multivariate statistics in studies of wildlife habitat. USDA For. Serv. Gen. Tech. Rep. RM-87. Rocky Mtn. For. and Range Exp. Sta., Ft. Collins, Col.
- Smith, T.M., H.H. Shugart, Jr., and D.C. West. 1982. Variation in territory size of the ovenbird (Seiurus aurocapillus): the role of habitat structure. ORNL/TM-8187. Oak Ridge National Laboratory, Oak Ridge, Tenn.
- Stenger, J., and J.B. Falls. 1959. The utilized territory of the ovenbird. Wilson Bull. 71:125-140.
- Temple, S.A. 1986. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. Pages 301-304 in J. Verner, M.L. Morrison, and C.J. Ralph (eds.), Modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison, Wis.

- Urban, D.L. 1981. Habitat relationships of birds and small mammals in second-growth forests. M.S. thesis, Southern Illinois University, Carbondale.
- Urban, D.L., and H.H. Shugart, Jr. 1986. Avian demography in mosaic landscapes: modeling paradigm and preliminary results. Pages 273-279 in J. Verner, M.L. Morrison, and C.J. Ralph (eds.), Modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison, Wis.
- Urban, D.L., and T.M. Smith. Microhabitat pattern and the structure of forest bird communities. (manuscript in review)
- Watt, A.S. 1925. On the ecology of British beech woods, with special reference to their regeneration. II. The development and structure of beech communities on the Sussex Downs. *J. Ecol.* 13:27-73.
- Watt, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* 35:1-22.
- Weinberg, G.M. 1975. An introduction to general systems thinking. Wiley, New York.
- Weise, C.M., and J.R. Meyer. 1979. Juvenile dispersal and development of site fidelity in the black-capped chickadee. *Auk* 96:40-55.
- Whitcomb, R.F., J.F. Lynch, P.A. Opler, and C.S. Robbins. 1976. Island biogeography and conservation: strategy and limitations. *Science* 193:1027-1032.
- Whitcomb, R.F., J.F. Lynch, M.K. Klimkiewicz, C.S. Robbins, B.L. Whitcomb, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-205 in R.L. Burgess and D.M. Sharpe (eds.), *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York.
- Whyte, L.L., A.G. Wilson, and D. Wilson. 1969. Hierarchical structures. Elsevier, New York.
- Wiens, J.A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornith. Monogr.* 8, AOU, Ithaca, N.Y.
- Wiens, J.A. 1974. Habitat heterogeneity and avian community structure in North American grasslands. *Am. Midl. Nat.* 91:195-213.

- Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.
- Willson, M.F. 1974. Avian community organization and habitat structure. *Ecology* 55:1017-1029.
- Zeigler, B.P. 1977. Persistence and stability of predator-prey systems induced by discrete event population exchange mechanisms. *J. Theoret. Biol.* 67:687-713.

APPENDIX A

COMMON AND SCIENTIFIC NAMES OF BIRD SPECIES

Table A.1. Common and scientific names of bird species (following AOU 1982).

AOU Common Name	Scientific Name
Mourning Dove	<i>Zenaida macroura</i>
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>
Downy Woodpecker	<i>Picoides pubescens</i>
Hairy Woodpecker	<i>Picoides villosus</i>
Northern Flicker	<i>Colaptes auratus</i>
Pileated Woodpecker	<i>Dryocopus pileatus</i>
Eastern Wood-Pewee	<i>Contopus virens</i>
Acadian Flycatcher	<i>Empidonax virescens</i>
Great Crested Flycatcher	<i>Myiarchus crinitus</i>
Blue Jay	<i>Cyanocitta cristata</i>
Black-capped Chickadee	<i>Parus atricapillus</i>
Tufted Titmouse	<i>Parus bicolor</i>
White-breasted Nuthatch	<i>Sitta carolinensis</i>
House Wren	<i>Troglodytes aedon</i>
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>
Veery	<i>Catharus fuscescens</i>
Wood Thrush	<i>Hylocichla mustelina</i>
American Robin	<i>Turdus migratorius</i>
Gray Catbird	<i>Dumetella carolinensis</i>
Brown Thrasher	<i>Toxostoma rufum</i>
European Starling	<i>Sturnus vulgaris</i>
Yellow-throated Vireo	<i>Vireo flavifrons</i>
Red-eyed Vireo	<i>Vireo olivaceus</i>
Yellow Warbler	<i>Dendroica petechia</i>
Cerulean Warbler	<i>Dendroica cerulea</i>
Black-and-white Warbler	<i>Mniotilta varia</i>
American Redstart	<i>Setophaga ruticilla</i>
Ovenbird	<i>Seiurus aurocapillus</i>
Common Yellowthroat	<i>Geothlypis trichas</i>
Scarlet Tanager	<i>Piranga olivacea</i>
Northern Cardinal	<i>Cardinalis cardinalis</i>
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>
Indigo Bunting	<i>Passerina cyanea</i>
Rufous-sided Towhee	<i>Pipilo erythrophthalmus</i>
Chipping Sparrow	<i>Spizella passerina</i>
Field Sparrow	<i>Spizella pusilla</i>
Song Sparrow	<i>Melospiza melodia</i>
Common Grackle	<i>Quiscalus quiscula</i>
Brown-headed Cowbird	<i>Molothrus ater</i>
Northern Oriole	<i>Icterus galbula</i>

APPENDIX B
DOCUMENTATION OF THE AVIAN DEMOGRAPHY SIMULATOR

DOCUMENTATION OF THE AVIAN DEMOGRAPHY SIMULATOR

Introduction

This appendix details the implementation of the simulation model described more generally in Chapter 3. In combination with Chapter 3, this and the following appendix (the listing of the source code) provide a comprehensive documentation and user's guide for the avian demographics simulator. The model was developed to be versatile, in that a wide variety of scenarios might be simulated with minimal changes in the basic program. The program was written, however, with certain kinds of applications in mind, and its configuration reflects this. Before documenting the program itself, it will be helpful to overview the structure of the model and the kinds of applications for which it was written.

The simulator was developed toward 2 kinds of applications: extrapolations and model experiments. Extrapolations simply extend local (patch-level) population dynamics to their longer-term or larger-scale implications. Model experiments contrast simulated scenarios, either in terms of species traits or mosaic characteristics. Because demographics are modeled as stochastic events, both sorts of applications require multiple replicates. An extrapolation is replicated to describe the variance associated with a mean population trend; experimental treatments are replicated, as with any experimental design, to satisfy the conditions for valid statistical inference.

The practical consequence of this application-oriented model is that the bulk of the program is relegated to control, replication, and

summary output routines. The program can be divided into 3 sections: (1) run control, initialization, and preview; (2) the annual demographics cycle; and (3) summary statistics and output utilities. After reviewing the main program, and a brief note on coding conventions, each of these 3 sections is detailed in turn.

Overview of Main Program

As discussed in Chapter 3, there are 2 versions of the simulator, available as single-species and multi-species programs. The 2 programs are identical in every regard except dimensionality and the amount of detail reported in output routines. This documentation focuses on the multi-species program; particulars of the single-species program are noted where appropriate.

The simulator is written in standard FORTRAN with no installation-specific extensions. The goal was to write code that could be easily deciphered by a novice user, hence tractability assumed a higher priority than computational efficiency or coding elegance. The program is modular, with 16 subroutines; nearly all variables are stored in COMMON blocks. These COMMON blocks contain run control parameters (labelled CONTRL), avian life-history parameters (BIRDS), and mosaic characteristics (MOSAIC).

Variable names are mnemonic insofar as possible. A few other coding conventions indicate the type of variable or its usage. The prefix K- is either a Boolean switch (e.g., KEDGE=1 invokes edge effects on natality) or a counter (KSP is the kth species).

N- prefixes a number or tally (NSPP is the number of simulated species), and I and J index patches. Mnemonics and descriptions of variables in COMMON blocks are summarized in Table B.1. Hereafter, capitalized names refer to variables or subroutines in the model.

Run Control, Initialization, and Preview

Subroutine INITL

The initialization routine sets control parameters and defines constants for the simulation. Run control parameters include the number of species simulated, the number of replicates, simulated years per replicate, and print interval for output censuses. Species constants include the site fidelity of breeders and floaters, and the minimum fraction of a territory that can be occupied by a breeder. Optional controls may be specified (1) to invoke edge effects on nesting success, (2) to increase mortality for floaters, (3) to begin simulation with random or user-provided initial populations (see subroutine IPOPN), and (4) to define the resolution of "usable habitat." If edge effects are invoked, intensities of brood parasitism and nest predation must be specified; these parameters represent the frequency of these events in edge habitats, above and beyond their occurrence in interior habitats. Mortality of floaters is adjusted by specifying their survivorship relative to breeders.

Habitat may be defined at 4 levels of resolution: (1) total patch area may qualify as usable habitat for all species; (2) species may be classified as generalists (using total patch area) or obligate edge species (using only a 50-m perimeter); (3) species may be

Table B.1. Names and definitions of variables stored in COMMON blocks.

VARIABLE	DEFINITION
COMMON/CONTRL:	Scalar Constants and Optional Control Parameters
NREPS	Number of replicate simulations; KREP is the counter
NSPP	Number of simulated species; indexed by KSP
NYRS	Number of years simulated; KYR is the counter
KPRT	Print interval (years) for output censuses
KHAB	Option to define level of resolution of "habitat"
KIP	Option to use random or user-provided initial populations
KFLTS	Option to adjust floater survivorship; if so, RSFLT is the relative survivorship of floaters
KEDGE	Option to adjust reproductive success in edge habitats; if so, XBP and XND are the probabilities of brood parasitism and nest depredation in edges
FBRD	Fidelity of breeders to nesting habitat, i.e., the probability of returning to the same site
FFLT	Site fidelity of floaters
TSMIN	Minimum territory fraction that can be occupied
IY	Seed and argument for uniform-random number generator
COMMON/MOSAIC:	Mosaic Characteristics, Arrayed per Habitat Patch
NI	Number of patches (islands) in simulation (indexed by I)
ML	Mosaic label used in output (4 characters maximum)
NAME	Mosaic name used in printed output (60 characters max)
IXY(I,L)	Cartesian grid coordinates for patch I; (L=1,2 for X,Y)
AREA(I)	Total area of habitat patch I
CORE(I)	Core (interior) area (more than 50 m from an edge)
EDGE(I)	Edge area (50-m perimeter)
CC(I,K)	Carrying capacity of patch I for species K
DIST(I,J)	Edge-to-edge distance from patch I to patch J
RECOL(I,J,K)	Probability of dispersal from patch I to J, for an individual of subpopulation K (1=breeders, 2=floaters)
COMMON/BIRDS:	Demographic Variables, Arrayed per Species
NBRD(I,K)	Number of breeders of species K in patch I
NFLT(I,K)	Number of floaters of species K in patch I
JUV(I,K)	Juveniles of species K in patch I
MSP(K)	Mnemonic for species K (4 characters max)
KGHAB(K)	Kind of gross habitat preferred (generalist, core, edge)
TS1(K)	Minimum territory size (ha)
TS2(K)	Territory size in intact forest; the reciprocal of maximum breeding density, MBD(K)
CLUTCH(K)	Clutch size (eggs per brood)
BROODS(K)	Number of broods per season
PND(K)	Probability of nest depredation in edges
PBP(K)	Probability of brood parasitism in edges
SURV(K)	Annual survivorship probability
RANGE(K)	Maximum likely distance for a single dispersal move (m)
MOBIL(K)	Mobility, the number of dispersal moves
PCCI(K)	% of carrying capacity initialized (random initials)
INPOP(I,K)	Initial populations (if provided by user)

classified as generalists, edge species, or interior species; or (4) the carrying capacity of each patch for each species may be provided as input data. This last option allows the demographics simulator to be coupled to an external habitat classification scheme (e.g., discriminant functions), or by extension, to be driven by a habitat simulation model (e.g., Smith et al. 1981).

Subroutine INPUT

Input data are provided as external data files read from logical units 3 (see subroutine IPOPN), 4 (species life-history parameters), and 5 (mosaic data). These separate files make it easier to configure model experiments by manipulating single files (mosaics or species) while holding others constant. The mosaic data file provides the number of patches in the mosaic, and a mosaic label and title used in printed output; an array of patches described by their grid coordinates and areas (total, core, and edge); and a matrix of inter-patch distances. These distances could be calculated internally (as Euclidean distances, using grid coordinates), but are provided externally so that the distance measure can incorporate shape complexity, or so distance can be weighted to reflect the "navigability" of intervening nonhabitats. This latter option is especially amenable to grid-based information management systems that include algorithms for computing weighted distances.

The species data file consists of an array of life-history parameters that are converted for use in subsequent demographics routines; only the converted parameters are retained as COMMON variables. These conversions concern (1) territory sizes, (2) clutch size, and (3) survivorship.

Two territory sizes are used in the model: minimum defended territory (TS1; as would be estimated from census spot-maps), and a second area (TS2) based on maximum reported densities in intact forest (calculated as the inverse of this maximum, in nested pairs per 100 ha). The former (usually smaller) territory defines the smallest patch that can be occupied by a species, while the latter (sometimes much larger) area prevents a species from packing large patches at extraordinary densities.

Clutch size is input as the average number of eggs per brood. This value is then adjusted for sex ratio and fledging success under optimal conditions. It is assumed that base fledging success is 60% and 66% for open- and hole-nesting species, respectively (Nice 1957; Ricklefs 1969, 1972). Given a 1:1 sex ratio, this yields adjusted clutch size correction factors of 0.30 and 0.33 for open- and hole-nesters.

Mortality is calculated from maximum reported age for wild birds, estimated to the nearest year. The calculation is based on the assumptions that survivorship is age-independent after the first (hatching) year, and that 1% of individuals survive to reach maximum age. Annual survivorship is then computed

$$\text{SURV}^{\text{MAXAGE}} = 0.01,$$

or

$$\text{MAXAGE} * \ln(\text{SURV}) = \ln(0.01),$$

or

$$\ln(\text{SURV}) = -4.605/\text{MAXAGE},$$

or

$$\text{SURV} = \exp(-4.605/\text{MAXAGE}).$$

Because this calculation is extremely sensitive to the estimated maximum age, and this input parameter can rarely be estimated precisely, a further adjustment is made if necessary. In this, survivorship is corrected so that net natality (adjusted clutch size times the number of broods per season) minus mortality is nonnegative. That is, it is assumed that no extant member of the species pool has a biologically untenable net recruitment rate under optimal conditions.

INPUT also assigns carrying capacities for each species in each patch. This assignment is based on the usable habitat area in a patch (HA), as dictated by the habitat resolution option in INITL, and on both territory sizes. Small patches ($HA \leq TS1$) have a fractional carrying capacity computed as $HA/TS1$. Patches of intermediate size ($TS1 < HA < TS2$) have a carrying capacity of 1.0 bird; larger patches have a carrying capacity computed as $HA/TS2$. A patch with a fractional territory less than the minimum occupiable fraction (TSMIN) has its carrying capacity truncated to 0.00. Otherwise, fractional territories are occupied probabilistically, so that a patch with carrying capacity for 1.8 birds could support 2 birds with chance 0.80, and 1 bird with probability 0.20. Again, territory fractions less than TSMIN cannot be occupied. Occupancy is determined on a per-bird basis, so small fractional territories are likely to be filled in times or locales of high population density. This implementation in effect allows territories to contract somewhat at high densities.

Subroutine PROBLY

PROBLY calculates the dispersal probability matrices for breeders and floaters. The calculation proceeds in 2 stages: a dispersal "flow" rate is computed for each pair of patches, and then these rates are adjusted so that the rows of the probability matrix sum to 1.0.

Emigrant flow from patch I to J is calculated as a negative-exponential function of inter-patch distance, subject to the assumption that 1% of individuals disperse to their maximum range. Flow is thus defined

$$\text{FLOW}(I,J)=\exp(-4.605*\text{DIST}(I,J)/R),$$

where -4.605, the natural log of 0.01, scales the function to equal 0.01 when inter-patch distance equals R, the maximum range of the species in question.

The matrix of flow rates between patches is then adjusted according to site fidelity and the relative proximity of patches. Because site fidelity is different for each subpopulation, separate dispersal matrices are computed for breeders and floaters. Each of these matrices initially has site fidelity (FBRD or FFLT, for breeders or floaters, respectively) as its diagonal elements, and flow rates as off-diagonal elements. For a patch surrounded by several other patches, the flow rates are relativized so that birds are apportioned according to the relative proximity of the patches. Reciprocally, for a patch in isolation, site fidelity is adjusted so that birds are retained. Thus, the configuration of a mosaic can effectively reshape

the negative-exponential dispersal-distance relationship. The dispersal probability matrix for breeders is defined

$$\text{RECOL}(I,J,1) = \frac{\text{FLOW}(I,J)}{\text{SUM}} \frac{1.0-\text{FBRD}}{1.0-\text{FBRD}}$$

for $I=J$, and site fidelity is

$$\text{RECOL}(I,I,1) = \frac{\text{FBRD}}{\text{SUM}} \frac{1.0-\text{FBRD}}{1.0-\text{FBRD}}$$

where SUM is the sum of FLOW(I,J) over all $I=J$. The dispersal probability matrix for floaters is similarly defined, except FFLT replaces FBRD in the calculations. These matrices must be recomputed for each species with a different dispersal range, so it is computationally efficient to stack species with the same range in the species data array.

Subroutine IPOPN

This routine establishes initial populations for each replicate simulation. There are 2 alternatives, specified as an option in subroutine INITL: random initial populations, or user-provided initials. If random initials are used, the program generates these anew for each replicate. The percentage of total mosaic carrying capacity initialized (PCCI) is set arbitrarily at 50%. Initial populations contain breeders only (no floaters), and these are randomly located within patches with available territories.

Alternatively, initial populations may be provided as input data (read from unit 3). This option might be used, for example, if actual census data were available for a particular habitat mosaic. If initials are provided, they are retained and reused for each replicate.

Because the starting locations of birds can conceivably affect future metapopulation dynamics, these 2 initialization options might result in different simulated results for an otherwise similar scenario. For example, 10 replicates initialized with 30 birds in a single patch would likely exhibit different dynamics, on average, than 10 replicates using randomly located initials. Care should be taken that the initialization mode is appropriate to a particular application or model experiment.

Subroutine PRINT1

This output routine, the first of 3 print options, overviews the simulation scenario (options in effect), tallies species parameters (as modified in INPUT), and prints a descriptive summary of the habitat mosaic being used. Much of the printout serves to record input data, since the input files are external to the program and may vary for each simulation.

The mosaic characterization includes patch areas and grid locations (i.e., input data), as well as summary spatial statistics. These statistics, based on a floater dispersal-probability matrix (with RANGE=5000 m), are (1) the number of patches that are functionally connected to each patch, (2) the total area of these connected patches, and (3) the nearest-neighbor distance for each

patch. For the entire mosaic, the routine prints the total habitat area, total and percentage core and edge habitat, and total and percentage of habitat included in patches larger than 40 ha ("refuges"); total dispersal flow among patches and this sum relative to the maximum possible flow (total connectedness); and the mean nearest-neighbor distance among patches (an index of patch dispersion).

The routine then summarizes the carrying capacity of the mosaic for each species, as well as the number of patches that can support each species and the total area of these patches. Finally, if initial populations are provided as input data and are to be retained for each replicate, these initial censuses are printed.

This output routine, as well as other print routines (PRINT2, PRINT3, and RSTATS), write to logical unit 8, which can be routed to a separate output file from the system compilation printout (which itself can be suppressed to save paper). Further, these routines are formatted to 80-column width, so the output can be printed on 8.5x11-inch paper.

Demographics Cycle

There are 5 subroutines devoted to the details of natality, mortality, and dispersal. The simulation cycle itself consists of a "replicate" loop, within which is nested the "annual" loop, within which is the "species" loop. Within the species loop, subroutine PROBLY must be recalled each time the dispersal range of the species changes. In the annual loop, various output routines can be called (described in the next section). Populations are reinitialized for each replicate.

Subroutine NATAL

The natality subroutine tallies successful breeding events for each brood of each breeding bird in each patch for each species. Because the adjusted mean clutch size for a species is rarely an integer and is often less than 1.0, the outcome of each nesting attempt is stochastically determined. Thus, a bird with a clutch size of 1.40 would produce 1 fledgling with probability 0.60, and 2 fledglings with chance 0.40. Similarly, a bird that averages 1.50 broods per season produces 2 broods half the time, otherwise, a single brood.

Nesting success may be subjected to stochastic predation and brood parasitism as edge effects. In this implementation, predation results in total nest failure, while parasitism costs 1 fledgling. The probability of predation or parasitism in edges is defined as the product of the base incidence rate (specified in INITL) and the relative susceptibility of each species (provided in INPUT). The actual probability of predation (the predation factor, PF) or brood parasitism (BPF) is derived by averaging these events in edges, over the entire patch area. For example, the edge-weighted average probability of predation is

$$PF = PND(KSP) * EDGE(I) / AREA(I),$$

where PND(KSP) is the probability of nest depredation for species KSP, and EDGE(I)/AREA(I) is the relative edge area for patch I. This probability is averaged over the entire patch because the exact

locations of territories within patches are not accounted; further, averaging smooths the discrete boundary of the 50-m "edge."

Note that specifying a species to be an edge species invokes predation and parasitism for all breeders of susceptible species (since none "escape" to interior habitats); reciprocally, strictly interior species are immune to edge effects by definition. That this latter case may result in somewhat tautologous distribution patterns in simulations underscores the need to carefully frame hypotheses in applications.

Subroutine MORTAL

Like natality, the mortality subroutine operates stochastically on a per-bird, per-patch, per-species basis. The base survivorship probability is that of breeders; this rate is adjusted to yield floater and juvenile survivorship. Relative floater survivorship is specified in subroutine INITL, and as a default value is 50% that of breeders. Juvenile survivorship is also set at 50% (after Ricklefs 1969, 1972). In each case, a bird "dies" if a uniform-random number on the interval (0,1) is greater than the chance of survivorship. Juveniles that survive their first winter are assigned floater status before dispersal.

Subroutines HOME, DISPRS, and REDISP

Dispersal of individuals is accomplished by 3 subroutines. HOME, called at the outset of dispersal, returns overwinter survivors to their home patch, and redefines breeder and floater subpopulations.

In this, floaters may become breeders if mortality has "emptied" any territories. This effectively allows within-patch dispersal for large patches (which frequently have available territories) but forces between-patch dispersal for small patches. This homing routine thus allows the use of edge-to-edge distances in subroutine PROBLY, which is computationally convenient.

Subroutine DISPRS is the first actual dispersal routine. In this, each bird is moved stochastically, guided by the dispersal probability matrix. This is done by drawing a uniform-random number on (0,1), and comparing it to the elements of the appropriate row of the dispersal matrix; the bird moves to the patch corresponding to the matching "window" in the row of probabilities. Immigrants to each patch are stored in a temporary array of colonists. After all birds have been dispersed once, birds in the colonist array are reassigned as breeders or floaters, as available territories dictate.

A redispersal subroutine (REDISP) is called for those species with nonzero mobility. For these species, REDISP repeats dispersal bouts as in DISPRS, but for floaters only (breeders do not redisperse). After each redispersal bout, breeder and floater subpopulations are reassigned as in HOME and DISPRS.

Summary Statistics and Output Routines

The model generates simulated data representing annual censuses of all birds in each habitat patch. Because the simulated mosaics often include more patches than could easily be censused in an actual field study, and the simulations extend to decades-long time scales,

the model can generate orders of magnitude more "data" than might be expected from a field study. The sheer volume of these data could easily be overwhelming, so model output is generally "sampled" or summarized for subsequent analyses. There are 5 subroutines devoted to sampling and summary statistics.

Subroutines PRINT2 and PRINT3

Two "census" routines are available for printed output at annual time steps or user-defined intervals. The print interval is specified in subroutine INITL, and may be further modified (with IF statements) where called from the MAIN program. PRINT2 tallies breeders and floaters per patch for each species in turn, and is useful in cases where focal species are of particular interest. The distribution among patches is highlighted for each species.

PRINT3 provides censuses that highlight individual patches (i.e., PRINT3 transposes PRINT2). Output from PRINT3 thus corresponds to conventional census data in that all species are tallied for each patch in turn. This routine also tallies the number of resident species and the total number of nested pairs for all species combined. Either of these routines can generate an intimidating volume of printed output, so they should be with moderation.

Subroutine PUNCH

Many, if not most, applications of the simulator involve subsequent analysis of model-generated census data. These analyses are conveniently performed by external statistical packages (e.g., SAS).

For such purposes, subroutine PUNCH writes a condensed data file to logical unit 7, which can be routed to disk or some other storage device. The output data file consists of a mosaic label, the replicate number, and simulation year, followed by patch number, patch area, and the number of breeders of each species in that patch. For less than 50 species, this routine produces 3 data records per patch per year. Given a sorting utility, this file can be partitioned to provide for a wide variety of statistical treatments.

Subroutine RSTATS

The final printout from the program is produced by RSTATS, which summarizes (averages) results from the pooled replicates. This routine provides means and standard deviations for breeder subpopulations per species per patch for the final simulation year. The form of the summary is as in PRINT2 and PRINT3; first, mean abundance patterns for each species (a "species" summary), followed by mean censuses for each patch (a "patch" summary).

Subroutine UTILT

The program also includes a utility subroutine to provide user-defined diagnostics or special-purpose output. These additional data are written to logical unit 6 (the system printout), hence do not interfere with the normal report generated by routines PRINT1, PRINT2, PRINT3, and RSTATS. The utility routine is currently used to tally the number and percentage of neotropical migrants, as well as the proportions of habitat generalists, edge species, and interior species

in annual censuses. UTILT can be modified to provide other diagnostics as desired.

Focal-Species Applications

When a single species is of interest it is more appropriate and much more computationally efficient to use the focal-species version of the simulator. The single-species program parallels the multi-species code in every particular except dimensionality (i.e., 2-dimensional arrays are reduced to vectors, and vectors become scalar variables), and the amount of detail available in output routines. For example, the single-species routine RSTATS reports on breeder as well as floater subpopulations for every simulation year, while the multi-species routine reports only on breeders in the final year. Three additional subroutines provide statistics on individual replicates.

Subroutines PSTATS, ESTATS, and FREQ

Each simulation year, breeder and floater subpopulations in each patch are copied into a storage array by subroutine AOPPN. This array is subsequently used by 3 statistics routines to summarize species abundance patterns for each replicate.

PSTATS computes population statistics, the mean and standard deviation of breeders and floaters per patch for the final 10 years of the simulation. This is an estimate of temporal variability in population dynamics (as compared to the among-replicate variation described by RSTATS). PSTATS also computes temporal statistics for the metapopulation.

ESTATS summarizes the dynamics of local extinctions and recolonizations for each patch and for the entire mosaic. The total number of these events indicates the relative spatial dynamics of the metapopulation (i.e., among-patch dynamics), while the ratio of recolonizations to extinctions indicates the trajectory of the metapopulation. Coupled with the spatial dispersion indices provided by PRINT1, ESTATS can be used to quantify isolation effects in the mosaic, or to describe the effects of connectedness.

FREQ tallies the frequency of occurrence of final-year, patch-level population sizes for discrete patch size classes, with an emphasis on the occurrence of empty patches. This simulated data is compatible with actual census data compiled to highlight "area-sensitivity" of bird species in fragmented forests (e.g., Forman et al. 1976, Whitcomb et al. 1981). FREQ prints tables that can be tested, with conventional contingency analyses, to determine whether a simulated species occurs differentially in patches of various sizes. Used together, subroutines FREQ and ESTATS comprehensively describe the dynamics of species abundance patterns for each replicate.

Final Notes on Usage

A few cautionary notes concerning model applications are appropriate. The simulator is a model, so is by definition inadequate and unrealistic. In particular, a wealth of biological detail is not represented in this implementation, so simulated demographics will always be unrealistic to some degree. Further, parameter uncertainties render the correspondence between simulated species and their real

counterparts somewhat unreliable, and to a degree that is difficult to specify. Finally, the stochastic nature of the simulated demographics, as expressed in model uncertainty (see Chapter 6), dictates that direct comparisons between model output and census data from real habitat mosaics should not be overinterpreted.

These caveats suggest that the question, "How many Yellow-throated Vireos will there be in Trelease Woods in the year 2000?" is not a particularly valid question to address with the simulator. Alternatively, the model can provide useful answers to questions such as, "What is the nature of the relationship between patch isolation and bird species richness?" or "Can edge effects on net natality be of sufficient magnitude (given biologically feasible intensities) to effect species abundance patterns in a mosaic?" In each of these cases, the general result can be informative even if the exact results are somewhat compromised by model uncertainties. The model is especially useful in implicating data criticalities, such as model formulations or parameters that are sufficiently sensitive and uncertain as to require verification or further refinement by field studies.

It should be emphasized that avian demographics, real or simulated, are implicitly scaled. This scaling dictates spatial and temporal domains over which it is reasonable to consider modeled demographics. Preliminary analysis of model output can indicate the degree of statistical closure for a particular habitat mosaic, which influences the consistency of modeled demographics for that mosaic. In this, output from subroutine PSTATS can be analyzed to determine

how many patches need to be simulated to yield consistent metapopulation-level demographics. Including too few patches will make the results statistically unstable and biologically misleading; including too many patches is statistically unnecessary and computationally expensive. It should be emphasized that the variability in metapopulation demographics increases with decreasing population size, so mosaics with fewer patches exhibit more variation than denser mosaics (all other things being equal). Output from subroutine RSTATS can indicate the number of replicates necessary to yield statistically stable characterizations of the pooled demographic trends. In this study, ten replicates were sufficient to describe general metapopulation trends, but were not always sufficient to completely stabilize among-replicate variation. Potential problems with statistical interpretations of model experiments were avoided by framing experiments so that the results were not biased by the number of replicates (e.g., the slope of the regression of population size for different clutch sizes, detailed in Chapter 6). Similar caution should be exercised in applying the model to other scenarios.

The temporal domain of avian demographics is dictated by the longevities of the bird species, and by the rate of change in habitat availability. Since most of the species simulated here have average lifespans of 2 or 3 years, demographic trends are usually expressed within a matter of a decade (a few generations). This time scale is the minimum necessary to witness the phenomenon of avian demographics in a habitat mosaic. At the other extreme, forest successional dynamics occur on time scales of decades or longer, and land use

changes may occur on these same time scales. At these longer temporal scales, the constraint of habitat availability itself becomes dynamic, and it would be unrealistic to consider demographics at these longer time scales without explicitly accounting for habitat dynamics. For these longer-term applications, the demographics simulator should be coupled to a habitat simulator (as provided for, in subroutines INITL and INPUT).

Finally, it should again be noted that the model is capable of generating data that are simultaneously very detailed and very extensive. This is in contrast to real data, where detail and extent are typically rather exclusive. The consequence of this is that the model can easily generate results that cannot be referenced to real data. While such results may be interesting to the modeler, it should be emphasized that model results or predictions that cannot possibly be verified or validated empirically are of limited scientific value. Model applications and experiments should be tailored such that the results can be compared to real data that, if not immediately available, are at least potentially obtainable. These latter applications are particularly useful in dictating critical directions for further empirical studies.

APPENDIX C
LISTING OF THE AVIAN DEMOGRAPHY SIMULATION PROGRAM

LISTING OF THE AVIAN DEMOGRAPHY SIMULATION PROGRAM

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C
C   POPN.FORTRAN
C   D.L. URBAN 1985
C
C   MAIN:
C
COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2   RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2   MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3   PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4   KGHAB(50), PCCI(50)
COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2   KIP, KHAB, KPRT, KFLT, RSFLT, KEDGE, XBP, XND,
3   FBRD, FFLT, TSMIN
C
C
CALL INITL
CALL INPUT
CALL PROBLY
CALL IPOPN
CALL PRINT1
DO 1 KREP=1,NREPS
IF (KREP.EQ.1) WRITE(8,999) KREP
999 FORMAT(/5X,'REPLICATE SIMULATION',I2)
IF (KREP.GT.1) CALL IPOPN
DO 2 KYR=1,NYRS
DO 3 KSP=1,NSPP
IF (KSP.GT.1.AND.RANGE(KSP).NE.RANGE(KSP-1)) CALL PROBLY
CALL NATAL
CALL MORTAL
CALL HOME
CALL DISPRS
IF (MOBIL(KSP).GT.0) CALL REDISP
C   IF (KREP.EQ.1.AND.MOD(KYR,KPRT).EQ.0) CALL PRINT2
C   IF (KREP.EQ.1.AND.MOD(KYR,KPRT).EQ.0.AND.KSP.EQ.NSPP) CALL PRINT3
3 CONTINUE
C   IF (KREP.LE.3.AND.KYR.EQ.NYRS) CALL PUNCH
C   CALL UTILT
2 CONTINUE
CALL RSTATS
1 CONTINUE
STOP
END

```

```

C   SUBROUTINES
C
C   'INITIAL' SETS CONSTANTS AND INITIAL CONDITIONS
C
C   SUBROUTINE INITL
COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2   RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2   MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3   PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4   KGHAB(50), PCCI(50)
COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2   KIP, KHAB, KPRT, KFLTS, RSFLT, KEDGE, XBP, XND,
3   FBRD, FFLT, TSMIN
C
C   CONTROL PARAMETERS:
C
C   NREPS=NO. OF REPLICATE SIMULATIONS, KREP IS THE COUNTER
NREPS=10
C   NYRS=NO. OF YEARS SIMULATED, KYR IS THE COUNTER
NYRS=30
KYR=0
C   KPRT=PRINT INTERVAL FOR OUTPUT
KPRT=30
C   KIP=1 IF INITIAL POPNS ARE PROVIDED AS INPUT DATA, =0 IF RANDOM
KIP=0
C   KHAB=0 IF NO HABITAT PREFERENCES ARE SPECIFIED, =1 IF GROSS
C   HABITATS ARE SPECIFIED (KGHAB=0, 1, 2, 3 FOR GENERALIST, CORE,
C   EDGE, OR FIELD/EDGE) AND SPECIES USE EITHER TOTAL (KGHAB=0,1)
C   OR EDGE (KGHAB=2,3) AREA, =2 IF SPECIES USE TOTAL (KGHAB=0),
C   CORE (=1), OR EDGE (=2,3), =3 IF CARRYING CAPACITIES PER PATCH
C   ARE PROVIDED AS INPUT DATA.
KHAB=1
C   KFLTS=1 IF FLOATERS' SURVIVORSHIP IS LESS THAN BREEDERS'
KFLTS=1
C   RSFLT=RELATIVE SURVIVORSHIP OF FLOATERS (.% OF BREEDERS')
RSFLT=0.50
C   KEDGE=1 IF EDGE EFFECTS ON NATALITY ARE INVOKED
KEDGE=1
C   XBP, XND=MULTIPLIERS FOR BROOD PARASITISM, NEST DEPREDATION
C   (USED IN SR INPUT TO CALCULATE PBP AND PND)
XBP=0.10
XND=0.10
C   NSPP=NO. OF BIRD SPECIES IN SIMULATION
NSPP=42
C   FBRD, FFLT=SITE FIDELITY OF BREEDERS, FLOATERS
FBRD=0.90
FFLT=0.10
C   TSMIN=MINIMUM TERRITORY SIZE THAT CAN BE OCCUPIED (.%)
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C   TSMIN=0.50  
    IY=INITIAL SEED FOR THE RANDOM NUMBER GENERATOR URAND  
    IY=0  
    RETURN  
    END
```

```

C   'INPUT' READS DISK FILES 'MOAIC.DAT' AND 'SPECIES.DAT'
C
  SUBROUTINE INPUT
  COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2    RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
  COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2    MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3    PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4    KGHAB(50), PCCI(50)
  COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2    KIP, KHAB, KPRT, KFLTS, RSFLT, KEDGE, XBP, XND,
3    FBRD, FFLT, TSMIN
  INTEGER ND, BP, MAXAGE

C
C   READ MOAIC DATA:
C   NI=NUMBER OF HABITAT ISLANDS, ML=MOAIC LABEL, NAME=MOAIC NAME
  READ(5,1001) NI, ML, (NAME(L),L=1,15)
1001 FORMAT(I5,1X,A4,2X,15A4)
C   IXY=GRID COORDINATES OF ISLAND; AREA'S ARE IN HA
  DO 11 I=1,NI
  READ(5,1002) IXY(I,1), IXY(I,2), AREA(I), CORE(I), EDGE(I)
1002 FORMAT(5X,2I5,3F9.5)
  11 CONTINUE

C
C   READ INTER-ISLAND DISTANCE MATRIX
  DO 12 I=1,NI
  READ(5,1003) (DIST(I,J),J=1,NI)
1003 FORMAT(8F9.3)
  12 CONTINUE

C
C   READ SPECIES LIFE-HISTORY PARAMETERS:
C   MSP=MNEMONIC FOR SPECIES, KGHAB=KIND OF GROSS HABITAT,
C   TS1=TERRITORY SIZE (HA), MBD=MAX BREEDING DENSITY (PAIRS/100 HA),
C   TS2=PACKED TERRITORY SIZE (FROM MBD);
C   CLUTCH=MEAN NO. EGGS, BROODS=NUMBER OF BROODS/SEASON,
C   ND=SENSITIVITY TO NEST DEPREDATION, BP=TO BROOD PARASITISM,
C   NEST=NEST TYPE (OPEN OR HOLE, WHICH DEFINES BASE NEST SUCCESS);
C   MAXAGE=MAXIMUM AGE IN YEARS; RANGE=DISPERSAL RANGE (M),
C   MOBIL=MOBILITY (NUMBER OF DISPERSAL EPISODES)
  DO 13 K=1,NSPP
  READ(4,1004) MSP(K), KGHAB(K), TS1(K), MBD(K), CLUTCH(K),
2    BROODS(K), ND, BP, NEST, MAXAGE, RANGE(K), MOBIL(K)
1004 FORMAT(1X,A4,5X,I1,F4.1,I4,4X,F5.2,F4.1,3I2,3X,I3,5X,F5.0,I3)
C   TERRITORY SIZE IN INTACT FOREST IS BASED ON MBD
  TS2(K)=100.0/FLOAT(MBD(K))
C   FLEDGING SUCCESS IS 60% IF OPEN-NESTER, 66% IF HOLE-NESTER
  IF (NEST.EQ.0) FS=0.60
  IF (NEST.EQ.1) FS=0.66
C   NET NATALITY (MALES FLEDGED) IS FS*50% MALE

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CLUTCH(K)=CLUTCH(K)*FS*0.50
C  PREDATION, BROOD PARASITISM FACTORS ARE SET IN SR INITL
PND(K)=FLOAT(ND)*XND
PBP(K)=FLOAT(BP)*XBP
C  SURVIVORSHIP ASSUMES 1% REACH MAX AGE (IN YEARS)
SURV(K)=EXP(-4.60517/FLOAT(MAXAGE))
C
C  A BANDAID FOR OPTIMISTIC APPLICATIONS - SET SURVIVORSHIP SO
C  THAT NET R IS NONZERO UNDER OPTIMAL CONDITIONS:
XN=CLUTCH(K)*BROODS(K)
XM=XN/(2.0+XN)
XS=1.0-XM
IF (SURV(K).LT.XS) SURV(K)=XS
C
C  ASSIGN PROPORTIONATE DENSITY FOR INITIALS
PCCI(K)=0.50
13 CONTINUE
C
C  ASSIGN CARRYING CAPACITY PER ISLAND PER SPECIES:
DO 14 I=1,NI
IF (KHAB.EQ.3) GO TO 16
DO 15 KS=1,NSPP
HA=AREA(I)
IF ((KHAB.EQ.1.OR.KHAB.EQ.2).AND.KGHAB(KS).GE.2) HA=EDGE(I)
IF (KHAB.EQ.2.AND.KGHAB(KS).EQ.1) HA=CORE(I)
IF (HA.LT.TS1(KS)) CC(I,KS)=HA/TS1(KS)
IF (TS1(KS).LE.HA.AND.HA.LE.TS2(KS)) CC(I,KS)=1.00
IF (HA.GT.TS2(KS)) CC(I,KS)=HA/TS2(KS)
IF (CC(I,KS).LT.TSMIN) CC(I,KS)=0.00
15 CONTINUE
GO TO 14
16 READ(5,1005) (CC(I,KS),KS=1,NSPP)
1005 FORMAT(12F6.2)
14 CONTINUE
RETURN
END

```

C 'PROBABILITY' CALCULATES DISPERSAL RATES FROM FLOW AND FIDELITY
 C SO THAT DISPERSAL PROBABILITIES SUM TO 1.0 IN EACH ROW.
 C THIS ENTAILS RE-RELATIVIZING FLOW RATES FOR VERY
 C CONTAGIOUS ISLANDS, OR INCREASING SITE FIDELITY FOR VERY
 C ISOLATED ISLANDS. THIS IS DONE SEPARATELY FOR BREEDERS
 C AND FLOATERS.

C

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SUBROUTINE PROBLY
COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2   RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2   MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3   PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4   KGHAB(50), PCCI(50)
COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2   KIP, KHAB, KPRT, KFLT, RSFLT, KEDGE, XBP, XND,
3   FBRD, FFLT, TSMIN

```

C

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REAL FLOW(75,75), SUM, MAX1, MAX2
IF (KYR.EQ.0) R=5000.0
IF (KYR.GT.0) R=RANGE(KSP)
B=-4.60517/R
DO 31 I=1,NI
DO 32 J=1,NI
IF (I.EQ.J) GO TO 32
D=DIST(I,J)
IF (D.LE.R) FLOW(I,J)=EXP(B*D)
IF (D.GT.R) FLOW(I,J)=0.00
32 CONTINUE
31 CONTINUE

```

C

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DO 41 I=1,NI
42 MAX1=1.00-FBRD
SUM=0.0
DO 43 J=1,NI
IF (I.EQ.J) GO TO 43
SUM=SUM+FLOW(I,J)
43 CONTINUE
IF (SUM.LT.MAX1) GO TO 44
IF (SUM.EQ.MAX1) GO TO 46
IF (SUM.GT.MAX1) GO TO 48
44 RECOL(I,I,1)=1.00-SUM
DO 45 J=1,NI
IF (I.EQ.J) GO TO 45
RECOL(I,J,1)=FLOW(I,J)
45 CONTINUE
GO TO 50
46 RECOL(I,I,1)=FBRD
DO 47 J=1,NI

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```
      IF (I.EQ.J) GO TO 47
      RECOL(I,J,1)=FLOW(I,J)
47  CONTINUE
      GO TO 50
48  RECOL(I,I,1)=FBRD
      DO 49 J=1,NI
      IF (I.EQ.J) GO TO 49
      RECOL(I,J,1)=(FLOW(I,J)/SUM)*MAX1
49  CONTINUE
50  MAX2=1.00-FFLT
      IF (SUM.LT.MAX2) GO TO 51
      IF (SUM.EQ.MAX2) GO TO 53
      IF (SUM.GT.MAX2) GO TO 55
51  RECOL(I,I,2)=1.00-SUM
      DO 52 J=1,NI
      IF (I.EQ.J) GO TO 52
      RECOL(I,J,2)=FLOW(I,J)
52  CONTINUE
      GO TO 41
53  RECOL(I,I,2)=FFLT
      DO 54 J=1,NI
      IF (I.EQ.J) GO TO 54
      RECOL(I,J,2)=FLOW(I,J)
54  CONTINUE
      GO TO 41
55  RECOL(I,I,2)=FFLT
      DO 56 J=1,NI
      IF (I.EQ.J) GO TO 56
      RECOL(I,J,2)=(FLOW(I,J)/SUM)*MAX2
56  CONTINUE
41  CONTINUE
      RETURN
      END
```

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C   'PRINT1' SUMMARIZES INITIAL CONDITIONS ON THE LANDSCAPE
C
SUBROUTINE PRINT1
COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2   RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2   MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3   PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4   KGHAB(50), PCCI(50)
COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2   KIP, KHAB, KPRT, KFLTS, RSFLT, KEDGE, XBP, XND,
3   FBRD, FFLT, TSMIN
DIMENSION NADJ(75), AADJ(75), NND(75)
C
C   PRINT OVERVIEW OF RUN CONTROL OPTIONS
WRITE(8,1006) (NAME(L),L=1,15), NSPP, NI
1006 FORMAT(/5X,'AVIAN DEMOGRAPHY IN MOSAIC LANDSCAPES',//5X,15A4,
2   ///5X,'SIMULATION INVOLVES',I5,' SPECIES UTILIZING',
3   I5,' HABITAT ISLANDS')
IF (KHAB.EQ.0) WRITE(8,1101)
1101 FORMAT(/10X,'CARRYING CAPACITIES ARE BASED ON TOTAL ISLAND AREA')
IF (KHAB.EQ.1) WRITE(8,1102)
1102 FORMAT(/10X,'CARRYING CAPACITIES ARE BASED ON TOTAL OR',
2   ' EDGE AREA')
IF (KHAB.EQ.2) WRITE(8,1103)
1103 FORMAT(/10X,'CARRYING CAPACITIES ARE BASED ON TOTAL, CORE,',
2   ' OR EDGE AREA')
IF (KHAB.EQ.3) WRITE(8,1104)
1104 FORMAT(/10X,'CARRYING CAPACITIES ARE PROVIDED AS INPUT DATA')
IF (KEDGE.EQ.0) WRITE(8,1106)
1106 FORMAT(10X,'THERE ARE NO EDGE EFFECTS ON NATALITY')
IF (KEDGE.EQ.1) WRITE(8,1107) XBP, XND
1107 FORMAT(10X,'NATALITY IS DECREASED IN EDGE HABITATS',
2   /15X,'BROOD PARASITISM MULTIPLIER IS:',F6.2,
3   /15X,'NEST DEPREDATION MULTIPLIER IS:',F6.2)
IF (KFLTS.EQ.0) WRITE(8,1108)
1108 FORMAT(10X,'MORTALITY IS THE SAME FOR BOTH SUBPOPULATIONS')
IF (KFLTS.EQ.1) WRITE(8,1109) RSFLT
1109 FORMAT(10X,'FLOATER SURVIVAL IS',F5.2,' TIMES THAT OF BREEDERS')
IF (KIP.EQ.0) WRITE(8,1110)
1110 FORMAT(10X,'POPULATIONS ARE INITIALIZED AT 50% OF CCL')
IF (KIP.EQ.1) WRITE(8,1111)
1111 FORMAT(10X,'INITIAL POPULATIONS ARE PROVIDED AS INPUT DATA')
C
C   PRINT AVIAN LIFE-HISTORY PARAMETERS
WRITE(8,1007)
1007 FORMAT(///5X,'BIRD SPECIES AND THEIR LIFE-HISTORY ATTRIBUTES:',
2   //10X,'SPECIES',3X,'TERRITORY',3X,' NATALITY ',3X,
3   ' ANNUAL ',3X,' DISPERSAL',/10X,' CODE',2X,'GH ONE MAX',2X,

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4 'BASE      P,BP',3X,'SURVIVAL',3X,'RANGE MOBILITY'/)
DO 21 K=1,NSPP
IF (KEDGE.EQ.1) IP=(PND(K)/XND)+0.05
IF (KEDGE.EQ.0) IP=0
IF (KEDGE.EQ.1) IBP=(PBP(K)/XBP)+0.05
IF (KEDGE.EQ.0) IBP=0
MR=RANGE(K)
WRITE(8,1008) K, MSP(K), KGHAB(K), TS1(K), TS2(K), CLUTCH(K),
2 BROODS(K), IP, IBP, SURV(K), MR, MOBIL(K)
1008 FORMAT(10X,I2,1X,A4,2X,I2,F4.1,F5.1,1X,F5.2,F4.1,1X,2I2,5X,F4.2,
2 5X,I5,3X,I2)
21 CONTINUE
C
C CALCULATE AND PRINT SPATIAL STATISTICS FOR MOSAIC
DO 22 I=1,NI
NADJ(I)=0
AADJ(I)=0.0
NND(I)=99999
DO 23 J=1,NI
IF (I.EQ.J.OR.RECOL(I,J,2).LT.0.01) GO TO 23
NADJ(I)=NADJ(I)+1
AADJ(I)=AADJ(I)+AREA(J)
IF (DIST(I,J).LT.NND(I)) NND(I)=DIST(I,J)
23 CONTINUE
22 CONTINUE
WRITE(8,1009)
1009 FORMAT(///5X,'THE LANDSCAPE MOSAIC:'
2 //10X,'HABITAT ',' LOCI ',2X,' AREA (HA) ',2X,
3 ' ADJ. ISLANDS',2X,'NEAREST-NEIGHBOR',/10X,' ISLAND ',
4 ' X Y',2X,'TOTAL CORE EDGE', ' NO. AREA',
5 4X,' DISTANCE'/)
TOTA=0.0
TOTC=0.0
TOTE=0.0
TOTF=0.0
TOTNND=0.0
REFUGE=0.0
DO 24 I=1,NI
WRITE(8,1010) I, IXY(I,1), IXY(I,2), AREA(I), CORE(I), EDGE(I),
2 NADJ(I), AADJ(I), NND(I)
1010 FORMAT(12X,I2,3X,2I5,1X,3F6.2,3X,I2,2X,F6.1,8X,I5)
DO 241 J=1,NI
IF (I.EQ.J) GO TO 241
D=DIST(I,J)
IF (D.GT.5000.0) GO TO 241
F=EXP((-4.605/5000.0)*D)
TOTF=TOTF+F
241 CONTINUE
TOTNND=TOTNND+FLOAT(NND(I))

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TOTA=TOTA+AREA(I)
TOTC=TOTC+CORE(I)
TOTE=TOTE+EDGE(I)
IF (AREA(I).GE.40.0) REFUGE=REFUGE+AREA(I)
24 CONTINUE
PCC=100.0*TOTC/TOTA
PCE=100.0*TOTE/TOTA
PCR=100.0*REFUGE/TOTA
SI=FLOAT(NI)
RELF=100.0*TOTF/(SI**2-SI)
XNND=TOTNND/SI
WRITE(8,1203) TOTA, TOTC, PCC, TOTE, PCE, REFUGE, PCR,
2 XNND, TOTF, RELF
1203 FORMAT(/10X,'TOTAL HABITAT AREA:',F7.2,' HA',/15X,'CORE AREA:',
2 F7.2,' HA (' ,F5.2,'%)',/15X,'EDGE AREA:',F7.2,' HA (' ,
3 F5.2,'%)',/10X,'TOTAL AREA IN LARGE PATCHES (40 HA +):',F7.2,
4 ' HA (' ,F5.2,'%)',//10X,'MEAN NEAREST-NEIGHBOR DISTANCE',
5 ' BETWEEN PATCHES:',F8.2,' M',/10X,'TOTAL FLOW AMONG PATCHES:',
6 F7.2,/15X,'RELATIVE TO MAXIMUM:',F6.2,'%')
C WRITE(7,1204) ML, NI, TOTA, TOTC, TOTE, REFUGE, XNND, TOTF,
C 2 RELF
C1204 FORMAT(A4,1X,I2,3X,4F7.2,3X,F8.2,F7.2,F6.2)
C
C SUMMARIZE CARRYING CAPACITY PER SPECIES
WRITE(8,1201)
1201 FORMAT(///5X,'CARRYING CAPACITY OF THE MOSAIC:',
2 //10X,'SPECIES',4X,'ISLANDS',2X,'AREA',2X,'TOTAL CC',
3 5X,'% INITIALIZED'/)
DO 25 K=1,NSPP
CCL=0.0
TA=0.0
NHI=0
DO 26 I=1,NI
IF (CC(I,K).LT.TSMIN) GO TO 26
NHI=NHI+1
TA=TA+AREA(I)
CCL=CCL+CC(I,K)
26 CONTINUE
PCI=100.0*PCCI(K)
WRITE(8,1202) K, MSP(K), NHI, TA, CCL, PCI
1202 FORMAT(10X,I2,1X,A4,6X,I2,4X,F6.2,1X,F7.2,10X,F6.3)
25 CONTINUE
C PRINT USER-PROVIDED INITIAL POPULATIONS
IF (KIP.EQ.0) RETURN
WRITE(8,1205)
1205 FORMAT(/5X,'INITIAL POPULATIONS:')
DO 27 I=1,NI
WRITE(8,1206) I
1206 FORMAT(/10X,'HABITAT ISLAND:',I5,//15X,'SPECIES',2X,

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2 'BREEDERS' /)
  DO 28 KS=1, NSPP
  IF (INPOP(I,KS).EQ.0) GO TO 28
  WRITE(8,1207) KS, MSP(KS), INPOP(I,KS)
1207 FORMAT(15X,I2,1X,A4,4X,I3)
  28 CONTINUE
  27 CONTINUE
  RETURN
  END
```

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C      'NATALITY' MAKES BABY BIRDS
C
      SUBROUTINE NATAL
      COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2      RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
      COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2      MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3      PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4      KGHAB(50), PCCI(50)
      COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2      KIP, KHAB, KPRT, KFLT, RSFLT, KEDGE, XBP, XND,
3      FBRD, FFLT, TSMIN
C
      DO 81 I=1,NI
      JUV(I,KSP)=0
      IF (NBRD(I,KSP).EQ.0) GO TO 81
      NB=NBRD(I,KSP)
      PF=PND(KSP)*EDGE(I)/AREA(I)
      BPF=PBP(KSP)*EDGE(I)/AREA(I)
      IF ((KHAB.EQ.1.OR.KHAB.EQ.2).AND.KGHAB(KSP).GE.2) PF=PND(KSP)
      IF ((KHAB.EQ.1.OR.KHAB.EQ.2).AND.KGHAB(KSP).GE.2) BPF=PBP(KSP)
      IF (KHAB.EQ.2.AND.KGHAB(KSP).EQ.1) PF=0.0
      IF (KHAB.EQ.2.AND.KGHAB(KSP).EQ.1) BPF=0.0
      DO 82 K=1,NB
      NC=BROODS(KSP)
      R=BROODS(KSP)-FLOAT(NC)
      IF (URAND(IY).LT.R) NC=NC+1
      DO 83 KC=1,NC
      CLTCH=CLUTCH(KSP)
      IF (KEDGE.EQ.0) GO TO 84
C      DO PREDATION - HIT OR MISS
      IF (URAND(IY).LT.PF) GO TO 83
C      DO BROOD PARASITISM - IT COSTS ONE FLEDGLING
      IF (URAND(IY).LT.BPF) CLTCH=CLTCH-0.30
      IF (CLTCH.LE.0.00) CLTCH=0.00
84      KJUV=CLTCH
      R=CLTCH-FLOAT(KJUV)
      IF (URAND(IY).LT.R) KJUV=KJUV+1
      JUV(I,KSP)=JUV(I,KSP)+KJUV
83      CONTINUE
82      CONTINUE
81      CONTINUE
      RETURN
      END

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C   'MORTALITY' KILLS BIRDS
C
  SUBROUTINE MORTAL
  COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2    RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
  COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2    MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3    PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4    KGHAB(50), PCCI(50)
  COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2    KIP, KHAB, KPRT, KFLTS, RSFLT, KEDGE, XBP, XND,
3    FBRD, FFLT, TSMIN
C
  DO 91 I=1,NI
  IF (NBRD(I,KSP).EQ.0) GO TO 93
  NB=NBRD(I,KSP)
C   KILL SOME BREEDERS
  DO 92 K=1,NB
  IF (URAND(IY).GT.SURV(KSP)) NBRD(I,KSP)=NBRD(I,KSP)-1
92 CONTINUE
93 IF (NFLT(I,KSP).EQ.0) GO TO 95
C   IF FLOATERS HAVE LOWER SURVIVORSHIP, ADJUST SURVIVAL PROBABILITY
  IF (KFLTS.EQ.0) SF=SURV(KSP)
  IF (KFLTS.EQ.1) SF=RSFLT*SURV(KSP)
  NF=NFLT(I,KSP)
C   KILL SOME FLOATERS
  DO 94 K=1,NF
  IF (URAND(IY).GT.SF) NFLT(I,KSP)=NFLT(I,KSP)-1
94 CONTINUE
95 IF (JUV(I,KSP).EQ.0) GO TO 91
C   JUVENILE MORTALITY IS 50% THAT OF ADULTS
  SJ=0.50*SURV(KSP)
  NJ=JUV(I,KSP)
C   KILL SOME JUVENILES
  DO 96 K=1,NJ
  IF (URAND(IY).GT.SJ) JUV(I,KSP)=JUV(I,KSP)-1
96 CONTINUE
C   JUVENILES NOW BECOME FLOATERS BEFORE DISPERSAL
  NFLT(I,KSP)=NFLT(I,KSP)+JUV(I,KSP)
91 CONTINUE
  RETURN
  END

```

```

C   'DISPERSAL' RECOLONIZES THE ISLANDS BY DISPERSING EACH BIRD
C   INDIVIDUALLY AND PROBABILISTICALLY, BY DRAWING A UNIFORM-
C   RANDOM NUMBER AND COMPARING IT TO A ROVING WINDOW THAT
C   SLIDES ALONG THE APPROPRIATE ROW OF THE 'PROBLY' MATRIX
C
SUBROUTINE DISPRS
COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2   RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2   MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3   PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4   KGHAB(50), PCCI(50)
COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2   KIP, KHAB, KPRT, KFLT, RSFLT, KEDGE, XBP, XND,
3   FBRD, FFLT, TSMIN

C   DIMENSION NCOL(50)
REAL MIN, MAX
DO 101 I=1,NI
  NCOL(I)=0
101 CONTINUE
  DO 102 I=1,NI
    IF (NBRD(I,KSP).EQ.0) GO TO 106
    NB=NBRD(I,KSP)
    DO 103 N=1,NB
      J=1
      MIN=0.00
      MAX=RECOL(I,J,1)
      X=URAND(IY)
104 IF (X.GE.MIN.AND.X.LT.MAX) GO TO 105
      J=J+1
      IF (J.GT.NI) GO TO 103
      MIN=MAX
      MAX=MAX+RECOL(I,J,1)
      GO TO 104
105 NCOL(J)=NCOL(J)+1
103 CONTINUE
106 IF (NFLT(I,KSP).EQ.0) GO TO 102
    NF=NFLT(I,KSP)
    DO 107 N=1,NF
      J=1
      MIN=0.00
      MAX=RECOL(I,J,2)
      X=URAND(IY)
108 IF (X.GE.MIN.AND.X.LT.MAX) GO TO 109
      J=J+1
      IF (J.GT.NI) GO TO 107
      MIN=MAX
      MAX=MAX+RECOL(I,J,2)

```

```
GO TO 108
109 NCOL(J)=NCOL(J)+1
107 CONTINUE
102 CONTINUE
```

```
C
C REASSIGN BREEDER/FLOATER SUBPOPULATIONS
C
```

```
DO 111 I=1,NI
NBRD(I,KSP)=0
NFLT(I,KSP)=0
IF (NCOL(I).EQ.0) GO TO 111
NC=NCOL(I)
DO 112 KB=1,NC
B=FLOAT(NBRD(I,KSP))
R=CC(I,KSP)-B
IF (R.LT.TSMIN) GO TO 113
IF (R.LT.1.0) GO TO 114
NBRD(I,KSP)=NBRD(I,KSP)+1
GO TO 112
113 NFLT(I,KSP)=NFLT(I,KSP)+1
GO TO 112
114 X=URAND(IY)
IF (X.LE.R) NBRD(I,KSP)=NBRD(I,KSP)+1
IF (X.GT.R) NFLT(I,KSP)=NFLT(I,KSP)+1
112 CONTINUE
111 CONTINUE
RETURN
END
```

C 'REDISP' REDISPERSSES FLOATERS AFTER INITIAL COLONIZATION
 C IN THE SAME MANNER THAT 'DISPERSAL' WORKS
 C

```

SUBROUTINE REDISP
COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2   RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2   MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3   PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4   KGHAB(50), PCCI(50)
COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2   KIP, KHAB, KPRT, KFLTS, RSFLT, KEDGE, XBP, XND,
3   FBRD, FFLT, TSMIN

```

C

```

DIMENSION NCOL(50)
REAL MIN, MAX
MOB=MOBIL(KSP)
DO 121 K=1,MOB
DO 122 I=1,NI
NCOL(I)=0
122 CONTINUE
DO 123 I=1,NI
IF (NFLT(I,KSP).EQ.0) GO TO 123
NF=NFLT(I,KSP)
DO 124 N=1,NF
J=1
MIN=0.00
MAX=RECOL(I,J,2)
X=URAND(IY)
125 IF (X.GE.MIN.AND.X.LT.MAX) GO TO 126
J=J+1
IF (J.GT.NI) GO TO 124
MIN=MAX
MAX=MAX+RECOL(I,J,2)
GO TO 125
126 NCOL(J)=NCOL(J)+1
124 CONTINUE
123 CONTINUE

```

C
 C REASSIGN BREEDER/FLOATER SUBPOPULATIONS AFTER EACH BOUT
 C

```

DO 127 I=1,NI
NFLT(I,KSP)=0
IF (NCOL(I).EQ.0) GO TO 127
NC=NCOL(I)
DO 128 KB=1,NC
B=FLOAT(NBRD(I,KSP))
R=CC(I,KSP)-B
IF (R.LT.TSMIN) GO TO 129

```

```
IF (R.LT.1.0) GO TO 130
NBRD(I,KSP)=NBRD(I,KSP)+1
GO TO 128
129 NFLT(I,KSP)=NFLT(I,KSP)+1
GO TO 128
130 X=URAND(IY)
IF (X.LE.R) NBRD(I,KSP)=NBRD(I,KSP)+1
IF (X.GT.R) NFLT(I,KSP)=NFLT(I,KSP)+1
128 CONTINUE
127 CONTINUE
121 CONTINUE
RETURN
END
```

```

C   'PRINT2' WRITES POPN STATUS PER ISLAND PER YEAR
C
  SUBROUTINE PRINT2
  COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2    RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
  COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2    MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3    PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4    KGHAB(50), PCCI(50)
  COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2    KIP, KHAB, KPRT, KFLTS, RSFLT, KEDGE, XBP, XND,
3    FBRD, FFLT, TSMIN
  CHARACTER*4 MSP
C
  WRITE(8,1012) KSP, MSP(KSP)
1012 FORMAT(/10X,'SPECIES',I3,' ': ' ',A4)
  WRITE(8,1013) KYR
1013 FORMAT(/15X,'SIMULATION YEAR:',I4)
  WRITE(8,1014)
1014 FORMAT(/15X,'ISLAND',4X,'AREA',4X,'CC',6X,'BREEDERS FLOATERS'/)
  LBRD=0
  LFLT=0
  DO 161 I=1,NI
  IF (NBRD(I,KSP).EQ.0.AND.NFLT(I,KSP).EQ.0) GO TO 161
  WRITE(8,1015) I, AREA(I), CC(I,KSP), NBRD(I,KSP), NFLT(I,KSP)
1015 FORMAT(17X,I2,4X,F6.2,1X,F6.2,7X,I3,6X,I3)
  LBRD=LBRD+NBRD(I,KSP)
  LFLT=LFLT+NFLT(I,KSP)
161 CONTINUE
  WRITE(8,1018) LBRD, LFLT
1018 FORMAT(/10X,'THE LANDSCAPE SUPPORTS',I4,' BREEDERS AND',I4,
2 ' FLOATERS')
  RETURN
  END

```

```

C   'PRINT3' WRITES SPECIES PER ISLAND (TRANSDPOSES PRINT2)
C
  SUBROUTINE PRINT3
  COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2    RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
  COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2    MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3    PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4    KGHAB(50), PCCI(50)
  COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2    KIP, KHAB, KPRT, KFLTS, RSFLT, KEDGE, XBP, XND,
3    FBRD, FFLT, TSMIN
C
  WRITE(8,1020) KYR
1020 FORMAT(/5X,'SPECIES ASSEMBLAGES PER ISLAND, YEAR',I4)
  DO 60 I=1,NI
  WRITE(8,1021) I, AREA(I), EDGE(I), CORE(I)
1021 FORMAT(/10X,'HABITAT ISLAND:',I5,/'AREA:',F7.2,
2 ' HA (EDGE:',F6.2,', CORE:',F6.2,')',
3 /15X,'SPECIES',3X,'BREEDERS FLOATERS'//)
  NSI=0
  NBI=0
  DO 61 KSP=1,NSPP
  IF (NBRD(I,KSP).EQ.0.AND.NFLT(I,KSP).EQ.0) GO TO 61
  IF (NBRD(I,KSP).EQ.0) GO TO 62
  NBI=NBI+NBRD(I,KSP)
  NSI=NSI+1
 62 WRITE(8,1022) KSP, MSP(KSP), NBRD(I,KSP), NFLT(I,KSP)
1022 FORMAT(15X,I2,1X,A4,5X,I3,6X,I3)
 61 CONTINUE
  WRITE(8,1023) NSI, NBI
1023 FORMAT(/15X,'THE ISLAND SUPPORTS',I3,' SPECIES, AND',
2 I4,' NESTED PAIRS')
 60 CONTINUE
  RETURN
  END

```

```

C   'IPOPNI' INITIALIZES ISLAND POPULATIONS FOR EACH SIMULATION
C
SUBROUTINE IPOPNI
COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2   RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2   MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3   PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4   KGHAB(50), PCCI(50)
COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2   KIP, KHAB, KPRT, KFLTS, RSFLT, KEDGE, XBP, XND,
3   FBRD, FFLT, TSMIN
C
IF (KIP.EQ.0) GO TO 200
IF (KIP.EQ.1.AND.KREP.EQ.1) GO TO 206
IF (KIP.EQ.1.AND.KREP.GT.1) GO TO 209
C   KIP=0: BEGIN WITH RANDOM INITIAL POPULATION
200 DO 201 KSP=1,NSPP
    CCL=0.0
    DO 202 I=1,NI
        CCL=CCL+CC(I,KSP)
202 CONTINUE
    IMP=PCCI(KSP)*CCL
    KPOP=0
    DO 203 I=1,NI
        NBRD(I,KSP)=0
        NFLT(I,KSP)=0
203 CONTINUE
204 X=URAND(IY)
    IF (X.EQ.1.00) GO TO 204
    I=X*FLOAT(NI)+1
    B=FLOAT(NBRD(I,KSP))
    R=CC(I,KSP)-B
    IF (R.LT.TSMIN) GO TO 204
    Y=URAND(IY)
    IF (Y.LE.R) GO TO 205
    IF (Y.GT.R) GO TO 204
205 NBRD(I,KSP)=NBRD(I,KSP)+1
    KPOP=KPOP+1
    IF (KPOP.LT.IMP) GO TO 204
201 CONTINUE
    GO TO 212
C   KIP=1: READ INITIAL POPULATION AS INPUT DATA
206 DO 207 I=1,NI
    READ(3,1019) (INPOP(I,KSP),KSP=1,NSPP)
1019 FORMAT(4X,33I2/4X,15I2)
    DO 208 KSP=1,NSPP
        NBRD(I,KSP)=INPOP(I,KSP)
        NFLT(I,KSP)=0

```

```
208 CONTINUE
207 CONTINUE
    GO TO 212
209 DO 210 I=1,NI
    DO 211 KSP=I,NSPP
        NBRD(I,KSP)=INPOP(I,KSP)
        NFLT(I,KSP)=0
211 CONTINUE
210 CONTINUE
212 RETURN
    END
```

C 'HOME' REASSIGNS BRD/FLT STATUS BEFORE DISPERSAL

C

SUBROUTINE HOME

```
COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2   RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2   MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3   PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4   KGHAB(50), PCCI(50)
COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2   KIP, KHAB, KPRT, KFLTS, RSFLT, KEDGE, XBP, XND,
3   FBRD, FFLT, TSMIN
```

C

```
DO 221 I=1,NI
NB=NBRD(I,KSP)+NFLT(I,KSP)
NBRD(I,KSP)=0
NFLT(I,KSP)=0
IF (NB.EQ.0) GO TO 221
DO 222 KB=1,NB
B=FLOAT(NBRD(I,KSP))
R=CC(I,KSP)-B
IF (R.LT.TSMIN) GO TO 223
IF (R.LT.1.0) GO TO 224
NBRD(I,KSP)=NBRD(I,KSP)+1
GO TO 222
223 NFLT(I,KSP)=NFLT(I,KSP)+1
GO TO 222
224 X=URAND(IY)
IF (X.LE.R) NBRD(I,KSP)=NBRD(I,KSP)+1
IF (X.GT.R) NFLT(I,KSP)=NFLT(I,KSP)+1
222 CONTINUE
221 CONTINUE
RETURN
END
```

```

C   'PUNCH' WRITES A PATCH X SPECIES (ROWXCOL) MATRIX TO DEC
C
  SUBROUTINE PUNCH
  COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2    RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
  COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2    MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3    PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4    KGHAB(50), PCCI(50)
  COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2    KIP, KHAB, KPRT, KFLTS, RSFLT, KEDGE, XBP, XND,
3    FBRD, FFLT, TSMIN
C
  DO 231 I=1,NI
  WRITE(7,3001) ML, KREP, I, AREA(I), (NBRD(I,K),K=1,NSPP)
3001 FORMAT(A4,1X,I2,I3,F7.2,3X,13I4/4X,17I4/4X,17I4)
  231 CONTINUE
  RETURN
  END

```

```

C   'UTILITY' PUNCHES OR WRITES USER-SPECIFIED STATS OR WHATEVER
C
  SUBROUTINE UTILT
    COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2     RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
    COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2     MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3     PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4     KGHAB(50), PCCI(50)
    COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2     KIP, KHAB, KPRT, KFLTS, RSFLT, KEDGE, XBP, XND,
3     FBRD, FFLT, TSMIN
    IF (KYR.EQ.1) WRITE(6,3002) KREP
3002 FORMAT('1',4X,'NEOTROPICAL MIGRANTS (% OF TOTAL)',
2   /5X,'REPLICATE:',I5,//10X,'YEAR',5X,'% NTM'/)
    NT=0
    MIGT=0
    DO 191 I=1,NI
    DO 192 KS=1,NSPP
    NT=NT+NBRD(I,KS)
    IF (MOBIL(KS).EQ.3) MIGT=MIGT+NBRD(I,KS)
192 CONTINUE
191 CONTINUE
    PMT=100.0*FLOAT(MIGT)/FLOAT(NT)
    WRITE(6,3003) KYR, PMT
3003 FORMAT(10X,I4,6X,F5.2)
C
    IF (KYR.LT.NYRS) RETURN
C
    WRITE(6,3004)
3004 FORMAT('1',4X,'SPECIES PER PATCH, YEAR 30:')
    WRITE(6,3005) KREP
3005 FORMAT(/5X,'REPLICATE:',I5,//10X,'ISLAND',5X,'AREA',5X,'NSPP',
2   3X,'GSPP',3X,'CSPP',3X,'ESPP',3X,'NONF'/)
    DO 193 I=1,NI
    NTS=0
    NGS=0
    NCS=0
    NES=0
    NONF=0
    DO 194 J=1,NSPP
    IF (NBRD(I,J).EQ.0) GO TO 194
    NTS=NTS+1
    IF (KGHAB(J).EQ.0) NGS=NGS+1
    IF (KGHAB(J).EQ.1) NCS=NCS+1
    IF (KGHAB(J).GE.2) NES=NES+1
    IF (KGHAB(J).EQ.3) NONF=NONF+1
194 CONTINUE
    WRITE(6,3006) I, AREA(I), NTS, NGS, NCS, NES, NONF

```

```
3006 FORMAT(12X,I2,5X,F6.2,6X,I2,5X,I2,5X,I2,5X,I2,5X,I2)
193 CONTINUE
    RETURN
    END
```

```

C   'REP STATS' WRITES AVERAGE OUTPUTS (PRINT2 AND PRINT3) OVER REPS
C
  SUBROUTINE RSTATS
    COMMON/MOSAIC/ NI, ML, NAME(15), IXY(75,2), DIST(75,75),
2     RECOL(75,75,2), AREA(75), CORE(75), EDGE(75), CC(75,50)
    COMMON/BIRDS/ NBRD(75,50), NFLT(75,50), JUV(75,50), INPOP(75,50),
2     MSP(50), RANGE(50), MOBIL(50), CLUTCH(50), BROODS(50),
3     PND(50), PBP(50), SURV(50), TS1(50), TS2(50), MBD(50),
4     KGHAB(50), PCCI(50)
    COMMON/CONTRL/ NREPS, KREP, NYRS, KYR, NSPP, KSP, IY,
2     KIP, KHAB, KPRT, KFLTS, RSFLT, KEDGE, XBP, XND,
3     FBRD, FFLT, TSMIN
    DIMENSION B(75,50,10), XB(75,50), SDB(75,50), XTOT(50),
2     SDTOT(50), CCL(50), XNS(75), SDNS(75)
    DO 301 I=1,NI
    DO 302 J=1,NSPP
      B(I,J,KREP)=FLOAT(NBRD(I,J))
302 CONTINUE
301 CONTINUE
    IF (KREP.LT.NREPS) RETURN
C
C   CALCULATE MEAN, STD. DEV., PER SPECIES, PER ISLAND
    REPS=FLOAT(NREPS)
    DO 303 J=1,NSPP
      TOTSUM=0.0
      TOTSSQ=0.0
      CCL(J)=0.0
      DO 304 I=1,NI
        SUM=0.0
        SSQ=0.0
        CCL(J)=CCL(J)+CC(I,J)
        DO 305 K=1,NREPS
          SUM=SUM+B(I,J,K)
          SSQ=SSQ+B(I,J,K)**2
305 CONTINUE
        XB(I,J)=SUM/REPS
        SDB(I,J)=SQRT((SSQ-(SUM**2/REPS))/(REPS-1.0))
304 CONTINUE
C   CALCULATE MEAN, S.D., FOR METAPOPOPULATIONS
    DO 306 K=1,NREPS
      BT=0.0
      DO 307 I=1,NI
        BT=BT+B(I,J,K)
307 CONTINUE
      TOTSUM=TOTSUM+BT
      TOTSSQ=TOTSSQ+BT**2
306 CONTINUE
      XTOT(J)=TOTSUM/REPS
      SDTOT(J)=SQRT((TOTSSQ-(TOTSUM**2/REPS))/(REPS-1.0))

```

```

303 CONTINUE
C   FIND MEAN NUMBER OF SPECIES PER ISLAND
    DO 308 I=1,NI
      SUMNS=0.0
      SSQNS=0.0
      DO 309 K=1,NREPS
        SP=0.0
        DO 310 J=1,NSPP
          IF (B(I,J,K).GT.0.0) SP=SP+1.0
310 CONTINUE
      SUMNS=SUMNS+SP
      SSQNS=SSQNS+SP**2
309 CONTINUE
      XNS(I)=SUMNS/REPS
      SDNS(I)=SQRT((SSQNS-(SUMNS**2/REPS))/(REPS-1.0))
308 CONTINUE
C   OUTPUT 'PRINT2': SPECIES ABUNDANCES BY SPECIES
    WRITE(8,4001) NREPS, NYRS
4001 FORMAT(//5X,'SIMULATION RAN',I3,' REPLICATES FOR',I3,
2  ' YEARS EACH',//5X,'MEAN ABUNDANCES PER SPECIES IN FINAL YEAR:')
    DO 321 J=1,NSPP
      WRITE(8,4002) J, MSP(J)
4002 FORMAT(/10X,'SPECIES',I3,5X,A4)
      IF (XTOT(J).EQ.0.0) GO TO 323
      WRITE(8,4003)
4003 FORMAT(/15X,'ISLAND',5X,' AREA ',5X,' BREEDERS',5X,'STD. DEV.'/)
      DO 322 I=1,NI
        IF (XB(I,J).EQ.0.0) GO TO 322
        WRITE(8,4004) I, AREA(I), XB(I,J), SDB(I,J)
4004 FORMAT(17X,I2,6X,F6.2,6X,F7.3,6X,F7.3)
322 CONTINUE
323 RCC=100.0*XTOT(J)/CCL(J)
      WRITE(8,4005) XTOT(J), SDTOT(J), RCC
4005 FORMAT(/15X,'TOTAL METAPOPOPULATION:',F8.3,6X,F7.3,
2  /15X,'RELATIVE TO MAX CCL:',F9.3,'%')
321 CONTINUE
C   OUTPUT 'PRINT3': SPECIES ASSEMBLAGES PER ISLAND
    WRITE(8,4006)
4006 FORMAT(/5X,'MEAN SPECIES ASSEMBLAGES PER ISLAND'/)
    DO 331 I=1,NI
      WRITE(8,4007) I, AREA(I), CORE(I), EDGE(I)
4007 FORMAT(/10X,'HABITAT ISLAND:',I4,//15X,'TOTAL AREA:',F7.2,
2  ' HA',/15X,'CORE:',F7.2,5X,'EDGE:',F7.2,//15X,'SPECIES',
3  5X,'BREEDERS',5X,'STD. DEV.'/)
      DO 332 J=1,NSPP
        IF (XB(I,J).EQ.0.0) GO TO 332
        WRITE(8,4008) J, MSP(J), XB(I,J), SDB(I,J)
4008 FORMAT(15X,I2,1X,A4,5X,F7.3,6X,F7.3)
332 CONTINUE

```

C-30

```
WRITE(8,4009) XNS(I), SDNS(I)
4009 FORMAT(/15X,'MEAN NUMBER OF SPECIES:',F6.2,' (S.D.:',
2 F6.2,')')
331 CONTINUE
STOP
END
```

C FUNCTION URAND(IY) RETURNS A UNIFORM RANDOM NUMBER ON (0,1).
C

```

REAL FUNCTION URAND(IY)
INTEGER IY
INTEGER IA, IC, ITWO, M2, M, MIC
DOUBLE PRECISION HALFM
REAL S
DOUBLE PRECISION DATAN, DSQRT
DATA M2/0/, ITWO/2/
IF (M2.NE.0) GO TO 20
M=1
10 M2=M
M=ITWO*M2
IF (M.GT.M2) GO TO 10
HALFM=M2
IA=8*IDINT(HALFM*DATAN(1.DO)/8.DO)+5
IC=2*IDINT(HALFM*(0.5DO-DSQRT(3.DO)/6.DO))+1
MIC=(M2-IC)+M2
S=0.5/HALFM
20 IY=IY*IA
IF (IY.GT.MIC) IY=(IY-M2)-M2
IY=IY+IC
IF ((IY/2).GT.M2) IY=(IY-M2)-M2
IF (IY.LT.0) IY=(IY+M2)+M2
URAND=FLOAT(IY)*S
RETURN
END

```


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