1

CANADIAN THESES ON MICROFICHE

I.S.B.N.

THÈSES CANADIENNES SUR MICROFICHE

National Library of Canada
Collections-Development Branch

Canadian Theses on
Microfiche Service

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Direction du développement des collections

Service des thèses canadiennes
sur microfiche

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

National Library
of Canada

Canadian Theses -
on Microfiche Service

Ottawa, Canada
K1A 0N4

Bibliothèque nationale
du Canada

Services des thèses canadiennes
sur microfiches

65772

0-315-17863-9

PERMISSION TO MICROFILM — AUTORISATION DE MICROFILMER

• Please print or type — Écrire en lettres moulées ou dactylographier

Full Name of Author — Nom complet de l'auteur

Kathryn Elizabeth FREEMARK

Date of Birth — Date de naissance

February 15, 1953

Country of Birth — Lieu de naissance

Canada

Permanent Address — Résidence fixe

R.R. 6
Renfrew, Ontario
Canada
K7V 3Z9

Title of Thesis — Titre de la thèse

The Species-Area Pattern of Forest Birds in an Agricultural Landscape

University — Université

Carleton

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

Ph.D.

Year this degree conferred — Année d'obtention de ce grade

1984

Name of Supervisor — Nom du directeur de thèse

Dr. H.G. Merriam

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication, ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

Date

2 December 1983

Signature

Kathryn Freemark

THE SPECIES-AREA PATTERN OF FOREST BIRDS
IN AN AGRICULTURAL LANDSCAPE

by

KATHRYN ELIZABETH FREEMARK, B.Sc.

A thesis submitted to the Faculty of
Graduate Studies and Research in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Department of Biology
Carleton University
Ottawa, Ontario

© December 1983

11055
Ph.D.
1984
F73

1123 5096 01 FE

© 1984 Kathryn Elizabeth Freemark

The undersigned hereby recommend to the faculty
of Graduate Studies and Research acceptance of this
thesis, submitted by Kathryn Elizabeth Freemark,
B.Sc., in partial fulfilment of the requirements for
the degree of Doctor of Philosophy.

.....
Chairman, Department of Biology

.....
External Examiner

.....
Thesis Supervisor

Carleton University

December 1983

ABSTRACT

Hypotheses relating habitat heterogeneity, population processes and passive sampling to species-area patterns of birds were examined for 21 forests (3-7620 ha) in an agricultural landscape near Ottawa, Canada.

Forests were typical of the Great Lakes-St. Lawrence forest region. Habitat heterogeneity within forests was quantified by an index of spatial variability (HH) in plant species and forest structure. Positive correlation of HH based on tree species with HH for ground species, shrub species or forest structure indicated importance of trees as determinants of spatial pattern in forests. HH based on tree species, shrub species or all species increased with forest size.

Both forest size and HH were significant determinants of spatial patterns of birds among forests, according to multiple regressions for 2 summers. Larger forests had more species in total and in 67% of 21 ecological classes. Increasing species number in 3- to 18-ha forests was consistent with random samples from the regional species pool. Greater HH also increased species number in total and in 24% of ecological classes by increasing the sample of individuals from the regional species pool and by including species with different habitat

requirements.

No turnover in species number within forests was observed between years after correction for sampling errors or 'pseudoturnover'. Corrected annual turnovers in species composition within forests did not decrease with larger area or greater HH, contrary to population process and habitat heterogeneity hypotheses, respectively. Turnover of species in a 3-ha forest was lower than expected at random, indicating that individual site-fidelity may determine dispersal of some species between years.

Observed distributions of 66 of 72 bird species were consistent with a passive sampling model of random dispersal of birds in each year. Species composition within forests appeared to be related to external factors affecting regional availability of dispersing individuals (e.g. regional production of young, post-breeding mortality, pre-breeding dispersal). Absences of a few species in smaller forests may be related to territory size, habitat suitability, interspecific interactions and regional configuration of forests.

ACKNOWLEDGMENTS

Financial support was provided by the Natural Science and Engineering Research Council of Canada, Carleton University, the Canadian Wildlife Service and Ottawa Valley Grain Products Ltd. Co-operation of land owners was greatly appreciated. Critical comment was provided by my supervisor, Dr. G. Merriam, my advisory committee, Dr. B. Fenton, Dr. G. Carmody, Dr. A. Barlow, Dr. H. Howden as well as by J. Wegner, Dr. J. Karr, Dr. R. Roth, Dr. D. Welsh and fellow graduate students. Special thanks to my parents, my husband, Tim, and his parents for their continuing support.

TABLE OF CONTENTS

	Page
1. INTRODUCTION	1
2. METHODS	11
2.1. Study Sites	11
2.2. Habitat Sampling	15
2.3. Habitat Heterogeneity Indices	19
2.4. Bird Sampling	25
2.5. Spatial Analyses of Birds	30
2.5.1. Bird Species Numbers	30
2.5.2. Species Variability	30
2.5.3. Bird Species Composition	32
2.5.4. Random Assemblages	35
2.6. Temporal Analyses of Birds	37
2.7. Statistical Analyses	38
3. RESULTS	43
3.1. Habitat Descriptions	43
3.1.1. Species Composition	43
3.1.2. Forest Structure	46
3.2. Evaluation of Habitat Methods	48
3.2.1. Habitat Sampling	48
3.2.2. Habitat Heterogeneity Indices	51
3.3. Habitat Heterogeneity Within Forests ..	53
3.4. Evaluation of Bird Survey Methods	57
3.5. Spatial Patterns in Birds	62
3.5.1. Bird Species Number by Census Point	62
3.5.2. Species Variability	64
3.5.3. Bird Species Numbers by Forest ..	68
3.5.4. Bird Species Number and Habitat Quality	68
3.5.5. Bird Species Number by Ecological Class	73
3.5.6. Birds by Species	79
3.6. Temporal Patterns in Birds	87
3.6.1. Regional Turnover	87
3.6.2. Forest Turnover	88
4. DISCUSSION	102
5. CONCLUSIONS	128
6. REFERENCES	130
7. APPENDICES	144

LIST OF TABLES

Table	Page
1. A numerical example of the habitat heterogeneity index, HH.....	20
2. Plant species detected in the tree stratum of over half of 21 forests sampled in 1980	44
3. Plant species detected in the shrub stratum of over half of 21 forests sampled in 1980	45
4. Plant species detected in the ground stratum of over half of 21 forests sampled in 1980	47
5. Habitat variables replicated in 5 forests with greater sampling intensity in 1979 than 1980	49
6. Habitat heterogeneity (HH) in 21 forests sampled in 1980	52
7. Mean habitat heterogeneity (HH) in 21 forests (3-7620 ha) sampled in 1980	55
8. Pearson correlations for forest size and habitat heterogeneity within 21 forests	56
9. Efficiency of the point-count method versus spot-mapping method for censusing forest birds	58
10. Multiple regression statistics for bird species numbers per census point on size (Log Area) and habitat heterogeneity (HH) within 21 forests	63
11. Multiple regression statistics for spatial variability in bird species on size (Log Area) and habitat heterogeneity (HH) within 16 forests.....	65
12. Spatial variability in bird species (SDc) and in bird species weighted by abundance (SDa) averaged for pairs of census points within 16 forests sampled in 1981	67
13. Multiple regression statistics for bird	

species numbers per forest on size (Log Area) and habitat heterogeneity (HH) within 21 forests	69
14. Multiple regression statistics for bird species number per forest on habitat quality (mean species number per census point) and habitat heterogeneity (HH) within 21 forests	72
15. Relative importance of forest size (Log Area) and habitat heterogeneity (HH) to bird species number by ecological class in 21 forests	78
16. Bird species composition in 21 forests surveyed in A. 1980 and B. 1981	80
17. Bird species number per forest observed and expected from a passive sampling model of random dispersal of individuals available in the regional species pool of 1980	85
18. Number of pairs for selected bird species in small forests observed in 1980, 1981 and expected from a passive sampling model of random dispersal of individuals available in the regional species pool	86
19. Number of bird species within ecological classes detected in 21 forests, 1980-81	89
20. Annual turnovers in bird species for 5 forests, 1979-1981	90
21. Pseudoturnover in bird species associated with point count sampling versus spot-map censusing of 5 Ontario forests (1979) and 2 Maryland forests (Whitcomb et al. 1981: Appendix B)	92
22. Annual turnovers in bird species for 21 forests, 1980-81	93
23. Species turnover observed and expected at random between 1980 and 1981 in a 3-ha forest	95
24. Pearson correlations (r) of bird species number between 1980 and 1981 for ecological classes within 21 forests	96

25. Ecological classes of birds exhibiting
nonrandom temporal variability
regionally between 1980 and 1981 98
26. Annual turnovers in obligate forest and
facultative forest bird species within
21 forests, 1980-81 100.

LIST OF FIGURES

Figure	Page
1. A. Geographic location of the study area west of Ottawa, Canada B. Aerial view representative of the regional configuration of forests in the agricultural landscape	12
2. Effect of variable mean and deviation on the index of habitat heterogeneity, HH	21
3. Bird species-time curves for 21 forests surveyed in 1980	60
4. Relative importance of A. forest size (Log Area) and B. habitat heterogeneity (HH) to ecological classes of birds in 21 forests in 1980 and 1981	75

1. INTRODUCTION

Patterns in species number have interested naturalists since the early 1800's. In particular, the general increase in number of species within a taxonomic group with increasing area has received a great deal of attention (Arrhenius 1921, Gleason 1922, Preston 1962, MacArthur & Wilson 1963, 1967, Williams 1964, Simberloff 1972, Connor & McCoy 1979, Williamson 1981). Three principal hypotheses advanced to account for the species-area pattern relate to habitat heterogeneity, population processes and passive sampling.

Williams (1964) proposed the habitat heterogeneity hypothesis on the basis that as area increases, a greater diversity of habitats with their associated species are encountered. Greater habitat heterogeneity in larger areas and species diversification through interspecific differences in habitat selection results in an increase in species number with area. Increased habitat heterogeneity may also increase the number of species in an area by adding species which meet their requirements by coupling habitat types (Dwyer 1972). More heterogeneous areas may also support more species as a consequence of greater temporal persistence of species. Within the limits imposed by their dispersal capability and biotic restrictions,

individuals may be able to move within a more heterogeneous mosaic and find habitats that meet seasonal variations in their requirements or that provide their requirements if resources vary annually within habitats (e.g. Root 1967, Leck 1972, Roughgarden 1974, Rice et al. 1980, Karr & Freemark 1983). Individuals may experience higher reproductive success in more heterogeneous areas and exhibit greater site-tenacity. Greater habitat heterogeneity may also provide "survival foci" (Birch 1971), "refuge areas" (Dwyer 1972) or "hot spots" (Diamond 1975) in which individuals can survive unfavourable environmental conditions and from which other habitats can be colonized when conditions improve (cf. Karr 1982). If conspecifics are capable of occupying a range of habitats, each subject to different selection pressures, species occurrences may be stabilized in a more heterogeneous area by reduction of extinction probabilities of populations from local perturbations (e.g. Reddingius & den Boer 1970, Wray & Whitmore 1979, Cooke & Abraham 1980).

I will call the second, the "population process hypothesis". In their theory of island biogeography, MacArthur and Wilson (1963, 1967) proposed that the number of species on different-sized islands was determined by an equilibrium between immigration and extinction. Immigration rates were inversely related

to distance from a source of colonists while extinction rates were directly related to population processes associated with island size. Population sizes were assumed to be directly proportional to area, and species extinction probabilities inversely proportional to population size. Given equivalent immigration rates, small islands should support fewer species because population sizes are small and extinction probabilities are high. Population sizes on large islands should be relatively large, implying low probabilities of species extinctions. At any particular time, then, large islands should contain more individuals and species, resulting in a positive correlation between species number and area. Furthermore, at equilibrium, temporal variability in species composition, or species turnover, should decrease as island size increases as a consequence of lower extinction probabilities of larger populations.

Connor and McCoy (1979) proposed a third hypothesis which related the species-area pattern to passive sampling from the regional species pool. Larger areas have more species because they receive larger samples of individuals than smaller areas. Species turnover within areas would then be related to the random probability of individuals of new species reaching an area and becoming established.

Recent studies of islands have shown relationships among species-area patterns, habitat heterogeneity, population processes and passive sampling which make these hypotheses viable. A positive relationship between species number and area has been observed on oceanic islands (MacArthur & Wilson 1963, 1967, Simberloff 1974, Williamson 1981, but cf. Gilbert 1980). Lack (1976) suggested that differences in species number were determined by ecological poverty of islands. Among the California Channel Islands, Power (1972, 1976) found that variation in number of bird species was explained principally by the habitat diversity indexed by number of plant species per island. Number of habitat types was the primary predictor of the number of landbird species on 61 islands throughout Britain (Reed 1983). Ecological diversity was considered to be the most important factor affecting bird species number on islands of the East Indies, east central Pacific and West Indies (Hamilton et al. 1964) and the Gulf of Guinea (Hamilton & Armstrong 1965) but only by assuming that the primary importance of area reflected interisland differences in environmental opportunity.

Analyses of annual breeding censuses on islands (Diamond 1969, 1980) supported both the habitat heterogeneity hypothesis and the population process

hypothesis. Short-term species turnover was inversely related to both habitat heterogeneity and island size, although the validity of the analyses has been debated (Lynch & Johnson 1974, Diamond & May 1977).

The importance of species-area hypotheses related to area per se has also been suggested by other studies. After summing relative importances from univariate analyses of species number for lizards and birds on many archipelagoes in the Bahamas, Schoener and Schoener (1983) concluded that area was a more significant correlate of species number than habitat heterogeneity. Simberloff (1976) demonstrated experimentally that the number of arboreal arthropod species increased with the size of mangrove islands, independently of habitat heterogeneity. The prediction of the population process hypothesis of higher turnover rates on smaller islands could not be conclusively tested because of small sample size.

Only one study appears to have explicitly tested the passive sampling hypothesis of the species-area relationship on islands. Coleman et al. (1982) observed an increase in number of resident bird species with island size in a North American lake. They concluded that the species number observed was that expected from random distribution of individuals

among islands.

As human populations increase throughout the world, extensive forest ecosystems continue to be fragmented as land is converted to agricultural, industrial, suburban and urban uses. The forests that remain have been viewed as islands in a sea of culturally modified habitats (MacArthur & Wilson 1967, Pickett & Thompson 1978, Whitcomb 1977, Burgess & Sharpe 1981, Weaver & Kellman 1981). Habitat islands differ from true islands in that they are not surrounded by habitat totally inhospitable to terrestrial species (Margules et al. 1982, McCoy 1982). However, like true islands, the size of forest remnants affects species number. For birds, larger forests contain more species during the breeding season (Gromadzki 1970, Moore & Hooper 1975, Galli et al. 1976, Howe & Jones 1977, Willis 1980, Whitcomb et al. 1981, Blake & Karr 1982a), during migration (Martin 1980, 1981, Blake & Karr 1982a,b) and overwinter (Staite et al. 1979, Blake & Karr 1982b). Theoretically, at least some of the principles regulating species number on true islands could be operative in these forest fragments.

The relevance of the habitat heterogeneity hypothesis to birds is suggested by the relationship between vegetation type and bird species composition, which was recognized early by numerous ornithologists.

(Grinnell 1917, Pitelka 1941, Kendeigh 1946, Svardson 1949). More recent studies suggest that bird species respond to differences in vegetation structure (MacArthur & MacArthur 1961, MacArthur et al. 1962, MacArthur et al. 1966, Karr 1968, 1971, Recher 1969, James 1971, Karr & Roth 1971, Blondel et al. 1973, Willson 1974, Cyr 1977, Cody 1980, Collins et al. 1982) and/or plant species composition (Bond 1957, Williamson 1970, Lovejoy 1972, Tomoff 1974, Robbins 1978, Holmes et al. 1979, Nilsson 1979, Holmes & Robinson 1981, Sabo & Holmes 1983).

When Roth (1976) analyzed the distribution of bird species across a vegetational gradient from grasslands to forest, bird species diversity was significantly correlated with an index of habitat heterogeneity based on variation in spacing of trees and shrubs. However, in North American grasslands, bird species number appeared to vary independently of spatial heterogeneity in plant structure, whether the data were analyzed using univariate (Wiens 1974a) or multivariate methods (Rotenberry & Wiens 1980a,b). Dwyer (1972) argued that bird species number of two woodlands in Australia was enhanced by habitats of structurally more diverse vegetation associated with streams or rocky outcrops. Diversity of foliage cover by height intervals in forested habitats has been reported to be both a good predictor (MacArthur

& MacArthur 1961) and a poor predictor (Willson 1974) of bird species diversity. Both Johnson (1975) and Thompson (1978) argued that habitat heterogeneity best explained bird species number of ecologically-isolated montane areas. In paramos and puna of the high Andes Mountains, the importance of habitat heterogeneity to bird species number was not as clear because of high correlation of the ecological diversity index and area (Vuilleumier & Simberloff 1980).

In contrast, the number of spring migratory bird species was highly correlated with area, not plant species diversity, of shelterbelts on the Great Plains (Martin 1980). Area, not foliage height diversity, was considered the more important factor in explaining increased bird species number in mixed oak forests on the New Jersey Piedmont (Forman et al. 1976, Galli et al. 1976). Blake and Karr (1982a) also found that area, not species composition or structure of the habitat, was the best predictor of bird species number in forests in Illinois. Whether the species-area relationship was mediated through differential population processes or merely through passive sampling was not explicitly examined in the above studies. However, the observation by Blake and Karr (1982a) that forest size was unrelated to bird species turnover suggests that extinction

probabilities were not related to area of forests in Illinois. Other temporal analyses available in the literature are not particularly useful because they are restricted to a few studies of birds in single isolated forests (Whitcomb et al. 1977, for a reanalysis see McCoy 1982; Butcher et al. 1981, Kendeigh 1982).

To date, each of the three hypotheses of the species-area pattern has been related separately to species number on islands or forest fragments. To the best of my knowledge, no studies have tested all three hypotheses simultaneously. The present study explicitly tested the habitat heterogeneity hypothesis, the population process hypothesis and the passive sampling hypothesis by spatial and temporal analyses of birds across a range of forest size and habitat heterogeneity. Forests were selected to represent a continuum from small size and high habitat heterogeneity to large size and low habitat heterogeneity, to separate the effects of heterogeneity and size on numbers of bird species in total and in a variety of ecological classes. Size effects were further analyzed to determine the importance of population processes versus passive sampling in determining patterns in numbers of bird

species. Bird species composition among forests was also examined and differences compared to passive sampling effects.

2. METHODS

Both birds and habitat within forests were analyzed by two different methodologies during the study. In the first year, birds and habitat within a small number of forests were sampled intensively. To improve the reliability of the results, a larger number of forests was sampled in subsequent years. To avoid problems of interobserver variability, I collected all data in all years. Consequently, less intensive sampling methodologies had to be employed for more extensive coverage in later years. Variables replicated between intensive and extensive methodologies were subsequently compared to evaluate consistency of results.

2.1. Study Sites

The study was conducted in a 1400 km² area west of Ottawa, Ontario, Canada (approximately centred at 45°21'N 76°05'W, Fig. 1A). The landscape is characterized by forests of differing areas separated by nonforest habitats, such as cultivated fields, pastures and roads, and variously interconnected by hedgerows and riparian strips (Fig. 1B). No major urban areas were located within the study area. Forests are typical of the Great Lakes-St. Lawrence forest region (Hosie 1969, this study Section 3.1.).

Forests were selected to represent gradients of

Figure 1. A. Geographic location of the study area west of Ottawa, Canada B. Aerial view representative of the regional configuration of forests in the agricultural landscape. Forest size (ha) is shown for 7 forests studied. Locations of all forests studied are given in Appendix III.

area and spatial variability in canopy tree species, and ranged from small size and high spatial variability in canopy tree species to large size and low spatial variability in canopy tree species. Only more mature forests with relatively continuous canopy were chosen. Forests with outstanding irregularities in shape were avoided.

Topographic relief was variable among forests but was at most 30 metres within any forest.

The degree of disturbance varied due to cattle grazing and selective cutting in some forests. Disturbance effects were incorporated in habitat measurements and did not change during the study.

Forests were located by road or airplane surveys using 1:50,000 topographical maps, followed by analysis of 1:15,000 air photos. Forest size was measured on air photos using a dot planimeter (Bruning Areagraph Chart No. 4850). On-site reconnaissance determined the suitability of forests. Approximately 150 forests were examined at varying degrees of intensity. Five forests (13-30 ha) were selected for intensive study in 1979. Sixteen additional forests (3-7620 ha) were studied in 1980 and 1981. Exact locations of forests are given in Appendix III.

2.2. Habitat Sampling

In 1979, approximately 2% of each of 5 forests (13, 22, 25, 27, 30 ha) was sampled. In the 13, 27 and 30 ha forests, sampling effort was apportioned according to area of vegetation types recognized by differences in canopy tree composition on 1:15,000 air photos. In each forest, habitat plots were located systematically at the intersection of grid lines superimposed on a 1:15,000 air photo so that the habitat sample spanned the entire area. Since most plant populations are contagiously distributed, regular placement of samples provides better coverage of the range of spatial variation than random sampling (Mueller-Dombois & Ellenberg 1974:39, Gauch 1982:60).

In 1979, plant species composition and forest structure were sampled within forests. Both are components of habitat complexity considered relevant to birds and have been used to examine species-area relationships in birds. For brevity, only habitat variables replicated in the 1980 sample will be discussed.

Species compositions of tree, shrub and ground strata were sampled in each habitat plot using a series of nested quadrats (after Levenson 1981) that generally conformed to the minimal sample areas for forests recommended by Mueller-Dombois and Ellenberg

(1974). Trees ≥ 8 cm diameter breast high (dbh) were identified to species and dbh in a 25 m x 10 m quadrat. Shrubs (woody vegetation < 8 cm dbh and > 1 m high) were identified to species in a 12.5 m x 2 m quadrat. Species abundance was quantified as number per 250 m² or 125 m² for tree and shrub strata, respectively. Ground flora (herbs, vines and woody vegetation ≤ 1 m high) was identified to species in two 1 m x 1 m quadrats from which percent cover was calculated.

Percent canopy closure was averaged from estimates at 12 points along the midline of the 25 m x 10 m quadrat using a 5 cm x 5 cm square gridded into 25 equal sections. Mean canopy height was also obtained from estimates at these 12 points. Height estimates were intermittently checked with a Brunton compass and were accurate to within 2 metres. The number of trees by diameter class (8-12, 12-20, 20-36, > 36 cm dbh) was tabulated for each habitat plot.

In 1980, 8 habitat plots were established in each forest from 1:15,000 air photos. Plots were located at all bird census points, and additional plots were variously located depending on forest size, shape, accessibility and sampling history.

Species composition of the tree, shrub and ground strata was sampled by a modification of the relevé method (Mueller-Dombois & Ellenberg 1974) using a series of nested quadrats as reference areas. Vegetation of the tree stratum was determined as in 1979 but shrub data were collected in the tree quadrat. For each stratum, the cover of each species was scored according to the Braun-Blanquet cover-abundance scale: 5, cover >75%; 4, cover 50 - 75%; 3, cover 25 - 50%; 2, cover 5 - 25%; 1, numerous or scattered <5% cover; +, few with small cover. The scale values were absolute insofar as the values related to the vertical crown projection per species in a fixed reference area of 250 m² (Mueller-Dombois & Ellenberg 1974:59). For quantitative analyses, cover values of 87.5, 62.5, 37.5, 15.0, 2.5 and 0.1 % were used for class 5 to +, respectively (Mueller-Dombois & Ellenberg 1974: 147). Plants in the ground stratum (herbs, woody vegetation <1 m high) were identified to species and Braun-Blanquet cover scale in a 12.5 m x 10 m quadrat. Only species with cover class 2 to 5 were recorded.

Components of forest structure were recorded at each plot. Tree density was estimated by the point-centred quarter method (Cottam & Curtis 1956). Two points were located 6 m on either side of the centre point along the midline of the 25 m x 10 m

quadrat. At each point, the distance to the nearest tree in each quarter was measured by calibrated pacing and trees were identified to species and dbh class (8-12, 12-20, 20-36, >36 cm dbh). Class designations were periodically checked using a diameter tape. The number of trees in each dbh class was later tabulated. Canopy closure was assessed from two 35-mm photographs taken vertically with a 50-mm lens at each point-quarter. Each negative was enlarged to 11.5 cm x 17.5 cm and percent canopy closure measured by the point-intercept method using a transparent dot-grid. A preliminary analysis of results for grids of 5 to 100 regularly-spaced dots indicated a 50 dot grid produced results similar with those obtained with greater sampling intensity. Percent canopy closure was then calculated from the proportion of the 50 dots that were intercepted by a portion of the canopy. The mean for the 2 photos was used to characterize canopy closure in the plot. Foliage cover in the 25 m x 10 m quadrat was estimated for 5 height intervals (0-1, 1-3, 3-5, 5-9, >9 m) using 20% cover classes. The average height of the canopy and herbaceous vegetation was also estimated. Ground cover was estimated in the 25 m x 10 m quadrat according to percent cover of rock, bare ground, water and litter. When pacing between habitat plots, the distances between fallen trees and

snags were recorded and later averaged. Diameters of canopy gaps greater than 5 m wide were also recorded and later converted to percent of the distance between habitat plots.

2.3. Habitat Heterogeneity Indices

Habitat heterogeneity in species composition of tree, shrub and ground strata and forest structure was indexed using a derivation of the Shannon entropy function (after Orloci 1970):

$$HH = \sum_{i=1}^r \sum_{j=1}^c X_{ij} \ln (X_{ij}/X_i)$$

where r is the total number of variables used in characterizing c habitat plots, X_{ij} is an observation on the i th variable of the j th habitat plot, X_i is the mean for variable i and $\ln$ specifies the natural logarithm. Extension of the numerical example presented in Table 1 results in a family of curves (Fig. 2) indicating differential sensitivity of HH to habitat heterogeneity depending on the mean and deviation of variables. Only variables which are heterogeneous contribute to HH as indicated by origin of all curves at zero. The multiplier, X_{ij} , accounts primarily for the geometric form of the curve and makes HH sensitive to scale of measurement of variables.

In 1979 and 1980, scale of measurement was standardized by proportioning each variable by its

TABLE 1

A numerical example of the habitat heterogeneity index, HH.

Mean $\bar{x}$	Observation		$\ln(x_1/\bar{x})$	$x_1 \ln(x_1/\bar{x})$	$\ln(x_2/\bar{x})$	$x_2 \ln(x_2/\bar{x})$	HH
	x_1	x_2	(1)	(2)	(3)	(4)	(2 + 4)
10	10	10	0	0	0	0	0
	9	11	-.105	-.949	.095	1.048	.099
	8	12	-.223	-1.785	.182	2.188	.403
	7	13	-.337	-2.497	.262	3.411	.914
	6	14	-.451	-3.065	.337	4.711	1.646
	5	15	-.693	-3.466	.406	6.083	2.617
	4	16	-.916	-3.665	.470	7.520	3.855
	3	17	-1.204	-3.612	.531	9.020	5.408
	2	18	-1.609	-3.219	.588	10.580	7.361
	1	19	-2.303	-2.303	.642	12.196	9.893
	0	20	0	0	.693	13.862	13.862

Figure 2. Effect of variable mean ($\bar{X} = (\sum_{i=1}^n X_i)/n$) and deviation ($\sum_{i=1}^n |X_i - \bar{X}|/n$) on the index of habitat heterogeneity, HH.

total in each forest. This effectively collapsed the index to a single set of values specified by the number of habitat plots. In 1979, theoretical maxima of the index for each variable ranged from 2.398 in the 13-ha forest (11 habitat plots) to 3.296 in the 27-ha forest (27 habitat plots). In 1980, this bias was removed by sampling 8 habitat plots in all forests, thereby setting theoretical maxima for each variable at 2.079.

Theoretical maximum of HH is approached as the data for each variable become more skewed. Skewness in data may arise from real spatial variability or from the way in which variables are defined and/or measured. For example, data skewness may be introduced by grouping diameters of trees into classes. Although this bias is potentially the same among forests, the effect of variable classification was reduced by proportioning the data by the total for all classes before the HH for each class was calculated (recalling the geometric nature of HH arises primarily as a result of the multiplier, X_{ij}).

HH was calculated separately for species composition of tree, shrub and ground strata. These HH indices were later summed to obtain HH for species composition as a whole. Within each stratum, the abundance data for each species were proportioned by the total for all species in the stratum before the

HH for each species was calculated. Since the HH for the stratum was obtained by summing HH across species, proportioning each species by the total for all species, scaled a species HH contribution to its relative abundance, as well as its spatial variability. Vegetation cover in each of 5 height intervals was weighted by vegetation cover totalled for all height intervals to incorporate differences in cover between the various height intervals, as well as spatial variability within each height interval, into the HH index.

Alternative methods for quantifying habitat heterogeneity within forests were examined using 1980 species composition data. The ratio of species number per forest to average species number per habitat plot was calculated for tree, shrub and ground strata as a first approximation of spatial variability associated with between-habitat or beta-diversity (Whittaker 1972). Data from all habitat plots for tree species occurring in greater than 3% of all quadrats were further subjected to principal component analysis (Sokal & Rohlf 1981). Ranking of forests by increasing heterogeneity was not pursued because PCA did not explain a significant amount of the variation.

2.4, Bird Sampling

In 1979, birds in 5 forests were censused using a modification of the spot-mapping method. Standard spot-mapping censuses (IBCC 1970, Ralph & Scott 1981) involve mapping of singing males as an observer travels regularly-spaced grid lines on each of 8 or more visits. This method is generally intractable for larger areas and/or larger numbers of sites. Consequently, the spot-mapping method was modified by intensively censusing circular plots within each forest. In the 22 to 30 ha forests, there were 12 nonoverlapping plots of 45-metre radius. Plots were located randomly on a grid pattern superimposed on 1:15,000 air photos except in the 27- and 30-ha forests, where they were stratified according to the area of vegetation strata delineated by differences in canopy tree composition evident on air photos. In the 13-ha forest, only 6 census plots were located using a stratified-random design. Centre points of plots were at least 90 m apart in all forests. With this procedure, 25 to 35% (mean 30%) of the total area of each forest was censused for birds. In contrast to the standard spot-mapping method, remaining stationary at census plots facilitated concentration on censusing birds rather than trail navigation (Reynolds et al. 1980).

Census plots were located within forests by

pacing along compass bearings. The circumference of each 45-m radius census plot was marked using flagging tape and natural features (e.g. snags, distinctive trees) visible from the centre point.

Each plot was censused from the centre point for 15 minutes. To equalize observation time in all forests, each plot in the 13-ha forest was censused twice during each survey. Registrations were recorded in 5-minute periods. Census plots in each forest were surveyed sequentially such that the first and last plots were easily accessible. Censuses began within 30 minutes before sunrise. Average duration of censuses was 235 minutes (± 17 SD). Plot order was reversed on alternate surveys to reduce the effect of decreased song activity later in the morning (Shields 1977, Robbins 1981a, Skirvin 1981).

All bird activity in each census plot was noted with respect to species, location in the plot, activity (e.g. song, call, visual contact, feeding young, etc.) and temporal relationship with conspecific individuals (simultaneous or separate registrations). Birds detected outside the plot were noted as to species and 5-minute period to compare spot-mapping and point count methods for surveying birds.

Birds were censused from late May to early July on days with little rain or wind to avoid conditions

which adversely affect detectability of birds (Best 1981, Robbins 1981b). Seven spot mapping surveys were completed in each forest.

Species maps were generated for each census plot in each forest by combining observations from all completed surveys. Individuals maintaining breeding territories were determined by interpretation of the maps following the guidelines established by the International Bird Census Committee (IBCC 1970). Flushing data supplemented spot-mapping for Ruffed Grouse and American Woodcock. (Scientific names for all bird species are given in Appendix I). Number of species breeding in each forest was calculated by summing census plot results.

In 1980 and 1981, point counts (hereafter census points) were used to sample birds in each forest (Ralph & Scott 1981). Census points were distributed in the interior of forests to sample the spatial heterogeneity in canopy tree species evident from 1:15,000 air photos. All census point were at least 210 metres apart to minimize double-counting (cf. Reynolds et al. 1980, Blondel et al. 1981). Only one census point could be accommodated in the 5 smallest forests (3-9 ha). In the 16 larger forests, the numbers of census points were : 2 (13-14 ha), 3 (16-22 ha), 4 (25-44 ha), 5 (58-79 ha) or 6 (116-7620 ha). Census points in 1979 forests were coincident

with census plots.

At each census point all birds heard or seen during 5-minute periods were mapped according to estimated distances from the centre point. Birds flying overhead and raptors were included. In forests with 4 or more census points, birds were sampled for 15 minutes per point per survey. In forests which accommodated fewer census points, census duration was prolonged to improve sampling of species composition (see Section 3.4.). In forests with only a single census point, birds were sampled for 30 minutes per survey. In forests with 2 or 3 census points, sampling time was 20 minutes per point per survey. For some spatial analyses (Sections 2.5.1., 2.5.2.) and temporal analyses (Section 2.6.), bird data were restricted to 15 minutes per census point per survey to equalize sampling intensity per census point. In smaller forests with more survey time per census point, only data from the first 15 minutes were used.

Forests were surveyed at least twice during each breeding season of 1980 and 1981. Calendar dates were on average, within 4.5 days (± 6 SD) of each other between years. Surveys began around sunrise and 1 or 2 forests were surveyed per day. Other survey procedures were similar to 1979.

Results at each census point were evaluated the

same day as the survey. For each species, data were translated into number of pairs according to the following rules: a singing male, a pair of birds, an occupied nest, a family party or a single bird seen or heard calling were all counted as a pair of birds. Simultaneous registrations of singing males were required before more than 1 pair per species was accepted. Abundance of each species at a point was then taken as the high of the 5-minute periods. The higher value of two surveys was used as the species abundance at that point. This procedure is very similar to that used in the IPA method (Ferry 1974, IBCC 1977, Blondel et al. 1981). As in that method, the effective area censused varies with differences in detectability of species. For each species, comparisons can be made between census points and forests assuming detectability within a species does not vary significantly among forest habitats. While these data do not necessarily provide an accurate estimate of absolute density, they do allow comparisons of levels of observable bird activity among census points and forests. Because a single observer was responsible for all data collection and interpretation, data obtained from point counts likely do provide relatively reliable information.

2.5. Spatial Analyses of Birds

2.5.1. Bird Species Numbers

Bird numbers were examined at the scale of both census points and forests. Analyses were based on census time standardized to 15 minutes per census point per survey to equalize sampling intensity per census point among forests.

The number of bird species per census point was taken as all species detected in 2 surveys. The number of pairs per census point was calculated as the sum of individual species maxima. Means for bird species per census point and pairs per census point were calculated by averaging census point data within forests.

The number of bird species per forest equalled the cumulative number of species over all census points. Number of pairs per forest was calculated by summing census point maxima for all species except those audible at greater distances (Common Crow, Pileated Woodpecker, raptors). For these species, only the maximum number of pairs detected at any census point was included in the forest total.

2.5.2. Species Variability

Spatial variability of bird species within forests was examined in a number of ways using data from census time standardized to 15 minutes per

census point per survey. With all methods, only forests with 2 or more census points could be analyzed. Methods included:

1. Analysis of between-habitat or beta-diversity in species composition within each forest. Beta-diversity was approximated by calculating the ratio of number of bird species per forest to mean number of bird species per census point.
2. Mean percent difference (after Karr et al. 1982) in species composition between census points within a forest calculated by averaging pairwise comparisons of all points for 1981 according to:

$$SDc = 100(a+b)/(a+b+c)$$

where a = number of species at point A only

b = number of species at point B only

c = number of species in common.

This index is equivalent to (1 - Jaccard Index) (Mueller-Dombois & Ellenberg 1974).

3. Mean percent difference in species composition weighted by abundance (after Karr et al. 1982) between census points within a forest calculated by averaging pairwise comparisons of all points for 1981 according to:

$$SDa = 100 \sum_{i=1}^n |X_i - Y_i| / (X + Y)$$

where X = number of pairs at point A

Y = number of pairs at point B

X_i = number of pairs of species i at

point A

Y_i = number of pairs of species i at

point B

r = total number of bird species

2.5.3. Bird Species Composition

Analyses of the cumulative number of species against census duration for 1980 and 1981 indicated that species compositions within smaller forests (3-22 ha) were more completely sampled by increased census duration at each census plot (see Section 3.4.). Consequently, bird species composition and species abundances within forests were determined from results of all 5-minute census periods over all census points for 2 surveys in each year.

For each species, except those audible at greater distances (see Section 2.5.1.), the number of pairs per forest was standardized by summing census point maxima and dividing by the number of 30-minute census periods. For the most audible species, the number of pairs per forest was calculated by dividing the maximum number of pairs detected at any census point by the number of 30-minute census periods.

Bird species in each forest were tabulated according to 6 ecological classifications: habitat use, territory size, nesting stratum, foraging stratum, migratory status and regional abundance.

Classifications were only an approximation in that they do not reflect the real variability in resource use within a species. Since all classifications were obtained independently of this study, species number in each class could be related to forest size and habitat heterogeneity within forests.

Habitat use by each species was evaluated from Godfrey (1966), Robbins et al. (1966), Tozer & Richards (1974), Galli et al. (1976), Erskine (1977), Bull & Farrand (1977), Butcher et al. (1981), Freedman et al. (1981), Whitcomb et al. (1981), Blake & Karr (1982a), Collins et al. (1982) and Kendeigh (1982). Habitat use classes were: edge, facultative forest and obligate forest. Species classified as 'edge' characteristically used more open habitats but also forest edges or openings in forests. 'Facultative forest' species used both forest edge and forest interior habitats as well as urban, open shrub, and young second growth habitats. In some cases (e.g. Pileated Woodpecker), species may integrate more than one discrete forest into a single territory. 'Obligate forest' species were restricted primarily to the interior of older forests.

The territory size for each species was calculated by averaging all estimates (except the largest estimate) either obtained or derived from the literature (Williams 1936, Kendeigh 1945, 1946,

Schoener 1968, Tozer & Richards 1974, Willson 1974, Erskine 1971, 1976, DesGranges 1980, McCracken et al. 1981, Whitcomb et al. 1981). Species were then assigned to 1 of 3 classes: <2 ha, 2-5 ha, >5 ha.

Nesting stratum classes were: ground, shrub, canopy, hole or other. Species were classified after reviewing information in Godfrey (1966), Robbins et al. (1966), Bull and Farrand (1977) and Butcher et al. (1981).

The height at which species characteristically foraged was assessed from personal observation and the literature (Bent 1918-1968, Godfrey 1966, Willson 1974, DesGranges 1980, Blake & Karr 1982a). Foraging stratum classes were: ground, shrub, canopy, trunk or other.

Migratory status classes were: resident, short-distance migrant or long-distance migrant. Species were classified according to Robbins et al. (1966), Erskine (1977), Bull and Farrand (1977), Butcher et al. (1981), Whitcomb et al. (1981) and Blake and Karr (1982a). Long-distance migrants winter south of continental U.S.A. Short-distance migrants usually winter south of eastern Ontario or when present in winter, are derived from more northerly populations. Residents typically remain in eastern Ontario year round with at most small scale movements.

The regional abundance of each species was assessed by the Breeding Bird Survey method (Erskine 1978). In 1980, three, 40-km road transects were established within the 1400 km² area of the present study so as to pass near all 21 forests censused by point counts. From 24 June to 7 July 1980, two routes were surveyed 4 times, the third, twice, by an experienced observer from the Canadian Wildlife Service. On each route, birds were observed at 50 stops that were .8 km apart. Every bird seen within .4 km and every bird heard were counted during 3 minutes at each stop. After each route was surveyed, the number of individuals detected was calculated for each species. For each species, the maximum number of individuals detected on any survey of each route was summed to obtain an estimate of regional abundance. Each species was then assigned to a regional abundance class according to total number of individuals detected: <10, 11-50, >50. Species with greater than 11 individuals regionally could occur in more than half of the forests studied.

2.5.4. Random Assemblages

Bird species assemblages were generated for the 3- to 18-ha forests using a passive sampling model of random dispersal of individuals available in the regional species pool. Forests in this size range

are typical of many agricultural landscapes and are of interest because their avifauna differs from that in larger forests.

The number of bird pairs actually observed in each forest in 1980 was randomly selected with replacement from the regional pool (after Karr et al. 1982). The regional pool was calculated by summing pairs observed during point counts in 1980. Five random assemblages were generated for each forest. Because generation of assemblages was laborious, only the smallest forest was analyzed using 1981 data, to facilitate between year comparisons (see Section 2.6.).

The expected abundance of each bird species observed in 1980 and 1981 was generated for 3- to 18-ha forests by extension of the random model. For each forest, the number of bird pairs was multiplied by the frequency of each species in the regional species pool to obtain expected abundances of species per forest. Observed and expected abundances of species within forests were then compared by visual inspection. Statistical comparisons were inappropriate because expected frequencies were generally less than 1 (see Section 3.5.6.).

2.6. Temporal Analyses of Birds

Annual variability in species number and composition between 1980 and 1981 were calculated for the region and for each of the 21 forests. Analyses were based on total survey time per forest in each year because smaller forests were more completely sampled by longer census duration (see Section 3.4.). The time base of the analyses was expanded by including 1979 data for 5 forests. Data were then restricted to 30 minutes survey time per census point in each year to allow comparison with 1979 data.

Differences in species composition were quantified as (after Diamond 1969, McCoy 1982):

1. Absolute turnover = $a + b$

where a = number of species in year 1 only i.e.
local 'extinctions' within forests

b = number of species in the next year only
i.e. local 'immigrations' within
forests

2. Relative turnover = $100(a + b)/(a + b + 2c)$

where a, b as above

c = number of species in common

Relative turnover in species composition is equivalent to (1 - Sorenson Index) (Mueller-Dombois & Ellenberg 1974).

Differences in species number were quantified as:

$$1. \text{ Absolute turnover} = |X - Y|$$

where X = total number of species in year 1

Y = total number of species in the next
year

$$2. \text{ Relative turnover} = 100|X - Y|/(X + Y)$$

where X, Y as above.

Estimates of species differences related solely to various sampling errors, or "pseudoturnover" (Lynch & Johnson 1974), were calculated by comparing spot-mapping and point count results for 5 forests surveyed in 1979.

Species turnovers, expected if birds randomly disperse among forests, were estimated by comparing species assemblages randomly generated from 1980 and 1981 data. Analyses were restricted to the smallest forest because random assemblages were too laborious to generate for both years for many forests. Future research should concentrate on more efficient methods for generating random assemblages.

2.7. Statistical Analyses

Significance for all statistical tests was accepted at probabilities less than 5%.

Coefficient of variation, CV (Zar 1974), was calculated for means of habitat variables as a measure of sample variability relative to the mean. The Mann-Whitney test (Zar 1974) was used to compare

habitat variables within forests replicated in 1979 and 1980 samples.

Spearman's coefficient of rank correlation, r_s (Siegel 1956), was used to evaluate association between variables when only qualitative relationships were important. Compared to Kendall's rank correlation, r_s gives greater weight to pairs of ranks that are farther apart and thus is more appropriate when there is less certainty about the reliability of close ranks (Sokal & Rohlf 1981: 607). When quantitative relationships were important, association between variables was analyzed using the Pearson product-moment correlation coefficient, r (Zar 1974, Sokal & Rohlf 1981). In both tests, probabilities for two-tailed tests were used to determine significance.

Multiple linear regression was used to analyze the functional relationship between bird numbers and forest size and habitat heterogeneity within forests. Multiple regressions were performed by stepwise elimination of variables (the step-down) method (Zar 1974). Each dependent variable was regressed on 3 sets of independent variables: (1) $\log(\text{area})$, HH in species composition of tree, shrub and ground strata, and HH in forest structure (2) $\log(\text{area})$, HH in species composition of all strata combined and HH in forest structure (3) $\log(\text{area})$, and HH in species

composition and forest structure combined.

For all regressions, forest size was represented by $\log_{10} \text{area}$ (hereafter $\log(\text{area})$) because this transformation reduces skewness in the distribution of forest sizes and linearizes species-area curves (cf. Connor & McCoy 1979) and the relationship between HH and forest size (personal observation). Since area was used as an independent variable, and by definition has no variance, a log transformation does not bias regression results. Representing forest size by $\log(\text{area})$ rather than maximum distance minimized intercorrelations with HH (cf. Nie et al. 1975). HH was entered for all plant species and separately for forest structure to test sensitivity to birds to these 2 components of total habitat heterogeneity. Within plant species composition, HH was entered for each stratum separately to analyze for differential sensitivity of birds with different ecological characteristics.

For each regression, the relative importance of significant variables was indicated by standard partial regression coefficients. Higher absolute value indicated greater influence of the independent variable on the dependent variable (Zar 1974). Scatter plots of residuals from significant regressions were examined for homoscedasticity. Regression residuals were also analyzed for normality.

using normal probability plots to ensure appropriate use of the t and F tests (Draper & Smith 1966). The t test, however, is robust enough to stand considerable departure from its theoretical assumptions of normality and homoscedasticity, particularly since two-tailed testing and lower significance levels ($p < .05$) were used (Zar 1974:107).

Chi-square analysis of contingency tables (Zar 1974) was used to test for interrelations of ecological classifications of bird species (for classifications, see Section 2.5.3.). Comparisons of classifications which differed significantly from random (e.g. habitat use vs. regional abundance) were examined for classes sharing more species than expected (e.g. obligate forest and regional abundance <11) (see Section 3.5.5.).

The distribution of temporal variability between 1980 and 1981 among classes in each ecological classification of bird species was analyzed using the chi-square test for goodness-of-fit (Zar 1974). The expected distribution of temporal variability among classes was generated using the proportion of the regional species pool in each class multiplied by the total number of local extinctions and immigrations. When the distribution of temporal variability within classifications differed significantly from random, classifications were examined for classes varying

more or less than expected.

The paired-sample t test (Zar 1974) was used to detect significant differences in species turnover within forests between 1980 and 1981 for all bird species versus only obligate forest and facultative forest species.

3. RESULTS

3.1. Habitat Descriptions

Habitat descriptions were based on data for species composition and forest structure of 21 forests (3-7620 ha) sampled in 1980 (Appendix II).

3.1.1. Species Composition

Of 30 tree species detected regionally, 33 were deciduous and 6 were coniferous. All but 3 of the 21 tree species mentioned by Hosie (1969) as characteristic of the Great Lakes-St. Lawrence forest region were detected. Eighteen species occurred in over half of the forests sampled (Table 2). Basswood and American elm were the most widespread of the deciduous species, although red maple and sugar maple had the highest cover where they occurred. Balsam fir was the most widespread coniferous species although with low average cover when present. The number of tree species per forest ranged from 8 to 22 (mean 16.3 species, CV = 21%) accumulated from a generally consistent number of species per habitat plot among forests (mean 6.7 species, CV = 16%).

Regionally, 57 species were detected in the shrub stratum. Of these, 36 were immature trees, 18 were shrub species and 3 were vines. Immature basswood and American elm again occurred in all 21 forests (Table 3). Sugar maple had the highest cover

TABLE 2

Plant species detected in the tree stratum of over half of 21 forests sampled in 1980. Nomenclature follows Hosie (1969).

SPECIES	NO. OF FORESTS WHERE DETECTED	MEAN % COVER ± 1 SD*
DECIDUOUS TREES		
Basswood, <u>Tilia americana</u> L.	21	19 + 7
American elm, <u>Ulmus americana</u> L.	21	17 + 8
Sugar maple, <u>Acer saccharum</u> Marsh.	20	29 + 19
Red maple, <u>Acer rubrum</u> L.	19	31 + 13
Red ash, <u>Fraxinus pennsylvanica</u> Marsh.	19	20 + 8
Black ash, <u>Fraxinus nigra</u> Marsh.	18	14 + 6
Yellow birch, <u>Betula lutea</u> Michx. f.	16	16 + 7
Ironwood, <u>Ostrya virginiana</u> (Mill.) K.Koch	16	15 + 8
Bur Oak, <u>Quercus macrocarpa</u> Michx.	13	16 + 8
White birch, <u>Betula papyrifera</u> Marsh.	13	12 + 10
Trembling aspen, <u>Populus tremuloides</u> Michx.	13	18 + 12
Black maple, <u>Acer nigrum</u> Michx. f.	11	18 + 13
American beech, <u>Fagus grandifolia</u> Ehrh.	11	14 + 6
CONIFEROUS TREES		
Balsam fir, <u>Abies balsamea</u> (L.) Mill.	17	13 + 10
White spruce, <u>Picea glauca</u> (Moench) Voss	14	17 + 10
White cedar, <u>Thuja occidentalis</u> L.	14	17 + 16
White pine, <u>Pinus strobus</u> L.	12	20 + 11
Hemlock, <u>Tsuga canadensis</u> (L.) Carr.	11	15 + 15

* Excludes habitat plots where species absent.

TABLE 3

Plant species detected in the shrub stratum of over half of 21 forests sampled in 1980. Nomenclature follows Hasle (1969), Gillett & White (1978).

SPECIES	NO. OF FORESTS WHERE DETECTED	MEAN % COVER ± 1 SD*
IMMATURE TREES		
Basswood, <u>Tilia americana</u> L.	21	11 + 7
American elm, <u>Ulmus americana</u> L.	21	9 + 6
Sugar maple, <u>Acer saccharum</u> Marsh.	20	18 + 13
Black ash, <u>Fraxinus nigra</u> Marsh.	20	11 + 9
Balsam fir, <u>Abies balsamea</u> (L.) Mill.	19	12 + 9
Red ash, <u>Fraxinus pennsylvanica</u> Marsh.	19	13 + 7
Ironwood, <u>Ostrya virginiana</u> (Mill.) K. Koch	18	14 + 11
Red maple, <u>Acer rubrum</u> L.	18	12 + 10
Yellow birch, <u>Betula lutea</u> Michx. f.	15	6 + 5
Bur oak, <u>Quercus macrocarpa</u> Michx.	14	4 + 5
White spruce, <u>Picea glauca</u> (Moench) Voss	14	9 + 12
Trembling aspen, <u>Populus tremuloides</u> Michx.	13	3 + 3
Blue-beech, <u>Carpinus caroliniana</u> Walt.	12	10 + 8
Green ash, <u>Fraxinus pennsylvanica</u> var. <u>subintegerrima</u> (Vahl) Fern.	12	5 + 5
White cedar, <u>Thuja occidentalis</u> L.	12	9 + 8
Black maple, <u>Acer nigrum</u> Michx. f.	11	11 + 14
Hemlock, <u>Tsuga canadensis</u> (L.) Carr.	11	6 + 7
White birch, <u>Betula papyrifera</u> Marsh.	11	3 + 1
SHRUBS		
Choke cherry, <u>Prunus virginiana</u> L.	17	4 + 5
Beaked hazelnut, <u>Corylus cornuta</u> Marsh.	15	8 + 6
Nannyberry, <u>Viburnum lentago</u> L.	13	2 + 2
Red elderberry, <u>Sambucus pubens</u> Michx.	11	6 + 7
VINES		
Virginia creeper, <u>Parthenocissus vitacea</u> (Knerr) A. S. Hitchc.	11	2 + 4

* Excludes habitat plots where species absent.

when present. Choke cherry was the most common shrub species; beaked hazelnut had the highest mean cover. Virginia creeper was the only common vine species. The number of shrub-stratum species per habitat plot ranged from 5.6 to 12.6 (mean 9.2 species, CV = 25%) with 24.0 species (CV = 21%) per forest, on average.

Regionally, 83 species were detected in the ground stratum. Of these, 15 were tree seedlings, 8 were immature shrubs and 3 were vines. Ground-stratum species exhibited high spatial variability. Thirty-two species were detected in only 1 forest and 23 species were detected in only 1 habitat plot. Only 14 species occurred in over half of the forests sampled (Table 4). Only 5.1 species (CV = 25%) were detected on average per habitat plot, partly because species with low cover were not recorded. A relatively consistent average of 17.5 species (CV = 25%) was detected in the ground stratum of each forest.

3.1.2. Forest Structure

Tree density averaged 21.3 trees per 250 m² and was relatively consistent among forests (CV = 34%). The older age of forests was evident in the widespread occurrence of trees with diameters over 36 cm. Forest canopy ranged from 12 to 21 m in height and was generally continuous (canopy closure averaged

TABLE 4

Plant species detected in the ground stratum of over half of 21 forests sampled in 1980. Nomenclature follows Gillett & White (1978).

SPECIES	NO. OF FORESTS WHERE DETECTED	MEAN % COVER ± 1 SD*
TREE SEEDLINGS		
Sugar Maple, <u>Acer saccharum</u> Marsh.	12	40 ± 15
VINES		
Virginia Creeper, <u>Parthenocissus vitacea</u> (Knerr) A. S. Hitchc.	13	19 ± 13
Poison Ivy, <u>Rhus radicans</u> L.	12	18 ± 7
OTHER		
Sedges, Cyperaceae	21	35 ± 10
Mosses, Bryophyta	18	23 ± 9
Lady Fern, <u>Athyrium filix-femina</u> (L.) Roth	15	23 ± 10
Sensitive Fern, <u>Onoclea sensibilis</u> L.	13	22 ± 10
Enchanter's Nightshade, <u>Circaea lutetiana</u> L. spp. <u>canadensis</u> (L.) Asch. & Magnus	13	20 ± 8
Spotted touch-me-not, <u>Impatiens capensis</u> Meerb.	13	32 ± 22
Dwarf raspberry, <u>Rubus pubescens</u> Raf.	13	19 ± 8
Ostrich fern, <u>Matteucia struthiopteris</u> (L.) Todaro	12	22 ± 8
Violets, Violaceae	11	21 ± 9
Grasses, Gramineae	11	31 ± 12
Wild sarsaparilla, <u>Aralia nudicaulis</u> L.	11	18 ± 5

* Excludes habitat plots where species absent.

over 87%; canopy gaps averaged less than 5% of distances between habitat plots). Vegetation cover averaged from 60-80% for most height intervals in forests. Ground cover was predominately leaf litter with bare rock and standing water occurring in only a few forests.

3.2. Evaluation of Habitat Methods

The following subsections assess the adequacy of the less-intensive 1980 sample (Appendix II) in representing forest habitats, by comparing 1980 results for 5 forests with results from a more intensive sample in 1979. The habitat heterogeneity index is also examined and results compared to alternative methods for quantifying spatial variability in habitat conditions within forests.

3.2.1. Habitat Sampling

Six variables for species composition and 7 for structure were replicated between 1979 and 1980 in 5 forests (Table 5). Numbers of tree species in forests were similar in total between years primarily because sampling trees by canopy cover in 1980 included more species per plot. The larger quadrat used in 1980 for sampling the shrub stratum produced ~~smaller~~ total number of species through elevated species detections per plot compared to 1979. Substantial differences in species number in the

TABLE 5

Habitat variables replicated in 5 forests with greater sampling intensity in 1979 than 1980. Entries are means ($\pm$ 1 SD) except where appropriate.

Habitat Variable	13	18	22	25	27	30
	1979	1980	1979	1979	1979	1980
SPECIES COMPOSITION						
Tree stratum						
Total no. species	17	16	22	18	23	22
No. species per plot	5.6 (1.8)	8.5 (1.4)	6.9 (3.0)	5.3 (2.2)	6.1 (1.1)	7.0 (3.6)
Shrub stratum						
Total no. species	16	24	27	28	29	33
No. species per plot	4.1 (2.4)	9.5 (3.4)	6.2 (2.6)	12.1 (1.6)	12.6 (3.2)	11.4 (4.2)
Ground stratum						
Total no. species	37	26	82	37	91	16
No. species per plot	15.3 (4.0)	7.8 (2.3)	16.8 (4.2)	17.3 (4.0)	19.3 (6.1)	11.8 (7.1)
FOREST STRUCTURE						
Tree Density (No./250 m ²)	27.3 (12.9)	24.1 (6.0)	35.0 (15.8)	49.1 (10.9)	24.2 (10.1)	15.2 (9.5)
No. Trees by diameter class (cm)						
8-12	11.8 (7.1)	4.0 (1.5)	19.4 (12.5)	4.9 (1.1)	11.6 (7.1)	3.0 (2.3)
12-20	9.9 (6.4)	3.1 (1.2)	11.5 (6.4)	2.5 (1.3)	6.9 (5.6)	2.5 (1.8)
20-36	4.9 (3.5)	0.9 (0.9)	3.1 (3.2)	0.5 (1.1)	1.4 (1.2)	1.4 (1.2)
> 36	0.6 (0.9)	0.6 (0.9)	1.5 (1.8)	0.1 (0.4)	1.7 (2.2)	1.0 (1.1)
Canopy height (m)	11.7 (3.5)	14.3 (3.7)	13.1 (3.6)	13.3 (3.1)	10.8 (5.2)	11.6 (7.1)
Canopy closure (%)	58.7 (20.4)	75.8 (18.9)	77.1 (15.0)	88.1 (5.8)	61.5 (18.5)	72.4 (23.2)
No. Habitat Plots	11	8	17	20	22	8

ground stratum were evident primarily because species with low cover were not recorded in 1980. Tree densities were not significantly different between years except in the 25-ha (Mann-Whitney $U = 154$, $n = 28$) and 27-ha ($U = 138$, $n = 30$) forests. Differences in tree densities were reflected in distribution of trees by diameter class. A higher proportion of trees over 20 cm dbh were detected in larger forests by the 1980 sample. Canopy height was slightly higher in the 1980 sample but no statistically significant differences were detected (all U 's $p > .20$). Canopy closure was also consistently higher in 1980 with significant differences in the 22-ha ($U = 110$, $n = 25$), 25-ha ($U = 143$, $n = 28$), and 30-ha ($U = 127.5$, $n = 27$) forests.

In summary, changes in sampling methodology accounted for most differences in species composition per plot for all strata. For forests as a whole, tree and shrub strata appeared to be adequately sampled by the less-intensive 1980 sample. Differences in forest structure were primarily related to sampling intensity, in particular, fewer habitat plots in 1980 and location of those plots in more continuously-canopied interiors of forests. Since bird sampling was also restricted to forest interiors, these differences represented reasonable changes in habitat descriptions within forests.

Despite differences in sampling methodology and intensity, habitat patterns among forests were similar between 1979 and 1980 samples. A composite of habitat comparisons was obtained by ranking each of the 13 replicated variables for the 5 forests in 1979 and 1980. When absolute values in rank differences were calculated for each forest for each habitat variable, 79% of all ranks differed by 1 rank or less between years.

3.2.2. Habitat Heterogeneity Indices

The intermittent occurrence of snags, canopy gaps and ground covers of rock and standing water within and among forests in 1980 resulted in large variation in HH values for those variables relative to other variables (Table 6). HH values of 2.079 in 8-, 25-, 116-, 220-, and 680-ha forests resulted from a variable occurring at only 1 of 8 habitat plots. These variables were omitted from further analysis because it seemed ecologically unreasonable that measures of habitat heterogeneity within forests should be dominated by variables of that nature. Fallen trees, although potentially important ecologically as nest sites or foraging substrates for birds, were also removed from further analyses because they remained the only component of forest structure measured between, rather than at, habitat

TABLE 6
Habitat heterogeneity (HH) in 21 forests sampled in 1980.

Habitat Variable	3	4	5	8	9	13	14	16	18	22	25	27	30	44	58	79	316	220	680	3350	7620
Species Composition																					
* Tree stratum	.484	.601	.801	.513	.401	.469	.813	.842	.376	.541	.477	.823	.995	.884	.635	.639	.972	1.010	.543	.917	.841
* Shrub stratum	.792	.561	.719	.701	.637	.653	.900	.922	.703	.474	.821	.587	.907	1.167	.746	.809	1.174	.841	1.744	.935	.730
* Ground stratum	.874	1.244	1.084	.962	.798	.877	1.236	.852	.804	.665	.651	.726	1.092	1.262	1.011	.814	1.192	1.211	1.103	1.028	1.147
Forest Structure																					
Tree density	.075	.044	.036	.053	.052	.027	.035	.173	.089	.147	.068	.146	.125	.036	.065	.036	.046	.073	.102	.148	.070
* Trees by diameter class	.203	.196	.257	.340	.194	.136	.253	.373	.384	.177	.333	.337	.333	.198	.349	.291	.317	.248	.142	.376	.262
* Canopy height	.007	.041	.020	.022	.005	.031	.016	.011	.017	.024	.007	.146	.012	.020	.033	.026	.010	.021	.015	.023	.035
Herb height	.113	.186	.172	.064	.082	.100	.036	.128	.039	.159	.046	.164	.150	.172	.088	.267	.184	.368	.129	.310	.216
Foliage cover by height interval	.013	.022	.030	.022	.029	.034	.031	.043	.020	.020	.012	.049	.045	.042	.021	.017	.045	.040	.009	.075	.024
* Canopy closure	.003	.001	.015	.017	.001	.029	.001	.123	.007	.002	.003	.050	.010	.015	.002	.011	.000	.009	.001	.044	.011
Bare ground	.024	.206	.335	.128	.036	.236	.388	.261	.060	.172	.087	.245	.344	.335	.091	.040	.000	.332	.000	.000	.173
Litter cover	.003	.006	.009	.001	.003	.004	.009	.008	.000	.002	.001	.005	.017	.009	.009	.050	.000	.042	.000	.003	.007
Rock cover	0	0	0	0	0	0	0	0	0	0	0	0	1.000	0	0	.633	.384	2.079	0	1.151	0
Water cover	1.511	0	0	0	0	0	0	0	0	0	0	2.079	0	0	1.443	0	0	0.992	0	0	0
Canopy gaps	1.030	1.040	.225	2.079	1.284	.415	.678	.343	.196	.618	.454	1.239	.697	.225	.788	1.207	2.079	0	2.079	1.257	.997
Snags	.143	.036	.030	.566	.698	.115	.228	.652	.222	.060	.184	.142	.101	.030	.086	.297	.273	.072	.055	.370	.348
Fallen trees																					

* Variables replicated from 1979.

plots.

The HH index was compared to other methods for quantifying spatial variability in habitat within forests. The ratio of species number per forest to mean species number per habitat plot in 1980 (Appendix II) was calculated by stratum as a first approximation of spatial heterogeneity associated with between-habitat or beta-diversity. Correlations of the HH index and the beta-diversity approximation were significant for the tree stratum ($r_s = .777$), shrub stratum ($r_s = .553$), ground stratum ($r_s = .730$) and species composition in total ($r_s = .848$).

Species composition of the tree stratum at habitat plots was further examined using principal components analysis, PCA, in order to rank forests by increasing heterogeneity. Only 16.5% of the total variance in tree species composition among habitat plots was explained by the first two principal components, making PCA an unuseful analysis for these data. (cf. Karr & Martin 1981). The third factor explained only an additional 7.3%; 9 factors were required to explain 50% of the total variance.

3.3. Habitat Heterogeneity Within Forests

On average, habitat heterogeneity in species composition within 21 forests was highest for the ground stratum and lowest for the tree stratum (Table

7). Comparisons between compositional and structural variables were inappropriate because of differences in data classification and the resulting effect on the habitat heterogeneity index, HH (discussed in Section 2.3.). According to HH, species composition in all strata combined was most heterogeneous in the 116-ha forest, the least in the 22-ha forest. Structurally, the 27-ha forest was the most heterogeneous, the 680-ha forest the least. In total, the 9-ha forest exhibited the lowest habitat heterogeneity; the 220-ha forest was the most spatially heterogeneous for habitat variables analyzed.

Overall, components of habitat heterogeneity were not significantly correlated with forest size represented by $\log(\text{area})$ (Table 8). Forest area was log transformed to reduce skewness in the distribution of forest sizes. Forest size was alternately represented by the greatest distance between habitat plots (hereafter maximum distance). Maximum distance reflects the spatial scale over which habitat heterogeneity was actually measured within forests. Theoretically, as distances between habitat plots increases, habitat heterogeneity should also increase because plant populations tend to be contagiously distributed (Mueller-Dombois & Ellenberg 1974). Larger forests generally had greater maximum

TABLE 7

Mean habitat heterogeneity (HH) in 21 forests (3-7620 ha) sampled in 1980.

Habitat Variable	HH		Forest Size (ha)	
	Mean	1 SD	Maximum HH	Minimum HH
Species Composition				
Tree stratum	.693	.209	220	18
Shrub stratum	.786	.178	116	22
Ground stratum	.982	.197	4	25
All strata	2.462	.489	116	22
Forest Structure*	.739	.232	27	680
Total Habitat	3.200	.631	220	9

* Variables included Tree density, Trees by diameter class, Canopy height, Herb height, Foliage cover by height interval, Canopy closure, Bare ground, Litter cover.

TABLE 8

Pearson correlations for forest size and habitat heterogeneity within 21 forests.

FOREST VARIABLE	1	2	3	4	5	6	7
SIZE							
1. Log Area							
2. Maximum Distance ^a	.667*						
HABITAT HETEROGENEITY							
Species Composition							
3. Tree Stratum	.430	.488*					
4. Shrub Stratum	.275	.540*	.603*				
5. Ground Stratum	.276	.181	.590*	.472*			
6. All Strata	.393	.477*	.881*	.809*	.825*		
7. Forest Structure ^b	.153	.128	.766*	.166	.209	.469*	
8. Total Habitat	.361	.416	.963*	.687*	.715*	.946*	.730*

^a Greatest distance between habitat plots^b Variables included listed in Table 7* $p < .05$

distances but not always so, as indicated by a Pearson correlation of less than one (Table 8). Habitat heterogeneity of species composition of tree stratum, shrub stratum and all strata combined increased significantly with greater maximum distance within forests.

The various components of habitat heterogeneity within forests were also intercorrelated to varying degrees (Table 8). The significant correlation of all components with tree species heterogeneity emphasizes the importance of trees as determinants of spatial pattern in forest vegetation.

3.4. Evaluation of Bird Survey Methods

From 1979 to 1981, birds were sampled in forests using point counts at habitat plots. The efficiency of the point count method for sampling forest birds was examined by comparing 1979 data from point counts with intensive spot-mapping censuses collected in 5 forests. Although the spot-mapping method introduces biases to census results (Berthold 1976, Oelke 1981), it is still the commonly accepted standard for comparison (Ralph & Scott 1981).

On average, the point count method detected 89% of the species enumerated as breeding species by the spot-mapping method (Table 9). The total number of species per forest was 11% higher, on average, for

TABLE 9

Efficiency of the point-count method versus spot-mapping method for censusing forest birds.

Forest Size (ha)	Spot-Mapping No. Species (1)	Point Counts Total No. Species (2)	No. Species Common to Spot-Mapping (3)	Efficiency Total Species $\left(\frac{2+1}{\times 100}\right)$	Species Common to Spot Mapping $\left(\frac{3+1}{\times 100}\right)$
ONTARIO ^a					
30	22	30	20	136	91
27	31	30	26	97	84
25	18	23	17	128	94
22	22	22	20	100	91
13	20	19	17	95	85
Mean $\pm$ 1 SD				111.2 $\pm$ 19.3	89.0 $\pm$ 4.3
MARYLAND ^b					
14.2 (North)	30	28	27	93	90
14.6 (South)	21	21	19	100	90
Mean $\pm$ 1 SD				96.5 $\pm$ 4.9	90.0 $\pm$ 0

^a Spot-mapping of circular plots. Details in Section 2.4.

^b Whitcomb et al. 1981: Appendix B. Spot-mapping of entire forest.

point counts than for spot-mapping. Percent differences in total species number between the 2 methods were not related to $\log(\text{forest area})$ ($r = .612$ $p > .20$). Higher species numbers from point counts reflected inclusion of species with territories outside census plot boundaries as well as detection of some transient species (i.e. bird species merely passing through a forest) and/or vagrant species (i.e. species that treat a forest only as part of a territory or home range). Differences attributable to modification of the spot-mapping method appeared minimal as similar results were evident for the 13-ha forest in the present study and two 14-ha forests in Maryland which were censused by point counts and by spot-mapping of the entire forest (Table 9).

The efficiency of point counts in representing bird species composition within forests was further evaluated by analyzing species-time curves for 1980 and 1981 data (1980 data displayed in Fig. 3). An asymptote in species number was achieved in 25- to 7620-ha forests by accumulating species over census points surveyed for 15 minutes on each of 2 surveys. Similar data for 3- to 22-ha forests did not produce an asymptote in species number. More census points could not be accommodated in these forests. Additional survey time at census points increased the

Figure 3. Bird species-time curves for 21 forests surveyed in 1980.

number of species by an average of 16.5% (± 12.1 SD). An asymptote was achieved in all smaller forests with longer census duration.

3.5. Spatial Patterns in Birds

3.5.1. Bird Species Numbers by Census Point

The number of bird species per census point increased significantly with number of pairs per census point in 1980 and 1981 ($r = .824, .835, n = 74$, respectively). The relationship was even stronger when data were averaged over all census points within each forest (1980 $r = .875$, 1981 $r = .897, n = 21$). This pattern was independent of forest size. No significant correlations were detected between $\log(\text{area})$ and species number per census point (1980 $r = -.105, p > .20$, 1981 $r = -.043, p > .50, n = 74$). Nor was $\log(\text{area})$ correlated with number of pairs per census point (1980 $r = -.025, p > .50$, 1981 $r = .104, p > .20, n = 74$). Mean species number per census point was not related to forest size in 1980 or 1981 by multiple linear regression (Table 10). Mean species number per census point did increase significantly with greater habitat heterogeneity in forest structure in 1980 but not in 1981. The mean number of pairs per census point increased significantly solely with habitat

TABLE 10

Multiple regression statistics for bird species numbers per census point on size (Log Area) and habitat heterogeneity (HH) within 21 forests.

BIRD VARIABLE	YEAR	F [#]	R ² (%) ^c	Y INTERCEPT	ENVIRONMENTAL VARIABLE	PARTIAL REGRESSION COEFFICIENT, b	t ^e	STANDARD b
Mean No. Bird Species	1980 1981	10.20* None Significant	35	11.3-	HH(Forest Structure)	7.6	3.193*	.591
Mean No. Pairs	1980 1981	4.45* 8.89*	19 32	18.4 12.3	HH(Forest Structure) HH(Shrub Species)	6.8 10.9	2.110* 2.981*	.436 .565

[#]F - ratio for multiple regression

^c Coefficient of determination

^et - ratio for partial regression coefficient

* p < .05

heterogeneity in forest structure in 1980 and with habitat heterogeneity in species composition of the shrub stratum in 1981.

3.5.2. Species Variability

Theoretically, more heterogeneous forests should exhibit greater spatial variability in bird species as a consequence of interspecific differences in habitat selection. Spatial variability in bird species composition within 16 forests with 2 or more census points was examined in several ways. The ratio of total bird species number per forest to species number per census point averaged for the whole forest (Appendix III) was calculated as a first approximation of between-habitat or beta-diversity in bird species composition. Multiple regression analyses indicated that beta-diversity increased significantly solely with forest size in 1980 and 1981 (Table 11). Beta-diversity results indicated that larger forests supported more bird species through differences in species composition between census points.

Interpoint differences in species composition within forests were quantified by averaging percent difference in species composition between pairs of census points for 1981 according to the SDC index (details in Section 2.5.2.). SDC is sensitive to

TABLE 11

Multiple regression statistics for spatial variability in bird species on size (Log Area) and habitat heterogeneity (HH) within 16 forests. Beta-diversity, SDC, SDa defined in text.

MEASURE OF SPATIAL VARIABILITY	YEAR	r^2	R^2 (%) ^c	Y INTERCEPT	ENVIRONMENTAL VARIABLE	PARTIAL REGRESSION COEFFICIENT, b	t °	STANDARD b
Beta-diversity	1980	106.48*	88	1.1	Log Area	.268	10.319*	.940
	1981	52.87*	79	1.2	Log Area	.275	7.271*	.889
	1981	11.47*	45	39.5	HH(Tree Species)	18.0	3.387*	.671
SDc		7.71*	54	36.4	Log Area	3.6	2.930*	.590
					HH(Forest Structure)	12.1	2.692*	.505
		7.53*	35	35.7	HH(Total Habitat)	5.1	2.745*	.592
SDa	1981	8.73*	38	36.9	Log Area	3.2	2.954*	.620

^aF - ratio for multiple regression

^c - Coefficient of determination

^bt - ratio for partial regression coefficient

* p < .05

species differences between points (Mueller-Dombois & Ellenberg, 1974) and is particularly appropriate for comparisons involving relatively few species. SDC varied from 42 to 63% among forests (Table 12). SDC increased significantly with increasing forest size and habitat heterogeneity within forests (Table 11). SDC was uncorrelated with number of bird species per forest in 1981 ($r_s = .394$, $p > .10$, $n = 16$).

SDC weights all species differences equally regardless of abundance. To incorporate differences in species abundances, SDA (details in Section 2.5.2.) was calculated by averaging percent difference in species composition weighted by abundance between pairs of census points within 16 forests. Mean differences in species composition between census points within a forest weighted by abundance varied from 37 to 53% among forests and were always lower than unweighted differences in species composition (Table 12). That is, relatively uncommon species appeared responsible for higher SDC than SDA values within forests. Only forest size was significantly predictive of SDA within forests (Table 11). Bird species composition weighted by abundance was more variable with the greater distances between census points in larger forests. SDA was uncorrelated with number of bird species per forest in 1981 ($r_s = .415$, $p > .10$, $n = 16$).

TABLE 12

Spatial variability in bird species (SDc) and in bird species weighted by abundance (SDa) averaged for pairs of census points within 16 forests sampled in 1981.

Forest Size (ha)	Pairs of Census Points Compared	Mean SDc	$\pm$ 1 SD	Mean SDa	$\pm$ 1 SD
13	1	50	--	44	--
14	1	55	--	39	--
16	3	56	12	45	6
18	3	42	8	38	8
22	3	52	7	39	8
25	6	47	8	42	12
27	6	51	5	42	5
30	6	50	12	42	12
44	6	49	5	37	7
58	10	56	7	43	8
79	10	50	8	43	9
116	15	55	9	47	10
220	15	62	8	49	8
680	15	48	10	39	10
3350	15	63	12	53	16
7620	15	58	10	48	7
Mean $\pm$ 1 SD		52.8 $\pm$ 5.5		43.1 $\pm$ 4.4	

3.5.3. Bird Species Numbers by Forest

Although bird numbers per census point were unrelated to forest size, the number of bird species per forest increased significantly in both 1980 and 1981 with forest size (Table 13). In 1980, structural heterogeneity was secondarily predictive as indicated by the lower absolute value of its standard partial regression coefficient (standard $b = .366$ versus $.673$ for forest area). The number of bird pairs per forest increased significantly with $\log(\text{area})$ in 1980 and 1981 (Table 13). In 1981, greater habitat heterogeneity in species composition of the shrub stratum also increased the number of pairs per forest.

Log species number has also been found to be significantly related to forest size (Connor & McCoy 1979, Martin 1981, Wright 1981). When multiple regressions were done using the log of bird species number per forest, $\log(\text{area})$ remained the best predictor in 1980 and 1981, although components of habitat heterogeneity were secondarily important in both years (Table 13).

3.5.4. Bird Species Number and Habitat Quality

Theoretically, a forest could be highly heterogeneous in habitat but, if the habitats were of poor quality, the number of bird species within the

TABLE 13

Multiple regression statistics for bird species numbers per forest on size (Log Area) and habitat heterogeneity (HH) within 21 forests.

BIRD VARIABLE	YEAR	F ^a	R ² (%) ^c	Y INTERCEPT	ENVIRONMENTAL VARIABLE	PARTIAL REGRESSION COEFFICIENT, b	t ^b	STANDARD b
Bird Species No.	1980	17.65*	66	7.2	Log Area	5.7	4.855*	.673
					HH(Forest Structure)	11.9	2.641*	.366
Log Bird Species No.	1981	20.51*	52	14.6	Log Area	6.4	4.529*	.721
	1980	14.37*	62	1.017	Log Area	.105	4.177*	.618
Log Bird Species No.					HH(Forest Structure)	.260	2.679*	.397
	1981	12.40*	69	1.185	Log Area	.118	4.878*	.700
No. Pairs					HH(Shrub Species)	.369	2.773*	.434
					HH(Ground Species)	-.297	-2.476*	-.387
No. Pairs	1980	35.09*	65	12.5	Log Area	42.5	5.924*	.805
	1981	30.17*	77	-44.3	Log Area	37.3	6.382*	.750
					HH(Shrub Species)	73.9	2.501	.294

^a F - ratio for multiple regression

^c Coefficient of determination

^b t - ratio for partial regression coefficient

* p < .05

forest could be comparable to the number of bird species within a less heterogeneous forest of better quality habitat. Not incorporating differences in habitat quality explicitly into the HH index could have obscured the relationship between habitat heterogeneity and bird species number per forest.

Any measure of habitat quality must be relevant to the organism in question, in this case, birds. In the following analyses I used the mean number of bird species per census point (Appendix III) as an approximation of habitat quality within forests. This approach was valid because the number of bird species at a particular census point is not predictable a priori from the total number of bird species per forest. The effect of habitat quality versus habitat heterogeneity can therefore be evaluated by regression on total bird species per forest because species number at a census point is independent of total species number in a forest.

The number of bird species detected at a census point was significantly correlated between 1980 and 1981 ($r = .476$, $n = 74$). When averaged within forests, species number per census point was not correlated between years ($r = .327$, $p > .05$, $n=21$), primarily because of high variability at the single census points in the 5 smallest forests. When forests with single census points were omitted, mean

bird species number per census point was significantly correlated between years ($r = .603$, $n = 16$). The mean number of bird species per census point appeared to be reasonably representative of the range of habitat quality within forests, at least for forests larger than 9 ha, since forests with higher mean numbers of bird species per census point were not more variable in species number between census points (measured by SE, Appendix III) than forests with lower mean numbers of bird species per census point (1980 $r = -.092$, 1981 $r = -.037$, $p > .50$, $n = 16$).

Habitat quality and habitat heterogeneity within forests were not consistently related (Table 10). In contrast, the number of bird species per forest increased primarily with habitat quality in 1980 and 1981 (Table 14). Differences in habitat quality among forests larger than 9 ha were not related to differential variability between census points in bird species composition (SDc for 1981 $r_s = .041$, $p > .50$, $n = 16$) or bird species composition weighted by abundance (SDa for 1981 $r_s = -.046$, $p > .50$, $n = 16$). That is, forests with different quality habitats were, on average, equally variable in bird species between census points despite differences in habitat heterogeneity. The positive relationship between habitat quality and bird species number per

TABLE 14

Multiple regression statistics for bird species number per forest on habitat quality^a
(mean species number per census point) and habitat heterogeneity (HH) within 21 forests.

YEAR	F [#]	R ² (%) ^c	Y INTERCEPT	ENVIRONMENTAL VARIABLE	PARTIAL REGRESSION COEFFICIENT, b	t ^e	STANDARD b
1980	12.06*	.57	-0.6	Habitat Quality HH(Tree Species)	1.1 11.1	3.100* 2.108*	.529 .360
1981	16.42*	.65	-9.9	Habitat Quality HH(Tree Species)	1.776 11.210	4.674* 2.505*	.664 .356

[#]F - ratio for multiple regression

^c - Coefficient of Determination

^et - ratio for partial regression coefficient

* p < .05

forest must then accrue from more species per census point in higher quality habitats. When coupled with the secondary importance of habitat heterogeneity, these results suggest that interaction of habitat quality and habitat heterogeneity was not as important in determining numbers of bird species per forest as differences in habitat quality among forests.

3.5.5. Bird Species Number by Ecological Class

The importance of habitat heterogeneity to bird species numbers may still have been obscured by lumping all species irrespective of ecological differences in resource use. To improve the sensitivity of the analyses, each of the 72 species detected in 1980 or 1981 was classified according to its habitat use, territory size, nesting stratum, foraging stratum, migratory status and regional abundance (Appendix I). Of 37 obligate and facultative forest species detected by point counts within 21 forests in 1980, 89% were also detected by Breeding Bird Surveys (BBS) conducted simultaneously within the study area. Regional abundances of these species were significantly correlated between BBS and point counts ($r_s = .789$), or even higher by Pearson correlation ($r = .796$). BBS appeared sensitive to species characteristically inhabiting forests

regionally and likely provided reasonable data for classifying bird species by regional abundance. Comparison of BBS and point count results also indicated that bird species in forests sampled were typical of the regional forest avifauna.

Bird species number in 11 ecological classes consistently increased, primarily with forest size (Fig. 3A, details in Appendix IV). Forest size was the most significant variable for 6 other classes in either 1980 or 1981. Chi-square analyses of contingency tables of ecological classifications indicated that many of these classes were positively interrelated (Fig. 3A).

Habitat heterogeneity was the most significant variable in both 1980 and 1981 for 2 interrelated classes (Fig. 3B). Six other classes exhibited inconsistent relationships with habitat heterogeneity between 1980 and 1981. The number of species characterized as edge, shrub nesters, shrub foragers and very abundant regionally increased primarily as heterogeneity of species composition of the ground stratum decreased (Appendix IV). Edge species were significantly positively interrelated with shrub foragers and species abundant regionally (Fig. 3B). Since larger, more continuously-canopied forests tended to exhibit greater heterogeneity in species composition of the ground stratum (Table 8), the

Figure 4. Relative importance of A. forest size (Log Area) and B. habitat heterogeneity (HH) to ecological classes of birds in 21 forests in 1980 and 1981. Results summarized from multiple regression analyses (Appendix IV) for ecological classes by habitat use (E:edge, FF:facultative forest, OF:obligate forest), territory size (T<2: <2 ha, T2-5: 2-5 ha, T>5: >5 ha), nesting stratum (GN:ground, SN:shrub, CN:canopy, HN:hole), foraging stratum (GF:ground, SF:shrub, CF:canopy, TF:trunk, Other F: raptors), migratory status (RES:resident, SD:short-distance, LD:long-distance) and regional abundance from 1980 Breeding Bird Surveys (RA<11: <11 individuals, RA11-50: 11-50 individuals, RA>50: >50 individuals). Other symbols explained in the key.

A. Log Area Most Significant Variable

B. HH Most Significant Variable

KEY

- Variable important 1980 only
- Variable important 1981 only
- ° Other variable secondarily important in 1980 and/or 1981
- Interrelated by χ^2
- Interrelated by trend only

inverse relationship of ground-stratum heterogeneity and ecological classes interrelated with edge species likely reflected differential availability of 'edge-like' habitat in smaller forests and/or less continuously-canopied forests. Other classes were positively related with habitat heterogeneity within forests. Greater habitat heterogeneity can substitute for forest area, except that very small forests contained few or no raptor species, species with large territory sizes, obligate forest species, trunk foragers, or species with low regional abundances, i.e. multiple regressions for these classes had low or negative y-intercept values (Appendix IV).

In summary, forest size was the only significant variable determining the number of bird species in half of the ecological classes in 1980 or 1981 (Table 15). In total, 67% of all classes analyzed over 2 years were significantly related, at least primarily, to forest size. Habitat heterogeneity was the most significant variable for 24% of all ecological classes. Only four classes (or 10% of all classes analyzed) were not significantly related to either forest size or habitat heterogeneity within forests.

TABLE 15

Relative importance of forest size (Log Area) and habitat heterogeneity (HH) to bird species number by ecological class in 21 forests. Results summarized from multiple regression analyses (Appendix IV).

Significant Variable	Percent of n Ecological Classes		
	1980 (n = 21)	1981 (n = 21)	1980 & 1981 (n = 42)
Log Area Only	43	57	50
Log Area Primarily*	19	14	17
HH Only	19	14	17
HH Primarily*	10	5	7
None	10	10	10

* Other variable secondarily important.

3.5.6. Birds by Species

Smaller forests did not have many of the bird species detected in larger forests (Table 16). Of species detected in at least 4 forests over both years, only the Starling was restricted to the smallest forests. However, many other species exhibited varying degrees of sensitivity to smaller forest size. For example, Veery and Ovenbird were not detected in forests less than 5 ha, Northern Waterthrush not less than 18 ha, and Winter Wren not less than 116 ha.

For each species, the number of pairs per 30 minutes survey time varied among forests where pairs were detected (Table 16). No consistent linear trend with forest size was evident for over 80% of the species (Table 16, Appendix I). The abundance of a few species increased significantly with increasing forest size in 1980 (Ovenbird, Red-eyed Vireo) or 1981 (Veery). The abundances of Common Crow, Common Grackle and Pileated Woodpecker were negatively correlated with forest size in both years. Six other species exhibited inconsistent decreases in abundance with increasing forest size.

Observed species distributions among forests were compared to distributions generated from a passive sampling model of random dispersal of pairs detected regionally. Numbers of species observed in

TABLE 16

Bird species composition in 21 forests surveyed in A. 1980 and B. 1981. Entries are number of pairs per 30 minutes census time. Species ordered by smallest forest in which detected in either year. Details of correlation analyses, regional abundance and scientific names of species in Appendix 1.

A. 1980

SPECIES	3	4	5	8	9	13	14	16	18	22	25	27	30	44	58	79	116	220	680	3350	7620
Brown-headed Cowbird	.5	1.0	1.0	.5	.5	1.1	.8	1.0	1.0	1.0	.8	1.3	1.8	1.5	1.0	1.4	.3	.2	.8	1.0	.2
Eastern Wood-Pewee	1.5	1.0	1.5	1.5	1.5	1.1	1.9	.8	1.8	1.0	2.0	.8	2.3	1.8	1.8	1.8	2.0	1.2	2.0	1.5	1.3
Great Crested Flycatcher	.5	1.0	1.0	.5	1.0	1.9	1.1	1.3	1.0	1.0	.8	1.0	1.3	1.0	1.2	1.2	1.7	1.0	1.3	1.2	.8
White-breasted Nuthatch	.5	1.0	.5	1.0	.5	.8	.8	.5	.5	.5	.3	1.0	.8	.8	1.0	.6	.8	.8	.7	.7	.5
Rose-breasted Grosbeak	.5	1.5	.5	.5	.5	.8	.8	1.0	1.0	2.8	1.8	1.8	1.0	1.3	.8	1.4	1.2	.8	.8	1.8	1.2
American Goldfinch	1.0	.5	1.0	.5	.5	.8	.8	1.3	.8	1.5	1.0	.5	1.3	1.6	.4	.5	.5	.5	.5	1.2	.8
American Robin	.5	1.5	.5	.5	.5	.8	.4	.8	.5	.5	.3	.8	1.0	.8	1.0	.6	.5	.5	.5	.5	.3
Common Grackle	1.5	1.0	1.0	.5	.5	1.5	.8	1.5	1.5	1.0	1.0	.8	1.3	.3	1.0	.8	.5	.5	.5	.8	.3
Black-capped Chickadee	1.0	.5	.5	.5	.5	.8	1.1	1.3	.5	.5	.5	1.8	1.5	.8	.8	.4	1.2	1.8	.7	.7	.5
American Crow	.5	.5	1.0	.5	1.0	1.1	.9	1.0	.8	.5	.8	.8	.8	.3	.6	.8	.2	.3	.3	.3	.2
Northern Oriole	.5	.5	.5	.5	.5	.8	.4	.5	.5	.5	1.0	1.0	1.0	.5	1.0	.4	.2	.4	.5	.5	.7
Song Sparrow	1.5	2.0	.5	.5	1.0	1.1	.4	1.3	1.3	.8	1.5	2.3	.5	.5	.4	.4	.2	.5	.5	.3	.3
Red-winged Blackbird	1.5	1.5	.5	.5	.5	1.5	.8	.5	.3	.8	1.0	.8	1.3	.5	.4	.4	.2	.2	.2	.3	.7
Yellow-bellied Sapsucker	.5	.5	.5	.5	.5	.4	.4	.3	.3	.3	.5	.3	.5	.3	.4	.4	.2	.2	.2	.3	.3
Northern Flicker	.5	.5	.5	.5	.5	.8	.4	.5	.3	.3	.5	.3	.5	.3	1.0	.2	.2	.2	.3	.3	.2
Mourning Dove	2.0	.5	.5	.5	.5	.8	.4	.5	.3	.3	.5	.3	.3	.3	.2	.2	.2	.2	.2	.3	.2
Chipping Sparrow	.5	.5	.5	.5	.5	.5	.4	.5	.5	.5	.3	.3	.3	.3	.2	.2	.2	.2	.2	.3	.2
Eastern Kingbird	1.0	.5	.5	.5	.5	.5	.4	.5	.5	.5	.3	.3	.3	.3	.2	.2	.2	.2	.2	.3	.2
Warbling Vireo	.5	.5	.5	.5	.5	.5	.4	.5	.5	.5	.3	.3	.3	.3	.2	.2	.2	.2	.2	.3	.2
Yellow Warbler	.5	.5	.5	.5	.5	.5	.4	.5	.5	.5	.3	.3	.3	.3	.2	.2	.2	.2	.2	.3	.2
European Starling	1.0	.5	.5	1.5	1.5	.4	1.5	.8	1.3	1.3	1.8	.5	1.8	2.0	2.6	1.2	1.8	.8	2.7	2.0	2.5
Red-eyed Vireo	.5	.5	.5	.5	.5	1.1	.4	1.0	.3	.8	.5	2.0	1.0	1.0	1.6	1.6	.5	.7	.8	.7	.7
Blue Jay	1.0	.5	.5	.5	.5	.5	.4	.3	.8	.3	1.0	1.0	1.0	1.0	.8	1.0	1.0	.5	.8	.5	.2
Brown Creeper	.5	.5	.5	.5	.5	.8	.8	.8	.3	.5	1.0	1.0	.3	.5	.2	.6	.7	.2	.2	.2	.2
Hairy Woodpecker	.5	.5	.5	.5	.5	.4	.4	.3	.3	.5	.5	.5	.3	.3	1.6	.6	.7	.2	.2	.5	.5
Cedar Waxwing	.5	.5	.5	.5	.5	.4	.4	.3	.3	.5	.5	.5	.3	.3	.2	.6	.7	.2	.2	.5	.5
Downy Woodpecker	.5	.5	.5	.5	.5	.4	.4	.3	.3	.5	.5	.5	.3	.3	.2	.6	.7	.2	.2	.5	.5
Brown Thrasher	.5	.5	.5	.5	.5	.4	.4	.3	.3	.5	.5	.5	.3	.3	.2	.6	.7	.2	.2	.5	.5
Veery	.5	.5	.5	.5	.5	.4	.4	.3	.3	.5	.5	.5	.3	.3	.2	.6	.7	.2	.2	.5	.5
Ovenbird	.5	.5	.5	.5	.5	.4	.4	.3	.3	.5	.5	.5	.3	.3	.2	.6	.7	.2	.2	.5	.5
Common Yellowthroat	.5	.5	.5	.5	.5	.4	.4	.3	.3	.5	.5	.5	.3	.3	.2	.6	.7	.2	.2	.5	.5
Pileated Woodpecker	.5	.5	.5	.5	.5	.4	.4	.3	.3	.5	.5	.5	.3	.3	.2	.6	.7	.2	.2	.5	.5
Bobolink	.5	.5	.5	.5	.5	.4	.4	.3	.3	.5	.5	.5	.3	.3	.2	.6	.7	.2	.2	.5	.5
Black-billed Cuckoo	.5	.5	.5	.5	.5	.4	.4	.3	.3	.5	.5	.5	.3	.3	.2	.6	.7	.2	.2	.5	.5
Wood Thrush	.5	.5	.5	.5	.5	.4	.4	.3	.3	.5	.5	.5	.3	.3	.2	.6	.7	.2	.2	.5	.5

Significant decrease in abundance with Log Area when detected

* Significant increase in abundance with Log Area when detected.

TABLE 16A (continued)

SPECIES	FOREST SIZE (ha)															3350	7620			
	3	4	5	8	9	13	14	16	18	22	25	27	30	44	58			79	116	220
Indigo Bunting				.5	.5				.3	.3	.3	.8			.6		.2			
Chestnut-sided Warbler									.8	.3					.2					.3
White-throated Sparrow									.5	.5	1.3			.8	.2	.2	.5	.3		.3
Mourning Warbler									.5	.3	.3	.5		.3				1.3		.2
Red-breasted Nuthatch									.3							.4				.5
Pine Warbler							.4								.6	.6	1.0	.7	.3	1.0
Scarlet Tanager								.8	.5											1.5
Ruby-throated Hummingbird									.3					.3						
Northern Waterthrush										.3					.2	.4	1.0	1.0	.2	.5
Ruffed Grouse											1.3								1.3	2.5
Least Flycatcher											.3								.7	.5
American Redstart														.5			.2			.2
Black-and-white Warbler												.8	.3							.3
Nashville Warbler																				.2
Purple Finch																		.2		.2
Red-shouldered Hawk																				.2
Magnolia Warbler																	.2	.2		.2
Blackburnian Warbler																	.7	1.0	.3	.5
Winter Wren																				
<u>Irregular</u>																				
Eastern Phoebe			.5																	
Gray Catbird			.5																	
House Sparrow								.4		.4									.2	
Swinson's Thrush																				
American Woodcock																				
Canada Warbler															.6	.2	.2			.2
Northern Goshawk																				
Red-tailed Hawk																				
Golden-crowned Kinglet																				.3
Broad-winged Hawk																	.2			
Hermit Thrush																			.2	
Black-throated Blue Warbler																				.3
Black-throated Green Warbler																				.2

0° Significant decrease in abundance with Log Area when detected
 .+ Significant increase in abundance with Log Area when detected.

TABLE 16B, 1981

SPECIES	FOREST SIZE (ha)																					
	3	4	5	8	9	13	14	16	18	22	25	27	30	44	58	79	116	220	680	3350	7620	
Brown-headed Cowbird	1.5	.5	.5	.5	1.0	.8	.8	1.0	.5	.5	1.3	1.3	1.0	1.3	1.0	1.4	.3	.7	.8	.8	.8	
Eastern Wood-Pewee	1.0	1.0	1.0	1.5	1.0	1.1	1.5	2.3	1.5	1.0	1.8	.8	2.3	3.0	2.2	1.2	1.3	.8	1.2	1.0	1.0	
Great Crested Flycatcher	.5	.5	.5	.5	.5	1.5	1.1	.5	.8	1.0	.8	1.3	.8	1.5	1.2	1.8	1.0	1.2	.8	1.0	1.0	
White-breasted Nuthatch	.5	.5	.5	.5	.5	.4	.8	.5	.5	.5	.5	.5	1.0	.5	.8	.6	.5	.3	.7	.8	.5	
Rose-breasted Grosbeak	.5	1.0	.5	1.0	.5	1.1	.8	1.5	1.0	1.0	1.3	1.3	1.3	1.3	1.0	1.6	1.2	.5	1.0	1.2	1.0	
American Goldfinch	.5	.5	.5	.5	.5	.8	.8	.5	.5	.5	1.0	1.0	.8	.8	.8	.8	.5	.2	.2	.7	.7	
American Robin	1.0	.5	.5	.5	.5	.8	.4	.5	.5	.5	.5	1.3	.5	.5	.6	.8	.7	.3	.5	.5	.5	
Common Grackle #	1.0	1.0	.5	.5	.5	.8	.4	.5	1.0	.8	.5	.8	.5	.8	.4	.2	.3	.3	.2	.5	.2	
Black-capped Chickadee	.5	.5	.5	.5	.5	.4	.4	1.0	.5	.8	.5	1.5	1.0	.5	.8	1.2	.7	1.7	.5	.3	.3	
American Crow #	.5	.5	.5	1.0	1.0	1.1	1.1	.5	.8	.5	.5	.8	.3	.5	.2	.4	.5	.5	.2	.2	.2	
Northern Oriole	1.0	.5	.5	.5	.5	.8	.4	.8	.5	.5	1.0	.8	.3	.3	.8	.6	.5	.5	.2	.3	.3	
Song Sparrow	1.5	.5	1.0	.5	.5	.8	.8	1.5	1.0	.8	.8	2.0	.8	.5	.8	.2	.2	.2	.2	.3	.2	
Red-winged Blackbird #	.5	.5	.5	.5	.5	.4	.4	.5	.5	.5	.5	.5	.5	.3	.5	.2	.4	.3	.5	.8	.2	
Yellow-bellied Sapsucker	.5	.5	.5	.5	.5	.4	.4	.3	.5	.5	.8	.8	.5	.5	.5	.4	.3	.2	.2	.7	.2	
Northern Flicker	.5	.5	.5	.5	.5	.4	.4	.5	.5	.8	.5	.8	.5	.5	.2	.4	.2	.2	.2	.2	.2	
Mourning Dove	1.0	.5	.5	.5	.5	.4	.8	.5	.5	.5	.5	.5	.5	.3	.2	1.0	.2	.2	.2	.2	.2	
Chipping Sparrow	.5	.5	.5	.5	.5	.8	.8	.8	.5	.5	.5	.5	.5	.3	.5	.2	.2	.2	.2	.2	.2	
Eastern Kingbird	.5	.5	.5	.5	.5	.8	.8	.8	.5	.5	.5	.5	.5	.3	.5	.2	.2	.2	.2	.2	.2	
Warbling Vireo	.5	.5	.5	.5	.5	.8	.8	.8	.5	.5	.5	.5	.5	.3	.5	.2	.2	.2	.2	.2	.2	
Yellow Warbler	.5	.5	.5	.5	.5	.8	.8	.8	.5	.5	.5	.5	.5	.3	.5	.2	.2	.2	.2	.2	.2	
European Starling	1.0	.5	1.0	1.5	.5	1.1	1.9	.8	1.3	.5	2.0	.3	1.0	1.5	2.2	1.0	1.7	.7	2.0	1.5	2.5	
Red-eyed Vireo	.5	.5	1.0	.5	.5	.8	.8	.8	.5	.5	.5	1.0	1.0	1.3	1.0	1.0	1.0	1.8	.7	.7	1.0	
Blue Jay	.5	.5	.5	.5	.5	.8	.8	.5	.8	.5	.5	.8	.5	1.0	.4	.6	.7	.8	.8	.3	.5	
Brown Creeper	.5	.5	.5	.5	.5	.8	.8	.5	.5	.5	.5	.5	.5	.3	.2	.2	.3	.3	.2	.5	.5	
Hairy Woodpecker	.5	.5	.5	.5	.5	.4	.4	.5	.5	.5	.5	.5	.5	.5	.4	1.6	.3	.3	.2	.5	.5	
Cedar Waxwing	.5	.5	.5	.5	.5	.4	.4	.5	.5	.5	.5	.5	.5	.5	.4	1.6	.3	.3	.2	.5	.5	
Downy Woodpecker #	.5	.5	.5	.5	.5	.4	.4	.5	.5	.5	.5	.5	.5	.5	.4	1.6	.3	.3	.2	.5	.5	
Brown Thrasher	.5	.5	.5	.5	.5	.4	.4	.5	.5	.5	.5	.5	.5	.5	.4	1.6	.3	.3	.2	.5	.5	
Veery*	.5	.5	.5	.5	.5	.4	.4	.5	.5	.5	.5	.5	.5	.5	.4	1.6	.3	.3	.2	.5	.5	
Ovenbird	.5	.5	.5	.5	.5	.4	.4	.5	.5	.5	.5	.5	.5	.5	.4	1.6	.3	.3	.2	.5	.5	
Common Yellowthroat	1.5	.5	.5	.5	.5	.8	.8	.8	.8	.3	1.0	.3	1.3	.5	.6	1.2	1.8	.8	1.7	1.2	1.8	
Pileated Woodpecker #	1.0	.5	.5	.5	.5	1.5	1.5	1.0	.5	.3	.3	1.5	1.5	3.3	1.4	1.8	2.3	2.5	3.3	2.0	2.2	
Bobolink	.5	.5	.5	.5	.5	.3	.3	.3	1.3	.3	.3	.3	.3	.3	.2	.2	.2	.2	.2	.2	.2	
Black-billed Cuckoo	.5	.5	.5	.5	.5	.3	.3	.3	.3	.3	.3	.3	.3	.3	.2	.2	.2	.2	.2	.2	.2	
Wood Thrush	.5	.5	.5	.5	.5	.4	.4	.5	.5	.5	1.5	.8	.8	1.0	.2	1.4	1.8	.5	1.2	1.0	.3	

* Significant decrease in abundance with Log Area when detected
 + Significant increase in abundance with Log Area when detected.

TABLE 16B. 1981 (continued)

SPECIES	3	4	5	8	9	13	14	16	18	22	25	27	30	44	58	79	116	220	680	3350	7620
Indigo Bunting #				.5	1.0				.8	.5		.3	.3		.4		.3				
Chestnut-sided Warbler									.5						.2						
White-throated Sparrow						.6			.5	.8		1.3	.8	.5	.4	.2	.5	.5		.8	
Mourning Warbler							.4		.5	.3					.4					.2	
Red-breasted Nuthatch							.4	.3							1.2	1.2	.7			.2	
Pine Warbler															.2	.2	1.0	1.0	1.3	.7	1.7
Scarlet Tanager								.8					1.0	.3	.8						
Ruby-throated Hummingbird #								.3	.3					.8		.2					
Northern Waterthrush																	1.0	.7	.7	.2	.5
Ruffed Grouse																					
Least Flycatcher											1.0				.2	.2	1.2		1.0	2.3	.7
American Redstart															.2				.2	.3	.2
Black-and-white Warbler											.3	.5				.2	.5	.2	.2	.5	
Nashville Warbler											.3				.4	.4	.3	.2	.2	.3	
Purple Finch													.3			.4		.3		.2	.2
Red-shouldered Hawk															.2			.2		.2	
Magnolia Warbler																.2		.2		.2	
Blackburnian Warbler																.2	.3	.2		.5	.3
Winter Wren																	.5	.5	.7		
Irregular																					
Eastern Phoebe																					.2
Blackpoll Warbler																					
Swainson's Thrush																					
American Kestrel																					
Tennessee Warbler																					
Northern Goshawk																.4					
Red-tailed Hawk																	.2		.2		
Golden-crowned Kinglet																					
Barred Owl																					
Black-throated Blue Warbler																		.2			.5
Black-throated Green Warbler																					.2
Northern Parula																					.2

Significant decrease in abundance with Log Area when detected

* Significant increase in abundance with Log Area when detected.

smaller forests in 1980 were generally in close agreement with species number predicted by the passive sampling model (Table 17). Presence of species such as Black-capped Chickadee, Brown-headed Cowbird, Eastern Wood Pewee and Great Crested Flycatcher in smaller forests in 1980 and 1981 was predicted by extension of the random model (Table 18). Similarly, the absences of some species in smaller forests were consistent with distributions expected from random dispersal of individuals among forests. Northern Waterthrush, Winter Wren and Pine Warbler, for example, were not expected to occur in smaller forests (particularly when expected abundances were $< .5$ pairs per forest) because of a small pool of individuals regionally. On the other hand, absences of species such as Bobolink, Chipping Sparrow, Eastern Kingbird and House Sparrow, which were abundant regionally according to the Breeding Bird Survey, reflected low numbers of individuals utilizing forests relative to other nonforest habitats more characteristic of these species. Overall, extension of the random model generated a reasonable fit to observed distributions for 66 of 72 bird species. In contrast, distributions of 6 species were not reasonably predicted from the random model. The absences of Brown Creeper, Least Flycatcher, Ovenbird, Scarlet Tanager, Veery and Wood

2 2
OF / DE

TABLE 17

Bird species number per forest observed and expected from a passive sampling model of random dispersal of individuals available in the regional species pool of 1980. Random values are means $\pm$ 1 SD of 5 assemblages.

FOREST SIZE (ha)	OBSERVED	RANDOM
3	16	18.8 $\pm$ 1.6
4	19	17.2 $\pm$ 1.6
5	22	18.8 $\pm$ 0.8
8	17	15.4 $\pm$ 0.9
9	14	15.0 $\pm$ 1.2
13	24	25.2 $\pm$ 1.8
14	25	25.2 $\pm$ 2.2
16	25	30.4 $\pm$ 0.5
18	28	29.0 $\pm$ 1.6

TABLE 18

Number of pairs for selected bird species in small forests observed in 1980, 1981 and expected from a passive sampling model of random dispersal of individuals available in the regional species pool. Entries are observed pairs (expected pairs). Scientific names in Appendix 1.

Species	Year	3	4	5	6	9	13	14	16	18
Forest Size (ha)										
Black-capped Chickadee	1980	2 (1.2)	1 (1.0)	1 (1.3)	(.9)	(.8)	2 (2.2)	3 (1.8)	5 (2.9)	2 (2.9)
	1981	1 (1.1)	1 (.7)	1 (.9)	1 (.9)	(.9)	1 (1.3)	1 (1.5)	4 (2.7)	1 (2.4)
Brown-headed Cowbird	1980	1 (1.3)	2 (1.1)	2 (1.3)	1 (.9)	1 (.8)	3 (2.2)	2 (1.9)	4 (3.0)	4 (3.0)
	1981	3 (1.4)	1 (.8)	1 (1.1)	1 (1.1)	2 (1.1)	2 (1.6)	2 (1.9)	4 (3.3)	2 (2.9)
Eastern Wood Pewee	1980	3 (2.3)	2 (1.9)	3 (2.3)	3 (1.7)	3 (1.5)	3 (4.0)	5 (3.4)	3 (5.3)	7 (5.3)
	1981	2 (2.2)	2 (1.4)	2 (1.7)	3 (1.9)	2 (1.9)	3 (2.7)	4 (3.1)	9 (5.3)	6 (4.8)
Great Crested Flycatcher	1980	0 (1.6)	1 (1.3)	2 (1.7)	2 (1.2)	1 (1.0)	5 (2.8)	3 (2.4)	5 (3.8)	4 (3.8)
	1981	1 (1.6)	1 (1.0)	1 (1.2)	1 (1.3)	1 (1.3)	4 (1.9)	3 (2.2)	2 (3.8)	3 (3.4)
Northern Waterthrush	1980	(.3)	(.3)	(.3)	(.2)	(.2)	(.5)	(.5)	(.7)	1 (.7)
	1981	(.4)	(.3)	(.3)	(.4)	(.4)	(.5)	(.6)	(1.0)	1 (.9)
Winter Wren	1980	(.2)	(.2)	(.2)	(.2)	(.1)	(.4)	(.5)	(.5)	1 (.5)
	1981	(.2)	(.1)	(.1)	(.2)	(.2)	(.2)	(.3)	(.4)	(.4)
Pine Warbler	1980	(.1)	(.0)	(.1)	(.0)	(.0)	(.1)	(.1)	(.1)	(.1)
	1981	(.0)	(.0)	(.0)	(.0)	(.0)	(.0)	(.0)	(.1)	(.1)
Bobolink	1980	(.1)	(.1)	1 (.1)	(.1)	(.1)	2 (.2)	(.2)	1 (.3)	(.3)
	1981	(.1)	(.0)	(.0)	(.1)	(.1)	(.1)	(.1)	1 (.1)	(.1)
Chipping Sparrow	1980	(.1)	(.1)	(.1)	(.0)	(.0)	(.1)	(.1)	(.1)	(.1)
	1981	1 (.3)	(.2)	(.2)	(.2)	1 (.2)	2 (.3)	2 (.4)	(.7)	(.6)
Eastern Kingbird	1980	2 (.2)	(.1)	(.2)	(.1)	(.1)	(.3)	(.2)	(.4)	(.4)
	1981	1 (.2)	(.1)	(.1)	(.2)	(.2)	(.2)	(.3)	3 (.4)	(.4)
House Sparrow	1980	(.0)	(.0)	(.0)	(.0)	(.0)	(.1)	1 (.1)	(.1)	(.1)
	1981	(.0)	(.0)	(.0)	(.0)	(.0)	(.0)	(.0)	(.0)	(.0)
Brown Creeper	1980	(.6)	1 (.7)	(.9)	(.6)	(.5)	(1.5)	2 (1.3)	1 (1.9)	3 (1.9)
	1981	(.7)	(.4)	(.5)	(.6)	(.6)	(.8)	(1.0)	2 (1.6)	3 (1.5)
Least Flycatcher	1980	(.7)	(.6)	(.7)	(.5)	(.4)	(1.2)	(1.0)	(1.6)	(1.6)
	1981	(.7)	(.4)	(.5)	(.6)	(.6)	(.8)	(1.0)	(1.6)	(1.5)
Ovenbird	1980	(1.8)	(1.5)	1 (1.8)	(1.3)	(1.1)	(3.1)	(2.7)	(4.2)	2 (4.2)
	1981	(2.4)	(1.4)	3 (1.8)	(2.0)	(2.0)	(2.8)	4 (3.3)	4 (5.6)	2 (5.0)
Scarlet Tanager	1980	(.7)	(.6)	(.7)	(.8)	(.4)	(1.2)	(1.0)	3 (1.6)	2 (1.6)
	1981	(1.0)	(.6)	(.8)	(.8)	(.8)	(1.2)	(1.4)	3 (2.3)	2 (2.1)
Veery	1980	(1.3)	(1.1)	(1.4)	(1.0)	(.9)	(2.6)	(2.0)	(3.1)	4 (3.1)
	1981	(1.3)	(.8)	(1.0)	(1.1)	(1.1)	(2.4)	2 (1.9)	(3.2)	3 (2.9)
Wood Thrush	1980	(1.1)	(.9)	(1.1)	(.8)	(.7)	(1.9)	1 (1.7)	3 (2.6)	2 (2.6)
	1981	(1.1)	(.6)	(.8)	1 (.9)	(.9)	(1.3)	1 (1.5)	(2.5)	(2.2)

Thrush from smaller forests were not expected from random dispersal of individuals available in the regional species pool in 1980 or 1981 (Table 18).

3.6. Temporal Patterns in Birds

Any temporal analysis should be done on a time base relevant to the life history traits of the species of interest. For temperate forest birds, a yearly interval from one spring to the next seems appropriate because it (1) spans the time from one reproductive season to the next and (2) includes the overwintering period during which high mortality typically occurs (Whitcomb et al. 1981).

Annual variability in species number and composition was analyzed for all forests between 1980 and 1981. Whether the results are typical can only be evaluated from longer-term, research quality data. Such data is not available for a large sample of forests appropriate to the present study. To expand the time base of the analyses, 1979 data for 5 forests were included so that variability among years could be evaluated.

3.6.1. Regional Turnover

Regionally, 39, 67 and 66 bird species were detected at census points within forests in 1979, 1980 and 1981, respectively. Changes in species number and species composition measured by either

absolute or relative turnovers between 1979 and 1980 existed because 16 more forests were surveyed in 1980. In contrast, the difference in species number between 1980 and 1981 was almost nil, reflecting detection of approximately equal numbers of species in only 1980 or 1981. Similar numbers of bird species in different ecological classes in 1980 or 1981 (Table 19) also reflected this temporal consistency. Regional turnover in species composition was 8% between 1980 and 1981.

3.6.2. Forest Turnover

Annual turnovers from 1979 to 1981 were generally similar in each of 5 forests (Table 20). However, estimates of species turnover were subject to "pseudoturnover" (Lynch & Johnson 1974) i.e. species differences associated solely with various sampling errors. Sampling errors involve inclusion of transient species (e.g. Blackpoll Warbler) and/or vagrant species (e.g. Bobolink, Eastern Kingbird, Red-winged Blackbird) and/or failure to detect breeding species as a result of incomplete sampling (e.g. Ruffed Grouse, Tennessee Warbler). Thus, real turnover equals apparent turnover minus pseudoturnover.

Temporal variability in species composition attributable to pseudoturnover was evaluated by

TABLE 19

Number of bird species within ecological classes detected in 21 forests, 1980-81.

CLASS	YEAR		
	1980 & 1981	1980	1981
ALL BIRDS	72	67	66
HABITAT USE			
Edge	31	30	28
Facultative Forest	17	16	17
Obligate Forest	24	21	21
TERRITORY SIZE (ha)			
< 2	36	33	32
2 - 5	26	26	25
> 5	10	8	9
NESTING STRATA			
Ground	17	16	14
Shrub	16	15	15
Canopy	24	23	23
Hole	13	11	12
Other	2	2	2
FORAGING STRATA			
Ground	22	21	19
Shrub	24	23	23
Canopy	13	11	12
Trunk	8	8	8
Other	5	4	4
MIGRATORY STATUS			
Resident	17	16	16
Short-distance	22	21	19
Long-distance	33	30	31
REGIONAL ABUNDANCE (No.)			
< 11	30	26	26
11 - 50	25	24	24
> 50	17	17	16

TABLE 20

Annual turnovers in bird species for 5 forests, 1979-81.

Forest Size (ha)	Species Turnover (No.)		Species Number Relative Turnover (%)		Absolute Turnover (No.)		Species Composition Relative Turnover (%)	
	79-80	80-81	79-80	80-81	79-80	80-81	79-80	80-81
30	1	5	2	9	9	15	15	26
27	4	3	6	5	10	13	16	20
25	0	2	0	5	10	8	22	18
22	2	1	4	2	10	9	22	18
13	4	6	10	15	10	10	24	25
Mean $\pm$ 1 SD	2.8 $\pm$ 1.9		5.8 $\pm$ 4.5		10.4 $\pm$ 2.1		20.6 $\pm$ 3.8	

comparing spot-mapping and point count results for 5 forests surveyed in 1979. Pseudoturnover in species composition was higher for both absolute and relative measures than pseudoturnovers in species number (Table 21). Pseudoturnovers in the 13-ha forest and two completely censused 14-ha forests in Maryland were similar (Table 21). Log(area) of the 5 Ontario forests was unrelated to absolute and relative pseudoturnovers in species number ($r = .553$, $r = .491$, respectively, $p > .20$) and in species composition ($r = .706$, $p > .10$, $r = .553$, $p > .20$, respectively).

On average, pseudoturnover in species composition was sufficient to account for three-quarters of apparent relative turnover (15.4% out of 20.6%) and apparent absolute turnover (7.4 species out of 10.4 species) annually from 1979 to 1981 in the 5 forests. Pseudoturnover in species number was, on average, sufficient to account for all of the apparent relative and absolute turnover observed.

Annual turnovers from 1979 to 1981 for 5 forests were, on average, similar to annual turnovers observed from 1980 to 1981 for all 21 forests (Table 22). In the 3-ha forest, turnover in species number was 5 species or 14%. Turnover in species composition was also 5 species or 14% because all 1980 species were detected in 1981. Compared to

TABLE 21

Pseudoturnover in bird species associated with point count sampling versus spot-map censusing of 5 Ontario forests (1979) and 2 Maryland forests (Whitcomb et al. 1981: Appendix B).

Forest Size (ha)	No. Species Spot- Mapping (1)	Species Point Counts (2)	Pseudoturnover			
			Species	Number	Species	Composition
			Absolute 1 - 2	Relative $\frac{100 1 - 2 }{(1 + 2)}$	Absolute (3)	Relative $\frac{100 (3)}{(1 + 2)}$

ONTARIO*

30	22	30	8	15	12	23
27	31	30	1	2	9	15
25	18	23	5	12	7	17
22	22	22	0	0	4	9
13	20	19	1	3	5	13
Mean $\pm$ 1 SD			3.0 $\pm$ 3.4	6.4 $\pm$ 6.7	7.4 $\pm$ 3.2	15.4 $\pm$ 5.2

MARYLAND#

14.2 (North)	30	28	2	3	4	7
14.6 (South)	21	21	0	0	4	10
Mean $\pm$ 1 SD			1.0 $\pm$ 1.4	1.5 $\pm$ 2.1	4.0 $\pm$ 0	8.5 $\pm$ 2.1

* Spot-mapping of circular plots. Details in Section 2.4.

Spot-mapping of entire forest.

TABLE 22

Annual turnovers in bird species for 21 forests, 1980-81.

Forest Size (ha)	Species Number		Species Composition	
	Absolute Turnover (No.)	Relative Turnover (%)	Absolute Turnover (No.)	Relative Turnover (%)
3	5	14	5 (5)*	14
4	3	9	13 (8)	37
5	5	13	7 (6)	18
8	3	8	11 (4)	30
9	5	15	9 (2)	27
13	5	12	9 (7)	21
14	2	4	14 (8)	29
16	2	4	10 (4)	19
18	3	6	5 (4)	9
22	0	0	10 (5)	18
25	2	5	8 (5)	18
27	3	5	13 (8)	20
30	5	9	15 (10)	26
44	2	4	10 (4)	18
58	4	6	8 (2)	14
79	8	11	18 (5)	24
116	1	2	7 (4)	11
220	3	5	11 (4)	19
680	0	0	8 (4)	14
3350	4	5	8 (6)	11
7620	1	2	15 (7)	25
Mean	3.1	6.6	10.2 (5.1)	20.1
+ 1 SD	1.8	4.4	3.2 (2.3)	7.1

* No. species detected in 1981 only.

random assemblages, observed turnovers in species number were higher (Table 23). Observed turnovers in species composition were substantially lower than those expected if birds were randomly distributed among forests.

Assuming pseudoturnovers within all forests were also comparable with pseudoturnovers in the smaller sample of 5 forests, no real absolute or relative turnovers in species number were observed, on average. Real absolute and relative turnovers in species composition averaged 2.9 species (28.8% of 10.2 species) and 5.1% (25.2% of 20.1%), respectively. Within forests, equal numbers of species were detected, on average, in only 1980 or 1981 i.e. local 'immigrations' balanced local 'extinctions' (Table 22). Ecological substitution of species within forests was suggested by significant correlations between 1980 and 1981 in species number for most ecological classes (Table 24). Species number in the 'Other' foraging and 'Other' nesting classes were not significantly correlated between years, in part because of few species (5 and 2 species respectively, Table 19) in these classes.

Simple linear regressions using corrected turnovers in species composition indicated that both absolute and relative annual turnovers were not significantly related to forest size (either

TABLE 23

Species turnover observed and expected at random between 1980 and 1981 in a 3-ha forest. Random values are means $\pm$ 1 SD of 25 comparisons of 5 assemblages generated using the regional species pool from 1980 or 1981.

TURNOVER	OBSERVED *	RANDOM
SPECIES NUMBER		
Absolute Turnover (No.)	5	1.5 $\pm$ 0.7
Relative Turnover (%)	13.5	4.0 $\pm$ 1.8
SPECIES COMPOSITION		
Absolute Turnover (No.)	5	18.4 $\pm$ 1.3
Relative Turnover (%)	13.5	47.7 $\pm$ 3.6

* Uncorrected for pseudoturnover.

TABLE 24

Pearson correlations (r) of bird species number
between 1980 and 1981 for ecological classes within
21 forests.

ECOLOGICAL CLASS	r
HABITAT USE	
Edge	.759 *
Facultative Forest	.706 *
Obligate Forest	.956 *
TERRITORY SIZE (ha)	
< 2	.758 *
2 - 5	.747 *
> 5	.637 *
NESTING STRATA	
Ground	.825 *
Shrub	.656 *
Canopy	.670 *
Hole	.601 *
Other	-.073
FORAGING STRATA	
Ground	.724 *
Shrub	.557 *
Canopy	.543 *
Trunk	.773 *
Other	.267
MIGRATORY STATUS	
Resident	.710 *
Short-distance	.682 *
Long-distance	.858 *
REGIONAL ABUNDANCE (No.)	
< 11	.821 *
11 - 50	.856 *
> 50	.631 *

* $p < .05$

log(area) or maximum distance) for forests ranging from 13-30 ha (n = 8), 3-30 ha (n = 13), 3-79 ha (n = 16) and 3-7620 ha (n = 21). Multiple regressions using 3-7620 ha forests indicated that neither forest size nor habitat heterogeneity was significantly related to turnover in species composition. Corrected turnovers were also uncorrelated to number of bird species per forest (contra Diamond 1969, 1980).

Observed absolute turnover in species composition was not randomly distributed among ecological classes of bird species. According to chi-square tests for goodness-of-fit, temporal variability within classifications by habitat use, migratory status, territory size and foraging stratum was significantly nonrandom (Table 25). Four unrelated classes exhibited more temporal variability than expected regionally; 5 generally interrelated classes exhibited less temporal variability than expected regionally. For example, obligate forest species exhibited less temporal variability regionally than expected at random despite generally low regional abundances. Most edge species, on the other hand, had high regional abundances, yet exhibited more temporal variability regionally than expected at random. This did not appear to be related to differential species abundances per

TABLE 25

Ecological classes of birds exhibiting nonrandom temporal variability regionally between 1980 and 1981. Interrelated pairs of classes (more species in common than expected by χ^2) are indicated by superscripts.

Ecological Classification	χ^2 ($p < .05$)	Ecological Classes showing Temporal Variability	
		More than expected	Less than expected
Habitat Use	9.98	Edge	Obligate Forest ^a
Migratory Status	12.09	Resident	Long-distance migrants ^{bc}
Territory Size	12.29	Territory 2-5 ha	Territory < 2 ha ^b
Foraging Stratum	17.39	Trunk foragers	Canopy Foragers ^{bc}
			Raptorial Foragers

forest, as about 65% and 70% of apparent absolute turnover in obligate forest and edge species, respectively, involved presence and absence between years of single pairs of birds.

McCoy (1982) argued that edge species are more likely to be vagrants i.e. species which are not entirely resident in a forest and thereby artificially inflate species turnovers. Potential pseudoturnover associated with edge species in forests was removed by limiting temporal analyses to obligate forest (OF) and facultative forest (FF) species (Table 26). Absolute turnover in number of OF and FF species per forest was significantly lower than absolute turnover in number of all bird species per forest (paired sample $t = 3.889$, $n = 21$). Relative turnover in number of OF and FF species was not significantly different than that for all birds (paired sample $t = -.767$, $p > .20$, $n = 21$) because fewer numbers of OF and FF species were detected per forest. Absolute turnover in composition of OF and FF species per forest was significantly lower than absolute turnover in all species (paired sample $t = 9.636$, $n = 21$). Local immigrations balanced local extinctions, on average (Table 26). Relative turnover in composition of OF and FF species per forest was not significantly different than forest values for all species (paired sample $t = 1.382$,

TABLE 26

Annual turnovers in obligate forest and facultative forest bird species within 21 forests, 1980-81.

Forest Size (ha)	Species Number		Species Composition	
	Absolute Turnover (No.)	Relative Turnover (%)	Absolute Turnover (No.)	Relative Turnover (%)
3	3	27	3 (3)*	27
4	2	11	4 (3)	22
5	2	11	2 (2)	11
8	4	20	6 (1)	30
9	2	14	4 (1)	29
13	1	5	3 (2)	16
14	1	4	9 (5)	36
16	0	0	6 (3)	20
18	2	8	2 (2)	8
22	1	4	5 (3)	22
25	1	5	3 (1)	14
27	3	7	7 (5)	26
30	1	3	6 (3)	19
44	1	3	3 (1)	9
58	3	9	3 (0)	9
79	3	7	6 (1)	14
116	1	2	3 (2)	7
220	2	5	6 (2)	14
680	0	0	8 (4)	19
3350	2	5	4 (3)	9
7620	1	2	9 (4)	19
Mean	1.7	7.2	4.9 (2.3)	18.1
+ 1 SD	1.1	6.6	2.2 (1.5)	8.2

* No. species detected in 1981 only.

$p > .10$, $n = 21$). Despite exclusion of potential vagrant species, turnover of OF and FF species within 21 forests was significantly positively correlated with turnovers of all species for absolute turnover in species number ($r = .553$), relative turnover in species number ($r = .685$), absolute turnover in species composition ($r = .681$) and relative turnover in species composition ($r = .638$).

Multiple regressions of uncorrected turnovers in composition of OF and FF species per forest indicated that both absolute and relative annual turnovers were not significantly related to either forest size or habitat heterogeneity within forests.

4. DISCUSSION

Habitat heterogeneity within forests, at least for species composition of tree and shrub strata, increased significantly with forest size. The number of bird species also increased with forest size suggesting that the bird species-area pattern may be related to species diversification associated with habitat heterogeneity.

The habitat heterogeneity hypothesis predicts that greater habitat heterogeneity within larger forests should increase bird species numbers (assuming successful overwintering), because of: (1) spatial coupling of habitats by birds in a more heterogeneous forest (Dwyer 1972), (2) interspecific differences in habitat selection (Williams 1964) and/or (3) greater temporal persistence of species (Birch 1971, Reddingius & den Boer 1970).

In the present study, more pairs of birds were detected per census point in forests with greater habitat heterogeneity. This relationship was not consistently translated into greater species number per census point in more heterogeneous forests.

Between-habitat or beta-diversity analyses of birds within forests over 9 ha in size indicated that increased number of bird species resulted from species differences among census points. Larger and

more heterogeneous forests exhibited, on average, greater spatial variability in bird species composition between pairs of census points than less heterogeneous forests and forests as small as 13 ha. When differences in bird species composition within forests were weighted by species abundance, species distributions were consistently less spatially variable. Spatial variability in birds was then significantly positively related to forest size alone, suggesting that the importance of habitat heterogeneity within forests was related to spatial variability of relatively uncommon bird species or potential 'habitat specialists'. In contrast, the importance of area per se to measures of spatial variability between pairs of census points and to bird species differences among points indicated by beta-diversity analyses suggested that species differences related to habitat heterogeneity were insufficient to account completely for the increase in bird species in larger forests. In 1981 at least, both measures of spatial variability in bird species within forests were not significantly related to number of bird species per forest. Furthermore, in both 1980 and 1981, habitat heterogeneity did not explain as much of the pattern in bird species number among forests as forest size. When bird species were classified according to a variety of ecological

characteristics intended to reflect interspecific differences in resource use, habitat heterogeneity was the most significant determinant of the number of bird species in only about one quarter of all classes.

Habitat heterogeneity was also not significantly related to turnover in bird species within forests between 1980 and 1981. When data were corrected for potential pseudoturnover by edge species, habitat heterogeneity was still not significantly predictive of species turnovers in forest birds. That is, habitat heterogeneity remained unrelated to persistence of bird species in temperate forests between years.

Perhaps the relationships of spatial and temporal distributions of bird species to habitat heterogeneity were weakened by problems with sampling of birds and habitat and/or by techniques used to quantify habitat heterogeneity. Bird species composition within forests appeared to be represented reasonably well by the point count method according to analyses of species-time curves and comparisons with spot-mapping results. Potential errors in temporal analyses were minimized by removing pseudoturnover associated with certain bird species.

Both compositional and structural variables were selected to characterize an array of habitat features

including many found to be significant in explaining bird species numbers in other studies. Habitat sampling methods used in the more extensive survey provided data which compared reasonably well with results from more intensive sampling of 5 forests in 1979.

Several methods were investigated for quantifying habitat heterogeneity within forests. The measure of beta-diversity developed in this study provided a first approximation of spatial variability in species composition of the habitat but could not incorporate variability in species abundances and was inappropriate for measures of forest structure. The multivariate method of principal components analysis proved analytically intractable for data containing many zeroes (e.g. species composition data for the tree stratum). Any variable which can be averaged however, can be incorporated into the HH index. HH is sensitive to both magnitude and spatial variability in forest structure and species abundances. Variables can be weighted to incorporate differences in ecological importance where known. The consistent results between beta-diversity and HH for compositional data suggested that HH was a reasonable index of habitat heterogeneity within forests.

Although differences in habitat quality were not

explicitly incorporated into the HH index, a posteriori analyses suggested that this was not a significant omission. At the spatial scale of the present study, bird species number per forest appeared to be influenced more by differences in habitat quality among forests than by species differences associated with habitat heterogeneity within forests. After examining the relationship between bird species number, and tree species densities and forest structure within and among forests in Illinois, Blake and Karr (1982a) also concluded that differences in habitat between forests had a greater influence on bird species number than differences in habitat conditions within forests.

Of course, the scale at which habitat heterogeneity was measured varied with forest size. For example, in the 3-ha forest, HH indexed spatial variability in habitat over 90 m, while in the 116-ha forest, habitat heterogeneity was indexed over 1100 m. Perhaps most birds were unable to utilize effectively the spatial variability at the scale measured in smaller forests. That is, the heterogeneity measured in smaller forests was below the effective threshold on a spatial scale gradient for most species. However, half of the bird species detected in the present study had territories less than 2 ha, yet the number of species in this class

was consistently related solely to forest size and not habitat heterogeneity within forests. But more importantly, one of the objectives of the present study was to determine the relative importance of area and habitat heterogeneity in explaining the number of bird species within different-sized forests. If habitat heterogeneity was functionally more important than area then habitat heterogeneity, not forest size, should have explained more of the variation in bird species numbers per forest.

Multiple regression analysis is an appropriate interpretive tool for evaluating the relative importance of independent variables to a dependent variable (Nie et al. 1975). The contribution of forest size and habitat heterogeneity to bird numbers per forest was evaluated after controlling for confounding effects arising from intercorrelations of independent variables. However, the greater the intercorrelations of the independent variables (extreme collinearity exists in the .8 to 1.0 range), the less the reliability of the relative importance indicated by the partial regression coefficients (ibid.). In the present study, the intercorrelation of forest size and habitat heterogeneity within forests was minimized by representing forest size as $\log_{10}$ area. The importance of habitat heterogeneity was assessed from three sets of independent variables

representing different degrees of data aggregation. Since components of habitat heterogeneity were intercorrelated, interpretive emphasis was placed on the importance of habitat heterogeneity in general, rather than on individual components. Visual inspection of residuals for significant regressions indicated that linear regression was generally an appropriate model.

Only the numbers of edge-related bird species were consistently predicted solely by habitat heterogeneity within forests. A quarter of all ecological classes were related, at least primarily, in 1980 and/or 1981 to habitat heterogeneity within forests. Habitat heterogeneity was also secondarily important to numbers of bird species in total per forest and in an additional 17% of all ecological classes in 1980 and/or 1981. Inconsistent results between years were presumably related to differences introduced by sampling variability. For at least some species then, greater habitat heterogeneity may provide a full range of necessary resources in a smaller area.

Forest size was not only the major determinant of bird species number per forest, but also was at least secondarily predictive of the number of species in about-75% of all ecological classes within forests in 1980 and 1981. The greater significance of forest

size rather than habitat heterogeneity suggests that the importance of habitat heterogeneity to birds is contingent upon both spatial and temporal scale. Wiens (1981a) argued that habitat specificity depends on centres of abundance and distribution of species relative to the spatial scale of the habitat gradient examined. For example, forest species may exhibit habitat specificity across a gradient from fields to forest (MacArthur et al. 1966, Karr 1968, 1971, James 1971, Karr & Roth 1971, Willson 1974) although in the portion of the gradient limited to forests alone, be much less specific (Sherry 1979, Willson 1974, Roth 1976, Whitcomb et al. 1981, Collins et al. 1982). Species number may then be enhanced by habitat heterogeneity across a gradient from fields to forest but within forests alone habitat heterogeneity may be much less effective.

In the present study, only the number of edge-related species was consistently related to habitat heterogeneity. Sensitivity of this class to habitat heterogeneity within forests should be expected because their centre of abundance and distribution lie more in nonforest habitats. Flexible use of forest habitats by other bird species, particularly facultative and obligate forest species, is suggested by a broader geographical analysis. The forest habitats studied locally were

typical of the Great Lake-St. Lawrence Forest Region. These forests are transitional mixtures of tree species characteristic of the Boreal Forest Region farther north and the Deciduous Forest Region farther south (Hosie 1969, Erskine 1977). Of the 72 bird species detected within forests, 60% also characteristically utilize boreal habitats (Erskine 1977) and more southerly deciduous forest habitats (Whitcomb et al. 1981, Blake & Karr 1982a). Thus, the range of forests sampled in the present study lies well within the centres of abundance and distribution of many of the forest bird species detected. Distribution of many bird species over most of the habitat spectrum sampled would result in few clear habitat associations. Habitat flexibility in many bird species of these temperate forests is further suggested by the variability in habitat use associated with the migratory habit of over three-quarters of all species detected (cf. Greenburg 1979, Keast & Morton 1980, Martin 1980, Rice et al. 1980). Such habitat flexibility could account for the reduced importance of habitat heterogeneity to bird species numbers in forests, at least within the Great Lakes-St. Lawrence Forest Region.

Wiens. (1981a) further argued that interpretation of habitat patterns among species is not only sensitive to the spatial scale at which sampling and

analysis are conducted but to temporal scale as well. Annual changes in population densities and/or redistribution of individuals resulting from migration and re-establishment of territories each spring can produce substantial variations in habitat associations (cf. Fretwell 1972, Wiens 1974b, O'Connor 1981). Most habitat studies conducted within temperate forests which suggest that bird species preferentially utilize only certain forest types (e.g. Bond 1957, MacArthur & MacArthur 1961, MacArthur et al. 1962, James 1971, Edington & Edington 1972, Anderson & Shugart 1974, Whitmore 1977) were not designed to assess variability in habitat use by species either spatially or temporally. Data collection was often confined to one part of the year, particularly the breeding season, and most often to only one year. This problem was compounded by combining or averaging data for species to enhance analytical tractability (e.g. Bond 1957, Hespenheide 1971, James 1971, Steele 1974, Whitmore 1975). Habitats 'preferentially selected' by species were inferred from abundance patterns, which in reality may reflect differences in sampling efforts among habitats or differences in availability of resources within habitats to support bird species (i.e. habitat quality). Interpretation of habitat associations by population density may be further

complicated by interspersions of habitats. For example, habitat patterns among species may reflect the "source-sink structuring" of populations (Wiens & Rotenberry 1985). 'Source' populations occupy habitats suitable for reproduction. The output of offspring exceeds local carrying capacity, leading to net dispersal of individuals. Densities may be temporally stable, but the true productivity of the habitat is underestimated by breeding density only. 'Sink' populations may occupy habitat types in which reproduction alone cannot maintain population levels. Persistence of these populations depends on emigrants from 'source' populations. The densities and dynamics that characterize populations in these sink habitats thus vary more as a consequence of events in nearby source populations than in response to local habitat conditions. Source areas could be considered equivalent to "survival foci" (Birch 1971), "refuge areas" (Paine 1969, Dwyer 1972) or "hot spots" (Diamond 1975) in which species reside during unfavourable conditions and from which other habitats can be colonized when conditions improve.

Importance of habitat heterogeneity inferred from patterns of habitat use from single sample surveys is based on data analyses which are not only subject to erroneous statistical interpretation (Wiens 1981a,b), but further assume that ecological

systems are relatively unchanging or at 'equilibrium'. Certainly, the equilibrium concept enabled biologists to justify the short-term studies characteristic of current research funding policies and university degree programs. Unfortunately, in avoiding the difficulties of sampling and data analysis associated with variable environments (Levins 1969; Smith 1972; Mulholland & Gowdy 1978; Hendrickson 1979), the temporal and spatial variability in habitat use by birds evident in the data was ignored or averaged away. The need for temporal plasticity in habitat use by forest birds may become more apparent as the importance of internal changes or "patch dynamics" (Pickett & Thompson 1978) of temperate forest habitats become better understood. Temporal variability, as well as spatial variability in habitat use by forest bird species could account for the secondary importance of habitat heterogeneity to bird species numbers within forests observed in the present study.

The number of bird species in total and in many ecological classes increased significantly primarily with forest area. In their theory of island biogeography, MacArthur and Wilson (1963, 1967) proposed that species number was related to population processes associated with island size. Changes in species composition as a result of

extinction of some species and their replacement by newly-colonizing species, or species turnover, were also partly related to island size. Theoretically, larger islands support larger populations per species with concomitant lower extinction probabilities. If species on larger islands experience lower extinction probabilities then not only should larger islands contain more species than smaller islands at any given time, but species turnover should be lower on large islands than small islands, all other things being equal. Forest fragments have been viewed as habitat 'islands' isolated in an agricultural matrix (e.g. MacArthur & Wilson 1967, MacArthur 1972, Whitcomb 1977, Pickett & Thompson 1978, Burgess & Sharpe 1981). Unlike true oceanic islands, temperate forest fragments exhibit annual 'extinction' and 'recolonization' of migrant birds, which comprise 76% of all species detected in the breeding season. Considering the high overwinter mortality in migrant species (Roberts 1971, Whitcomb et al. 1981) and site-tenacity of successful breeders (Whitcomb et al. 1981), the decreased probability of local extinctions of large populations could account for the increase in bird species observed in larger forests.

The number of bird species in 5 forests was constant over three years when species turnovers were corrected for sampling errors or pseudoturnover.

Between 1980 and 1981, bird species numbers within all 21 forests were also constant, on average, when corrected for pseudoturnover. The constant number of species within forests reflected detection of equal numbers of bird species within forests, on average, in only 1980 or 1981 i.e. a balancing of 'immigrations' and 'extinctions'. On average, 73% of turnover in species composition within forests was related to pseudoturnover. Nilsson and Nilsson (1983) found 63% of apparent species turnover in vascular plants of small islands in a Swedish lake to be attributable to pseudoturnover. The higher value for birds reflects, in part, greater mobility of birds compared to plants, leading to increased probability of missing breeding species and/or of including transients or vagrants in surveys of forests. Real turnover in species composition within forests was conservatively estimated at 5% on average between 1980 and 1981. In Illinois, point counts in forests ranging from 2 to 600 ha exhibited, on average, 17% apparent turnover in species composition annually over 3 years (Blake & Karr 1982a). In a 13-ha deciduous forest in southern Sweden, numbers of small passerine species were constant over a 10-year period (Järvinen 1980). Annual species turnover was about 10% and was due mainly to immigration and disappearance of species with 1- to 2-pair

populations. In a completely censused 14-ha forest in Maryland, annual turnover was 16.9%, or 10.8% when corrected for possible observational artifacts (Whitcomb et al. 1977), compared to 6.6% in the 14-ha forest surveyed in the present study. McCoy (1982) argued that Maryland turnovers were still inflated by inclusion of vagrant species within years. Comparisons with species turnover rates over longer time intervals between censuses (e.g. Diamond 1969, Whitcomb et al. 1977, Butcher et al. 1981) are invalid because apparent turnover underestimates real turnover as species may colonize and become extinct between surveys without being recorded (Diamond & May 1977, Diamond 1980, Nilsson & Nilsson 1983).

Although a balanced turnover of species was observed within forests annually, turnovers in species composition were unrelated to forest size (cf. MacArthur-Wilson model). That is larger forests were as temporally variable in species composition as smaller forests. In Illinois, Blake and Karr (1982a) also found that annual species turnovers in 15 forests ranging from 2 to 600 ha were unrelated to forest size. Unlike true oceanic islands, forests are not surrounded by habitat totally inhospitable to terrestrial bird species. Bird species inhabiting forests were capable of surviving in the intervening agricultural matrix and many even had large

populations in surrounding habitats (cf. Margules et al. 1982). Consequently, forest 'islands' may contain many vagrant and/or transient species (Howe 1979, McCoy 1982). The significantly higher temporal variability of edge species within forests perhaps reflected the transient and/or vagrant nature of these birds in forest habitats. However, even when potential vagrants were removed by excluding edge species, annual species turnover remained similar within and among forests. High immigration rates of birds into forests each spring may counterbalance greater extinction rates of populations within smaller forests by the 'rescue effect' of demographic and genetic contributions from conspecifics (sensu Brown & Kodric-Brown 1977). Further, the annual redistribution of individuals may result in compensating shifts of species among forests, producing the consistent species number and composition observed in the region as a whole. Whitcomb et al. (1977) were premature in concluding that the MacArthur-Wilson model was appropriate for forests in fragmented landscapes just because they observed species turnover in a single forest. Others have also argued that many, if not all, insular continental situations do not fit the tenets of the island biogeographic model (Brown 1971, Kushlan 1979, Gilbert 1980, Butcher et al. 1981, Weaver & Kellman

1981, Margules et al. 1982, McCoy 1982, Middleton & Merriam 1983).

Smaller forests contained only a limited subset of bird species detected in larger forests. For some species, smaller forests were insufficient to meet minimum territory requirements e.g. species with territories over 5 ha (cf. Forman et al. 1976, Galli et al. 1976). Many species with much smaller territory sizes were also restricted to larger forests, indicating that minimum territory size alone is insufficient to explain increasing bird species number with forest size. Connor and McCoy (1979) suggested that the species-area pattern reflects random sampling from the regional species pool. Larger areas contain more species merely as a consequence of supporting a larger sample of individuals. Species with low regional abundances do not occur in smaller areas because their probability of doing so is low. The larger forests studied contained more species with low regional abundance; small forests contained few or no species with low abundance regionally (which included a significant number of obligate forest species). In Maryland, bird species with low regional abundance (which again included a significant number of obligate forest

species) were also significantly more abundant in forests over 70 ha than in 6- to 14-ha forests (Whitcomb et al. 1981:Table 8-7).

The general applicability of the passive sampling hypothesis was explicitly examined by comparing species distributions observed among forests to species distributions generated from the passive sampling model of random dispersal of individuals available in the regional species pool. The number of species occurring in forests as large as 18 ha was generally consistent with the random model (cf. Coleman et al. 1982). Distributions of over 90% of species within years appeared consistent with the random model. Species with low regional abundances within forests did not occur in smaller forests because their probability of doing so was low. For species with large territories, distributions among forests must be constrained by a minimum size. Random distribution between years is also constrained by site-tenacity of successful breeders, as reflected in unexpectedly low species turnovers. Absences of 6 bird species from smaller forests were not predicted by the random model. Differential distribution of these species could be related to a number of factors such as habitat suitability, interspecific interactions and dispersal probabilities.

Habitat suitability may be related to physical factors (e.g. resources for nesting, feeding) or behavioural factors. The tendency for Ovenbirds to occur in loose 'colonies' may result in new colonists actively avoiding unoccupied forests and choosing forests with existing colonies (Whitcomb et al. 1981). This could account for the increased abundance of Ovenbirds observed in larger forests in at least some years. A similar phenomenon could be applicable to the Least Flycatcher (pers. obs.). In 1981, Veery were also more abundant in larger forests, suggesting that physical conditions in smaller forests may be less suitable, in at least some years.

Secondly, species may be absent from smaller forests because of lower success of individuals in establishing territories or fledging young. Martin (1980) suggested that the number of spring migratory bird species in shelterbelts on the Great Plains was determined by competition for limited food resources. From analyses of population trends in a 23-ha mixed forest in Connecticut, Butcher et al. (1981) suggested that the decline of forest species could be related to increased competition with increasing numbers of birds of suburban species. In the present study, most of the species exhibiting significantly higher abundances in smaller forests were

characterized as edge species. Increased predation by species characteristic of agricultural areas such as domestic cats, skunks, raccoons, Blue Jays or Common Crows (Matthaie & Stearns 1981, Whitcomb et al. 1981) could account for lower success of individuals, particularly of ground-stratum species such as Ovenbird, Veery and Wood Thrush. Both Common Crow and Common Grackle were significantly more abundant in smaller forests.

Species absences in smaller forests may also reflect lower probability of dispersal of individuals into smaller forests. Whitcomb et al. (1981) argued that, at least for obligate forest birds, species number within forests is strongly dependent on the mortality rate of previous residents and on subsequent colonisation by first-year birds produced elsewhere. That is, the number of forest species is largely regulated by events external to forests such as regional production of young, post-breeding mortality and pre-breeding dispersal. Particularly in smaller forests, maintenance of viable long-term breeding populations of forest species thus depends on regular subsidization from outside the forest.

The probability of individuals dispersing between forests appears to be influenced by the degree of forest isolation. Isolation is related to distance between forests, the size of those forests,

and interconnectivity of forests via corridors of forested habitat such as hedgerows or riparian strips. Theoretically, bird movement among forests is inversely related to the distance between forests and facilitated by greater interconnectivity. The size distribution of forests potentially affects the species composition of the regional pool of dispersing individuals. For example, Butcher et al. (1981) suggested that species turnover during a 23 year period in a 23-ha forest in Connecticut was related to increased urban/suburban development of the surrounding area. They attributed the disappearance of obligate forest species and increased numbers of species characteristic of suburban habitats to 'greater isolation' of the forest from similar forests. Greater isolation could reflect reduced dispersal of obligate forest birds into the forest because of greater distances between forests compounded by fewer wooded connections. Greater isolation could also reflect a simultaneous decline in availability of dispersing obligate forest birds as a result of destruction of forest habitat regionally. Species disappearances could then result from a passive sampling effect (cf. Haila et al. 1979). The relative importance of each mechanism cannot be evaluated from this study. However, information is available for birds from a single

breeding season in 30 forests (1-905 ha) in Maryland with respect to an isolation index which included interforest distances and forest size (Whitcomb et al. 1981). Analysis of the data indicated that more isolated forests contained significantly fewer species in total ($r = -.419$), primarily because they contained significantly fewer obligate forest species ($r = -.588$, although misreported by Whitcomb et al. 1981:149). Unfortunately, more isolated forests were also significantly smaller than less isolated forests ($r = -.660$), confounding interpretation of the results in terms of distance between forests versus passive sampling associated with forest size. Circumstantial evidence suggests that distances between forests and interconnectivity of forests was involved. Firstly, a single 12-ha forest in Maryland, connected to a large forest nearby by a 6-ha corridor of grazed woodland and early second growth, supported more obligate forest species than more isolated forests of similar size (MacClintock et al. 1977, Whitcomb et al. 1981). Secondly, birds appear to preferentially use woody vegetation between forests, as indicated by more frequent movement of forest birds along wooded fencerows than over open fields in Ontario (Wegner & Merriam 1979) and by concentration of bird-disseminated seeds along field-forest edges and under real or

artificially-constructed woody plants in old fields in New Jersey (McDonnell & Stiles 1983).

The importance of regional configuration of forests to bird species distributions is also suggested by comparisons of studies conducted in different geographic areas. Galli et al. (1976) censused birds in 10 forests (.01 - 24 ha) replicated for 3 geographic sections within a 2000 km² area in the New Jersey Piedmont. Differences in species numbers from one forest size to another were not the same from section to section, according to analysis of variance. Although the authors concluded that this size-by-section interaction was not ecologically significant, an alternative interpretation could be that differences in regional configuration of forests among geographic sections affected bird species distributions.

In the present study, statistical independence of bird species number per census point and forest size contrasted with the positive correlation observed by Blake & Karr (1982a) among 15 forests (1.8 - 600 ha) in Illinois. Birds were censused similarly in both studies, but Blake and Karr did not accumulate species at a census point over a season. Importance of this discrepancy was evaluated by comparing species differences (measured by SDC) between intraseasonal surveys for 1980 and 1981 in

the 21 forests of the present study. Between-survey variability in species composition was not significantly correlated with $\log(\text{area})$ of forests in 1980 ($r = -.233$ $p > .20$) but decreased significantly with forest size in 1981 ($r = -.552$). Greater accumulation of species between surveys in smaller forests could account for the difference in species number per census point between the Ontario and Illinois study. This difference in method may not be critical however, as a significant positive correlation between species per census point and forest size was also evident for 30 forests in Maryland ($r = .484$, although misreported by Whitcomb et al. 1981:148) which were censused by accumulating species at census points between surveys. The relationship between species number at a census point and forests size was consistent among studies when all analyses were restricted to sets of similar-sized forests (cf. Martin 1981). Different results in the present study cannot simply be attributed to undersampling of bird species at census points within larger forests. If larger forests have more species at a census point, then, for equal survey time, a census point in a larger forest will be undersampled relative to a census point in a smaller forest. Because of similar shapes of species-time curves in all forests, more species would still be detected at

census points in larger forests than at census points in smaller forests. Differences in species number at census points perhaps more reasonably reflect the effect of differences in regional configuration of forests on bird species distributions in Ontario, Illinois and Maryland. As forests become more fragmented regionally, bird species, particularly obligate forest species, may concentrate in larger forests as a result of reduced availability of dispersing individuals and/or reduced dispersal of those birds over greater distances between forests, compounded with fewer wooded interconnections. As a consequence, smaller forests contain relatively fewer species and larger forests, relatively more. Preliminary analyses suggest that differences in regional configuration of forests may account for a general increase in minimum forest size occupied by obligate forest species comparable among studies from Ontario to Maryland and Illinois. Differential abundances of obligate forest and facultative forest species in large versus small forests among Ontario, Maryland and Illinois may also be related to varying degrees of forest fragmentation and interconnectivity in these landscapes. Further research is necessary to examine the importance of isolation factors in determining the spatial distribution of birds inhabiting forests in fragmented landscapes.

To summarize, forest size was the most significant variable determining the number of bird species in forests. Larger forests had more species because they had a larger sample of individuals from the regional species pool.

Habitat heterogeneity was secondarily important to bird patterns among forests. More heterogeneous forests supported more species, in part, by including species with different habitat requirements. Perhaps more importantly, forests with greater heterogeneity supported more individuals. By increasing the number of individuals from the regional species pool, a larger number of species was also included in more heterogeneous forests.

Species composition within forests was related to external factors affecting regional availability of dispersing individuals (e.g. regional production of young, post-breeding mortality, pre-breeding dispersal, individual site-fidelity). Absences of a few species from smaller forests appeared related to large territory size, unsuitable habitat, detrimental interspecific interactions and/or low dispersal probabilities associated with landscape configuration.

5. CONCLUSIONS

1. Habitat heterogeneity, of at least species composition of tree and shrub strata, increased with forest size.
2. Trees were important determinants of spatial pattern in plant species and structure of forests.
3. Bird species number in total and in 67% of ecological classes increased, primarily with forest size.
4. Increasing species number in 3- to 18-ha forests was consistent with random samples from the regional species pool in each year.
5. Greater habitat heterogeneity also increased species number in total and in 24% of 21 ecological classes.
6. More heterogeneous forests had more species because of a larger sample of individuals from the regional species pool and by inclusion of 'habitat specialists'.
7. Temporal variability in bird species composition within forests did not decrease with larger area or greater habitat heterogeneity, contrary to population process and habitat heterogeneity hypotheses, respectively.
8. Unexpectedly low turnover in species composition

of a 3-ha forest indicated that all birds may not disperse randomly among forests between years.

9. Distributions of over 90% of species were consistent with a passive sampling model of random dispersal of birds among small forests in each year.
10. Species composition within temperate forests appears related to external events affecting the regional availability of dispersing individuals (e.g. regional production of young, post-breeding mortality, pre-breeding dispersal, individual site-fidelity).
11. Unexpected absences of a few species from smaller forests may be related to habitat suitability, interspecific interactions or regional configuration of forests.

6. REFERENCES

- Anderson, S.H. and H.H. Shugart Jr. 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. *Ecology* 55:828-837.
- Arrhenius, O. 1921. Species and area. *J. Ecology* 9:95-99.
- Bent, A.C. 1919-1968. Life-histories of North American Birds. U.S. National Museum Bulletin Nos. 107-237.
- Berthold, P. 1976. Methods of population determination in ornithology: Review and critical consideration. *J. fur Ornith.* 117:1-69 (translation).
- Best, L.B. 1981. Seasonal changes in detection of individual bird species. *Studies in Avian Biology* 6:252-261.
- Birch, L.C. 1971. The role of environmental heterogeneity and genetical heterogeneity in determining distribution and abundance. Pp. 109-128 IN: P.J. den Boer and G.R. Gradwell (eds.). *Dynamics of Populations*. Centre for Agricultural Publishing, Wageningen. 611 pp.
- Blake, J.G. and J.R. Karr. 1982a. Ecology of forest island bird communities in east-central Illinois. U.S. Fish & Wildlife Service Contract No. 14-16-0009-79-023.
- Blake, J.G. and J.R. Karr. 1982b. Avian community ecology of forest patches in east-central Illinois: Migrants and winter residents. U.S. Forestry Service Contract No. FS-NC-1701(80-03).
- Blondel, J., C. Ferry and B. Frochot. 1973. Avifaune et vegetation essai d'analyse de la diversite. *Alauda* XLI(1/2):63-84.
- Blondel, J., C. Ferry and B. Frochot. 1981. Point counts with unlimited distance. *Studies in Avian Biology* 6:414-420.
- Bond, R.R. 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. *Ecol. Monogr.* 27:351-384.
- Brown, J.H. 1971. Mammals on mountaintops: Nonequilibrium insular biogeography. *Am. Nat.* 105:467-478.

Brown, J.H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology* 58:445-449.

Bull, J. and J. Farrand Jr. 1977. The Audubon Society Field Guide to North American Birds. Alfred A. Knopf, Inc. N.Y. 718 pp.

Burgess, R.L. and D.M. Sharpe (eds.). 1981. Forest Island Dynamics in Man-Dominated Landscapes. Springer-Verlag, N.Y. 294 pp.

Butcher, G.S., W.A. Niering, W.J. Barry and R.H. Goodwin. 1981. Equilibrium biogeography and the size of nature preserves: An avian case study. *Oecologia (Berl)* 49:29-37.

Cody, M.L. 1980. Evolution of habitat use: Geographic perspectives. *Proc. 17th Internat. Ornith. Congr.*:1013-1018.

Coleman, B.D., M.A. Mares, M.R. Willig and Y.H. Hsieh. 1982. Randomness, area and species richness. *Ecology* 63:1121-1133.

Collins, S.L., F.C. James and P.G. Risser. 1982. Habitat relationships of wood warblers (Parulidae) in north central Minnesota. *Oikos* 39:50-58.

Connor, E.F. and E.D. McCoy. 1979. The statistics and biology of the species-area relationship. *Am. Nat.* 113:791-833.

Cooke, F. and K.F. Abraham. 1980. Habitat and locality selection in Lesser Snow Geese: The role of previous experience. *Proc. 17th Internat. Ornith. Congr.*:998-1004.

Cottam, G. and J. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451-460.

Cyr, A. 1977. A method of describing habitat structure and its use in bird population studies. *Pol. Ecol. Studies* 3:41-52.

DesGranges, J.L. 1980. Avian community structure of six forest stands in La Mauricie National Park, Quebec. Canadian Wildlife Service Occasional Paper No. 41. 34 pp.

Diamond, J.M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proc. Nat. Acad. Sci. U.S.A.* 64:57-63.

Diamond, J.M. 1975. Assembly of species communities. Pp. 342-444 IN: M.L. Cody and J.M. Diamond (eds.). Ecology and Evolution of Communities. Harvard University Press, Cambridge, Mass. 545 pp.

Diamond, J.M. 1980. Species turnover in island bird communities. Proc. 17th Internat. Ornith. Congr.:777-782.

Diamond, J.M. and R.M. May. 1977. Species turnover rates on islands: Dependence on census interval. Science 197:266-270.

Draper, N.R. and H. Smith. 1966. Applied Regression Analysis. John Wiley & Sons, Inc., N.Y. 407 pp.

Dwyer, P.D. 1972. Feature, patch and refuge area: Some influences on diversity of bird species. Emu 72:149-156.

Edington, J.M. and M.A. Edington. 1972. Spatial patterns and habitat partition in breeding birds of an upland wood. J. Animal Ecology 41:331-357.

Erskine, A.J. 1971. A preliminary catalogue of bird census studies in Canada, Part 1. Canadian Wildlife Service Progress Notes No. 20. 78 pp.

Erskine, A.J. 1976. A preliminary catalogue of bird census plot studies in Canada, Part 3. Canadian Wildlife Service Progress Notes No. 59. 24 pp.

Erskine, A.J. 1977. Birds in Boreal Canada: Communities, Densities and Adaptations. Canadian Wildlife Service Report Series No. 41. 73 pp.

Erskine, A.J. 1978. The First Ten Years of the Co-operative Breeding Bird Survey in Canada. Canadian Wildlife Service Report Series No. 42. 61 pp.

Ferry, C. 1974. Comparison between breeding bird communities in an oak forest and a beech forest censused by the IPA method. Acta Ornith. 20:302-309.

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 (Berl) 26:1-8.

Freedman, B., C. Beauchamp, I.A. McLaren and S.I. Tingley. 1981. Forestry management practices and populations of breeding birds in a hardwood forest in Nova Scotia. *Can. Field-Nat.* 95:307-311.

Fretwell, S.D. 1972. *Populations in a Seasonal Environment*. Princeton University Press, Princeton, N.J. 217 pp.

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.

Gauch, H.G. Jr. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge, Mass. 298 pp.

Gilbert, F.S. 1980. The equilibrium theory of island biogeography: Fact or fiction? *J. Biogeography* 7:209-235.

Gillett, J.M. and D.J. White. 1978. Checklist of Vascular Plants of the Ottawa-Hull Region, Canada. National Museum of Natural Sciences, Ottawa, Canada. 155 pp.

Gleason, H.A. 1922. On the relationship between species and area. *Ecology* 3:158-162.

Godfrey, W.E. 1966. The Birds of Canada. National Museums of Canada Bulletin No. 203. Biological Series No. 73. 428 pp.

Greenburg, R. 1979. Body size, breeding habitat, and winter exploitation systems in *Dendroica*. *Auk* 96:756-766.

Grinnell, J. 1917. Field tests of theories concerning distributional control. *Am. Nat.* 51:115-128.

Gromadzki, M. 1970. Breeding communities of birds in mid-field afforested areas. *Ekologia Polska* 18:1-44.

Haila, Y., O. Järvinen and R.A. Väisänen. 1979. Effect of mainland population changes on the terrestrial bird fauna of a northern island. *Ornis Scand.* 10:48-55.

Hamilton, T.H. and N.E. Armstrong. 1965. Environmental determination of insular variation in bird species abundance in the Gulf of Guinea. *Nature* 207:148-151.

Hamilton, T.H., R.H. Barth Jr. and I. Rubinoff. 1964. The environmental control of insular variation in bird species abundance. *Proc. Nat. Acad. Sci. U.S.A.* 52:132-140.

Hendrickson, J.A. Jr. 1979. Estimates of species diversity from multiple samples. Pp. 145-158 IN: J.F. Grassle, G.P. Patil, W. Smith and C. Taillie. *Ecological Diversity in Theory and Practice*. International Co-operative Publishing House, Fairland, Maryland. 365 pp.

Hespenheide, H.A. 1971. Flycatcher habitat selection in the eastern deciduous forest. *Auk* 88:61-74.

Holmes, R.T., R.E. Bonney Jr. and S.W. Pacala. 1979. Guild structure of the Hubbard Brook bird community: A multivariate approach. *Ecology* 60:512-520.

Holmes, R.T. and S.K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. *Oecologia (Berl)* 48:31-35.

Hosie, R.C. 1969. *Native Trees of Canada*. Canadian Forestry Service, Dept. of the Environment, Ottawa, Canada. 380 pp.

Howe, R.W. 1979. Distribution and behaviour of birds on small islands in northern Minnesota. *J. Biogeography* 6:379-390.

Howe, R. and G. Jones. 1977. Avian utilization of small woodlots in Dane County, Wisconsin. *Passenger Pigeon* 39:313-319.

International Bird Census Committee (IBCC). 1970. Recommendations for an international standard for a mapping method in bird census work. *Aud. Field Notes* 24:722-726.

International Bird Census Committee (IBCC). 1977. Censusing breeding birds by the IPA method. *Pol. Ecol. Studies* 3:15-17.

James, F.C. 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bull.* 83:215-237.

Järvinen, O. 1980. Dynamics of north European bird communities. Proc. 17th Internat. Ornith. Congr.:770-776.

Johnson, N.K. 1975. Controls of number of bird species on montane islands in the Great Basin. Evolution 29:545-563.

Karr, J.R. 1968. Habitat and avian diversity on strip-mined land in east central Illinois. Condor 70:348-357.

Karr, J.R. 1971. Structure of avian communities in selected Panama and Illinois habitats. Ecol. Monogr. 41:207-233.

Karr, J.R. 1982. Avian extinction on Barro Colorado Island, Panama: A reassessment. Am. Nat. 119:220-239.

Karr, J.R. and K.E. Freemark. 1983. Habitat selection and environmental gradients: Dynamics in the 'stable' tropics. Ecology. In press.

Karr, J.R. and T.E. Martin. 1981. Random numbers and principal components: Further searches for the Unicorn? Pp. 20-25 IN: D.E. Capen (ed.). The Use of Multivariate Statistics in Studies of Wildlife Habitat. USDA Forest Service Gen. Techn. Report RM-87. 249 pp.

Karr, J.R. and R.R. Roth. 1971. Vegetation structure and avian diversity in several new world areas. Am. Nat. 105:423-435.

Karr, J.R., D.W. Schemske and N. Brokaw. 1982. Temporal variation in the undergrowth bird community of a tropical forest. IN: E.G. Leigh, A.S. Rand and D. Edwards (eds.). Seasonal Rhythms in a Tropical Forest. Smithsonian Institution Press, Washington, D.C.

Keast, A. and E. Morton (eds.). 1980. Migrant Birds in the Neotropics: Ecology, Behaviour, Distribution and Conservation. Smithsonian Institution Press, Washington, D.C. 578 pp.

Kendeigh, S.C. 1945. Nesting behaviour of wood warblers. Wilson Bull. 57:144-164.

Kendeigh, S.C. 1946. Breeding birds of the beech-maple-hemlock community. Ecology 27:226-245.

Kendeigh, S.C. 1982. Bird Populations in East-central Illinois: Fluctuations, Variations, and Development over a Half-century. Illinois Biological Monographs No. 52. 136 pp.

Kushlan, J.A. 1979. Design and management of continental wildlife reserves: Lessons from the everglades. Biol. Conserv. 15:281-290.

Lack, D. 1976. Island Biology: Illustrated by the Land Birds of Jamaica. Blackwell Scientific Publications, Oxford, G.B. 445 pp.

Leck, C.F. 1972. Seasonal changes in feeding pressures of fruit- and nectar-eating birds in the neotropics. Condor 74:54-60.

Levenson, J.B. 1981. Woodlots as biogeographic islands in southeastern Wisconsin. Pp. 13-39 IN: R.L. Burgess and D.M. Sharpe (eds.). Forest Island Dynamics in Man-Dominated Landscapes. Springer-Verlag, N.Y. 310 pp.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Entomol. Soc. Am. 15:237-240.

Lovejoy, T.E. 1972. Bird species diversity and composition in Amazonian rain forests. Am. Zoologist 12:711-712.

Lynch, J.R. and N.K. Johnson. 1974. Turnover and equilibria in insular avifaunas, with special reference to the California Channel Islands. Condor 76:370-384.

MacArthur, R.H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Harper & Row, N.Y. 269 pp.

MacArthur, R.H. and J.W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

MacArthur, R.H., J.W. MacArthur and J. Peer. 1962. On bird species diversity. II. Prediction of bird censuses from habitat measurements. Am. Nat. 96:167-174.

MacArthur, R.H., H. Recher and M. Cody. 1966. On the relation between habitat selection and species diversity. Am. Nat. 100:319-332.

MacArthur, R.H. and E.O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-387.

MacArthur, R.H. and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, N.J. 203 pp.

MacClintock, L., 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.

Margules, C., A.J. Higgs and C.W. Rafe. 1982. Modern biogeographic theory: Are there any lessons for nature reserve design? *Biol. Conserv.* 24:115-128.

Martin, T.E. 1980. Diversity and abundance of spring migratory birds using habitat islands on the Great Plains. *Condor* 82:430-439.

Martin, T.E. 1981. Species-area slopes and coefficients: A caution on their interpretation. *Am. Nat.* 118:823-837.

Matthiae, P.E. and F. Stearns. 1981. Mammals in forest islands in southeastern Wisconsin. Pp. 55-66 IN: R.L. Burgess and D.M. Sharpe (eds.). *Forest Island Dynamics in Man-Dominated Landscapes*. Springer-Verlag, N.Y. 310 pp.

McCoy, E.D. 1982. The application of island-biogeographic theory to forest tracts: Problems in the determinations of turnover rates. *Biol. Conserv.* 22:217-227.

McCracken, J.D., M.S.W. Bradstreet and G.L. Holroyd. 1981. *Breeding Birds of Long Point, Lake Erie*. Canadian Wildlife Service Report Series No. 44. 74 pp.

McDonnell, M.J. and E.W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia (Berl)* 56:109-116.

Middleton, J. and H.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.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, N.Y. 547 pp.

Mulholland, R.J. and C.M. Gowdy. 1978. Determination of sampling intervals for ecological processes. Pp. 71-86 IN: H.H. Shugart Jr. (ed.). Time Series and Ecological Processes. SIAM-SIMS Conference Series No. 5. 303 pp.

Nie, N.H., C.H. Hull, J.G. Jenkins, K. Steinbrenner and D.H. Bent. 1975. Statistical Package for the Social Sciences. McGraw-Hill Book Co., N.Y. 675 pp.

Nilsson, S.G. 1979. Effect of forest management on the breeding bird community in southern Sweden. Biol. Conserv. 16:135-144.

Nilsson, S.G. and I.N. Nilsson. 1983. Are estimated species turnover rates on islands largely sampling errors? Am. Nat. 121:595-597.

O'Connor, R.J. 1981. Habitat correlates of bird distribution in British census plots. Studies in Avian Biology 6:533-537.

Oelke, H. 1981. Limitations of the mapping method. Studies in Avian Biology 6:114-118.

Orlowski, L. 1970. Automatic classification of plants based on information content. Can. J. Botany 48:793-802.

Paine, R.T. 1969. The Pisaster-Tegula interaction: Prey patches, predator food preference and intertidal community structure. Ecology 50:950-961.

Pickett, S.T.A. and J.N. Thompson. 1978. Patch dynamics and the design of nature preserves. Biol. Conserv. 13:27-37.

Pitelka, F.C. 1941. Distribution of birds in relation to major biotic communities. Am. Midl. Nat. 25:113-137.

Power, D.M. 1972. Numbers of bird species on the California islands. Evolution 26:451-463.

Power, D.M. 1976. Avifauna richness on the California Channel Islands. Condor 78:394-398.

Preston, F.W. 1962. The canonical distribution of commonness and rarity. *Ecology* 43:185-215, 410-432.

Ralph, C.J. and J.M. Scott (eds.). 1981. Estimating numbers of terrestrial birds. *Studies in Avian Biology* No. 6. Cooper Ornithological Society. 630 pp.

Recher, H.F. 1969. Bird species diversity and habitat diversity in Australia and North America. *Am. Nat.* 103:75-80.

Reddingius, J. and P.J. den Boer. 1970. Simulation experiments illustrating stabilization of animal numbers by spreading of risk. *Oecologia (Berl)* 5:240-284.

Reed, R.M. 1983. The role of species-area relationships in reserve choice: A British example. *Biol. Conserv.* 25:263-271.

Reynolds, R.T., J.M. Scott and R.A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. *Condor* 82:309-313.

Rice, J., B.W. Anderson and R.D. Ohmart. 1980. Seasonal habitat selection by birds in the lower Colorado River valley. *Ecology* 61:1402-1411.

Robbins, C.S. 1978. Determining habitat requirements of nongame species. *Transactions of the 43rd North American Wildlife and Natural Resources Conf.*:57-68.

Robbins, C.S. 1981a. Effect of time of day on bird activity. *Studies in Avian Biology* 6:275-286.

Robbins, C.S. 1981b. Bird activity levels related to weather. *Studies in Avian Biology* 6:301-310.

Robbins, C.S., B. Bruun and H.S. Zim. 1966. *Birds of North America*. Golden Press, N.Y. 340 pp.

Roberts, J.O.L. 1971. Survival among some North American wood warblers. *Bird-Banding* 42:165-184.

Root, R.B. 1967. The niche exploitation pattern of the Blue-grey Gnatcatcher. *Ecol. Monogr.* 37:317-350.

Rotenberry, J.T. and J.A. Wiens. 1980a. Habitat structure, patchiness and avian communities in North American steppe vegetation: A multivariate analysis. *Ecology* 61:1228-1250.

Rotenberry, J.R. and J.A. Wiens. 1980b. Temporal variation in habitat structure and shrub steppe bird dynamics. *Oecologia (Berl)* 47:1-9.

Roth, R.R. 1976. Spatial heterogeneity and bird species diversity. *Ecology* 57:773-782.

Roughgarden, J.R. 1974. Population dynamics in a spatially varying environment: How population size 'tracks' spatial variation in carrying capacity. *Am. Nat.* 108:649-664.

Sabo, S.R. and R.T. Holmes. 1983. Foraging niches and the structure of forest bird communities in contrasting montane habitats. *Condor* 85:121-138.

Schoener, T.W. 1968. Sizes of feeding territories among birds. *Ecology* 49:123-141.

Schoener, R.W. and A. Schoener. 1983. Distribution of vertebrates on some very small islands. II. Patterns in species number. *J. Animal Ecology* 52:237-262.

Sherry, T.W. 1979. Competitive interactions and adaptive strategies of American Redstarts and Least Flycatchers in a northern hardwoods forest. *Auk* 96:265-283.

Shields, W.M. 1977. The effect of time of day on avian census results. *Auk* 94:380-383.

Siegel, S. 1956. Nonparametric Statistics for the Behavioural Sciences. McGraw-Hill Book Co., Inc., N.Y. 312 pp.

Simberloff, D. 1972. Models in biogeography. Pp. 160-191 IN: T.J.M. Schopf (ed.). Models in Paleobiology. Freeman, Cooper & Co., San Francisco. 250 pp.

Simberloff, D. 1974. Equilibrium theory of island biogeography and ecology. *Ann. Rev. Ecol. Syst.* 5:161-182.

Simberloff, D. 1976. Experimental zoogeography of islands: Effects of island size. *Ecology* 57:629-642.

Skirvin, A.A. 1981. Effect of time of day and time of season on the number of observations and density estimates of breeding birds. *Studies in Avian Biology* 6:271-275.

Smith, F.E. 1972. Spatial heterogeneity, stability, and diversity in ecosystems. *Tran. Conn. Acad. Arts Sci.* 44:309-335.

Sokal, R.R. and F.J. Rohlf. 1981. *Biometry*. 2nd ed. Freeman and Co., San Francisco. 859 pp.

Staite, P., P. Adams and K. Wilson. 1979. The area-species relationship of wintering birds in Waterloo Region woodlots. Dept. of Man-Environment Studies, Faculty of Environmental Studies, University of Waterloo, Waterloo, Ontario, Canada. 58 pp.

Steele, J.H. 1974. Spatial heterogeneity and population stability. *Nature* 248:83.

Svardson, G. 1949. Competition and habitat selection in birds. *Oikos* 1:157-174.

Thompson, L.S. 1978. Species abundance and habitat relations of an insular montane avifauna. *Condor* 80:1-14.

Tomoff, C.S. 1974. Avian species diversity in desert scrub. *Ecology* 55:396-403.

Tozer, R.G. and J.M. Richards. 1974. *Birds of the Oshawa-Lake Scugog Region, Ontario*. Alger Press Ltd., Oshwawa, Ont. 382 pp.

Vuilleumier, F. and D. Simberloff. 1980. Ecology versus history as determinants of patchy and insular distributions in high Andean birds. *Evol. Biol.* 12:235-379.

Weaver, M. and M. Kellman. 1981. The effects of forest fragmentation on woodlot tree biotas in southern Ontario. *J. Biogeography* 8:199-210.

Wegner, J. and G. Merriam. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitat. *J. Appl. Ecol.* 16:349-357.

Whitcomb, B.L., R.F. Whitcomb and D. Bystrak. 1977. Island biogeography and 'habitat islands' of eastern forest. III. Long-term turnover and effects of selective logging on the avifauna of forest fragments. *Am. Birds* 31:17-23.

Whitcomb, R.F. 1977. Island biogeography and 'habitat islands' of eastern forest. I. Introduction. *Am. Birds* 31:3-5.

Whitcomb, R.F., C.S. Robbins, J.F. Lynch, B.L. Whitcomb, M.K. Klimkiewicz and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pp. 125-206 IN: R.L. Burgess and D.M. Sharpe (eds.). Forest Island Dynamics in Man-Dominated Landscapes. Springer-Verlag, N.Y. 294 pp.

Whitmore, R.C. 1975. Habitat ordination of passerine birds of the Virgin River Valley, southwestern Utah. Wilson Bull. 87:65-74.

Whitmore, R.C. 1977. Habitat partitioning in a community of passerine birds. Wilson Bull. 89:253-265.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21:213-251.

Wiens, J.A. 1974a. Habitat heterogeneity and avian community structure in North American grasslands. Am. Midl. Nat. 91:195-213.

Wiens, J.A. 1974b. Climatic instability and the 'ecological saturation' of bird communities in North American grasslands. Condor 76:385-400.

Wiens, J.A. 1981a. Scale problems in avian censusing. Studies in Avian Biology 6:513-521.

Wiens, J.A. 1981b. Single-sample surveys of communities: Are the revealed patterns real? Am. Nat. 117:90-98.

Wiens, J.A. and J.T. Rotenberry. 1981. Censusing and the evaluation of avian habitat occupancy. Studies in Avian Biology 6:522-531.

Williams, A.B. 1936. The composition and dynamics of a beech-maple climax community. Ecol. Monogr. 6:318-408.

Williams, C.B. 1964. Patterns in the Balance of Nature. Academic Press, N.Y. 324 pp.

Williamson, K. 1970. Birds and modern forestry. Bird Study 17:167-176.

Williamson, M. 1981. Island Populations. Oxford University Press, Oxford, G.B. 286 pp.

Willis, E.O. 1980. Species reduction in remanescent woodlots in southern Brazil. Proc. 17th Internat. Ornith. Congr.:783-786.

Willson, M.F. 1974. Avian community organization and habitat structure. Ecology 55:1017-1029.

Wray, R. II and R.C. Whitmore. 1979. Effects of vegetation of nesting success of Vesper Sparrows. Auk 96:802-804.

Wright, S.J. 1981. Intra-archipelago vertebrate distributions: The slope of the species-area relation. Am. Nat. 118:726-748.

Zar, J.H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J. 620 pp.

APPENDIX I

Ecological characteristics of bird species detected in 21 forests according to habitat use (E:edge, FF:facultative forest, OF:obligate forest), territory size, nesting stratum (G:ground, S:shrub, C:canopy, H:hole, O:other), foraging stratum (G:ground, S:shrub, C:canopy, T:trunk, O:other), migratory status (R:resident, SD:short-distance, LD:long-distance), regional abundance from 1980 Breeding Bird Surveys, Pearson correlation (r) between pairs per 30 minutes survey time and $\log(\text{forest area})$ where present and number of pairs detected regionally by point counts, 1980-81. Nomenclature follows the 34th supplement to the American Ornithologists' Union Checklist of North American Birds (Auk 99(3), 1982 Suppl.).

SPECIES	Habitat Use	Territory Size (ha)	Nesting Stratum	Foraging Stratum	Migratory Status	Regional Abundance (no.)	Pairs/30' - Log Area r (n)		Regional No. Pairs	
							1980	1981	1980	1981
Northern Goshawk	OF	>5	C	O	R	< 11	ISS ^d	ISS	1	1
Accipiter gentilis (Linnaeus)										
Red-shouldered Hawk	FP	>5	C	O	SD	< 11	.000(3)	.000(3)	3	3
Buteo lineatus (Gmelin)										
Broad-winged Hawk	OF	>5	C	O	LD	< 11	ISS	ISS	1	0
Buteo platypterus (Vieillot)										
Red-tailed Hawk	E	>5	C	O	SD	< 11	ISS	ISS	1	1
Buteo jamaicensis (Gmelin)										
American Kestrel	E	>5	H	O	SD	11-50	ISS	ISS	0	1
Falco sparverius Linnaeus										
Ruffed Grouse	FP	>5	C	G	R	< 11	.202(5)	---	6	1
Bonasa umbellus (Linnaeus)										
American Woodcock	E	2-5	C	G	SD	< 11	ISS	ISS	1	0
Scolopax minor Gmelin										
Mourning Dove	E	2-5	C	G	SD	> 50	-.660(9)	-.413(4)	19	9
Zenaidura macroura (Linnaeus)										
Black-billed Cuckoo	E	2-5	S	S	LD	< 11	-.521(4)	---	5	1
Coccyzus erythrophthalmus (Wilson)										
Barred Owl	OF	>5	H	C	R	< 11	ISS	ISS	0	1
Strix varia Barton										
Ruby-throated Hummingbird	E	2-5	C	S	LD	< 11	ISS	-.998*(3)	1	3
Archilochus colubris (Linnaeus)										
Yellow-bellied Sapsucker	FP	2-5	H	T	SD	11-50	.475(14)	.066(14)	27	28
Sphyrapicus varius (Linnaeus)										
Downy Woodpecker	FP	2-5	H	T	R	11-50	-.253(7)	-.688*(13)	9	17
Picoides pubescens (Linnaeus)										
Hairy Woodpecker	OF	>5	H	T	R	< 11	-.501(15)	-.581(10)	29	12
Picoides villosus (Linnaeus)										
Northern Flicker	FP	2-5	H	G	SD	11-50	-.533(12)	-.573(8)	21	14
Colaptes auratus (Linnaeus)										

.... 2

SPECIES	Habitat Use	Territory Size (ha)	Nesting Stratum	Foraging Stratum	Migratory Status	Regional Abundance (no)	Pairs/30' - Log Area $r(n)$		Regional No. Pairs	
							1980	1981	1980	1981
Pileated Woodpecker <u>Dryocopus pileatus</u> (Linnaeus)	PF	> 5	H	T	R	< 11	-.719*(8)	-.961*(8)	8	8
Eastern Wood-Pewee <u>Contopus virens</u> (Linnaeus)	PF	2-5	C	S	LD	11-50	.136(21)	-.109(21)	129	117
Least Flycatcher <u>Empidonax minimus</u> (Baird & Baird)	E	< 2	C	S	LD	11-50	.033(5)	.373(6)	38	36
Eastern Phoebe <u>Sayornis phoebe</u> (Latham)	PF	> 5	D	S	SD	11-50	ISS	ISS	2	1
Great Crested Flycatcher <u>Myiarchus crinitus</u> (Linnaeus)	PF	2-5	H	C	LD	11-50	.144(20)	.348(21)	91	83
Eastern Kingbird <u>Tyrannus tyrannus</u> (Linnaeus)	E	2-5	S	S	LD	> 50	-.632(6)	-.375(6)	9	9
Blue Jay <u>Cyanocitta cristata</u> (Linnaeus)	PF	2-5	C	S	R	11-50	.077(19)	.356(18)	67	67
American Crow <u>Corvus brachyrhynchos</u> Brehm	E	< 2	C	G	R	> 50	-.592*(20)	-.604*(15)	47	31
Black-capped Chickadee <u>Parus atricapillus</u> Linnaeus	PF	< 2	H	S	R	> 50	-.065(18)	-.020(20)	69	59
Red breasted Nuthatch <u>Sitta canadensis</u> Linnaeus	OF	2-5	H	T	R	11-50	-.424(4)	-.141(5)	15	13
White-breasted Nuthatch <u>Sitta carolinensis</u> Latham	PF	2-5	H	T	R	11-50	-.008(20)	.202(21)	54	47
Brown Creeper <u>Certhia americana</u> Bonaparte	OF	2-5	S	T	R	< 11	-.272(15)	-.413(11)	47	36
Winter Wren <u>Troglodytes troglodytes</u> (Linnaeus)	OF	2-5	C	S	SD	< 11	-.692(3)	.934(3)	12	10
Golden-crowned Kinglet <u>Regulus satrapa</u> Lichtenstein	OF	< 7	C	C	SD	< 11	ISS	ISS	2	1

...3

4.

SPECIES	Habitat Use	Territory Size (ha)	Nesting Stratum	Foraging Stratum	Migratory Status	Regional Abundance (no.)	Pairs/30' - Log Area $r_m(n)$			Regional No. Pairs	
							1980	1981	1981	1980	1981
<u>Veery</u>	OF	< 2	G	G	LD	11-50	.489(14)	.623*(13)		76	70
<u>Catharus fuscescens</u> (Stephens)											
<u>Swinson's Thrush</u>	OP	< 2	S	G	LD	< 11	ISS	ISS		1	2
<u>Catharus ustulatus</u> (Muttall)											
<u>Hermit Thrush</u>	OP	< 2	G	G ^a	SD	< 11	ISS	---		1	0
<u>Catharus guttatus</u> (Pallas)											
<u>Wood Thrush</u>	FF	< 2	S	G	LD	11-50	.017(13)	-.020(13)		62	55
<u>Hylocichla ustellina</u> (Gmelin)											
<u>American Robin</u>	E	< 2	C	G	SD	> 50	-.151(19)	-.221(20)		43	43
<u>Turdus migratorius</u> Linnaeus											
<u>Gray Catbird</u>	E	< 2	S	S	SD	11-50	ISS	---		1	0
<u>Dumetella carolinensis</u> (Linnaeus)											
<u>Brown Thrasher</u>	E	2-5	G	G	SD	11-50	-.998*(3)	ISS		3	1
<u>Toxostoma rufum</u> (Linnaeus)											
<u>Cedar Waxwing</u>	E	2-5	C	S	R	> 50	-.036(7)	.004(14)		17	129
<u>Bombicilla cedrorum</u> Vieillot											
<u>European Starling</u>	E	< 2	H	G	R	> 50	ISS	-.885(13)		3	5
<u>Sturnis vulgaris</u> Linnaeus											
<u>Warbling Vireo</u>	E	2-5	C	C	LD	11-50	-.954*(5)	-.829(5)		5	5
<u>Vireo gilvus</u> (Vieillot)											
<u>Red-eyed Vireo</u>	FF	< 2	C	C	LD	11-50	.620*(20)	.426(20)		128	113
<u>Vireo olivaceus</u> (Linnaeus)											
<u>Tennessee Warbler</u>	FF	< 2	G	S	LD	< 11	---	ISS		0	2
<u>Vermivora peregrina</u> (Wilson)											
<u>Nashville Warbler</u>	E	< 2	G	S	LD	< 11	-.517(3)	-.200(5)		6	8
<u>Vermivora ruficapilla</u> (Wilson)											
<u>Northern Parula</u>	OF	< 2	C	C	LD	< 11	---	ISS		0	1
<u>Parula americana</u> (Linnaeus)											

SPECIES	Habitat Use	Territory Size (ha)	Nesting Stratum	Foraging Stratum	Migratory Status	Regional Abundance (no.)	Pairs/30' - Log Area $r(n)$	Regional No. Pairs 1980	Regional No. Pairs 1981
Yellow Warbler <u>Dendroica petechia</u> (Linnaeus)	E	< 2	S	S	LD	11-50	-.806(4)	5	4
Chestnut-sided Warbler <u>Dendroica pensylvanica</u> (Linnaeus)	E	< 2	S	S	LD	< 11	-.392(4)	7	5
Magnolia Warbler <u>Dendroica magnolia</u> (Wilson)	OF	< 2	S	S	LD	< 11	.635(3)	2	6
Black-throated Blue Warbler <u>Dendroica caerulescens</u> (Gmelin)	OF	< 2	S	S	LD	< 11	ISS	2	3
Black-throated Green Warbler <u>Dendroica virens</u> (Gmelin)	OF	< 2	C	C	LD	< 11	ISS	1	1
Blackburnian Warbler <u>Dendroica fusca</u> (Muller)	OF	< 2	C	C	LD	< 11	.990(3)	5	5
Pine Warbler <u>Dendroica pinus</u> (Wilson)	OF	< 2	C	C	SD	< 11	ISS	3	2
Blackpoll Warbler <u>Dendroica striata</u> (Forster)	OF	< 2	S	C	LD	< 11	---	0	1
Black-and-white Warbler <u>Mniotilta varia</u> (Linnaeus)	OF	2-5	C	T	LD	11-50	-.730(4)	5	12
American Redstart <u>Setophaga ruticilla</u> (Linnaeus)	OF	< 2	S	S	LD	< 11	-.467(4)	10	5
Ovenbird <u>Seiurus aurocapillus</u> (Linnaeus)	OF	< 2	C	G	LD	11-50	.727*(12)	101	123
Northern Waterthrush <u>Seiurus noveboracensis</u> (Gmelin)	OF	2-5	G	G	LD	< 11	-.091(5)	17	22
Mourning Warbler <u>Opornis philadelphia</u> (Wilson)	E	< 2	C	C	LD	< 11	-.573(7)	9	8
Common Yellowthroat <u>Geothlypis trichas</u> (Linnaeus)	E	< 2	C	S	SD	> 50	-.329(10)	16	19

... 5

SPECIES	Habitat Use	Territory Size (ha)	Nesting Stratum	Foraging Stratum	Migratory Status	Regional Abundance (no.)	Pairs/30' - Log Area r (n)	1980	1981	1980	1981	Regional No. Pairs
Canada Warbler <i>Vireo canadensis</i> (Linnaeus)	OF	< 2	C	C	LD	< 11	ISS	---	---	4	0	0
Wilson's Warbler <i>Vireo gilvus</i> (Linnaeus)	OF	2-5	C	C	LD	11-50	.579(9)	.567(10)	38	51		
Scarlet Tanager <i>Piranga olivacea</i> (Gmelin)	FF	2-5	C	C	LD	> 50	.346(20)	.212(20)	92			
Rose-breasted Grosbeak <i>Phainopepla nitens</i> (Linnaeus)	FF	2-5	C	C	LD	11-50	-.243(7)	-.773*(7)	11	13		
Indigo Bunting <i>Passerina cyanea</i> (Linnaeus)	E	2-5	S	S	LD	> 50	-.923(3)	-.551(9)	3	14		
Chipping Sparrow <i>Spizella passerina</i> (Bechstein)	E	< 2	S	G	SD	> 50	-.455(15)	-.460(18)	52	44		
Song Sparrow <i>Melospiza melodia</i> (Wilson)	E	< 2	G	S	SD	11-50	-.474(10)	.037(10)	73	28		
White-throated Sparrow <i>Zonotrichia albicollis</i> (Gmelin)	E	< 2	G	G	SD	> 50	-.389(5)	-.947(3)	7	3		
Bobolink <i>Dolichonyx oryzivorus</i> (Linnaeus)	E	< 2	G	G	LD	> 50	-.473(17)	-.759*(15)	45	17		
Red-winged Blackbird <i>Agelaius phoeniceus</i> (Linnaeus)	E	< 2	S	S	SD	> 50	-.573*(20)	-.625*(19)	68	38		
Common Grackle <i>Quiscalus quiscula</i> (Linnaeus)	E	< 2	C	C	SD	> 50	-.218(21)	-.056(21)	72	72		
Brown-headed Cowbird <i>Molothrus ater</i> (Boddaert)	E	< 2	O	G	SD	11-50	-.288(17)	-.450(16)	37	33		
Northern Oriole <i>Icterus galbula</i> (Linnaeus)	E	2-5	C	C	LD	11-50	ISS	-.830(5)	1	7		
Purple Finch <i>Cardinalis purpureus</i> (Gmelin)	FF	2-5	C	S	R	> 50	-.000(20)	-.090(19)	67	47		
American Goldfinch <i>Carduelis tristis</i> (Linnaeus)	E	2-5	S	S	R	> 50	ISS	---	2	0		
House Sparrow <i>Passer domesticus</i> (Linnaeus)	E	< 2	H	G	R	> 50	ISS	---	2	0		

† Insufficient sample size for analysis

* $p < .05$

APPENDIX II

Habitat profiles for forests sampled in 1980.

HABITAT PROFILES, 1980. Entries are mean ($\pm$ 1 SD) where appropriate.

Forest Size (ha)	Tree Stratum		Shrub Stratum		Ground Stratum		Tree Density ₂ (No/250 m ²)	No. Trees by Diameter (cm)			
	Total	Per Plot	Total	Per Plot	Total	Per Plot		8-12	12-20	20-36	>36
3	14	6.5 (1.6)	25	11.6 (2.6)	16	5.6 (1.5)	19.7 (8.4)	3.0 (1.7)	3.1 (1.1)	1.3 (1.0)	0.6 (0.7)
4	12	5.5 (1.8)	18	7.3 (1.6)	13	3.3 (1.3)	19.2 (6.5)	2.5 (1.5)	2.1 (1.5)	2.5 (1.5)	0.9 (0.8)
5	17	7.4 (1.5)	25	12.0 (2.6)	21	5.0 (1.3)	17.6 (8.0)	2.1 (1.9)	2.9 (2.1)	2.6 (1.6)	1.1 (0.8)
8	12	5.6 (1.8)	18	5.9 (1.9)	12	4.1 (1.9)	11.5 (4.3)	0.8 (1.0)	1.5 (1.4)	1.6 (1.1)	4.4 (2.4)
9	8	3.9 (1.1)	24	9.3 (3.4)	18	4.9 (1.6)	18.4 (6.6)	0.8 (0.9)	1.4 (1.2)	4.4 (1.1)	2.3 (2.1)
13	16	8.5 (1.4)	24	9.5 (3.4)	26	7.8 (2.5)	22.9 (8.4)	4.0 (1.5)	3.1 (1.2)	0.8 (0.9)	0
14	19	7.3 (2.0)	13	6.0 (1.5)	14	3.9 (1.5)	21.9 (6.1)	1.8 (1.4)	1.6 (1.2)	3.4 (1.6)	1.3 (1.0)
16	19	7.9 (3.4)	24	10.5 (2.6)	25	7.3 (2.1)	22.2 (13.3)	3.0 (2.3)	1.8 (1.7)	2.5 (2.2)	0
18	12	5.6 (2.0)	18	7.3 (2.9)	19	6.4 (1.9)	23.0 (10.3)	2.5 (3.0)	2.9 (1.7)	2.1 (1.4)	0.4 (0.7)
22	14	6.9 (2.2)	25	12.1 (1.6)	18	6.6 (1.7)	48.0 (27.8)	4.9 (1.1)	2.5 (1.3)	0.5 (1.1)	0.1 (0.4)
25	20	7.3 (2.3)	30	11.5 (3.7)	14	5.3 (1.4)	22.8 (9.0)	2.6 (1.8)	2.9 (1.6)	2.4 (1.6)	0.1 (0.4)
27	17	6.1 (1.1)	31	12.6 (3.2)	16	5.8 (1.5)	15.2 (9.5)	3.0 (2.3)	2.5 (1.8)	1.4 (1.2)	1.0 (1.1)
30	22	7.0 (3.6)	33	11.4 (4.2)	16	3.9 (2.2)	19.9 (10.6)	2.6 (1.9)	1.8 (1.8)	2.8 (1.7)	0.6 (0.9)
44	18	7.8 (1.3)	29	9.6 (2.1)	24	5.5 (2.7)	18.5 (5.3)	2.3 (0.9)	2.4 (1.8)	2.5 (1.4)	0.9 (0.8)
58	16	7.8 (3.2)	30	10.8 (3.6)	22	5.8 (1.3)	19.7 (7.7)	3.4 (2.3)	1.8 (1.1)	2.0 (1.6)	1.5 (1.6)
79	20	8.1 (2.5)	28	9.0 (2.5)	16	4.9 (1.1)	17.2 (4.8)	2.9 (1.7)	2.6 (1.6)	1.9 (1.5)	0.6 (0.7)
116	17	6.0 (2.0)	23	6.9 (4.6)	15	4.1 (2.2)	20.7 (6.4)	1.8 (1.2)	2.5 (2.0)	2.3 (2.3)	1.5 (1.1)
220	18	6.3 (3.2)	20	5.6 (2.6)	11	3.0 (1.4)	22.6 (9.5)	2.8 (1.6)	2.9 (1.8)	2.1 (1.5)	0.4 (0.5)
680	15	6.0 (3.0)	25	10.4 (4.9)	19	5.6 (2.2)	24.1 (11.9)	3.0 (1.9)	1.4 (0.9)	3.8 (1.7)	1.0 (0.8)
3350	17	6.0 (2.7)	21	6.3 (1.8)	12	3.3 (1.0)	28.7 (17.4)	2.3 (2.1)	2.4 (1.8)	2.9 (1.9)	0.5 (0.5)
7620	19	6.9 (2.2)	21	7.3 (1.8)	20	4.6 (1.8)	13.0 (6.6)	1.8 (1.3)	2.6 (1.8)	2.1 (1.1)	1.5 (1.7)

Continued...

HABITAT PROFILES, 1980 ... continued

Forest Size (ha)	Canopy Height (m)	Herb Height (m)	Foliage Cover (20% cover class)					Canopy Closure (%)
			0-1 m	1-3 m	3-5 m	5-9 m	>9 m	
3	13.8 (1.8)	0.9 (0.6)	5.0 (0.0)	3.9 (1.6)	4.0 (1.5)	4.4 (1.4)	3.9 (1.1)	88.6 (7.3)
4	18.4 (5.3)	0.3 (0.3)	3.8 (0.7)	4.6 (1.2)	3.6 (1.1)	4.5 (1.1)	4.0 (1.3)	93.6 (3.6)
5	17.0 (1.9)	0.4 (0.2)	3.4 (0.9)	3.6 (1.1)	3.6 (1.2)	3.9 (1.1)	3.9 (0.8)	91.9 (5.2)
8	20.1 (4.4)	0.3 (0.1)	4.4 (1.3)	3.4 (1.2)	3.6 (0.9)	4.3 (0.7)	4.4 (1.4)	87.6 (16.3)
9	19.0 (2.0)	0.4 (0.2)	5.0 (0.0)	2.8 (1.3)	2.6 (1.8)	2.9 (1.0)	4.5 (1.4)	92.5 (3.9)
13	14.3 (3.7)	0.4 (0.2)	4.9 (1.1)	3.5 (1.9)	4.3 (1.6)	4.3 (1.5)	3.9 (1.6)	75.8 (18.9)
14	19.9 (3.8)	0.3 (0.1)	2.8 (1.2)	2.1 (0.6)	2.5 (0.5)	4.0 (1.1)	3.9 (1.0)	93.4 (3.2)
16	16.4 (2.6)	0.4 (0.2)	4.4 (0.5)	2.9 (0.8)	3.0 (1.1)	3.9 (1.5)	3.9 (1.1)	77.5 (31.8)
18	17.5 (3.5)	0.8 (0.2)	4.6 (0.5)	3.1 (0.6)	3.3 (0.9)	4.4 (1.5)	4.5 (1.1)	88.1 (10.7)
22	13.3 (3.1)	0.7 (0.4)	4.9 (0.4)	4.6 (0.7)	4.8 (0.5)	4.5 (1.1)	3.6 (1.5)	88.1 (5.8)
25	18.6 (2.4)	0.9 (0.3)	4.9 (0.4)	3.8 (0.9)	3.8 (1.5)	4.1 (0.8)	4.9 (0.4)	91.5 (6.9)
27	11.6 (7.1)	0.6 (0.4)	5.0 (0.0)	3.5 (0.9)	3.5 (1.2)	3.6 (1.2)	2.5 (1.6)	72.4 (23.2)
30	16.3 (2.7)	0.3 (0.2)	3.6 (1.7)	2.8 (0.7)	3.0 (0.5)	3.6 (0.7)	4.1 (1.2)	90.0 (12.9)
44	18.1 (3.9)	0.4 (0.3)	3.5 (1.5)	3.3 (1.6)	3.4 (0.9)	4.6 (1.2)	4.4 (0.7)	87.1 (15.1)
58	16.1 (4.3)	0.4 (0.2)	3.9 (0.8)	3.3 (0.9)	4.4 (1.2)	4.6 (0.9)	4.0 (1.1)	92.3 (5.9)
79	14.1 (4.2)	0.2 (0.2)	4.1 (0.6)	3.4 (0.7)	4.5 (1.2)	4.8 (1.2)	4.3 (1.7)	73.9 (28.9)
116	20.9 (3.1)	0.4 (0.2)	4.1 (1.1)	3.1 (1.5)	3.1 (1.2)	4.1 (1.6)	4.8 (0.9)	93.4 (2.1)
220	16.6 (3.6)	0.3 (0.3)	3.5 (1.1)	3.6 (1.3)	3.5 (1.2)	4.1 (1.5)	4.3 (0.9)	85.6 (11.6)
680	20.4 (3.7)	0.6 (0.3)	4.4 (1.4)	3.6 (1.6)	3.4 (0.5)	4.1 (1.9)	5.0 (0.0)	93.9 (4.4)
3350	17.6 (4.0)	0.3 (0.3)	3.6 (0.9)	2.9 (0.6)	3.1 (0.8)	3.6 (0.9)	4.5 (0.8)	83.3 (23.3)
7620	16.8 (4.9)	0.5 (0.3)	4.3 (1.7)	3.6 (1.7)	3.8 (1.6)	4.4 (1.3)	4.0 (1.1)	79.6 (12.1)

Continued ...

HABITAT PROFILES, 1980 ... continued

Forest Size (ha)	Bare	Ground Cover (z/250 m ²)	Water	Canopy Gaps (% Interplot) Distance	Snags (m apart)	Fallen Trees (m apart)
		Mitter				
		Rock				
3	8.1 (7.0)	91.8 (7.0)	0	4.0 (11.3)	18.0 (4.2)	18.5 (11.2)
4	14.4 (9.8)	85.6 (9.8)	0	0	13.4 (20.2)	12.3 (3.7)
5	15.0 (12.0)	85.0 (12.0)	0	0.9 (2.5)	27.4 (27.0)	37.3 (24.9)
8	8.4 (4.4)	91.9 (4.6)	0	0.5 (1.4)	8.4 (23.7)	14.4 (14.5)
9	5.6 (1.8)	94.4 (1.8)	0	4.8 (5.8)	35.6 (68.9)	24.8 (30.2)
13	10.3 (8.9)	89.3 (8.6)	0	3.5 (6.0)	49.5 (49.5)	35.4 (17.3)
14	10.3 (12.3)	89.4 (12.1)	0	4.4 (8.5)	36.3 (42.0)	27.3 (21.5)
16	16.3 (11.3)	83.8 (11.3)	0	18.2 (32.4)	32.0 (27.1)	42.0 (52.1)
18	7.0 (2.5)	93.1 (2.6)	0	0	29.6 (20.2)	20.8 (16.5)
22	7.5 (5.3)	92.5 (5.3)	0	4.1 (8.3)	35.6 (38.7)	11.9 (4.6)
25	10.0 (4.6)	90.0 (4.6)	0	1.1 (3.2)	62.0 (61.2)	26.6 (17.7)
27	6.3 (4.4)	91.9 (9.2)	1.9 (5.3)	15.0 (12.8)	42.8 (82.6)	17.3 (10.1)
30	11.3 (11.8)	78.8 (15.5)	10.0 (14.1)	4.6 (5.9)	55.1 (71.3)	37.0 (18.2)
44	13.4 (11.9)	86.6 (11.9)	0	0	61.0 (45.0)	18.9 (4.9)
58	18.8 (8.3)	77.5 (11.0)	3.8 (7.4)	11.9 (15.6)	52.0 (65.0)	22.3 (10.9)
79	6.0 (1.9)	73.3 (23.4)	20.6 (23.4)	4.0 (7.2)	49.5 (56.0)	48.8 (43.3)
116	5.0 (0.0)	95.0 (0.0)	0	0.4 (1.1)	55.3 (53.7)	14.8 (12.5)
220	4.4 (3.2)	79.8 (23.7)	13.6 (21.9)	0	70.6 (77.8)	14.3 (6.2)
680	5.0 (0.0)	95.0 (0.0)	0	0.6 (1.8)	74.1 (80.0)	13.6 (5.0)
3350	5.0 (0.0)	91.4 (6.8)	0	11.9 (21.7)	66.4 (86.4)	40.3 (39.4)
7620	5.3 (2.8)	81.9 (10.0)	13.1 (10.3)	1.0 (1.4)	77.2 (84.9)	45.1 (75.0)

APPENDIX III

Bird numbers and locations for forests, 1979-81.
Bird entries based on 30 minutes survey time per
census point per year; bird entries in parentheses
based on total survey time per forest per year.

Forest Site (ha)	1979	No. Species 1980	Per Forest		No. Pairs * 1981	No. Census Points	National Topographic System		National Air Photo No.
			1981	1980			Map No.	Co-ordinates	
1		12 (16)	19 (21)	22 (31)	24 (31)	1	318/8	24-13	A31191-82
4		17 (19)	12 (16)	20 (26)	14 (19)	1	318/8	24-96	A31191-192
5		19 (22)	13 (17)	26 (32)	19 (24)	1	318/8	25-5-00	A31191-72
8		15 (17)	16 (20)	21 (23)	21 (26)	1	318/8	27-03	A31191-37
9		10 (14)	13 (19)	15 (20)	19 (26)	1	318/1	01-15.5	A31186-30
13		23 (24)	18 (19)	49 (53)	31 (37)	2	318/8	27-99.5	A31191-59
14	19	22 (25)	20 (23)	40 (47)	37 (43)	2	318/2	29-5-00.5	A31190-134
16		25 (25)	27 (27)	69 (73)	68 (74)	3	318/1	25-5-98.5	A31191-72
18		26 (28)	25 (25)	67 (73)	59 (66)	3	318/8	90-5-13.5	A31186-44
22		24 (27)	25 (27)	52 (62)	50 (57)	3	318/8	27-5-08.5	A31191-53
25	22	23	21	89	67	4	318/4	06-37	A31007-112
27	30	34	31	118	89	4	318/8	27-04	A31191-55
30	30	31	26	105	83	4	318/8	28-5-06.5	A31191-53
44		27	29	83	93	4	318/8	26-5-00.5	A31191-72
58		27	31	113	102	5	318/8	28-5-02.5	A31191-57
79		33	41	128	137	5	318/8	30-5-07	A31190-139
116		33	32	150	141	6	318/4	06-29	A31194-31
220		28	31	122	116	6	318/8	38-5-11.5	A31190-14
680		29	29	139	128	6	318/4	02-30	A31194-107
3350		40	36	163	137	6	318/8	30-5-11.5	A31190-143
7620		30	31	113	120	6	318/8	21-5-92	A31191-196

* Not recorded for 1979.

Forest Size (ha)	1979			No. Species			Per Census Point			No. Pairs *		
	Mean ± 1SE			1980			1981			1980		
	Mean	±	1SE	Mean	±	1SE	Mean	±	1SE	Mean	±	1SE
3				12	—	—	19	—	—	22 ^a	—	24
4				17	—	—	12	—	—	20	—	14
5				19	—	—	13	—	—	26	—	19
8				15	—	—	16	—	—	21	—	21
9				10	—	—	14	—	—	15	—	19
13	14.5	1.5		19.0	0.0		13.5	1.5		25.0	1.0	16.0
14				15.0	1.0		14.5	3.5		21.5	0.5	19.5
16				18.0	1.0		17.3	3.5		24.7	1.7	24.7
18				17.7	0.7		16.3	1.4		23.7	1.2	20.7
22	14.0	1.2		15.7	0.9		16.3	0.9		18.3	2.4	17.3
25	14.5	1.3		15.0	0.4		12.8	1.3		23.3	1.7	16.8
27	18.8	2.1		24.0	1.7		18.8	1.1		30.3	2.2	23.0
30	14.8	2.3		19.8	2.1		16.3	0.9		27.8	1.6	21.0
44				17.3	1.5		17.5	1.5		22.0	1.4	25.0
58				18.2	0.8		16.6	0.9		24.6	1.5	20.8
79				19.6	0.4		22.6	1.2		27.2	0.5	28.8
116				18.3	0.7		17.2	1.2		25.5	1.2	23.8
220				15.8	1.3		15.3	1.3		21.3	1.3	19.7
680				16.2	1.6		15.5	0.7		24.0	2.2	21.5
3350				19.3	0.9		17.2	1.9		27.8	0.8	23.0
7620				14.2	1.6		14.2	0.6		19.7	1.1	20.0

* Not recorded for 1978.

APPENDIX IV

Multiple regression analyses for bird species number by ecological class on size (Log Area) and habitat heterogeneity (HH) of 21 forests, 1980-81.

HABITAT USE

Class	Year	P [#]	R ² (%) ^c	Y Intercept	Environmental Variable	Partial Regression Coefficient, b	t ^e	Standard b
Edge	1980	5.52*	38	18.4	HH(Ground species)	-12.4	-3.300*	-.759
					HH(Tree species)	-8.1	2.261*	.520
Facultative Forest	1981	7.64*	46	20.0	HH(Ground species)	-14.2	-3.909*	-.840
					HH(Tree species)	8.0	2.318*	.498
Facultative Forest	1980	18.07*	67	2.7	HH(Forest structure)	6.3	4.158*	.572
					Log Area	1.4	3.654*	.503
		11.52*	56	1.4	HH(Total Habitat)	2.0	2.957*	.495
					Log Area	1.2	2.460*	.412
Obligate Forest	1981	11.60*	38	7.6	Log Area	1.4	3.407*	.616
Obligate Forest	1980	71.31*	79	-1.3	Log Area	3.8	8.445*	.889
	1981	46.5*	84	-5.9	Log Area	3.7	8.205*	.810
					HH(Shrub species)	6.0	2.625*	.259
		44.45*	83	-6.3	Log Area	3.6	7.414*	.780
					HH(All species)	2.2	2.439*	.256

#P - ratio for multiple regression

c - Coefficient of determination

e - ratio for partial regression coefficient

* p < .05

TERRITORY SIZE (ha)

Class	Year	F [#]	R ² (%) ^c	Y Intercept	Environmental Variable	Partial Regression Coefficient, b	t ^e	Standard b
<2	1980	11.20*	37	8.5	Log Area	2.4	3.347*	.609
	1981	14.93*	44	8.9	Log Area	2.3	3.864*	.663
2 - 5	1980	9.55*	63	9.6	HH(Tree species)	8.7	3.297*	.644
					Log Area	1.4	2.783*	.456
	1981	11.16*	37	8.7	HH(Ground species)	-5.9	-2.261*	-.415
					Log Area	2.3	3.341*	.608
>5	1980	15.67*	45	0.5	Log Area	0.8	3.958*	.672
	1981	4.79*	20	0.4	Log Area	0.6	2.190*	.449

F - ratio for multiple regression

c Coefficient of determination

e t - ratio for partial regression coefficient

* p < .05

NESTING STRATUM

Class	Year	P [#]	R ² (%)	Y Intercept	Environmental Variable	Partial Regression Coefficient, b	t [*]	Standard b
Ground	1980	4.99*	36	5.1	HH(Tree species)	9.4	3.127*	.732
					HH(Ground species)	-7.0	-2.217*	-.519
	1981	10.25*	35	2.0	Log Area	1.6	3.202*	.592
Shrub	1980	7.58*	29	3.1	Log Area	1.0	2.754*	.534
	1981	6.61*	54	4.8	Log Area	1.1	3.338*	.575
					HH(Ground species)	-4.2	-2.671*	-.465
					HH(Forest structure)	2.9	2.254*	.382
Canopy	1980	28.98*	60	6.9	Log Area	1.8	5.383*	.777
	1981	23.56*	55	6.7	Log Area	2.0	4.854*	.744
Hole	1980	9.95*	53	1.6	Log Area	1.0	3.057*	.502
					HH(Forest Structure)	3.5	2.744*	.451
		9.47*	51	0.3	HH(Total Habitat)	1.3	2.623*	.463
					Log Area	0.8	2.294*	.405
	1981	None significant						

#P - ratio for multiple regression

c - Coefficient of determination

*t - ratio for partial regression coefficient

* p < .05

FORAGING STRATUM

Class	Year	F ^a	R ² (%) ^c	Y Intercept	Environmental Variable	Partial Regression Coefficient, b	t ^b	Standard b
Ground	1980	4.91*	21	4.9	HH(Forest structure)	-5.3	2.216*	.453
	1981	4.96*	36	6.6	HH(Shrub species)	7.8	3.058*	.656
					HH(Ground species)	-4.8	-2.108*	-.452
Shrub	1980	None significant						
	1981	14.83*	68	8.5	Log Area	2.1	4.860*	.702
					HH(Ground species)	-6.2	-3.181*	-.464
Canopy	1980	11.96*	39	3.3	HH(Forest structure)	4.3	2.642*	.375
	1981	15.72*	45	3.2	Log Area	0.9	3.459*	.622
					Log Area	1.0	3.964*	.673
Trunk	1980	29.32*	77	0	Log Area	1.5	6.630*	.766
					HH(Forest structure)	2.4	2.771*	.320
		29.72*	77	-1.0	Log Area	1.3	5.677*	.692
Other	1981	8.40*	48	-0.6	HH(Total Habitat)	0.9	2.818*	.343
					HH(Shrub species)	4.4	2.475*	.436
					Log Area	0.9	2.462*	.434
Other	1980	20.52	52	-0.5	HH(All species)	2.1	3.015*	.569
	1981	7.00*	27	-0.2	HH(Total Habitat)	1.2	2.285*	.423
					Log Area	0.8	2.168*	.401
Other	1980	20.52	52	-0.5	Log Area	0.5	4.530*	.721
	1981	7.00*	27	-0.2	Log Area	0.3	2.646*	.519

F^a - ratio for multiple regression

c - Coefficient of determination

t^b - ratio for partial regression coefficient

* p < .05

MIGRATORY STATUS

Class	Year	F ^a	R ² (%) ^c	Y Intercept	Environmental Variable	Partial Regression Coefficient, b	t ^b	Standard b
Resident	1980	9.07*	32	5.9	Log Area	1.2	3.011*	.568
	1981	8.36*	31	5.9	Log Area	1.2	2.891*	.553
Short- Distance	1980	4.88*	20	4.9	HH(Forest structure)	4.1	2.209	.452
	1981	None significant						
Long- Distance	1980	21.40*	79	7.0	Log Area	3.2	6.010*	.739
					HH(Tree species)	7.8	2.853*	.418
					HH(Ground species)	47.1	-2.636*	-.363
	1981	32.15*	63	5.1	Log Area	3.5	5.670*	.793

F^a - ratio for multiple regressionR² - Coefficient of determinationt^b - ratio for partial regression coefficient

* p < .05

REGIONAL ABUNDANCE (No. from Breeding Bird Surveys)

Class	Year	F ^a	R ² (%) ^c	Y Intercept	Environmental Variable	Partial Regression Coefficient, b	t ^b	Standard b
<11	1980	77.83*	90	-1.7	Log Area HH(Tree species)	2.7	10.150*	.853
						2.6	2.193*	.184
		81.33*	90	-1.8	Log Area HH(Forest structure)	2.9	12.013*	.904
						2.2	2.393*	.180
11 - 50	1981	28.05*	60	-0.1	Log Area	2.8	5.297*	.772
	1980	21.36*	53	7.2	Log Area	2.7	4.621*	.728
	1981	31.12*	62	7.2	Log Area	3.0	5.579*	.788
	1980	None significant						
>50	1981	5.63*	23	15.3	HH(Ground species)	-5.2	-2.373*	-.478

F^a - ratio for multiple regressionC^c - Coefficient of determinationt^b - ratio of partial regression coefficient

* p < .05

END

3 1 H 1 0 H 8 5

FIN