AN ECOLOGICAL ANALYSIS OF FOREST EDGE SUITABILITY FOR AVIAN POPULATIONS

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ABSTRACT

AN ECOLOGICAL ANALYSIS OF FOREST EDGE SUITABILITY FOR AVIAN POPULATIONS

By

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Observations of twenty-one species of open-nesting passerines breeding in contiguous field and forest habitats at Rose Lake Wildlife Research Area, Michigan, were made during 1974 and 1975. Data were collected on nest dispersion and fledging success in relation to the field-forest edge. Losses of eggs or nestlings were attributed to predation, inclement weather, Brown-headed Cowbird parasitism, nest desertion, hatching failure, or adult death.

Nests were not evenly distributed on the area, but had a definite pattern. Over one-half of the nests were found within 15 m of the habitat discontinuity. Seventy-five percent of the nests belonged to birds characteristic of mixed breeding habitats, i.e., birds requiring open areas with dense cover for nesting and feeding and elevated singing and observation perches. These birds also accounted for the increase in species nesting near edges. Nest dispersion seemed to be influenced by the openness of the forest and the amount of woody vegetation in the field.

Based on Kendall rank and partial rank correlation tests, numbers of nests were found to be negatively correlated with distance from a habitat discontinuity. Correlation between fledging success and distance from the edge was positive and highly significant. Of the several mortality factors investigated, predation was found to be the major one influencing the observed trend in fledging success. Although losses due to cowbird parasitism were also significantly correlated with fledging success, number of nests, and distance from the edge in the same manner as predation loss, its influence was not as important. The increased predation was attributed primarily to a functional response to higher numbers of nests and a greater activity of potential nest predators in the vicinity of the habitat discontinuities.

Results indicated that habitat suitability decreased with increasing numbers of nests toward the narrow field-forest edges. Although such abrupt habitat discontinuities did attract a variety and abundance of birds characteristic of habitats with mixed life-form, they seemed to function as ecological traps for birds nesting in their vicinity. Ironically, the cowbird was also a victim of the increased predation rate. As these man-made forest edges are of recent origin, they are perhaps unrepresentative of the ecological niche in which these species evolved, and thus they may be poorly adapted to cope with the increased nest predation.

AN ECOLOGICAL ANALYSIS OF FOREST EDGE SUITABILITY FOR AVIAN POPULATIONS

By

John Edward Gates

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INTRODUCTION

The ecological relationships which exist at the natural junction of different plant communities form the basis of the edge effect concept. Simply stated, it is a tendency for increased variety and density of organisms at the junction of different plant communities (Odum 1971). This phenomenon is due in part to the presence of species characteristic of each of the overlapping communities plus species inhabiting only the region of overlap. These edge species may find habitats at the community junction not present in either community alone, or require two or more adjacent communities differing greatly in structure.

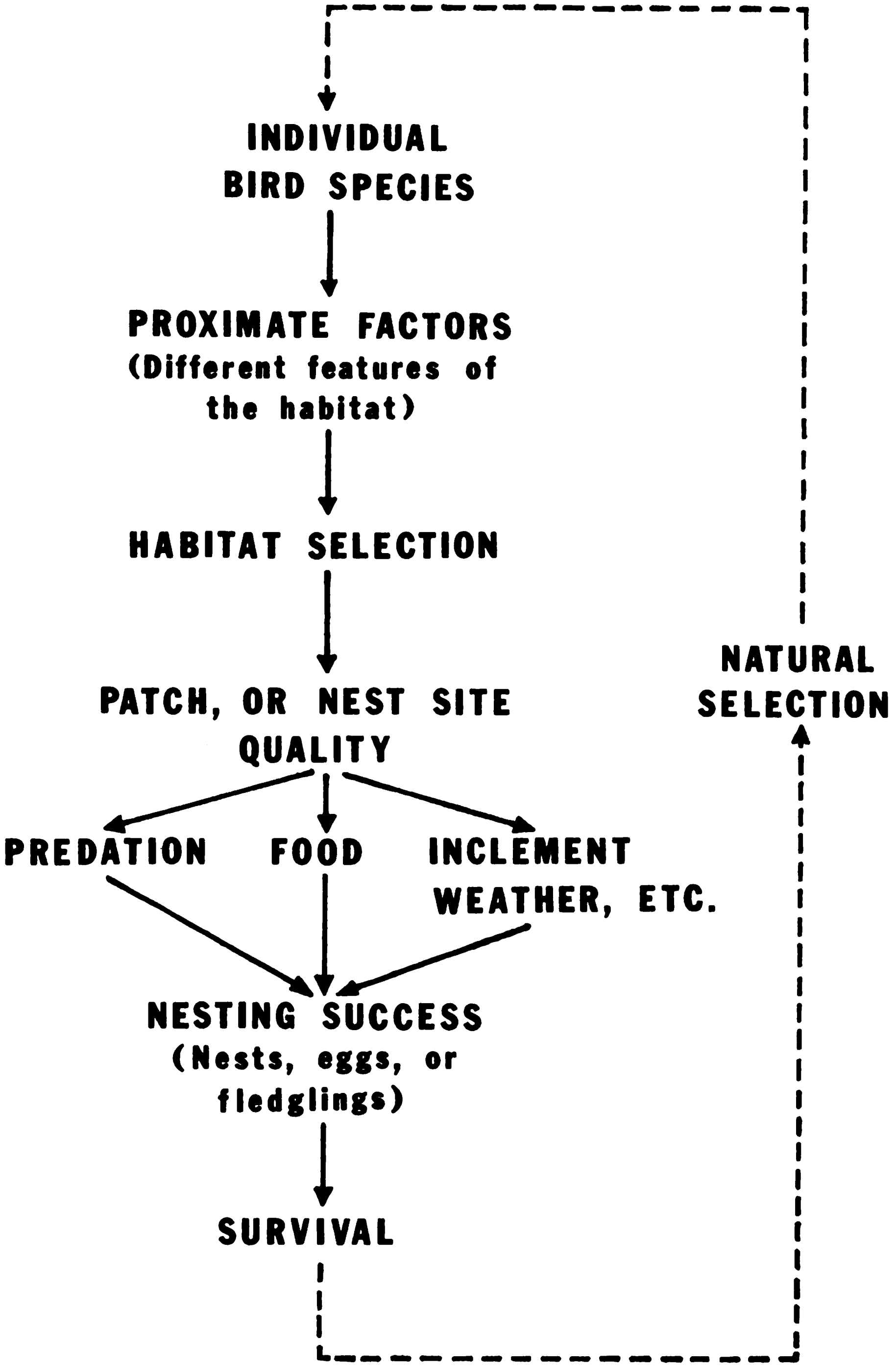
The idea of bringing different vegetation types into close association through habitat manipulation has also become an important principle to the wildlife biologist. It is called interspersion, and the borderline, considered so favorable to game, is referred to as edge (Leopold 1933, Allen 1962, Dasmann 1964). It is generally assumed that the close association of diverse plant communities results in optimum conditions for reproduction and survival of certain wildlife species.

Although many terrestrial vertebrates of economic importance are considered to be edge species or utilize edges to a large extent, the concept of edge effect is especially applicable to avian populations. Studies have shown that greater numbers of avian species exist in areas of mixed habitat, and consequently more edge, than in generally uniform vegetation (Johnston 1947, Johnston and Odum 1956). Other investigators have demonstrated a greater density of birds in mixed habitats, or in the margin, as compared with the interior of large tracts of uniform vegetation (Lay 1938, Good and Dambach 1943, Edeburn 1947, Johnston 1970). Nest densities have also been shown to be affected by proximity to habitat discontinuities. Beecher (1942) attempted to locate all bird nests on an area containing several marsh and upland communities. He found the greatest density of nests in sample plots containing two or more community types, and consequently more edge.

Because of the importance of the edge effect concept to the field of wildlife management and the increasing need and demand for the management of nongame species, this study was initiated to evaluate the effect of habitat discontinuities on avian populations. The main objectives of the research were to investigate the spatial distribution patterns of bird nests in relation to habitat discontinuities, and to determine some of the mechanisms operating at such boundaries which might influence their suitability as breeding habitat for avian populations.

If we assume that the conceptual model presented in Fig. 1 is correct, then one of the most important components determining the suitability of a habitat is nesting success rather than size of territory, population density, or any other factor considered alone (see Dow 1969, Fretwell 1968, 1969, Nettleship 1972), i.e., those individuals selecting a better quality patch or nest site will have increased nesting success over those selecting a poorer quality one. Nettleship (1972) has indicated that, if habitat selection is an adaptive activity, then the only measure of habitat suitability during the breeding season is nesting success and the degree of productivity attained in it. Other researchers have presented data supporting the view of increased nesting success in optimum habitats (Krebs 1971, Heppleston 1972, Robertson 1972, Holm 1973).

Fig. 1. A model representing the important components determining whether or not a bird will be successful in a certain patch of vegetation.


INDIVIDUAL BIRD SPECIES
PROXIMATE FACTORS (Different features of the habitat)
HABITAT SELECTION
PATCH, OR NEST SITE QUALITY
PREDATION
FOOD
INCLEMENT WEATHER, ETC.
NESTING SUCCESS (Nests, eggs, or fledglings)
SURVIVAL
NATURAL SELECTION

Although previous studies have primarily been concerned with overall success in relatively uniform habitats rather than with the effect of habitat discontinuities on nest dispersion and nesting success within such habitats, the same logic should be applicable to the latter situation. Here I appraise the suitability of narrow man-made forest edges for open-nesting passerines breeding in contiguous grassy field and oak-hickory forest habitats in central Michigan.

MATERIALS AND METHODS

Field Studies

Study sites were surveyed and gridded with wire-stake flags set at 50 m intervals using the cardinal points as a reference. The wire-stake flags were coded with black letters and numerals. The grids were later used to map bird nests for determining spatial distribution patterns in relation to the junction between field and forest, and to locate sample points for analyzing the composition and structure of vegetation on each site. A somewhat detailed vegetation analysis was done in order to adequately describe the field and forest habitats and the interface used by the breeding avifauna on the study sites.

Observations of avian populations on each study site were begun in March 1974 and continued through September 1975. An intensive search for all nests was made by systematically walking through the gridded study sites. To determine if nests had been missed, a 30 m rope was dragged through the field habitats (Wiens 1969), i.e., incubating birds should be flushed from the nest. A combination pole and mirror device was used to check the contents of nests in the canopy (Parker 1972). Open canopy nests above 12 m were ignored for the most part due to the difficulty of examining these nests on a daily basis. Nests in this category made up a very small percentage of nests located on the study area. Throughout most of the breeding season, daily trips to each site were made to check nest contents and to locate new nests. Several precautionary measures were undertaken to reduce the likelihood of predation due to the frequency of trips to check nest contents. When checking the contents of nests located below eye level, the observer was careful to stand as far from the nest as possible. Care was also taken not to create paths leading to nest sites, or to approach a nest when possible predators or Brown-headed Cowbirds (Molothrus ater) were observed nearby. All nests were marked in the field by placing a small strip of plastic flagging on vegetation 3 m north of the nest. Nest locations were plotted on scale maps of the study sites. Distances to habitat discontinuities were determined by range finders or measuring tapes for nearby nests.

Since open-nesting birds in the same locality generally have the same nest success regardless of their own species density (Nice 1957, Nolan 1963, Ricklefs 1970, Fretwell 1972), I decided to combine all open nests and to consider differences in fledging success and mortality patterns at the community level. Only those nests in which at least one egg had been laid were used in these analyses. This restriction was imposed so that all nests would initially have the same potential of being successful.

Measurements of environmental variables associated with avian breeding habitats on the study sites were made in July and August 1975. The methods used to collect data in each habitat were generally similar to that of James and Shugart (1970) using a modification of the range finder circle technique. Sample points were located randomly within each habitat type. Due to the possible influence of adjacent habitats, I decided to avoid all points lying within 30 m of a habitat discontinuity. Each sample point served as the center of a 0.1-acre (0.04-ha) circular plot, which was used for recording data on the composition and structure of the vegetation associated with each habitat. Adequacy of the sample was determined by the method outlined by James and Shugart (1970).

Within the 0.1-acre circle at each sample point, the species and diameter at breast height (dbh) of trees ($\geq$ 7.62 cm) were recorded on data sheets. Canopy cover was determined from point samples (James and Shugart 1970, Shugart and Patten 1972). The age of the dominant tree in each circular plot was estimated by counting growth rings on an increment core. Total height of vegetation directly over the sample plot was measured directly, or obtained from a Haga altimeter.

The number of species of understory plants (< 7.62 cm dbh, $\geq$ 1.0 m in height) within 4 m of the sample point was determined in each plot. Density of understory vegetation was estimated by averaging two 0.01-acre (0.004-ha) arm length rectangular plots centered on the sample point (Penfound and Rice 1957). Dominant understory vegetation cover ($\geq$ 2.54 cm, < 7.62 cm dbh) was estimated from point samples (James and Shugart 1970, Shugart and Patten 1972).

Within 1 m of the sample point, the number of species of ground-level vegetation (< 1.0 m in height) was determined by counting. Plotless point samples were made with an ocular tube to estimate percent cover (Winkworth and Goodall 1962).

A vegetation profile of the interface between field and forest habitats was estimated at each site by use of a measuring rod and a range finder mounted on a tripod. Transects were located at a representative portion of the interface and directed perpendicular to the habitat discontinuity at each site. They extended 20 m into each habitat type. Height of overstory, dominant understory, and dominant herbaceous and woody ground-layer (< 2.54 cm dbh) vegetation were recorded at each sample point. These data were used to construct vegetation profiles.

Analytical Procedures

Since I demonstrated that the assumptions of the parametric statistical model were not met in the data under analysis, especially that of normality (i.e., too many zeros), nonparametric techniques were used to determine the significance of observed differences and trends in the data. These distribution-free techniques result in conclusions which require fewer qualifications, and thus have greater generality than corresponding parametric tests. Siegel (1956) adequately discusses the advantages and disadvantages of both techniques of inference.

Chi-squared values (X^2) shown with tables have been derived from contingency tables testing the significance of the difference between the proportions indicated, unless otherwise stated. For those variables which met the assumptions of ordinal measurement and underlying continuity, the Kruskal-Wallis test statistic (H) (Siegel 1956, 184-193) was calculated to determine whether differences among means in the k populations were significant.

Kendall rank correlation coefficients (Siegel 1956, 213-223) were used to determine the effect of distance from the habitat discontinuity on nest dispersion, fledging success, and the different mortality factors affecting fledging success and their interrelationships. When two variables are correlated, there is always the possibility that the correlation may result from both being associated with a third variable. The observed correlation may not reflect any direct association between the two variables. Partial correlation provides a statistical method of attacking this problem. The association between $\underline{X}$ and $\underline{Y}$ is found with the third variable $\underline{Z}$ kept constant. The correlation between these adjusted variables is the partial correlation. Kendall partial rank correlation coefficients (Siegel 1956, 223-229) were calculated for certain observed correlations to understand and clarify the relationships between the variables.

Because these nonparametric correlation techniques require ordinal measurement and assume that the variables have underlying continuity, data were grouped in the following manner to meet these assumptions. Nests were first ranked according to their distance in meters from the edge, which is here defined as the point at which woody vegetation is first encountered in proceeding from field to forest habitats. Based on a cumulative frequency distribution of distances, nests were next partitioned into ten distance categories, each containing approximately ten percent of the total number of nests. Each category, therefore, had approximately an equal number of nests. The percent fledged and lost to different mortality factors were then determined relative to the total number of eggs laid. A nest distribution index (NDI) was finally calculated to correct for unequal distance intervals in each category:

$$\text{NDI} = \frac{\underline{X}_i/\underline{Y}_i}{\sum_{i=1}^{\underline{n}} (\underline{X}_i/\underline{Y}_i)} \text{ X } 100$$

where $\underline{X}_i$ is the number of nests in the ith distance category, $\underline{Y}_i$ is the number of meters in the ith distance category, and $\underline{n}$ is the number of distance categories. Calculation of NDI allowed a comparison to be made of the interrelationships between numbers of nests and the other variables.

STUDY SITES

The study sites were located on the Rose Lake Wildlife Research Area in Clinton and Shiawassee counties, Michigan. The Research Area is 19.3 km northeast of Lansing, just north of highway M-78 (I-69). It consists of 1350.3 ha of moderately undulating farmland, abandoned fields and pastures, oak and swamp woods, and marsh. Rose Lake Wildlife Research Center staffed by several wildlife biologists and technicians is located on the area. Three sites were selected from among a larger series to represent the abrupt habitat discontinuity characteristic of edges created by many agricultural, forestry, and wildlife management programs, and because of the control I would have over all management operations on the sites. General features of the sites and their vegetation are given in Tables 1, 2, and 3 and Fig. 2.

Site 1.--This site consisted of a forest stand (woodlot #1, 4.28 ha) and an abandoned field (4.46 ha) located immediately north (woodlot numbers are those designated by the biologists at the Research Center). The forest habitat was dominated by *Quercus velutina* with *Prunus serotina* and *Carya glabra* present as subdominants. *Prunus serotina* was important due to an observed higher density of individuals in the smaller size classes, especially those trees between 3-6 inches (7.62-15.24 cm) dbh. The field habitat was dominated by *Bromus inermis* (95% cover, N = 40) with *Agropyron repens* present in smaller proportion (5%, N = 40). It was also composed of isolated patches of goldenrod (*Solidago graminifolia*,

Table 1. Density, basal area, and frequency of trees ($\geq$ 7.62 cm dbh) by species in the forest habitat on each study site based on five 0.1-acre (0.04-ha) circular plots per site.

	Density (stems·ha^{-1})			Basal area (sq m.ha^{-1})			Frequency (%)		
Species	1	2	3	1	2	3	1	2	3
Acer rubrum	74	44	10	1.98	3.24	0.58	80	80	20
Amelanchier canadensis	25	5	20	0.18	0.16	0.15	40	20	40
Carpinus caroliniana	-	5	-	-	0.04	-	-	20	-
Carya glabra	104	133	84	3.29	7.90	6.26	100	100	80
C. ovata	-	30	5	-	1.52	0.32	-	80	20
Crataegus sp.	-	5	5	-	0.03	0.02	-	20	20
Prunus americana	5	-	-	0.05	-	-	20	-	-
P. serotina	282	79	124	4.23	2.81	0.95	100	100	100
Quercus alba	40	49	153	2.52	2.03	13.63	80	100	100
Q. borealis	-	-	10	-	-	0.88	-	-	20
Q. velutina	118	40	59	16.50	5.45	4.70	100	80	60
Sassafras albidum	-	20	44	-	0.22	0.34	-	20	60
Ulmus rubra	5	-	-	0.03	-	-	20	-	-
Tilia americana	-	10	-	-	0.07	-	-	20	-
Total	653	420	514	28.78	23.47	27.83			

Table 2. Density and basal area of trees ($\geq$ 7.62 cm dbh) by size class in the forest habitat on each study site based on five 0.1-acre (0.04-ha) circular plots per site.

Size class (dbh)	Density (stems·ha^{-1})			Basal area (sq m·ha^{-1})		
	1	2	3	1	2	3
3-6 inches (7.62-15.24 cm)	306	138	257	2.95	1.40	2.07
6-9 inches (15.24-22.86 cm)	138	99	69	3.83	2.70	1.97
9-15 inches (22.86-38.1 cm)	128	109	104	8.91	8.09	8.29
15-21 inches (38.1-53.34 cm)	69	69	64	10.52	10.12	9.66
21-27 inches (53.34-68.58 cm)	10	5	15	2.57	1.16	4.02
27-33 inches (68.58-83.82 cm)	0	0	5	0.00	0.00	1.82
Total	653	420	514	28.78	23.47	27.83

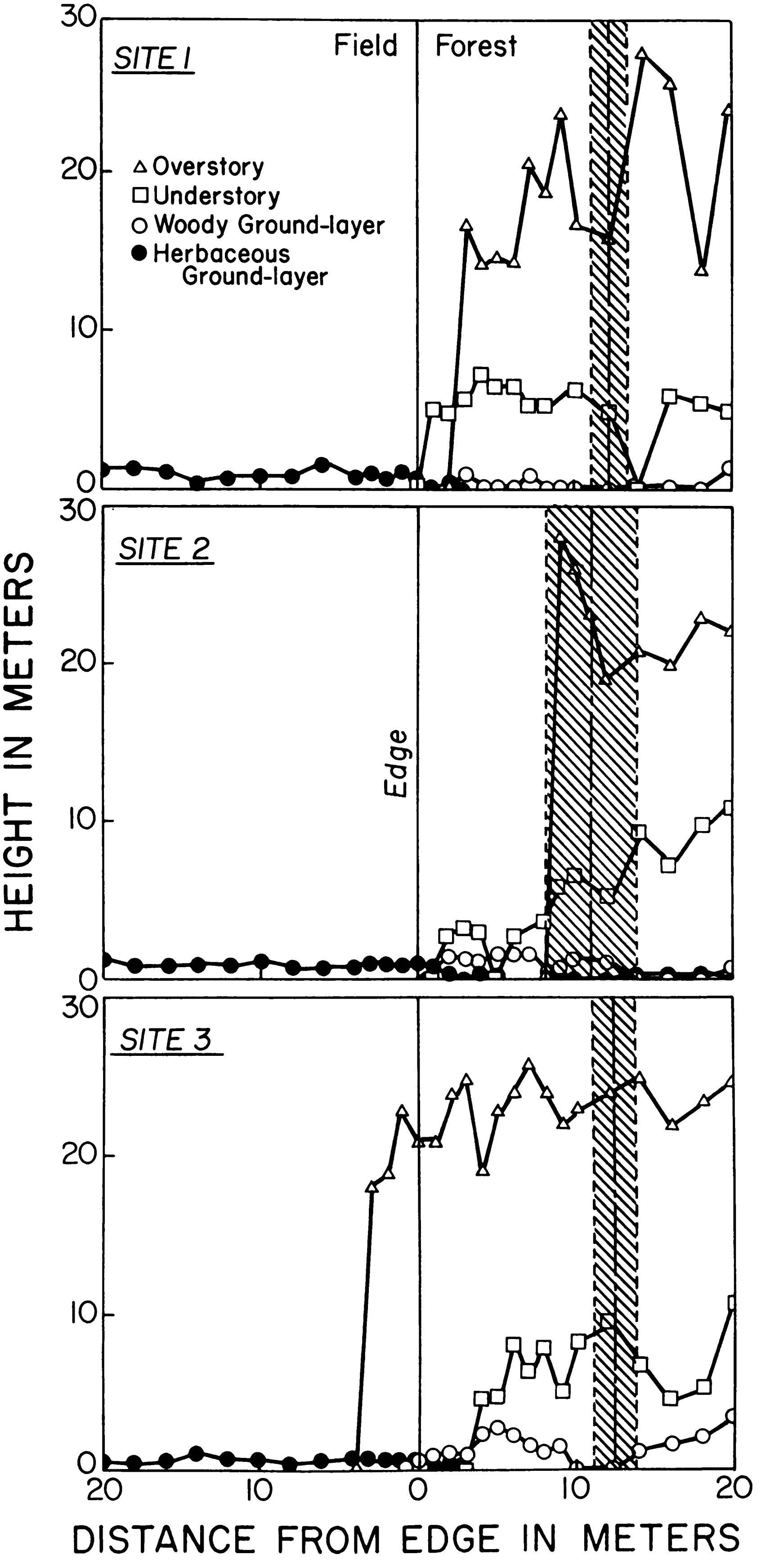
Table 3. Means, standard deviations, and sample size ( ) of variables used to describe habitats on each study site. Chi-squared (X^2) and Kruskal-Wallis (H) tests were used to determine whether or not observed differences were significant.

Variable	Study site 1	 2	 3	X^2	H	p
Forest habitat						
Maximum age of stand (years)	108 ± 5.4 (5)	108 ± 11.6 (5)	97 ± 19.7 (5)	-	1.10	>0.05
Tree density (stems·0.04 ha^{-1})	26 ± 2.6 (5)	17 ± 3.5 (5)	21 ± 6.1 (5)	-	6.78	<0.05
Basal area (sq m·0.04 ha^{-1})	1.17 ± 0.394 (5)	0.95 ± 0.157 (5)	1.13 ± 0.226 (5)	-	1.52	>0.05
Maximum height of canopy (m)	25.5 ± 3.60 (5)	23.6 ± 2.72 (5)	25.8 ± 5.64 (5)	-	1.82	>0.05
Canopy cover (%)	83 (100)	71 (100)	76 (100)	4.07	-	>0.05
Understory species (# ·0.005 ha^{-1})	3 ± 0.4 (5)	5 ± 0.8 (5)	5 ± 1.3 (5)	-	8.55	<0.01
Understory density (stems·0.004 ha^{-1})	19 ± 8.0 (10)	31 ± 16.9 (10)	38 ± 38.3 (10)	-	11.39	<0.01
Dominant understory cover (%)	65 (100)	37 (100)	61 (100)	18.48	-	<0.001

Table 3 (cont'd.).

Variable	Study site			$\underline{X}^2$	$\underline{H}$	$\underline{p}$
	1	2	3			
Forest habitat (cont'd.)						
Ground-level species (#·3 m^{-2})	4 ± 1.5 (5)	11 ± 2.0 (5)	9 ± 2.9 (5)	-	10.14	<0.01
Ground-level cover (%)	43 (100)	82 (100)	66 (100)	33.24	-	<0.001
Field habitat						
Maximum height of herbs (cm)	100 ± 29.0 (100)	74 ± 24.1 (100)	80 ± 27.6 (100)	-	42.15	<0.001
Herbaceous cover (%)	97 (100)	92 (100)	93 (100)	2.48	-	>0.05

Fig. 2. Representative vegetation profiles of the interface between field and forest habitats on the study sites derived from the maximum height of overstory ($\geq$7.62 cm dbh), dominant understory ($\geq$2.54 cm, <7.62 cm dbh), and dominant herbaceous and woody ground-layer (<2.54 cm dbh) vegetation. The zone at which dominant overstory trees (30.48-38.10 cm dbh) first occurred in the stand is represented by cross-hatched areas, which designate ± 1 SD of the mean. Sample sizes are 10 (site 1), 30 (site 2), and 15 (site 3). Differences between sites were not significant ($H = 3.91$, $p > 0.05$).


SITE 1
Field
Forest
△ Overstory
□ Understory
○ Woody Ground-layer
● Herbaceous Ground-layer
SITE 2
Edge
SITE 3
HEIGHT IN METERS
0
10
20
30
DISTANCE FROM EDGE IN METERS
20
10
0
10
20

S. canadensis), aster (*Aster pilosus*), burdock (*Arctium minus*), milkweed (*Asclepias syriaca*), and other forbs. A discontinuous row of rose (*Rosa multiflora*) paralleled the northern edge at about 60 m into the field.

Site 2.--About 0.4 km due east of site 1, site 2 was chosen. It was a forest stand (woodlot #5, 8.98 ha) with an abandoned pasture (9.09 ha) located just north of the forest. *Carya glabra* was dominant and *Q. velutina* and *Acer rubrum* were subdominant species in the stand. *Prunus serotina* and *Quercus alba* were also important constituents in the stand, but primarily in the smaller size classes. *Bromus inermis* was again the dominant species in the field habitat (95%, N = 40) with *Phleum pratense* composing a small percentage of dominant herbaceous cover (5%, N = 40). Furthermore, the field habitat contained several isolated patches of goldenrod (*S. graminifolia*, *S. canadensis*), aster (*A. pilosus*), sweet clover (*Melilotus alba*, *M. officinalis*), wild carrot (*Daucus carota*), thistle (*Cirsium arvense*, *C. vulgare*), and other forbs. Several isolated large trees and a few scattered shrubs were located throughout the field.

Site 3.--This site was located 0.2 km east of site 2. It consisted of a forest stand (woodlot #6, 5.27 ha) with an old field (5.79 ha) situated immediately east. The tree species dominant in the forest stand was *Q. alba* with *C. glabra* and *Q. velutina* associated with it as subdominants. *Prunus serotina* was again an important species in the 3-6 inch size class. Dominance in the field habitat was shared by *B. inermis* (55%, N = 40) and *A. repens* (45%, N = 40). Besides the dominant grasses, isolated patches of solidago (*S. graminifolia*, *S. canadensis*), aster (*A. pilosus*), burdock (*Arctium minus*), milkweed (*Asclepias syriaca*), wild carrot (*Daucus carota*), hedge-parsley (*Torilis japonica*), and other forbs were also present.

Although structurally the habitats on the three sites were quite similar, there were several significant differences. The forest on site 2 was noted to be quite open beneath the canopy with dominant understory cover of 37% and fewer trees per plot, especially individuals between 3-9 inches (7.62-22.86 cm) dbh, than at sites 1 or 3. Light penetration to the forest floor was observed to be greater here than at sites 1 or 3. This situation is perhaps reflected in the increased forest ground-level cover at site 2. Other differences included greater numbers of forest understory and ground-level species, and an increase in forest understory density at sites 2 and 3 than at site 1. These differences are most likely attributed to man's past influence on grazing practices and lumbering operations. Herbaceous vegetation was also found to be much taller in the field habitat at site 1 than at sites 2 or 3.

Vegetation profiles of the interface between field and forest habitats on the study sites indicate fairly abrupt structural changes between the two habitats. The edge represents a rather distinct discontinuity between short herbaceous field vegetation and tall woody forest vegetation. However, along the edge of the forest habitats, patches of blackberry (*Rubus allegheniensis*), raspberry (*R. occidentalis*, *R. strigosus*), gray dogwood (*Cornus racemosa*), hawthorne (*Crataegus* sp.), as well as saplings of black cherry (*P. serotina*), red maple (*A. rubrum*), hickory (*C. glabra*, *C. ovata*), and oak (*Q. velutina*, *Q. alba*) created a somewhat intermediate shrubby vegetation zone of varying width. Reflecting a wildlife habitat improvement program of the early 1950's (Robert Ankney, pers. comm.), the presence of rose (*R. multiflora*) along the northern edge of forests at sites 1 and 2 and honeysuckle (*Lonicera tartarica*) and rose along the eastern edge of the forest at site 3 added to the shrubby appearance. This shrubby vegetation zone was for the most part quite narrow. Trees characteristic of dominant forest overstory (30.48-38.10 cm dbh) were found on the average 11.1-12.3 m from the edge. The major structural difference between sites appeared to be a generally more gradual vertical transition from field to forest habitat at site 2 than at sites 1 or 3.

Soils on the study sites were primarily Fox sandy loam (Typic Hapludalfs) with a small percentage of Washtenaw loam (Typic Haplaquents). Fox soils are on nearly level to sloping areas of glacial outwash plains, terraces, and moraines. These are well-drained soils developed in loamy outwash overlying stratified calcareous sand and gravel at depths of 51-102 cm commonly on a slope of 1-12%. The small areas of Washtenaw loam were located in the field sections of sites 2 and 3. These soils are on nearly level areas in depressions or moraines, till plains, and outwash plains. They are poorly-drained soils formed in 51-102 cm of recent alluvium from adjacent soils and in drift of Wisconsin age.

Due to the influence of the Great Lakes, the climate of the region alternates between continental and semimarine, depending upon the force and direction of the wind (summaries presented here are from U.S. Dept. of Commerce, Local Climatological Data, 1936-1975). The increased cloudiness associated with the prevailing westerly winds during the fall and winter months helps to moderate minimum temperatures. When winds diminish or change to the north or northeast, skies often clear to give the cooler temperatures more commonly associated with an inland location. The prevailing wind is southwesterly averaging about 16.6 $km \cdot hr^{-1}$. Mean maximum temperatures are above freezing from March through December and between 23 and 28° C in the summer. Mean minimum temperatures are above freezing from April through October. Precipitation is well-distributed throughout the year and averages about 7,861 mm annually, with 50% occurring from April through August. May and June, with 874 and 876 mm respectively, are the wettest months of the year. Summer precipitation is mainly in the form of afternoon showers or thundershowers.

RESULTS

Nest Distribution Patterns

During the two-year study 194 nests of twenty-one species of open-nesting passerines were found on the area (Table 4). These nests were not evenly dispersed on the study sites, but had a definite pattern. Most of the nests were found within about 10-20 m of the habitat discontinuity at each site (Fig. 3). Seventy-five percent of the nests belonged to birds characteristic of mixed breeding habitats, i.e., birds requiring open areas with dense cover for nesting and feeding and elevated singing and observation perches (Kendeigh 1944, Johnston 1947, Johnston and Odum 1956). These birds also accounted for the increase in number of bird species found nesting near the edge. Indeed, each species seemed to have a definite preference as to nest site location relative to the habitat discontinuity at each site (Appendix).

The distribution patterns of nests almost represent a symmetrical bell-shaped curve with some variation in height between sites. Nest distribution patterns at study sites 1 and 3 were quite similar. However, site 1 had an increased frequency of nests toward mid-field because of Song Sparrows, generally considered a mixed-habitat species, nesting in some multiflora rose. Song Sparrows also used the multiflora rose for singing and observation posts and cover. The somewhat less clumping of nests near the habitat discontinuity at site 2 when compared to sites 1 and 3 is attributed to the relatively gradual change in

Table 4. Characteristic life-form of nesting habitat and numbers of nests of open-nesting passerines located on the study area. Numbers of nests in which eggs were determined to be present are in parentheses.

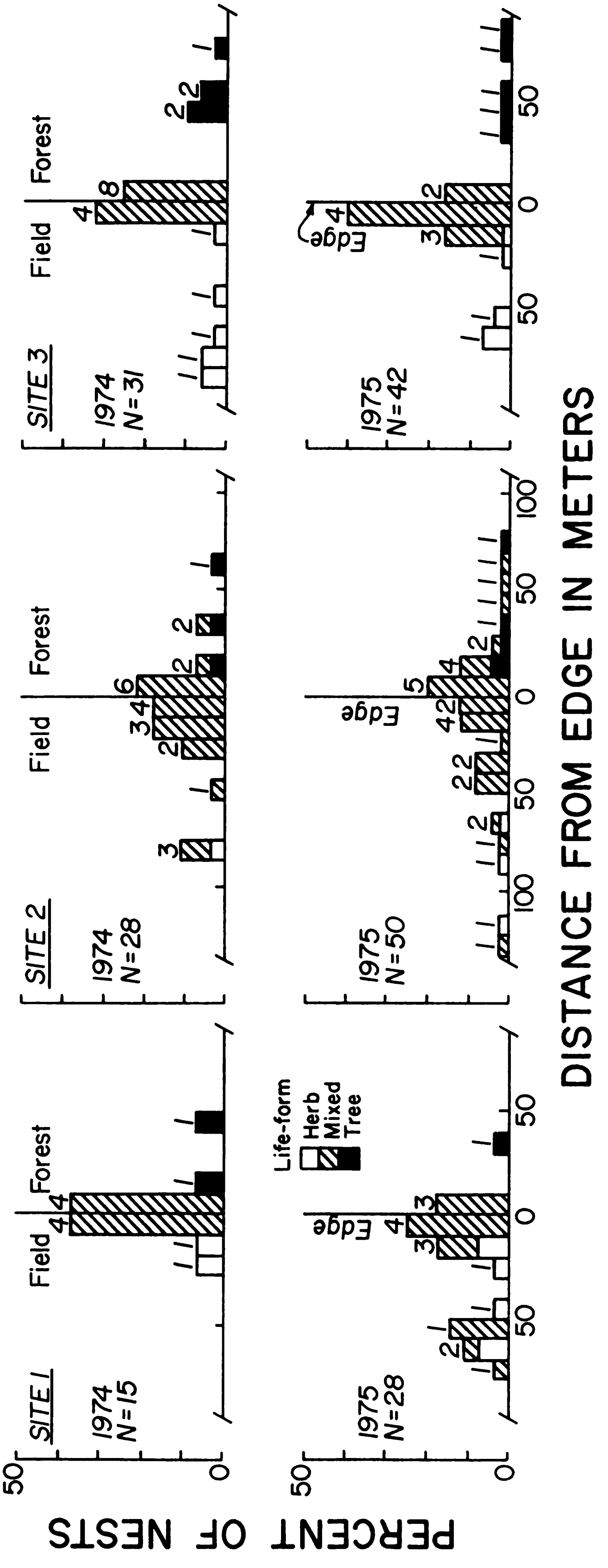
Species	Life-form	# Nests
Acadian Flycatcher (*Epidonax virescens*)	Tree	1 (1)
Eastern Wood Pewee (*Contopus virens*)	Tree	3 (1)
Blue Jay (*Cyanocitta cristata*)	Mixed[a]	1 (1)
American Crow (*Corvus brachyrhynchos*)	Tree	1 (0)
Gray Catbird (*Dumetella carolinensis*)	Mixed	4 (3)
Brown Thrasher (*Toxostoma rufum*)	Mixed	1 (1)
American Robin (*Turdus migratorius*)	Mixed	3 (3)
Wood Thrush (*Hylocichla mustelina*)	Tree	7 (4)
Red-eyed Vireo (*Vireo olivaceus*)	Tree	9 (5)
Blue-winged Warbler (*Vermivora pinus*)	Mixed	1 (1)
Chestnut-sided Warbler (*Dendroica pensylvanica*)	Mixed	4 (2)
Eastern Meadowlark (*Sturnella magna*)	Herb	1 (1)
Red-winged Blackbird (*Agelaius phoeniceus*)	Herb	26(22)
Northern Oriole (*Icterus galbula*)	Mixed	1 (0)

Table 4 (cont'd.)

Species	Life-form	# Nests
Scarlet Tanager (*Piranga olivacea*)	Tree	1 (1)
Cardinal (*Cardinalis cardinalis*)	Mixed	15(10)
Indigo Bunting (*Passerina cyanea*)	Mixed	32(27)
American Goldfinch (*Spinus tristis*)	Mixed	2 (2)
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	Mixed	5 (5)
Field Sparrow (*Spizella pusilla*)	Mixed	59(59)
Song Sparrow (*Melospiza melodia*)	Mixed	17(15)
Total		194(164)

[a] Mixed--Herb-Shrub, Herb-Tree, or Herb-Shrub-Tree.

Fig. 3. Cumulative nest distribution patterns of open-nesting passerines on the study sites according to characteristic life-form of nesting habitat and number of species (numerals above histograms).


SITE 1
1974
N=15
1975
N=28
SITE 2
1974
N=28
1975
N=50
SITE 3
1974
N=31
1975
N=42
Field
Forest
Edge
Life-form
Herb
Mixed
Tree
PERCENT OF NESTS
0
50
100
DISTANCE FROM EDGE IN METERS

vegetation profile (structure) at site 2. For example, open-canopied, shrub-nesting passerines found a wider zone of acceptable nesting cover which resulted in somewhat less clumping of nests near the habitat discontinuity. The presence of several isolated large trees and shrubby vegetation as well as patches of stout, erect herbs scattered throughout the field habitat at site 2 also provided singing posts or suitable nesting cover farther into the field interior for several mixed-habitat species (e.g., Indigo Bunting, Field Sparrow, and Song Sparrow). Indigo Buntings, another species typical of mixed habitats, were attracted into the fields on all study sites by patches of burdock, milkweed, goldenrod, and sweet clover, all of which were used as nest sites. Indigo Buntings were also observed nesting farther into the forest interior at site 2 than at sites 1 or 3. This phenomenon was probably due to the increased openness of the stand which resulted in suitable, low vegetation cover for nesting. Patches of blackberry and raspberry were used for the most part as nest sites in the forest interior. Cardinals, which generally nested in shrubs along the habitat discontinuity, were also found nesting somewhat farther into the forest habitat at site 2 than at sites 1 or 3. Nests were located in multiflora rose, hawthorne, and a grapevine (*Vitis* sp.) tangle. Nests of mixed-habitat species were especially concentrated near the edge at site 3. The closed forest stand and complete absence of woody vegetation in the field seemed to restrict these species to the interface.

Fledging Success and Mortality Patterns

Since overall nest distribution patterns were basically the same between sites (i.e., high numbers of nests near the habitat discontinuity) and the observed trends in fledging success and losses due to different mortality factors relative to the habitat discontinuity were consistent during the period of the study, the major emphasis was placed on the effect of the habitat discontinuity on these factors and their interrelationships with each other. Graphical presentation of the relationship of the different variables with distance from the edge revealed several interesting trends (Fig. 4).

Nest distribution index, calculated as previously described, initially dropped quickly and then gradually fell to a low of around one percent. Over one-half of the nests were found within 15 m of the habitat discontinuity. This trend is comparable to the frequency distributions of the raw data presented in Fig. 3. Fledging success steadily increased with distance from lows of 20-30% near the edge to highs of 60-70% away from the edge. Parallel but opposite to the trend in fledging success, losses due to predation dropped from 40-50% near the edge to 0-10% away from the edge. Predation appeared to drop steadily with increasing distance until about 45 m from the habitat discontinuity, where it quickly fell. Brown-headed Cowbird parasitism more or less followed the same trend as predation, but it was more variable. Parasitism was as high as 15-25% near the edge to as low as 0-5% farther from it. Losses due to nest desertions appeared to be relatively constant oscillating between 0-10% until about 65 m and then sharply rising to 15-20%. Losses due to inclement weather, adult death, and hatching failure did not show any definite trend with distance from the habitat discontinuity.

Table 5 compares the degree of correlation between all variables using the Kendall rank correlation test. Kendall partial rank correlation coefficients were then calculated for certain correlations observed

Fig. 4. Graphical presentation of the relationship of different nest variables with distance from the habitat discontinuity. Distances covered by each distance category are as follows: (1) 0.0-0.82 m; (2) 0.82-2.19 m; (3) 2.19-4.34 m; (4) 4.34-6.86 m; (5) 6.86-10.06 m; (6) 10.06-14.18 m; (7) 14.18-26.74 m; (8) 26.74-46.24 m; (9) 46.24-65.58 m; and (10) 65.58-123.00 m. Sample sizes are in parentheses.

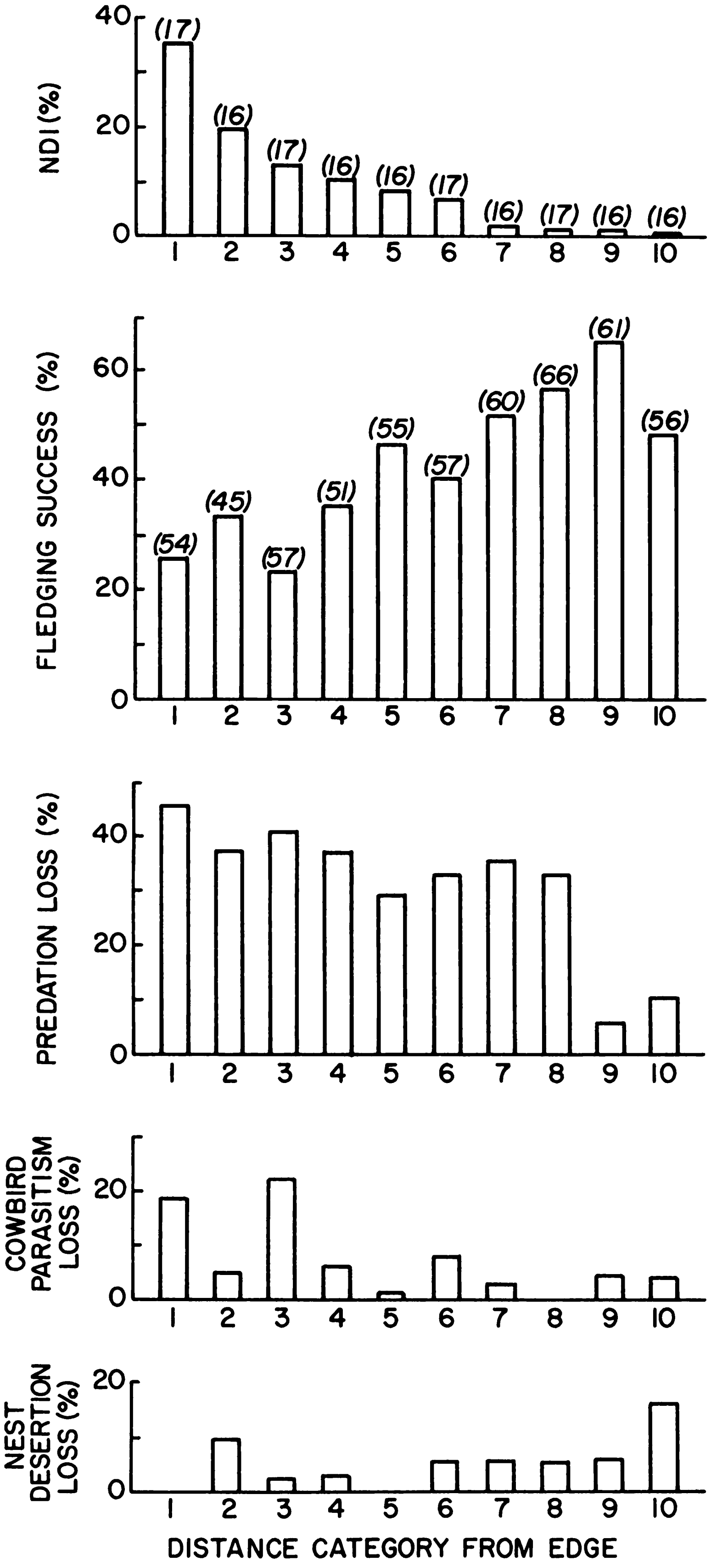

NDI (%)
40
20
0
(17)
(16)
(17)
(16)
(16)
(17)
(16)
(17)
(16)
(16)
1 2 3 4 5 6 7 8 9 10
FLEDGING SUCCESS (%)
60
40
20
0
(54)
(45)
(57)
(51)
(55)
(57)
(60)
(66)
(61)
(56)
1 2 3 4 5 6 7 8 9 10
PREDATION LOSS (%)
40
20
0
1 2 3 4 5 6 7 8 9 10
COWBIRD PARASITISM LOSS (%)
20
0
1 2 3 4 5 6 7 8 9 10
NEST DESERTION LOSS (%)
20
0
1 2 3 4 5 6 7 8 9 10
DISTANCE CATEGORY FROM EDGE

Table 5. Matrix of Kendall rank correlation coefficients, τ (tau), comparing the interrelationships between distance from a habitat discontinuity (edge), nest distribution index (NDI), fledging success, and the different mortality factors affecting fledging success.

					Mortality factors					
		Distance from edge	NDI	Fledging success	Predation	Inclement Weather	Cowbird parasitism	Nest desertion	Hatching failure	Adult death
	Distance from edge	1.000								
	NDI	-1.000****	1.000							
	Fledging success	0.733****	-0.733****	1.000						
Mortality factors	Predation	-0.674****	0.674****	-0.674****	1.000					
	Inclement weather	0.163	-0.163	-0.023	-0.283	1.000				
	Cowbird parasitism	-0.422*	0.422*	-0.600***	0.405*	0.023	1.000			
	Nest desertion	0.506**	-0.506**	0.322	-0.349	0.048	-0.230	1.000		
	Hatching failure	-0.090	0.090	0.090	-0.023	-0.188	0.090	0.116	1.000	
	Adult death	-0.050	0.050	0.050	-0.251	0.260	-0.348	-0.412*	-0.201	1.000

* Significant at 0.05; ** Significant at 0.025; *** Significant at 0.01; **** Significant at 0.005.

in Table 5 to understand and clarify the relationships between the variables by uncovering spurious relationships and searching for intervening linking variables (Table 6). Since distance from a habitat discontinuity and nest distribution index (NDI) had a perfect negative correlation, both will be considered together when presenting the results of partial correlation. The most significant inferences are summarized as follows.

The significant correlation observed between fledging success and distance (NDI) became $\tau_{xy \cdot z}$ = 0.511 (-0.511) when the influence due to predation was held constant. Since this value is smaller than τ_{xy} = 0.733 (-0.733), the relation between fledging success and distance (NDI) is affected by losses due to predation. Controlling for distance (NDI), the relationship between fledging success and predation was not as strong, which indicates that distance from a habitat discontinuity or numbers of nests influences the predation rate which in turn affects fledging success.

Partialling out losses due to Brown-headed Cowbird parasitism had little effect on the relationship between fledging success and distance (NDI). The correlation between fledging success and distance (NDI) seems to be relatively independent of the influence of losses due to parasitism. Furthermore, when the effect of distance (NDI) was held constant, the correlation between fledging success and parasitism became less important. This suggests that the relations between fledging success and distance (NDI) and between parasitism and distance (NDI) are influencing the observed relation between fledging success and cowbird parasitism. Moreover, the correlation between parasitism and predation was nearly eliminated when distance (NDI) was kept constant, indicating that both are affected by distance (NDI) in the same manner.

Table 6. Kendall partial rank correlation coefficients, $\tau_{xy \cdot z}$, of the relation between the X and Y variables when the effect of variation of a third variable, Z, is eliminated.

X	Y	Z	τ_{xy}	$\tau_{xy \cdot z}$[a]
Fledging success	Distance (NDI)	Predation	0.733 **** (-0.733)****	0.511 (-0.511)
Fledging success	Predation	Distance (NDI)	-0.674 ****	-0.358
Fledging success	Distance (NDI)	Cowbird parasitism	0.733 **** (-0.733)****	0.662 (-0.662)
Fledging success	Cowbird parasitism	Distance (NDI)	-0.600 ***	-0.472
Predation	Cowbird parasitism	Distance (NDI)	0.405 *	0.180
Nest desertion	Distance (NDI)	Predation	0.506 ** (-0.506)**	0.392 (-0.392)
Nest desertion	Predation	Distance (NDI)	-0.349	-0.013
Nest desertion	Adult death	Distance (NDI)	-0.412 *	-0.449

[a] Since the sampling distribution of the Kendall partial rank correlation is unknown, no tests of the significance of an observed $\tau_{xy \cdot z}$ are possible.

* Significant at 0.05.
** Significant at 0.025.
*** Significant at 0.01.
**** Significant at 0.005.

Partialling out the effect due to predation, the uncontaminated relation between losses due to nest desertion and distance (NDI) is expressed by $\tau_{xy.z} = 0.392$ (-0.392), which is less than $\tau_{xy} = 0.506$ (-0.506). Controlling for the effect of distance (NDI), the association between nest desertion and predation became essentially non-existent. The conclusion is that the observed significant correlation between losses due to nest desertion and distance (NDI) is relatively dependent on both being associated with losses due to predation. A logical explanation is that the increased predation rate nearer the edge results in loss of a certain proportion of nests which otherwise would have been deserted by the adult birds. This is based on the assumption that nest desertions are random and constant over the entire area. Losses due to nest desertion would, thereby, be less nearer the edge than farther from it, producing the observed correlation. Nevertheless, I cannot refute the likelihood that a real difference might exist farther from the habitat discontinuity caused by lack of secure cover or nearby conspecifics, i.e., the need of some form of social facilitation (Johnsgard 1967), but I find it doubtful.

When distance from a habitat discontinuity or NDI was held constant, the relation between losses due to nest desertion and adult death was observed to be similar. Therefore, it might be assumed that the relation between these two sources of mortality is relatively independent of the effect of distance (NDI). It appears that the constancy of incubation and brooding increases the probability that an adult bird may be taken by a predator while on the nest.

Differential Mortality Patterns

Because of the observation that several mortality factors may have a differential effect on the eggs or nestlings, the chi-squared one-sample test (Siegel 1956, 42-47) was employed to determine the significance of any observed differences. The results are presented in Table 7.

Parental activity at the nest site was noted to increase greatly once the eggs had hatched. Predators might be able to locate nests more easily during the nestling stage due to increased activity of parents feeding nestlings, especially where many nesting birds are concentrated. However, there was no significant difference in percent predation between the egg and nestling periods. In fact, predation appears to be evenly distributed throughout the nesting cycle. Losses due to heavy storms and death of one or both parents also seem to fall into this same category.

Brown-headed Cowbird parasitism was found to be significantly more destructive of eggs than nestlings. Most egg losses occurred from the female removing an egg of the host after depositing her own egg. Losses which occurred during the nestling period resulted either from the remaining nestling(s) of the host species being crowded out of the nest by the generally larger and stronger cowbird nestling(s), or from slow starvation due to the cowbird nestling(s) dominating the feeding sequence. The majority of parasitized nests (62%) had only one cowbird egg, while the remaining nests had two or three. One exceptional nest had a total of five cowbird eggs deposited in it.

Nest desertions which resulted in losses occurred early in the nesting cycle, usually before incubation began. Eighty-two percent of the deserted nests had only one or two eggs in them. Only 18% of the deserted nests had clutches of three or four eggs. Causes of nest desertion were difficult to determine. Several nests may have been deserted because of cowbird egg deposition. Due to the difficulty in

Table 7. Differential effects of mortality factors on eggs and nestlings at Rose Lake.

Variable	Percent Loss[a]		X^2	p
	Eggs	Nestlings		
Predation	17.1	15.5	0.44	>0.05
Inclement weather	3.2	5.0	2.17	>0.05
Cowbird parasitism	5.3	0.7	19.88	<0.001
Nest desertion	3.2	0.0	18.00	<0.001
Hatching failure	3.7	-	-	-
Adult death	0.9	0.0	-	>0.05[b]

[a] Sample size = 562.

[b] Since the expected frequencies were less than five, the binomial test was used to determine the two-tailed probability.

ascertaining whether or not the parent was killed, several recorded desertions could have been losses due to adult death rather than desertion. Some nest desertions were possibly due to the disturbance at the nest caused by checking nest contents. Others were perhaps due to inadequate cover near the nest.

Seasonal Effects

Seasonal differences in mortality were for the most part nonexistent (Table 8). However, Brown-headed Cowbird parasitism was found to be important only to birds initiating nesting in late spring (June). Birds breeding in early spring (May) or in the summer (July and August) were essentially free from the depredations wrought by the cowbird. Losses due to nest desertion were also greater in June, which may be a result of the higher incidence of cowbird parasitism.

Predator Activity

Predation, which was the major factor affecting fledging success, accounted for 59.6% of all losses. In most instances, the cause of the loss was impossible to ascertain.

Several nests in the study area may have been predated by eastern chipmunks (*Tamias striatus*). Field Sparrows nesting in or near an edge seemed especially vulnerable. On one occasion, I witnessed two adult Field Sparrows chirping and flying about their nest site. On closer inspection I saw one chipmunk in the small *Juniperus communis* in which the nest was located, and another on the ground at the base of the shrub. Only one nestling remained in the nest from a brood of four. The eastern chipmunk was the most frequently observed mammal on the study sites,

Table 8. Comparison of losses due to different sources of mortality by month of nest initiation at Rose Lake. Sample sizes are in parentheses.

Variable	Percent loss			X^2	p
	May (232)	June (223)	July-August[a] (107)		
Predation	29.7	36.8	29.9	2.97	>0.05
Inclement weather	8.6	7.2	9.3	0.55	>0.05
Cowbird parasitism	2.6	11.2	2.8	17.30	<0.001
Nest desertion	1.7	6.3	0.0	12.05	<0.01
Hatching failure	3.9	3.6	3.7	0.02	>0.05
Adult death[b]	2.2	0.0	0.0	-	-

[a] Two nests occurred in August, each contained three eggs.

[b] Expected frequencies in each cell were too small; therefore, no value for X^2 or probability could be calculated.

and could have been a very important predator on eggs and nestlings. Nolan (1963) believed that the chipmunk was a significant predator of nests of deciduous shrub birds. Other potential mammalian predators observed or known to be in the area included shorttail shrew (*Blarina brevicauda*), white-footed mouse (*Peromyscus leucopus*, *P. maniculatus*), ground squirrel (*Citellus tridecemlineatus*), red squirrel (*Tamiasciurus hudsonicus*), fox squirrel (*Sciurus niger*), longtail weasel (*Mustela frenata*), striped skunk (*Mephitis mephitis*), opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), domestic cat (*Felis catus*), and red fox (*Vulpes vulpes*).

Other predators of open-nesting birds included the Blue Jay and possibly the Common Crow, several raptors (*Buteo jamaicensis*, *Falco sparverius*, *Otus asio*), and various snakes (*Lampropeltis doliata triangulum*, *Coluber constrictor foxi*, *Thamnophis sirtalis sirtalis*). Blue Jays were considered the cause of broken eggs and dead nestlings in several nests of Red-eyed Vireos and Cardinals. Based on the observed presence of a Screech Owl (*O. asio*) and blood-stained feathers at the nest site, a Blue Jay and Wood Thrush were thought predated by an owl while incubating and brooding, respectively. A milk snake (*L. d. triangulum*) was observed near the nest of an Eastern Meadowlark, which was later predated. No direct observations of predation were made during the study, thus much of the above information is speculative.

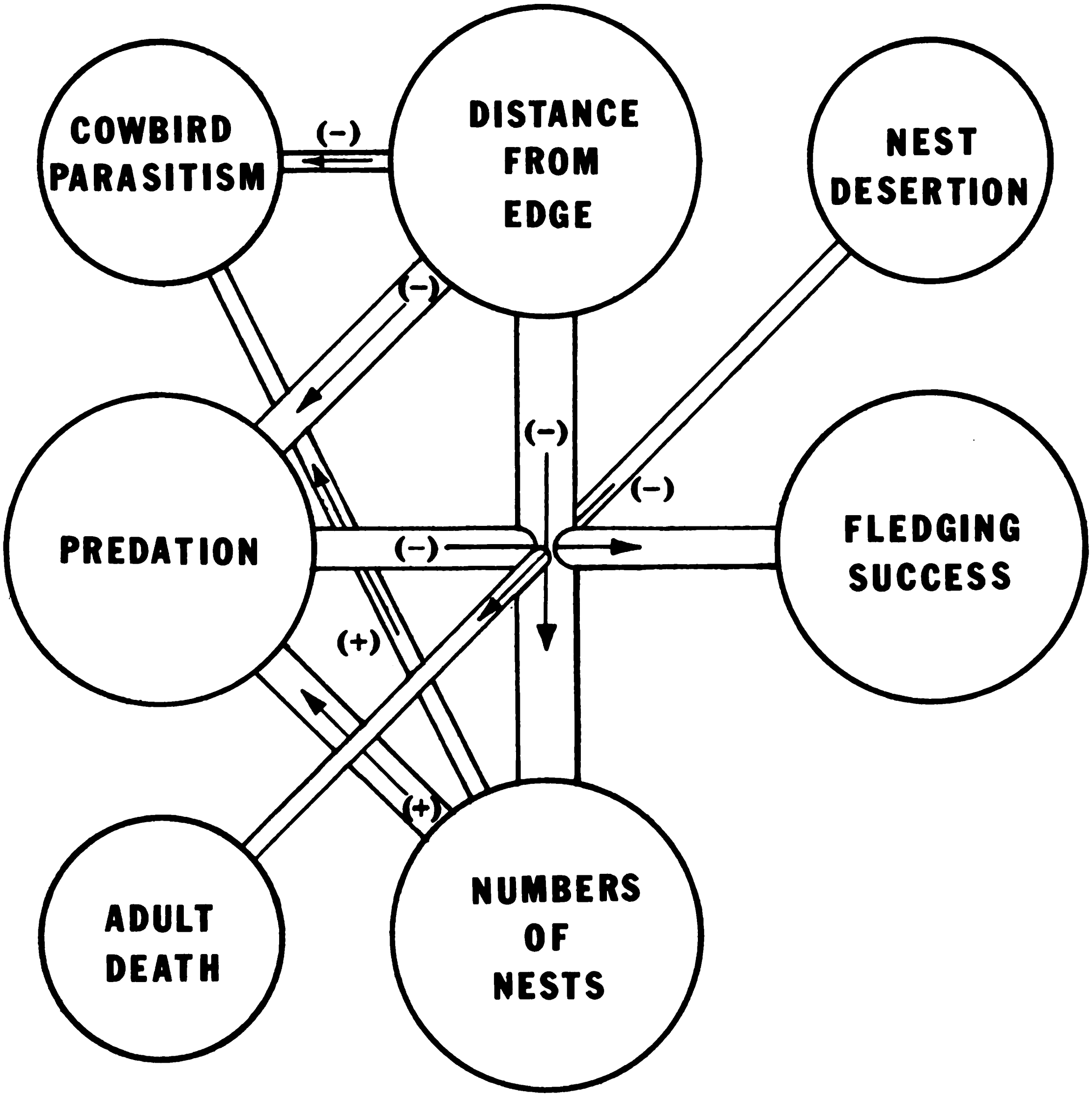
DISCUSSION

A summary of the biologically important as well as statistically significant pathways by which the habitat discontinuity at Rose Lake affected nest distribution, fledging success, and losses due to different mortality factors in open-nesting passerines is presented in Fig. 5.

Distance from a habitat discontinuity, which also represents changes in habitat composition and structure, inversely affects numbers of nests. Some nest sites, especially those associated with an open canopy and dense shrubby vegetation (Cardinal, Gray Catbird, Brown Thrasher, Rufous-sided Towhee), are not found in either adjoining habitat interiors. Since availability of nest sites is probably limiting, such birds are restricted to nesting near edges which effectively concentrates nests. Birds that may require an open canopy and high singing or observation perches near their nest sites but nest and feed close to the ground in low vegetation (Field Sparrow, Song Sparrow, Indigo Bunting) would also be limited to nesting near edges. The increase in woody ground-layer vegetation resulting from the openness of the forest stand and the presence of woody vegetation in the field habitat seemed to influence the nest location of these mixed-habitat species.

According to the data, distance from a habitat discontinuity and numbers of nests, separately or in concert, influence the percent predation which is the primary factor affecting fledging success. Because predation was higher near edges than in habitat interiors, fledging success was lower. Holling (1959) has demonstrated that predation is

Fig. 5. A summary of the biologically important as well as statistically significant pathways by which the habitat discontinuity (edge) affected nest distribution, fledging success, and losses due to different mortality factors in open-nesting passerines. The width of connecting lines designate the significance of the relationship. The direction and sign of the arrows indicate probable cause-and-effect relationships and whether or not it is direct or inverse.


COWBIRD PARASITISM
(−)
DISTANCE FROM EDGE
NEST DESERTION
(−)
(−)
(−)
PREDATION
(−)
FLEDGING SUCCESS
(+)
(+)
ADULT DEATH
NUMBERS OF NESTS

affected mainly by prey and predator density. The increase in numbers of prey consumed per predator as prey density increases is termed the functional response. An increase in the numbers of predators with increasing prey density is the numerical response. Fretwell (1972) has also shown that, within a habitat, avian breeding success is mainly density-dependent, due to density-dependent nest predation. In fact, the nest mortality of each open nest is dependent upon the density of all open nests, regardless of species (Fretwell 1972). A major portion of the increased predation is attributed to a functional response of predators to increased nest numbers near edges. Because losses due to predation did not significantly differ during the breeding season, it is improbable that predator density was able to increase sufficiently by reproduction or immigration in order to have a direct numerical response.

There is some indication that the number of prey consumed per predator is not just directly proportional to prey density, but that the activity of predators searching for prey is greater near habitat discontinuities. Bider (1968) observed that such small mammals as red squirrels, eastern chipmunks, shrews, and weasels were significantly more active in the vicinity of the forest edge. Raccoons were also found to extend their activity to a greater ecotonal depth than smaller animals, and to utilize forest interiors only sparingly (Bider, Thibeault, and Sarazin 1968, Bider 1968). Bider (1968) thought that the forest edge may function as a biological barrier which causes animals to move parallel to it for some distance. This would result in animals whose home ranges are delineated by barriers to be more active along it, thus creating an activity vacuum at some distance away from the barrier (Bider 1968). This fact could also explain the increased activity of eastern chipmunks in the ecotone between field and forest habitats studied by Forsyth and Smith (1973). They observed that 69-90% of all home ranges were entirely within, or extended into, the ecotone. It seems likely that higher predation observed near habitat discontinuities at Rose Lake can be attributed to both an increase in numbers of nests and a greater activity of potential nest predators in the vicinity of edges.

Brown-headed Cowbird parasitism was also observed to be higher near edges. It too was affected by distance from a habitat discontinuity or nest numbers, separately or in combination. Although its effect upon fledging success was not as important as predation, McGeen (1972) has demonstrated that as cowbird pressures increase fledging success of open-nesting birds can decrease. Because cowbird pressure is dependent upon parasite and host nest density (McGeen 1972), a parasite can also be considered to have a response to prey density (egg laying), which can be identified as a functional response (Holling 1959). However, cowbirds would not be expected to show a direct numerical response during one breeding season for obvious reasons. Therefore, the increased incidence of parasitism can be attributed in part to a functional response of Brown-headed Cowbirds to increased nest numbers in the vicinity of edges.

Furthermore, there is evidence that cowbirds exhibit increased activity near habitat discontinuities due to their nest searching behavior (Berger 1951, Johnston 1960, Payne 1973, Norman and Robertson 1975). Cowbirds at Rose Lake were often observed on a high perch near the habitat discontinuity in a position to see nest building activity of potential host species, or on several occasions moving about in the vegetation along the field-forest edge presumably searching for nests (see Norman and Robertson 1975). I seldom observed cowbirds in the forest or field interiors on the study sites. This indicates that cowbirds may find it difficult to locate nests in habitats where their view of nesting birds is obscured by dense foliage. It would also be a more economical use of time and energy to concentrate their search in areas where host nest density is high. Because cowbirds in northern, lower Michigan begin egg laying in late May or early June and terminate in July (Payne 1965, 1973), birds nesting in June and near a habitat discontinuity at Rose Lake were especially susceptible to cowbird parasitism. Ironically, the cowbird also became a potential victim of increased predator activity due to its parasitism of nests near habitat discontinuities. In fact, cowbirds had a fledging success of only 11.8% during the study period.

In conclusion, the creation of narrow forest edges by agricultural, forestry, or wildlife management programs does seem to attract a variety and abundance of open-nesting passerines. This phenomenon is what is classically known as the edge effect. Based on these observations, earlier workers assumed that edges had high suitability for certain avian species. However, this study has shown that birds nesting near habitat discontinuities at Rose Lake are subject to high rates of predation and Brown-headed Cowbird parasitism due in part to large numbers of nests near such areas. I would furthermore add that total production of independent avian off-spring appears to be comparatively constant over the entire area, or slightly higher near edges (unpublished data). I conclude that actual habitat suitability decreases with increasing nest frequencies toward relatively narrow field-forest edges. But why should open-nesting passerines nest in the vicinity of edges in such

numbers? I propose that the narrow man-made forest edges studied in central Michigan could well function as ecological traps for avian species characteristic of habitats with mixed life-form. All the normal structural cues, indicating good nest sites, singing and observation perches, cover, and food availability, are presumably present for these species near edges. Those birds selecting to nest in the vicinity of the edge perceive it as a suitable nesting area. However, they are perhaps "tricked" by the juxtaposition of field and forest into settling near the narrow zone of shrubby vegetation bordering these forested areas. Extensive areas of narrow field-forest edge have only been in existence for a brief period relative to the evolutionary time-scale. Forests, which once covered this part of Michigan almost entirely, have been reduced about 90% since logging first began around 1865 (information derived from soil surveys of Clinton and Shiawassee counties, Michigan). Therefore, these man-made situations are perhaps unrepresentative of the ecological niche in which these mixed-habitat species evolved, and thus they may be poorly adapted to cope with the increased predation near them.

APPENDIX

Means, standard deviations, and sample size ( ) of distances from the habitat discontinuity used by open-nesting passerines as nest locations on study sites 1, 2, and 3. Positive values are forest locations, while negative values are field.

Species	Distance in Meters		
	1	2	3
Acadian Flycatcher	-	-	70.7 (1)
Eastern Wood Pewee	11.7 (1)	36.4 (1)	72.0 (1)
Blue Jay	-	7.6 (1)	-
American Crow	32.0 (1)	-	-
Gray Catbird	5.6 ± 1.95 (2)	2.6 (1)	6.6 (1)
Brown Thrasher	-	-	0.0 (1)
American Robin	-6.7 (1)	-13.4 ± 4.45 (2)	-
Wood Thrush	-	28.0 ± 22.81 (4)	48.4 ± 2.34 (3)
Red-eyed Vireo	41.0 (1)	45.4 ± 42.61 (2)	53.7 ± 15.63 (6)
Blue-winged Warbler	-	6.3 (1)	-
Chestnut-sided Warbler	-	9.2 ± 4.40 (4)	-

APPENDIX (cont'd.)

Species	Distance in Meters		
	1	2	3
Eastern Meadowlark	-	-	-41.1 (1)
Red-winged Blackbird	-34.1 ± 22.93 (8)	-86.0 ± 21.21 (4)	-54.5 ± 27.04** (14)
Northern Oriole	-	-	0.0 (1)
Scarlet Tanager	-	31.5 (1)	-
Cardinal	0.2 ± 3.25 (4)	1.2 ± 6.55 (9)	0.1 ± 3.01 (2)
Indigo Bunting	-9.6 ± 26.65 (8)	8.2 ± 32.93 (17)	-5.0 ± 5.28 (7)
American Goldfinch	-	-38.7 ± 10.37 (2)	-
Rufous-sided Towhee	-	0.0 (1)	-0.4 ± 2.20 (4)
Field Sparrow	-4.9 ± 5.37 (7)	-29.5 ± 21.16 (23)	-5.7 ± 6.40**** (29)
Song Sparrow	-33.7 ± 27.80 (10)	-32.2 ± 51.62 (5)	-2.4 ± 3.45 (2)

** $\underline{H} = 8.02$, $\underline{p} < 0.025$.
**** $\underline{H} = 26.78$, $\underline{p} < 0.005$.

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