

THE UNIVERSITY OF MANITOBA

NEST SITE SELECTION AND COEXISTENCE IN EASTERN  
AND WESTERN KINGBIRDS AT DELTA MARSH, MANITOBA

by

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A dissertation submitted to the Faculty of Graduate Studies of  
the University of Manitoba in partial fulfillment of the requirements  
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Master of Science

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For my parents,  
who know best why

"As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera."

— Darwin, 1859

## TABLE OF CONTENTS

	PAGE
ABSTRACT .....	i
ACKNOWLEDGEMENTS .....	iii
LIST OF TABLES .....	v
LIST OF FIGURES .....	ix
INTRODUCTION .....	1
The Approach .....	1
The Species .....	3
The Study Area .....	5
REVIEW OF CONCEPTS .....	9
Competition and Niche Theory .....	9
Resource Use and the Coexistence of Species .....	13
The Multivariate Approach to Habitat Selection ...	16
METHODS .....	19
Sampling Methods .....	19
Nest Site Characteristics .....	19
Characteristics of the Study Area Vegetation ...	21
Statistical Analysis .....	23
Univariate Methods .....	23
Multivariate Methods .....	23
RESULTS .....	28
Distribution of Nests on the Study Area .....	28
Characteristics of the Study Area .....	35
Overstory Composition and Structure .....	35
Environmental Gradient and Vegetation	
Heterogeneity .....	38

	PAGE
Analysis of Habitat Variables .....	42
Characteristics of the Nest Sites .....	52
Importance Values of the Tree Species .....	52
Analysis of Individual Variables .....	54
i) Macrosite Variables .....	54
ii) Microsite Variables .....	54
iii) Nest Tree Variables .....	54
Multivariate Analysis of Combined Data Sets .....	61
i) Macrosite and Nest Tree Variables .....	61
ii) Microsite and Nest Tree Variables .....	61
Principal Component Analysis .....	64
i) Macrosite Variables .....	64
ii) Microsite Variables .....	73
Discriminant Function Analysis .....	75
i) Macrosite Variables .....	75
ii) Microsite Variables .....	82
iii) Nest Tree Variables .....	86
iv) Combined Macrosite and Nest Tree Variables .	88
Intraspecific Variation in Eastern Kingbird Nest Sites .....	93
DISCUSSION .....	97
Pattern of Variation in the Ridge Vegetation .....	97
Kingbird Species' Responses to the Pattern of Variation .....	98
Nest Site Selection and Coexistence in Kingbirds ..	103
CONCLUSIONS .....	106
LITERATURE CITED .....	109

## ABSTRACT

Characteristics of nest sites of eastern and western kingbirds on the forested ridge, Delta Marsh, Manitoba, were studied during 1976 and 1977. Habitat analysis was performed around each nest site at three levels of resolution: macrosite (.07 ha), microsite (.01 ha), and nest tree.

Principal component analysis of overstory vegetation characteristics of randomly selected plots (.01 ha) defined the 'habitat space' of the study area in terms of the major components of variation in the vegetation. Discriminant function analysis of the random plots identified the major gradient in the variation of the vegetation (corresponding roughly to a microgeographical gradient from north to south), and characterized the differences between north- and south-zone type microhabitats.

Principal component analysis of the vegetation characteristics of kingbird nest sites at both macrosite and microsite levels determined the relative position of each species in the 'habitat space'. Projection of the nest site data onto the random plot ordination indicated that eastern kingbird nest sites were more evenly distributed than those of western kingbirds along the major components of variation in the ridge vegetation. Virtually all of the western kingbird sites and most of the eastern kingbird sites appeared to be situated in north-zone type microhabitat. Discriminant function analysis of the nest sites at

all three levels of resolution identified the variables most important in characterizing the differences between the nest sites of the two species. At the microhabitat (macrosite and microsite) level, western kingbird sites were characterized by fewer but larger trees than eastern kingbird sites. Western kingbird nest trees were larger and taller, and their nests were placed higher than those of eastern kingbirds. Eastern kingbirds employed the fine-grained strategy of a habitat generalist in their selection of nest sites from both available microhabitat types, and in their selection of nest trees from a wide range of tree sizes. Western kingbirds exhibited the coarse-grained response of a specialist, selecting sites in only the north-zone type microhabitat, and nest trees from the larger sizes.

A combination of macrosite and nest tree variables achieved the best statistical separation between eastern and western kingbird nest sites, using discriminant function analysis of the combined data sets. The degree of separation of the species along the resource dimension of nesting habitat, defined in terms of the best discriminating variables, is considered sufficient to permit coexistence of these species in the event nesting habitat should prove to be the resource limiting the population of either species.



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## LIST OF TABLES

TABLE	PAGE
1. Wisconsin school summary statistics for the major tree species on the forested dune ridge, Delta Marsh.....	36
2. Means, standard errors, and results of t-tests for habitat variables from random plot samples from the forested ridge, Delta Marsh.....	43
3. Correlation coefficients between 13 habitat variables from random plot samples from the forested ridge, Delta Marsh. Symbols represent the variables in their order of appearance in Table 2 (* $P \leq .01$ ).....	45
4. Correlations of the habitat variables with the four principal components extracted from the analysis of the random plot matrix.....	46
5. Standardized discriminant function coefficients from the analysis of the random plots.....	50
6. Importance values of the major tree species at kingbird nest sites on the forested ridge, Delta Marsh.....	53
7. Means, standard errors, and results of t-tests for habitat variables from eastern and western kingbird macrosites.....	55

## LIST OF TABLES (CONT'D)

TABLE	PAGE
8. Means, standard errors, and results of t-tests for habitat variables from eastern and western kingbird microsites.....	56
9. Means, standard errors, and results of t-tests for variables associated with eastern and western kingbird nest trees.....	57
10. Frequency of use of tree species as nest trees by eastern and western kingbirds on the forested ridge, Delta Marsh.....	59
11. Correlation coefficients between 22 habitat variables from the combined kingbird macrosite and nest tree data sets. Symbols represent the variables in their order of appearance in Tables 7 and 9.....	62
12. Correlation coefficients between 22 habitat variables from the combined kingbird microsite and nest tree data sets. Symbols represent the variables in their order of appearance in Tables 8 and 9.....	63
13. Correlations of the habitat variables with the five principal components extracted from the analysis of the combined kingbird species macrosite matrix.....	65

## LIST OF TABLES (CONT'D)

TABLES	PAGE
14. Correlations of the habitat variables with the first two principal components extracted from the analysis of the individual species macrosite matrices.....	71
15. Correlations of the habitat variables with the four principal components extracted from analysis of the combined kingbird species macrosite matrix.....	74
16. Standardized discriminant function coefficients from the analysis of the kingbird scaled macrosite data.....	79
17. Standardized discriminant function coefficients from the analysis of the kingbird macrosite data.....	83
18. Means, standard errors, and results of t-tests of comparisons of habitat variables from kingbird macrosites with those from random plots on the forested ridge, Delta Marsh.....	85
19. Standardized discriminant function coefficients from the analysis of the kingbird nest tree data.....	87

## LIST OF TABLES

TABLE	PAGE
20. Standardized discriminant function coefficients from the analysis of the combined macrosite and nest tree data sets.....	91
21. Results of $T^2$ -tests for all levels of resolution using north-zone eastern kingbird, south-zone eastern kingbird, and western kingbird nest sites.....	95

## LIST OF FIGURES

FIGURE	PAGE
1. Breeding distributions of eastern and western kingbirds. Arrow indicates the location of the study area at Delta Marsh, Manitoba. Map prepared using American Ornithologists' Union Checklist Committee (1957), Godfrey (1966), Breeding Bird Survey (1975).....	4
2. Map of Delta Marsh, Manitoba, showing the location of the study area. Map prepared using a Map of Delta Waterfowl Control Area, Department of Mines and Natural Resources, Manitoba.....	6
3. Map of the study area showing the disposition of the random plots. Consecutive numbers identify the cells of the study area grid.....	7
4. Map of the study area showing the location of eastern (E) and western (W) kingbird nests in 1976. Circles represent the microsite plots..	29
5. Map of the study area showing the location of eastern (E) and western (W) kingbird nests in 1977. Circles represent the microsite plots..	30
6. Nesting chronology of eastern and western kingbirds at Delta Marsh, Manitoba, 1976 and 1977. Time intervals correspond roughly to visits to the nests.....	31

## LIST OF FIGURES (CONT'D)

FIGURE	PAGE
7. Frequency distribution of nests (1976-1977) along the length of the study area.....	32
8. Frequency distribution of nests (1976-1977) across the study area. The ridge forest has been divided into ten zones of equal width from north to south.....	34
9. Mean density per hectare by size class for the major tree species on the forested ridge, Delta Marsh. Stems are grouped into size classes of 5 cm dbh.....	37
10. Diagrammatic cross-section of the forested ridge, Delta Marsh.....	39
11. Frequency distribution of the major tree species across the width of the ridge.....	40
12. Ordination of random plots along the first two principal components of the random plot analysis. Polygons surround the respective scatters of north and south plots. Straight line fitted by eye through the origin maximizes the separation between north and south plots..	48
13. Frequency distribution of discriminant scores obtained from analysis of the random plot data.....	51



## LIST OF FIGURES (CONT'D)

FIGURE	PAGE
14. Frequency distribution of tree size classes (all species) selected as nest trees by eastern and western kingbirds, in relation to their relative availability on the study area.....	60
15. Ordination of kingbird macrosite plots along the first two principal components extracted from the analysis of the combined species macrosite matrix. Straight line through the random plot scatter (Fig. 12) is superimposed on the macrosite ordination.....	67
16. Ordination of the kingbird macrosite plots obtained by weighting the macrosite data with the principal component weights derived from the analysis of the random plots.....	68
17. Ordination of eastern and western macrosite plots along the first two principal components extracted from each of the separate species analyses.....	72
18. Ordination of kingbird microsite plots along the first two principal components extracted from the analysis of the combined species microsite matrix.....	76

## LIST OF FIGURES (CONT'D)

FIGURE	PAGE
19. Ordination of the kingbird microsite plots obtained by weighting the microsite data with the principal component weights derived from the analysis of the random plots.....	77
20. Frequency distribution of discriminant scores obtained from the analysis of the kingbird scaled macrosite data.....	80
21. Frequency distribution of discriminant scores obtained by weighting the kingbird scaled macrosite data with the discriminant weights derived from the analysis of the random plots.	81
22. Frequency distribution of discriminant scores obtained from the analysis of the kingbird microsite data.....	84
23. Frequency distribution of eastern and western kingbird nest heights on the forested ridge, Delta Marsh.....	89
24. Frequency distribution of eastern and western kingbird nest heights recorded in the Prairie Nest Records Scheme.....	90
25. Frequency distribution of discriminant scores obtained from the analysis of the five best discriminating variables from the combined macrosite and nest tree data set.....	92

## INTRODUCTION

Animals partition resources in three basic ways: spatially, trophically, and temporally (Pianka 1973). Schoener (1974) observed that, in general, habitat dimensions are important more often than food dimensions, which are, in turn, important more often than temporal dimensions.

Selection of different habitats within the same area is the commonest means of ecological segregation among passerine birds (Lack 1971). Bird species select nest sites within specific habitats (Lack 1933; Lack and Venables 1939), and show species-specific responses to certain visual combinations of the structure of the habitat (Svårdson 1949; Hildén 1965; James and Shugart 1970). Among closely related species slight differences in habitat preference are common, coinciding with subtle differences in habitat pattern (Lack 1971).

## The Approach

In this study data are presented on the use of the same nesting habitat by eastern kingbirds (Tyrannus tyrannus) and western kingbirds (T. verticalis). The area examined is an island of forest habitat, bordered along one edge by marsh and upland meadow, and along the other by open water. Both species are primarily insectivorous (Beal 1912), and the food supply in the area appears to be superabundant throughout the breeding season (see Busby 1978; MacKenzie unpubl. data). However, availability of suitable nest sites could

be an important limiting factor for these species. Nesting habitat would then constitute a resource dimension along which segregation would be expected to occur, if the species were to coexist indefinitely.

The purpose of this study was to determine how such similar species share the nesting habitat resources available to them. The approach involved the application of multivariate techniques to a set of habitat variables which were considered relevant to an assessment of niche breadth and overlap along the resource dimension of nesting habitat.

The following objectives were pursued: 1) to describe the distribution of the nests of each species on the study area; 2) to determine the structural and floristic characteristics of the vegetation on the study area, thereby defining the 'habitat space' (after James 1971) in terms of these characteristics; 3) to determine the breadth of use of the available habitat by each species, hence, the relative position of each in the habitat space; 4) to determine the overlap of the two species' niches along the dimension of nesting habitat; 5) to identify, through reduction in the dimensionality of the habitat component of the species' niches, those factors which appeared most important in characterizing the difference in nesting habitat resource use between the species.

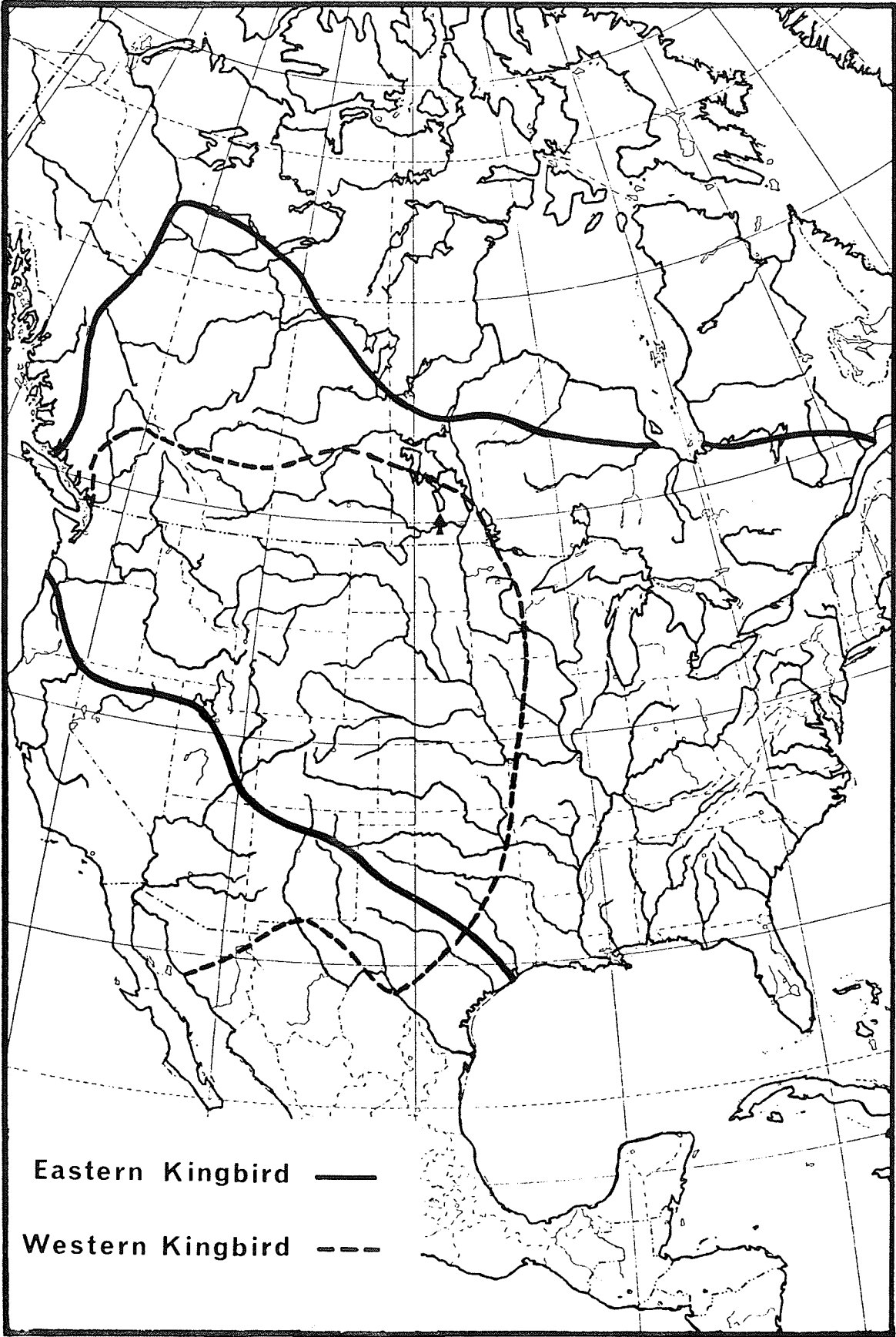
## The Species

The eastern kingbird and the western kingbird are sympatric over much of western North America (Fig. 1). The area of sympatry constitutes only 35% of the breeding range of the eastern kingbird, but 60% of the western kingbird's breeding range. Within their common range, where one species is abundant, the other is usually much less so, and there is also regional variation as to which species exploits the wider range of habitats (see Hiatt 1942; Hamilton 1962).

Over much of its range the eastern kingbird nests along the edges of woodlots, in orchards, frequently in riparian communities, and near marshes (Bent 1942; Smith 1966). In the parts of its range where wooded areas are scarce, the eastern kingbird inhabits open country, often nesting in low shrubs.

The western kingbird is typical of dry, grassland areas, but over much of its range its distribution appears to be dependent on the presence of at least a few trees for nesting. It is therefore a common inhabitant of prairie riparian woodlands, where it often reaches high nesting densities (e.g., see Carothers *et al.* 1974). The apparent dependence on trees or other tall structures (e.g., hydro poles) for nesting suggests that the expansion of the breeding range of this species since 1900 may have been influenced by the planting of trees and erection of man-made structures which accompanied settlement of the plains at the turn of the century (see Nice 1924).

Figure 1. Breeding distributions of eastern and western kingbirds. Arrow indicates the location of the study area at Delta Marsh, Manitoba. Map prepared using American Ornithologists' Union Check-list Committee (1957), Godfrey (1966), Breeding Bird Survey, 1975 (D. Bystrak pers. comm.).



The sympatric association of eastern and western kingbirds in southern Manitoba is the result of this breeding range expansion. The first record of the western kingbird in Manitoba was apparently a specimen collected in 1907 at Oak Lake, but by 1927 the species had become common in southwestern Manitoba (Taverner 1927). Nevertheless an analysis of census data from the Breeding Bird Survey (for details see Robbins and Van Velzen 1967) for the years 1970-1975 reveals that, for the routes summarized in the surveys, eastern kingbirds were 4 times as abundant as western kingbirds in Manitoba. Data from the same source indicated that eastern kingbirds were 3 times as abundant as western kingbirds throughout the Prairie Provinces.

Both species breed on the forested dune ridge at Delta Marsh in high densities, the eastern kingbird being about 3 times as abundant as the western kingbird (Smith 1966). Both species arrive on the ridge in early May, the western kingbird being observed usually a few days before the eastern. Nest construction begins in late May, and egg laying usually begins in the first week of June. By the end of August both species have usually disappeared from the ridge.

#### The Study Area

The study area (Figs. 2,3) is a 2000-meter portion of the forested dune ridge which separates the south shore of Lake Manitoba from Delta Marsh ( $50^{\circ}11'N$ ,  $98^{\circ}19'W$ ). The ridge is a remnant shore-line of Glacial Lake Agassiz



Figure 2. Map of Delta Marsh, Manitoba, showing the location of the study area. Map prepared using a Map of Delta Waterfowl Control Area, Department of Mines and Natural Resources, Manitoba.

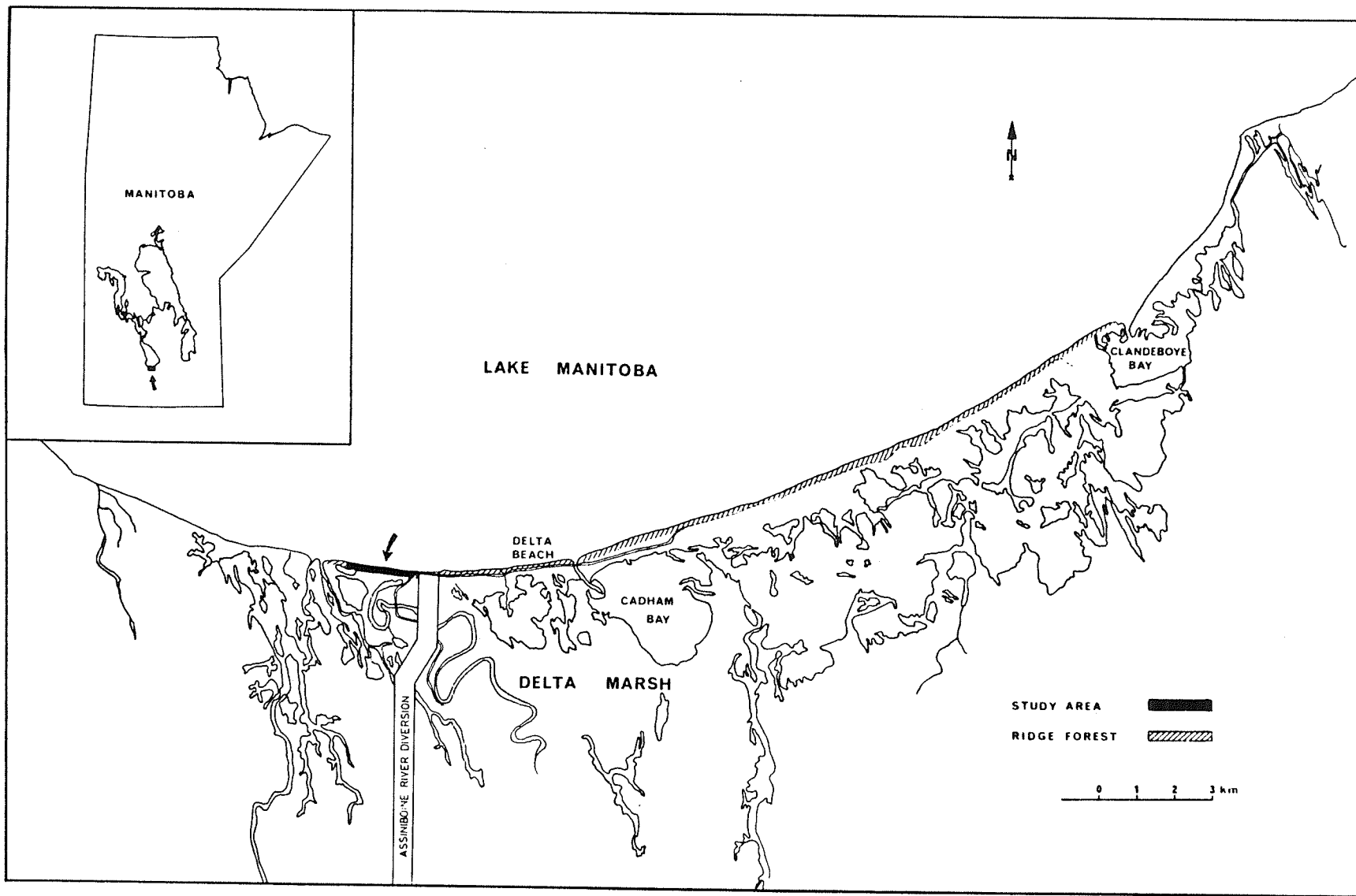
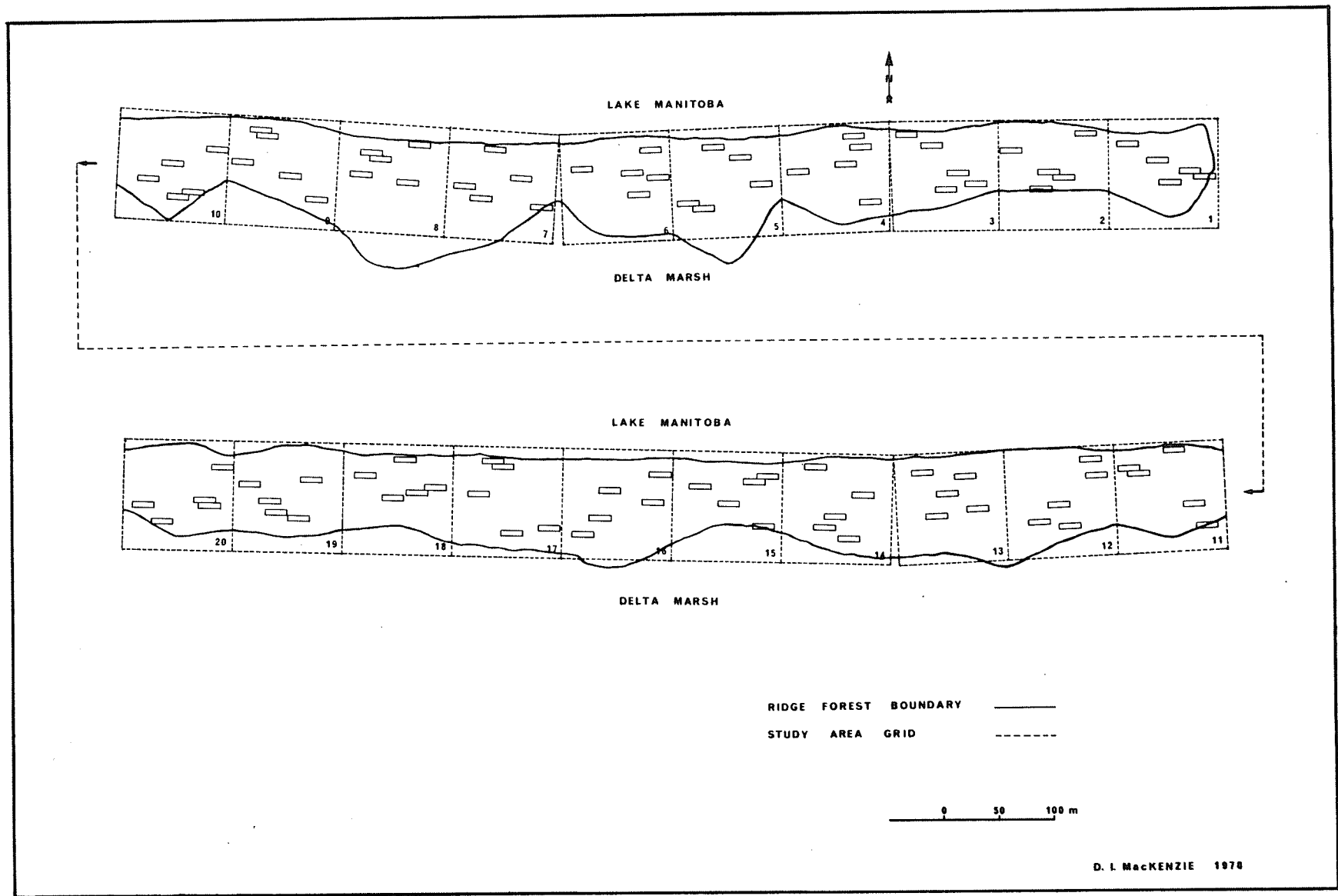


Figure 3. Map of the study area showing the disposition of the random plots. Consecutive numbers identify the cells of the study area grid.



(Walker 1965; Sproule 1972) formed by wind, wave, and ice action (Löve and Löve 1954). The dune formation per se, averages 2.5 m high and seldom exceeds 30 m in width on the study area. However, the ridge forest averages 80 m in width.

The vegetation of the ridge has been described by Löve and Löve (1954) and Walker (1959, 1965). The common trees on the study area are peach-leaved willow (Salix amygdaloides Anderss.), Manitoba maple (Acer negundo L.), green ash (Fraxinus pennsylvanica Marsh.), and cottonwood (Populus deltoides Marsh.). The common shrubs include sandbar willow (Salix interior Rowlee), red-berried elder (Sambucus pubens Michx.), and red osier (Cornus stolonifera Michx.). The common herbs and climbers include nettle (Urtica dioica L.), great burdock (Arctium lappa L.), wild cucumber (Echinocystis lobata (Michx.) T. & G.), and common hop (Humulus lupulus L.).

Seven species in addition to the kingbird species nest on the forested ridge in high numbers: mourning dove (Zenaidura macroura), least flycatcher (Empidonax minimus), northern oriole (Icterus galbula), warbling vireo (Vireo gilvus), yellow warbler (Dendroica petechia), gray catbird (Dumetella carolinensis), and robin (Turdus migratorius).

## REVIEW OF CONCEPTS

## Competition and Niche Theory

Whenever populations of closely related species come into direct contact, the potential for interspecific competition exists. Competition will normally occur either when the simultaneous demand for resources shared by these populations exceeds their current supply (exploitation competition), or when, in seeking those resources, one population limits access by another to them (interference competition) (see Brian 1956; Birch 1957; Miller 1967).

Following the work of Gause (1934) and others, it has become generally accepted that two closely related species cannot coexist indefinitely if their niches are similar with respect to any limited environmental resource(s). The principle of competitive exclusion (Hardin 1960) predicts that the better adapted, hence more efficient, of the two species will ultimately exclude the other species through competition for the same limited resource(s). Stated another way, this principle maintains that if two species coexist they must occupy different niches. In this context the concept of the niche has gradually become inextricably linked with competition theory.

The term 'ecological niche' was introduced by Grinnell (1904, 1917) as the ultimate distributional unit of a species, but was used by Elton (1927) to describe an animal's 'role' in the community, particularly in terms of its food habits.

Thus, the term was defined almost simultaneously to mean two different things (MacArthur 1968). Grinnell's concept of the niche has been interpreted as that of the 'pre-competitive' or 'pre-interactive' niche, while Elton's concept is considered to resemble that of the 'post-competitive' or 'post-interactive' niche (Vandermeer 1972).

Hutchinson (1944, in Miller 1967, p. 16) developed the formal hyperspace concept of the niche as "the sum of all the environmental factors acting on an organism". More importantly, perhaps, he incorporated both the pre- and post-competitive aspects of the niche in his concepts of fundamental and realized niches (Hutchinson 1958). He defined fundamental niche as an N-dimensional hypervolume in which every point corresponds to a different state of the environmental resources which would permit a given species to exist indefinitely in the absence of competitors. He defined realized niche as that subset of a species' fundamental niche which remained occupied by the species following competitive interaction with another species. This model of the niche provided a useful framework in which to view competitive interactions between species, for it was now theoretically possible, at least, to evaluate the influence of competition by comparing a species' fundamental and realized niches (see Miller 1967).

Levins (1968) refined the Hutchinsonian concept of the niche and made it more applicable to empirical data by defining a set of 'sufficient parameters' for the theory of

the niche, which included niche breadth, niche dimension, and niche overlap.

Niche breadth can be thought of as the distribution of a species over the range of environmental resources. The breadth of a species along any given dimension of the niche (e.g., prey size) can be evaluated quantitatively by determining the extent of exploitation by the species along that dimension. Thus, niche breadth can be used as an actual measure of the plasticity or 'versatility' (Maguire 1967) of a species, and as such is an inverse measure of ecological specialization of a species (Colwell and Futuyma 1971).

Niche dimensionality, according to Levins (p. 48), refers "not to the number of biologically relevant factors in the environment, which may be virtually unlimited, but to the number of factors which serve to separate species". This reduction in the multidimensional complexity of the Hutchinsonian niche concept coincides with MacArthur's (1968) suggestion of restricting discussion of the niches of species to only a few dimensions, and facilitates the quantitative comparison of niches.

Niche overlap can be defined as the joint use of a resource or resources by two or more species (Colwell and Futuyma 1971), and as such is a measure of the ecological similarity among species (Levins 1968).

Recently, the concept of the niche has become increasingly framed in terms of resource utilization spectra by a growing school of population biologists (see Pianka 1976).



Niche relationships among potentially competing species are depicted using bell-shaped resource utilization curves (e.g., Pianka 1976, Fig. 7.1). These functions are derived from the distribution of individuals in populations along the gradients representing a particular resource or resources (Platt and Weis 1977), and therefore characterize the species' use of the resource spectrum (May and MacArthur 1972). Using this model, niche breadth with respect to a given dimension is the length of the interval along the axis representing that dimension in which the population obtains most of its resources (Roughgarden 1972). Niche overlap in the context of this model is the overlap of the resource utilization curves of the species potentially competing along a given dimension of the niche. Such an approach lends itself well to an examination of the ecological similarity between species because, with a reduction in the dimensionality of the niche to the one or two critical dimensions in relation to which competition is most likely to occur, the similarity of the species can be assessed quantitatively and depicted graphically, in terms of niche breadth and overlap along these dimensions.

## Resource Use and the Coexistence of Species

When two species are found coexisting, they may or may not be similar in their exploitation of resources. If they are similar, their observed coexistence may be explained by one of the following hypotheses:

- 1) the resources they share are superabundant, and, therefore, not limiting factors;
  - 2) their populations are subject to density-dependent factors other than the shared resources (e.g., predator-mediated coexistence (Janzen 1970; Caswell 1978) such that the populations never reach levels sufficient to exhaust the supply of shared resources;
  - 3) the resources which they share do, in fact, limit the sizes of their populations, in which case competition exists between them, and the degree of competition will be directly related to the degree of overlap in their use of the limiting resources (Sale 1974). In this case the species appear to coexist in the presence of competition because displacement or exclusion may not yet be complete.
- Thus, overlap in resource use ( $\approx^1$  niche overlap) may indicate the absence of competition if the shared resources are superabundant, or the presence of incipient competition if the resources are limiting (see Colwell and Futuyma 1971).

If the coexisting species do not show substantial overlap, then one of the following hypotheses may apply:

<sup>1</sup>  $\approx$ : approximately equal to

- 1) the resources under consideration may not be relevant to both species, or the same range of those resources may not be critical to the survival of each species;
- 2) coexistence may have been facilitated by the retreat of both species to their adaptive peaks along the dimension considered in the face of interspecific competition (see Svardson 1949), or by the niche shift of one of the species as a result of the competitive interference of the other (see Jenssen 1973; Schoener 1975; Werner and Hall 1977).

Thus, the absence of resource overlap indicates that interspecific competition is not currently occurring, at least along the dimensions considered, but it does not indicate whether or not competition was an important influence during the history of coexistence of the species.

As Colwell and Futuyma (1971) have pointed out, the existence of competition can be demonstrated only if the 'actual' ( $\approx$  realized) niche overlap between suspected competitors is shown to be less than the 'virtual' ( $\approx$  fundamental) niche overlap — i.e., the demonstration of a change in resource use by one species in the presence of a competitor. In practice, this involves measuring resource use by a species both in the presence and in the absence of a competitor, and often means experimentally perturbing the system (see Sale 1974).

Following studies such as MacArthur's (1958) classic analysis of resource use by a community of coexisting

Dendroica warbler species, attention has been focussed increasingly on how much overlap is permissible — i.e., how similar species can be and still coexist. This has resulted in the introduction of concepts such as 'limiting similarity' (MacArthur and Levins 1967), 'species packing' (MacArthur 1969, 1970) and 'maximum tolerable overlap' (May and MacArthur 1972; May 1974). May and MacArthur (1972) have developed a model which indicates that there is a limit to niche overlap, and that this limit is not significantly dependent on the degree of environmental fluctuation. The model sets the limiting similarity of two or more species on a resource dimension such that  $d/w \approx 1$ , where  $d$  is the distance between the mean positions of species adjacent on the resource continuum (i.e., an index of species packing), and  $w$  is the standard deviation of a species' utilization function. The theoretical model assumes that all species' resource utilization functions are bell-shaped gaussian curves with common width,  $w$ , and that they are uniformly spaced along the resource continuum (i.e., common  $d$ ). Nevertheless, studies of coexisting species have, in fact, reported species separated along a resource continuum such that  $d/w \approx 1$  (e.g., see Terborgh 1972, in May 1974). Assuming that this model is valid, it is possible to determine from empirical data whether or not species found coexisting at a given point in time exceed the maximum tolerable overlap along a given resource dimension. Although excessive overlap ( $d/w < 1$ ) is not evidence of the existence

of competition, evidence that the maximum resource overlap has not been achieved along a given dimension ( $d/w > 1$ ) does indicate that competition along that dimension is not occurring. If the dimension under consideration is potentially the most limiting, then one should be able to predict with reasonable confidence the stable coexistence of the species in question.

#### The Multivariate Approach to Habitat Selection

It is generally accepted that avian habitat selection is based largely on gross visual aspects of the vegetation configuration (Hildén 1965; Shugart and Patten 1972; Smith 1977). James (1971) introduced the term 'niche-gestalt' to describe that combination of habitat factors which characterizes the occurrence of a species. The Gestalt approach to habitat selection depends upon a species' ability to perceive its Umwelt or 'relevant environment' (von Uexküll 1921) as distinct from the total environment, and to respond to it as an organized perceptual field (James 1971). Thus, according to the Gestalt view of perception (e.g., see Koffka 1935; Köhler 1947), the composite picture of a species' Umwelt is more than the sum of its constituent parts (see Hinde 1970).

Several authors (e.g., see Svårdson 1949; Hildén 1965) have viewed habitat selection as the reaction to certain specific environmental cues or 'sign stimuli' (Russell 1943). According to the principle of summation of heterogeneous stimuli (Tinbergen 1951) it is not necessary that a habitat

possess all the features characteristic of the species' optimal habitat in order that it be selected; it is sufficient that the combined effect of the few key sign stimuli exceed the threshold of the species' settling reaction (Hildén 1965).

Hildén considered habitat selection a two-staged process: the first stage, settling down and exploring the area, is released by features of the landscape; the second stage, selection of a breeding territory within the approved habitat, depends on whether the sign stimuli exceed the threshold of the bird's settling reaction. Carrying this mechanism one stage further, the selection of the specific nest site within the approved territory would depend on the recognition of relevant cues. Such a process could involve aspects of both Gestalt perception and stimulus summation. Habitat analysis would then consist of two stages: describing the Umwelt of a species (sensu immediate environment), and then attempting to identify those proximate factors or sign stimuli according to which the selection is made. The validity of such an approach depends, of course, on the ability of the investigator to select relevant variables.

The role of multivariate methods in habitat analysis is 1) to consider simultaneously the various factors which are considered to describe the Umwelt of a species, and to express these in simplified form (e.g., principal component analysis); and 2) to reduce the dimensionality of the data set to those factors which contribute most to characterizing the habitat of the species, and which differentiate it best

from the habitats of other species (e.g. discriminant function analysis).

The application of multivariate techniques to avian habitat selection is a relatively recent trend. James (1971) used principal component analysis (PCA) and discriminant function analysis (DFA) to ordinate the breeding habitats of 46 species along vegetation gradients in Arkansas. Whitmore (1975, 1977) employed the same techniques in a comparable study of 24 species in Utah. These studies emphasized the detection of habitat relationships among species over a large area rather than within a community, in order to determine which habitat variables characterized the occurrence and distribution of each species.

Wiens (1973) maintained that the value of examining within-site habitat selection was as important as understanding variation in habitat selection over a range of habitats. Conner and Adkisson (1977) applied PCA to the nesting habitat of a community of woodpecker species on a 20 km<sup>2</sup> study area. Smith (1977) applied PCA and DFA to a community of passerine species in a small watershed in order to assess the importance of the environmental gradient to the distribution of the species. McCrimmon (1978) used PCA to describe those aspects of the habitat associated with nest site selection among 5 species of herons, and to assess the separation of the species' nest sites. Rice (1978) used PCA and DFA to assess the habitat relationships of two interspecifically territorial vireo species.

## METHODS

## Sampling Methods

Nest Site Characteristics

Kingbird nests were located through intensive searching of the study area during the 1976 and 1977 breeding seasons. The nests were observed throughout the breeding season, and, where possible, the contents of each nest were examined at least once a week. Some nests were not reached because of either their height and position in the nest tree, or the condition of the nest tree (i.e., spindly, deteriorating, or dead). The rest were reached only with much time spent in the nest tree and, as a consequence, much disturbance to the nesting birds. Therefore, no attempt was made to relate nest site selection to breeding success.

Once the young had fledged from the nests, habitat analysis was performed around each nest site at three levels of resolution: macrosite, microsite, and nest tree. Concentric circular plots, .07 ha (macrosite) and .01 ha (microsite) in area, were established with the location of the nest as their common centre. The macrosite plots were used to sample on a large scale the vegetation surrounding the nest, in the event that kingbirds, which forage largely off the ridge, responded to large scale habitat differences. The microsite plots were employed, firstly, to achieve a finer resolution of habitat analysis around the nest sites, in case subtler differences proved important, and, secondly, to provide a



nest site sampling unit which would be more comparable in area to the .01 ha random plots used to sample the study area vegetation.

In both macrosite and microsite plots every tree  $\geq 5$  cm in diameter at breast height (dbh) was identified to species and was recorded in the appropriate size class (intervals of 5 cm dbh). From these data 13 variables were generated: total density of stems, total basal area of stems, 7 stem size classes, total density of Manitoba maple, green ash, peach-leaved willow, and sandbar willow. The establishment of several size classes ensured that even subtle structural differences in nest site composition would be identified if they proved important to the kingbird species. Stems  $< 5$  cm dbh were considered too small to be selected as nest trees, and too short to constitute a major influence on nest site selection. Stems  $> 35$  cm dbh were sufficiently infrequent ( $< 5\%$  of total stems occurred in any larger size class) that they were combined in one size class. The major tree species were included as potentially important habitat variables because their life forms represent distinctly different structural configurations, which could elicit different responses from kingbirds.

Two additional variables describing height and extent of the canopy were also included. Average tree height within the macrosite plots was determined from the heights of 10 randomly selected trees, measured with a Haga altimeter. Within the microsite plots maximum tree height was determined

by measuring the tallest tree. An estimate of canopy cover at or above the height of each nest was obtained by taking plus or minus readings for the presence or absence, respectively, of foliage, along each of two perpendicular diameters of each plot (both macrosite and microsite). These cover readings were made using an ocular sighting tube held at armslength and perpendicular to the ground (see James and Shugart 1970, p. 735).

At each nest tree 5 characteristics were measured: distance of the nest from the north edge of the ridge (an index of horizontal separation of the nests), nest tree height, dbh and crown volume, and nest height. Two more variables were then generated: relative nest tree height (i.e., relative to the average tree height in the macrosite), and relative nest height (i.e., relative to the height of the nest tree).

#### Characteristics of the Study Area Vegetation

The overstory vegetation was sampled in order to characterize the floristic and structural composition of the study area. This permitted the detection of any vegetation patterns with which the distribution of kingbird nests might be correlated. The method employed ensured objective evaluation of the variation in community structure by avoiding the prior arbitrary designation of synecological units.

The study area was surveyed and gridded into twenty 100 x 100 m cells using surveyor's transit and tape. The

north and south edges of the ridge were arbitrarily delimited on the basis of the north and south extent of stems  $\geq 3$  m in height. Rectangular quadrats (random plots), 5 x 20 m, were set according to a stratified random sampling scheme in which 5 plots were established randomly within each cell of the grid (Fig. 3). The location of each plot was determined by randomly selecting pairs of coordinates along two sides of a cell to describe the location of the northeast corner of the plot. Each plot was then positioned as precisely as possible, with the long axis of the plot parallel to the long axis of the study area. The shape and orientation of the plots were chosen in order to better elucidate the north-south pattern of heterogeneity considered to exist in the vegetation of the ridge (Löve and Löve 1954; M. Levin pers. comm.). The use of rectangular plots oriented perpendicular to the axis of the vegetation gradient maximized the probability that a plot would fall completely within a vegetation zone, thereby minimizing the within-plot variance (see LaFrance 1972).

In each plot all trees  $\geq 5$  cm dbh were identified to species and were recorded in the appropriate size class. From these data the 13 habitat variables used in the nest site analyses were generated. In addition, the conventional Wisconsin school summary statistics (Curtis and McIntosh 1950) were calculated to provide a descriptive overview of the study area vegetation.

Voucher specimens of each species identified were deposited in the herbarium of the University of Manitoba Field Station, Delta Marsh. Botanical nomenclature follows Scoggan (1957).

## Statistical Analysis

### Univariate Methods

Because of the small sample sizes, particularly of western kingbird nests, the samples from both years for each species were lumped in the analysis. The results of t-tests performed on the individual variables between the years for each species indicated that the lumping of samples was statistically valid. Student's t-tests were also performed on all variables to assess the significance of differences in species means. Where the variances of any variable were unequal between the two samples (as revealed by F-test), the  $t^*$ -test (see Noether 1971) was used instead of the Student's t-test.

Correlation matrices were constructed for the nest site and random plot data sets. These matrices were examined to determine the degree of interrelationship of the habitat variables within each data set.

### Multivariate Methods

While univariate analyses yield detailed information about individual variables, they ignore the covariance structure of the variables. Therefore, the multivariate techniques of principal component analysis, discriminant

function analysis, and Hotelling's  $T^2$ -test were used on the various data sets. For details of the theoretical and computational aspects of these techniques see Anderson (1958), Rao (1964, 1970), Seal (1966), and Morrison (1967).

The objective of principal component analysis (PCA) is to summarize the variation contained in the original set of variables in a smaller set of transformed variables. These principal components are mutually orthogonal (hence, independent) linear combinations of the original variables, of the form

$$Y = a_1 Z_1 + a_2 Z_2 + \dots + a_p Z_p$$

where  $Z_1, Z_2, \dots, Z_p$  is the set of standardized values for the original variables, and  $a_1, a_2, \dots, a_p$  is the vector of character coefficients (eigenvector) associated with a given principal component. Principal components explain progressively smaller amounts of the total variation within the original data set. Thus, the first few principal components can usually account for most of the variation in the original data. The result is a reduction in the dimensionality of the data set from several original variables to a few principal components. Furthermore, since each principal component is a linear combination of the original variables, the contribution of each variable to the multivariate complexity of the original data can be discerned by examining the character coefficients associated with each principal component.

In this study PCA was used to identify the major axes of variation in the habitat, and to project the cluster of points representing the plots (nest site and random) onto these major axes of variation. In this manner it was hoped to determine whether the patterns of variation in the ridge vegetation were reflected in the nest site data, or whether the distribution of nests was being influenced by factors other than those characterizing the vegetation of the ridge. The initial 13 habitat variables of the macrosite plots of both kingbird species were collectively subjected to PCA to discover the relative position of each species in the habitat space. This procedure was repeated using the microsite data. The resulting ordinations were compared to a similar ordination derived from a PCA of the random plots for the same set of variables. Next, the habitat data for each species were subjected to PCA separately at both the macrosite and microsite levels so that the importance of habitat factors to each kingbird species could be assessed without the influence of the other species' data set (PCA is somewhat weighted toward larger data sets).

While PCA is very useful in reducing the dimensionality of the original data to a conceptually manageable level, it does not identify those variables which are most important in contributing to the statistical separation of groups. Nor does PCA provide the basis for tests of significant differences between group means, especially when performed on correlation matrices, as in this study.

Discriminant function analysis (DFA) provides a mathematically objective method for separating groups. The goal of DFA is to weight and linearly combine the original variables in such a way that the groups are forced to be as statistically distinct as possible. The analysis computes a linear function of the form

$$D = w_1 Z_1 + w_2 Z_2 + \dots + w_p Z_p$$

where  $D$  is the score on the discriminant function, the  $w$ 's are weighting coefficients, and the  $Z$ 's are the standardized values of the original variables. This function defines a linear axis through the cluster of points representing the individuals of the two groups to be discriminated, such that the distance between the groups is maximized. Whereas in PCA as many principal components can be extracted as there are original variables, in DFA the number of functions derived is either one less than the number of groups, or equal to the number of variables, whichever is smaller. In the present study, because only two groups are compared, only one function is generated.

Since the discriminant function can be considered as an axis, the distribution of discriminant scores (one for each plot) for each group can be plotted along the axis to graphically depict the spatial separation of the groups, a separation that would not necessarily be obvious in the principal component ordination. All data sets were subjected to DFA, and their discriminant scores were plotted as frequency distributions along the discriminant axis. In the

random plot analyses, north and south plots were compared. In the nest site analyses eastern kingbird and western kingbird groups were compared at 4 levels: macrosite, microsite, nest tree, and combined macrosite and nest tree.

The hypothesis of significant differences between the group means in each data set was tested using Hotelling's  $T^2$ -test, the multivariate analogue of Student's t-test.

To test the hypothesis that the kingbird species were separating along the major axis of habitat variation, the data for all nest sites at both the macrosite and microsite levels were multiplied by the discriminant coefficients obtained from the random plot DFA, and the products were summed to produce a discriminant score for each nest site. The significance of the difference in mean discriminant scores between the species was tested using the t-test. For this analysis the macrosite data were scaled by division of the data matrices by 3. Inspection of the variance structure of both the macrosite and random plot data sets revealed that the variances of the macrosite variables were larger by a factor of approximately 3. The purpose of this procedure was to make the variance-covariance matrices of the macrosite data comparable to that of the random plot data without affecting the interrelationship of the variables within a matrix.

All statistical analyses were performed on an IBM 360/65 computer at the University of Manitoba, using programs from the SPSS (Nie et al. 1975) and BMDP (Dixon 1975) packages.



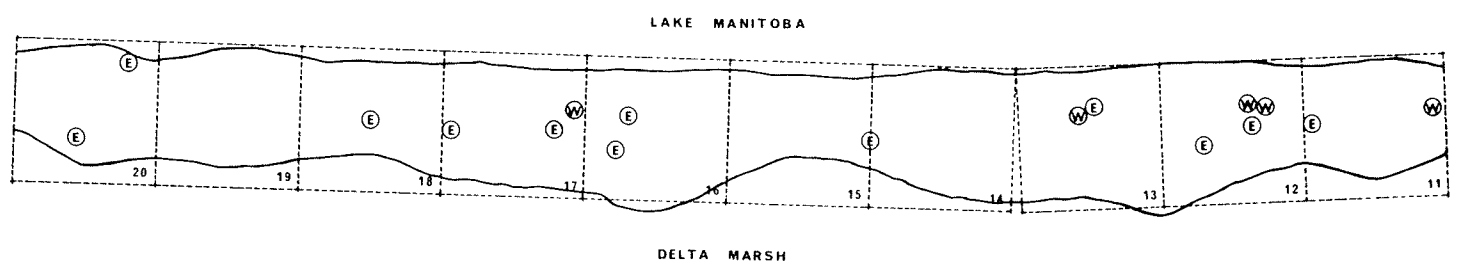
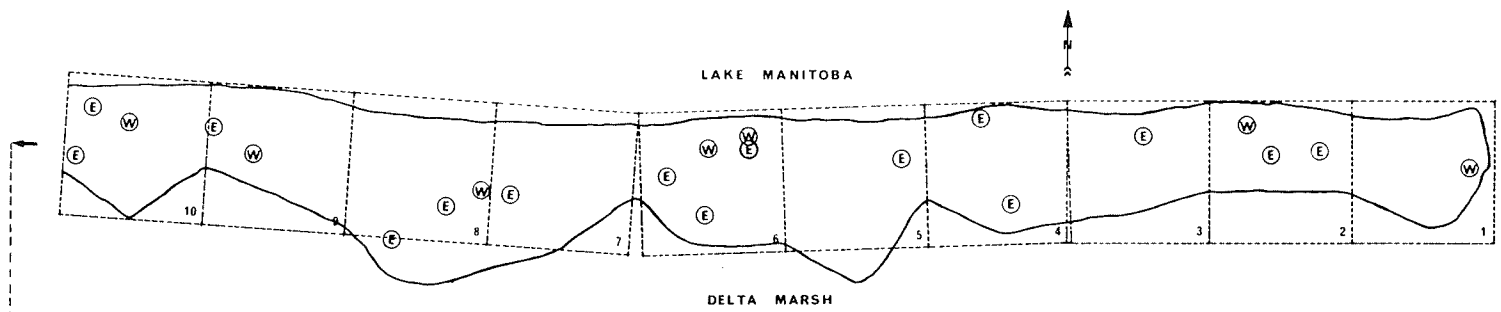
## RESULTS

## Distribution of Nests on the Study Area

Twenty-seven eastern kingbird nests and 12 western kingbird nests were found in 1976 (Fig. 4); 31 eastern and 10 western nests were found in 1977 (Fig. 5). The high degree of overlap in breeding chronology in both seasons indicates an absence of temporal partitioning of nest sites (Fig. 6).

Both species showed similar distributions along the length of the study area (Fig. 7). The hypothesis of uniform distribution of the nests of each species over the length of the study area was tested using a  $\chi^2$ -test for deviations of observed frequency from expectation (Sokal and Rohlf 1973, p. 289) using the combined yearly samples. The only significant clumping occurred in cell 6 (eastern:  $P < .05$ ; western:  $P < .005$ ). In this cell the ridge width exceeds the average of 80 m, and the vegetation appears to be more homogeneous, both floristically and structurally, from north to south than in most cells. The dominant tree species here is peach-leaved willow, the species chosen as the nest tree in nearly every case in cell 6. This cell is also on the edge of the relatively disturbed and sparsely forested area which includes most of the field station buildings. Smith (1966) reported a higher density of both kingbird species in the area around Delta Village inhabited by humans than in the uninhabited areas of the ridge. He suggested that the greater width of

Figure 4. Map of the study area showing the location of eastern (E) and western (W) kingbird nests in 1976. Circles represent the microsite plots.



RIDGE FOREST BOUNDARY ———  
 STUDY AREA GRID - - - - -

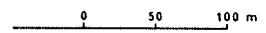
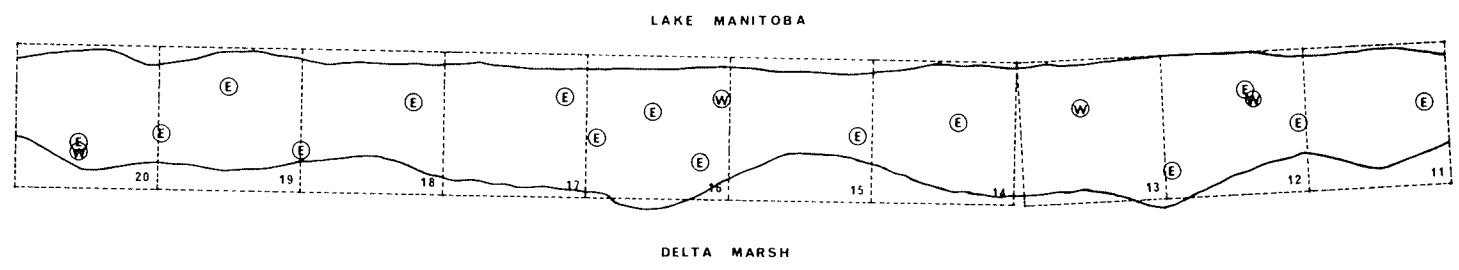
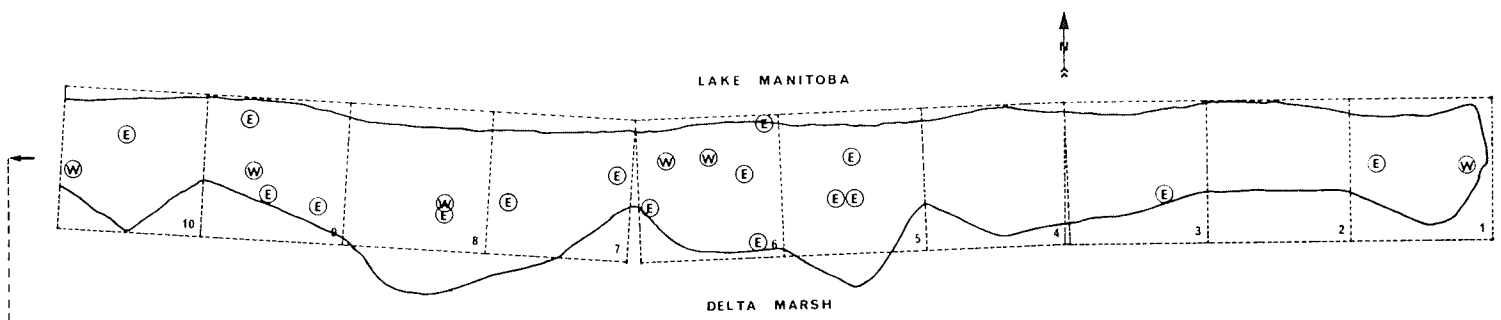
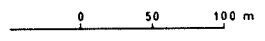


Figure 5. Map of the study area showing the location of eastern (E) and western (W) kingbird nests in 1977. Circles represent the microsite plots.



RIDGE FOREST BOUNDARY ———

STUDY AREA GRID - - - - -



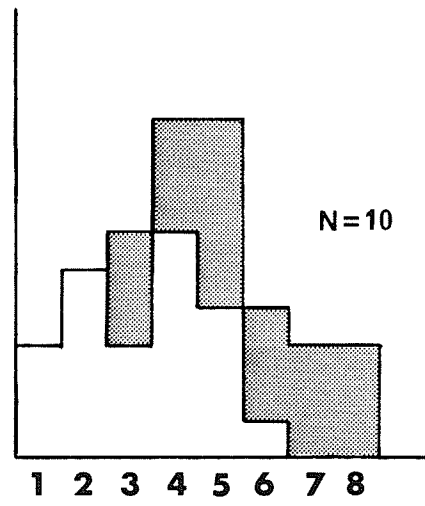
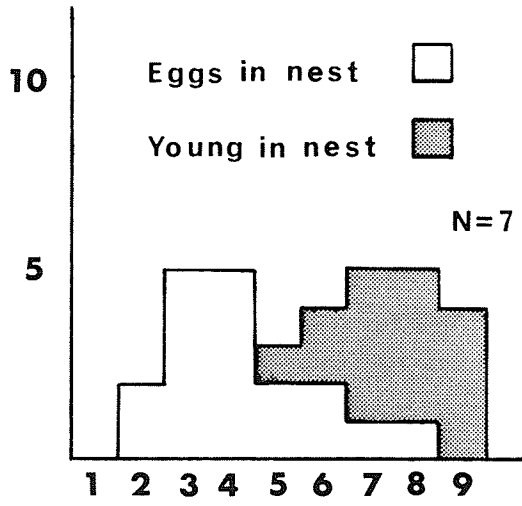
D. I. MacKENZIE 1978

Figure 6. Nesting chronology of eastern and western kingbirds at Delta Marsh, Manitoba, 1976 and 1977. Time intervals correspond roughly to visits to the nests.

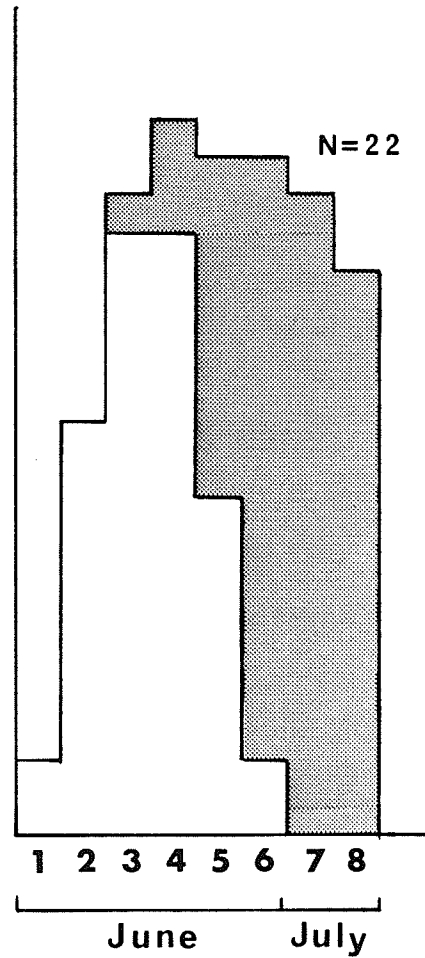
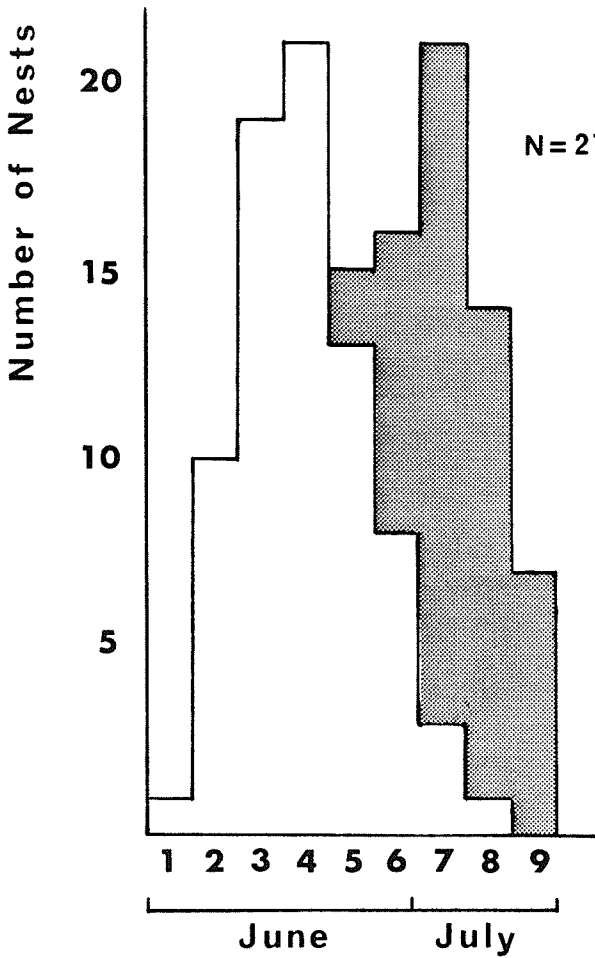
1976

1977

Western Kingbird



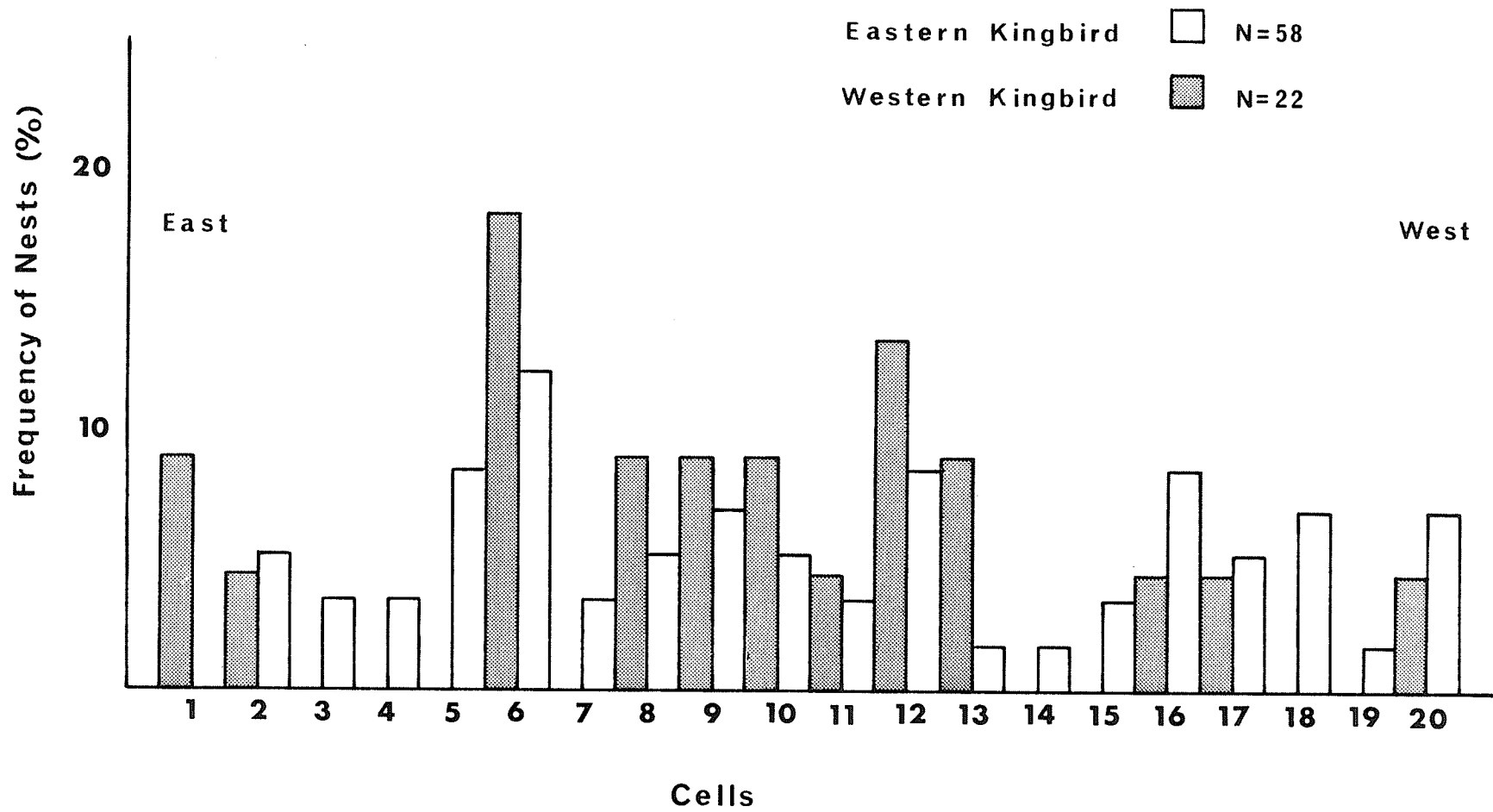
Eastern Kingbird



Time Periods

Figure 7. Frequency distribution of nests (1976-1977)  
along the length of the study area.





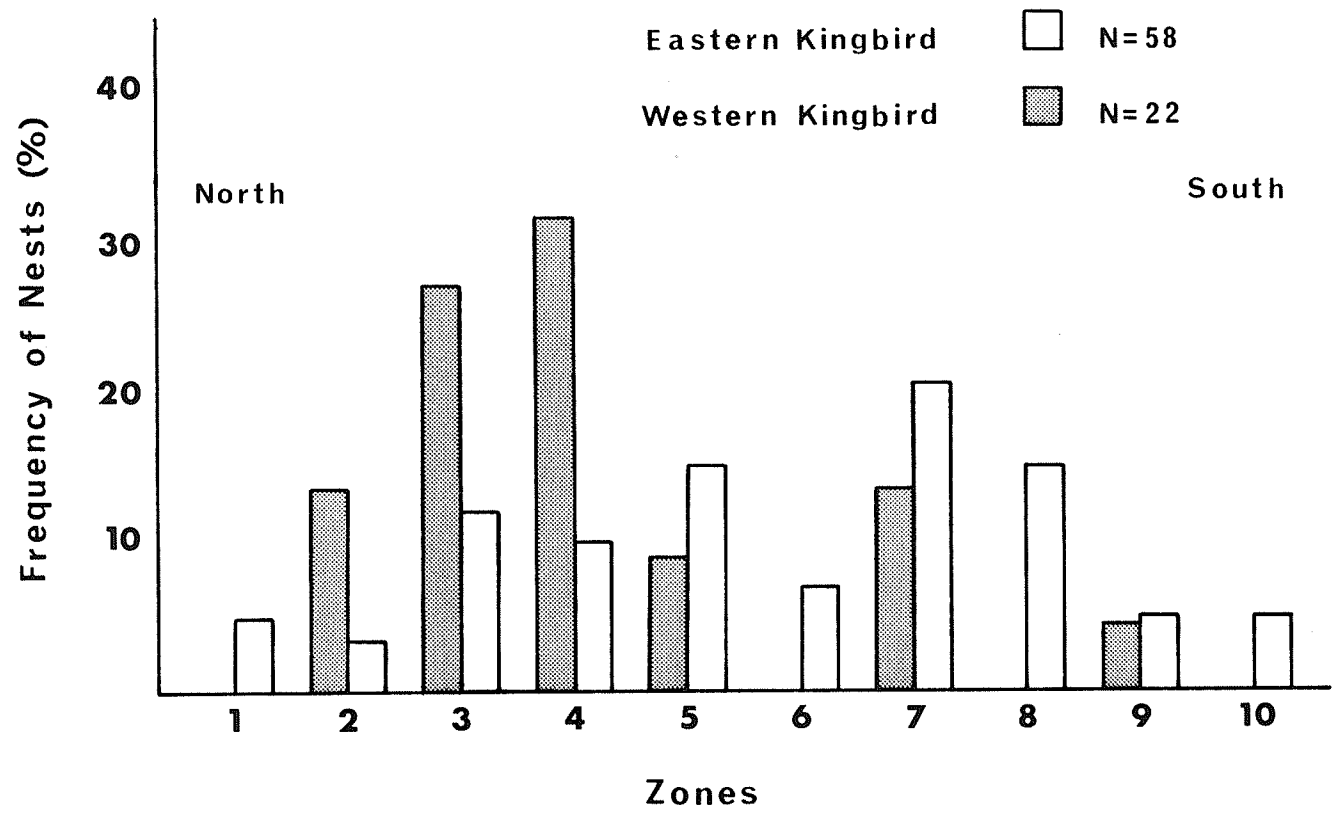
the ridge in the former area might explain the difference. In cell 6 virtually all of the nests were located within the most northerly 80 m, suggesting that the kingbirds did not make use of the increase in ridge width for nesting, or indeed, for spacing their nests, as they were quite clumped within the cell.

The hypothesis that the nests of each species were distributed with equal frequency in the inhabited (cells 6-9 inclusive) versus uninhabited parts (all other cells) of the study area was tested using the  $\chi^2$ -test. There was no significant difference in the distribution of nests between these areas for either species ( $P > .05$ ).

In contrast to the longitudinal distribution of nests, there was a marked difference in their distribution across the study area (Fig. 8). In both years most western kingbird nests were located in the north half of the ridge, whereas the eastern kingbird nests were distributed over both halves of the ridge with almost equal frequency.  $\chi^2$ -test revealed a highly significant difference in the distribution of western kingbird nests (combined samples) between the north and south halves of the ridge ( $P < .005$ ), but the difference in eastern kingbird nest distribution was not significant ( $P > .05$ ).

The discovery of this difference in horizontal distribution of the two species' nests led to the hypothesis that differences existed in the habitat of the study area from north to south, and that the difference in nest distribution

Figure 8. Frequency distribution of nests (1976-1977) across the study area. The ridge forest has been divided into ten zones of equal width from north to south.



was related to floristic and/or structural differences in the pattern of vegetation on the study area.

Because the differences between the species' nest sites are more meaningful when viewed in the context of the pattern of vegetation on the ridge, that pattern will be elucidated first.

### Characteristics of the Study Area

#### Overstory Composition and Structure

Peach-leaved willow, Manitoba maple, and green ash had, respectively, the highest importance values (Table 1). Of the three, peach-leaved willow exhibited the greatest density of stems and by far the greatest basal area. Maple was the most ubiquitous, occurring with a relative frequency of 31.7%, but was half as dominant as peach-leaved willow. This apparent discrepancy is attributable to the differential distribution of the stems of each species among the various diameter size classes (Fig. 9). More than 20% of the stems of peach-leaved willow were greater than 20 cm dbh, compared to 18% for ash, but only 7% for maple.

All species showed a maximum density in the smallest size class and a sharp drop in density thereafter. The curves for maple, peach-leaved willow, and to a lesser extent, ash approximate the classic inverse J-shaped curve suggested by Meyer (1952) as characteristic of any large forest which contains a reasonable diversity of size classes or stand ages. The curves can be interpreted to mean that mortality in these

Table 1. Wisconsin school summary statistics for the major tree species on the forested dune ridge, Delta Marsh.

Tree species	Relative density <sup>1</sup>	Relative dominance <sup>2</sup>	Relative frequency <sup>3</sup>	Importance value <sup>4</sup>
Manitoba maple	24.6	23.0	31.7	26.4
Green ash	16.9	19.1	26.9	21.0
Cottonwood	0.9	5.9	2.1	3.0
<u>Prunus</u> spp.	2.2	0.6	3.8	2.2
Peach-leaved willow	25.6	43.2	22.6	30.4
Sandbar willow	29.8	8.2	12.9	17.0
Total	100.0	100.0	100.0	100.0

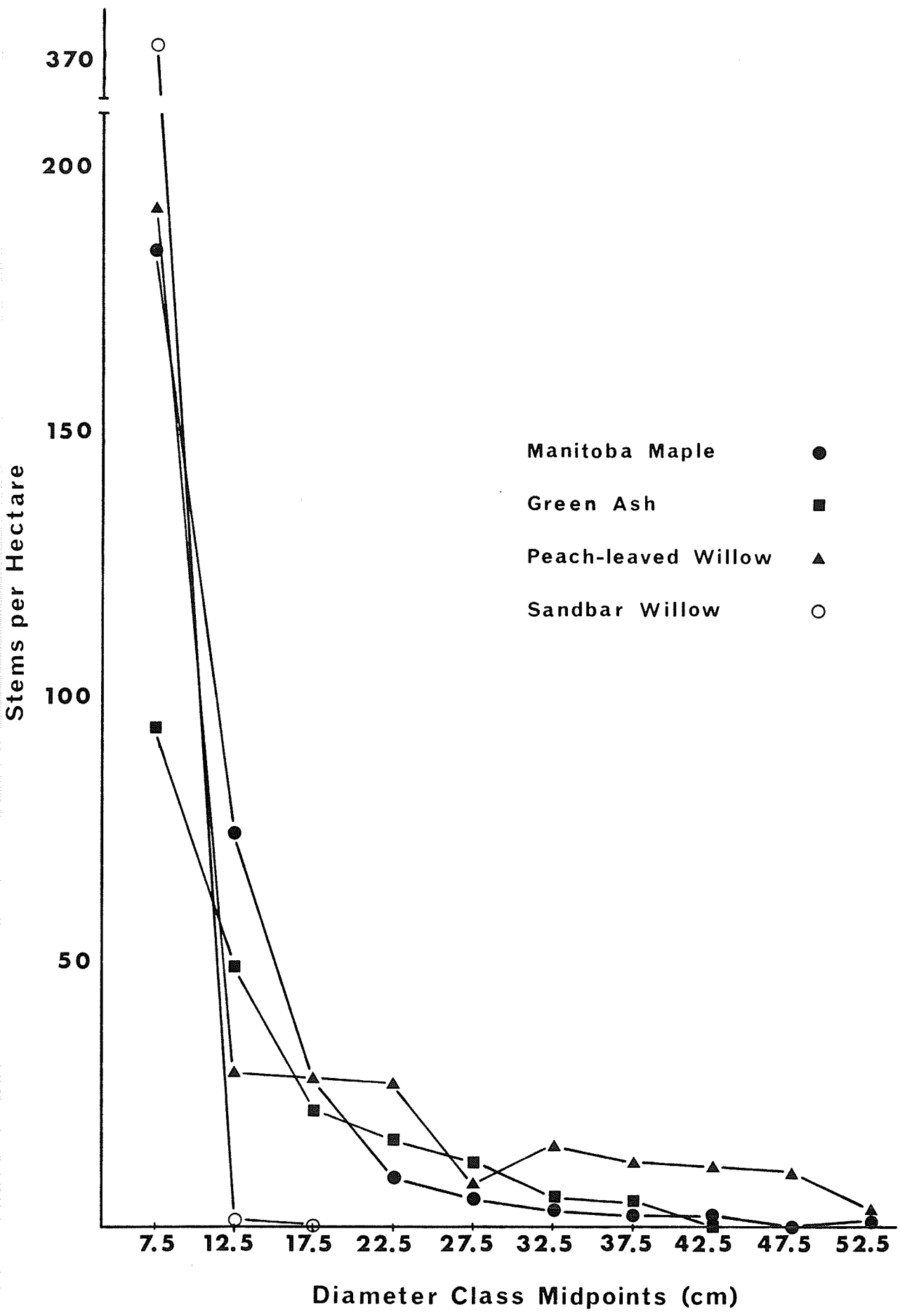
<sup>1</sup>  $\frac{\text{Number of individuals of the species}}{\text{Number of individuals of all species}} \times 100$

<sup>2</sup>  $\frac{\text{Total basal area of the species}}{\text{Total basal area of all species}} \times 100$

<sup>3</sup>  $\frac{\text{Number of points of occurrence of the species}}{\text{Number of points of occurrence of all species}} \times 100$

<sup>4</sup> (relative density + relative dominance + relative frequency) ÷ 3

Figure 9. Mean density per hectare by size class for the major tree species on the forested ridge, Delta Marsh. Stems are grouped into size classes of 5 cm dbh.





species occurs as a constant percentage from one size class to the next, but that sufficient numbers of small trees are established to maintain a balanced population (Johnson et al. 1976).

Sandbar willow is not a true tree, and therefore cannot be expected to show the same size distribution as the other species. On the ridge it seldom exceeds 10 cm dbh, but because its life form here resembles that of a sapling more than that of a shrub, it has been included as a tree species.

#### Environmental Gradient and Vegetation Heterogeneity

For much of the length of the study area the extreme north edge, between the foreshore vegetation and the ridge forest proper, is colonized by sandbar willow (Fig. 10). Here this species takes the form of a low shrubby band and, in places, a narrow zone (< 5 m wide) of dense saplings, too small to have been included in the sampling scheme. Inward from the north edge the sandbar willow density decreases quickly, being replaced by peach-leaved willow, maple and ash. These species, in turn, decrease in density toward the south edge, being replaced by a broad zone of sandbar willow saplings, which become progressively more shrub-like until they disappear in the transition to marsh vegetation.

A plot of the frequency distribution of the stems of the four major tree species across the width of the ridge (Fig. 11) indicates a different pattern for each species.

Figure 10. Diagrammatic cross-section of the forested ridge, Delta Marsh.

Vertical Scale  
1cm = 2m

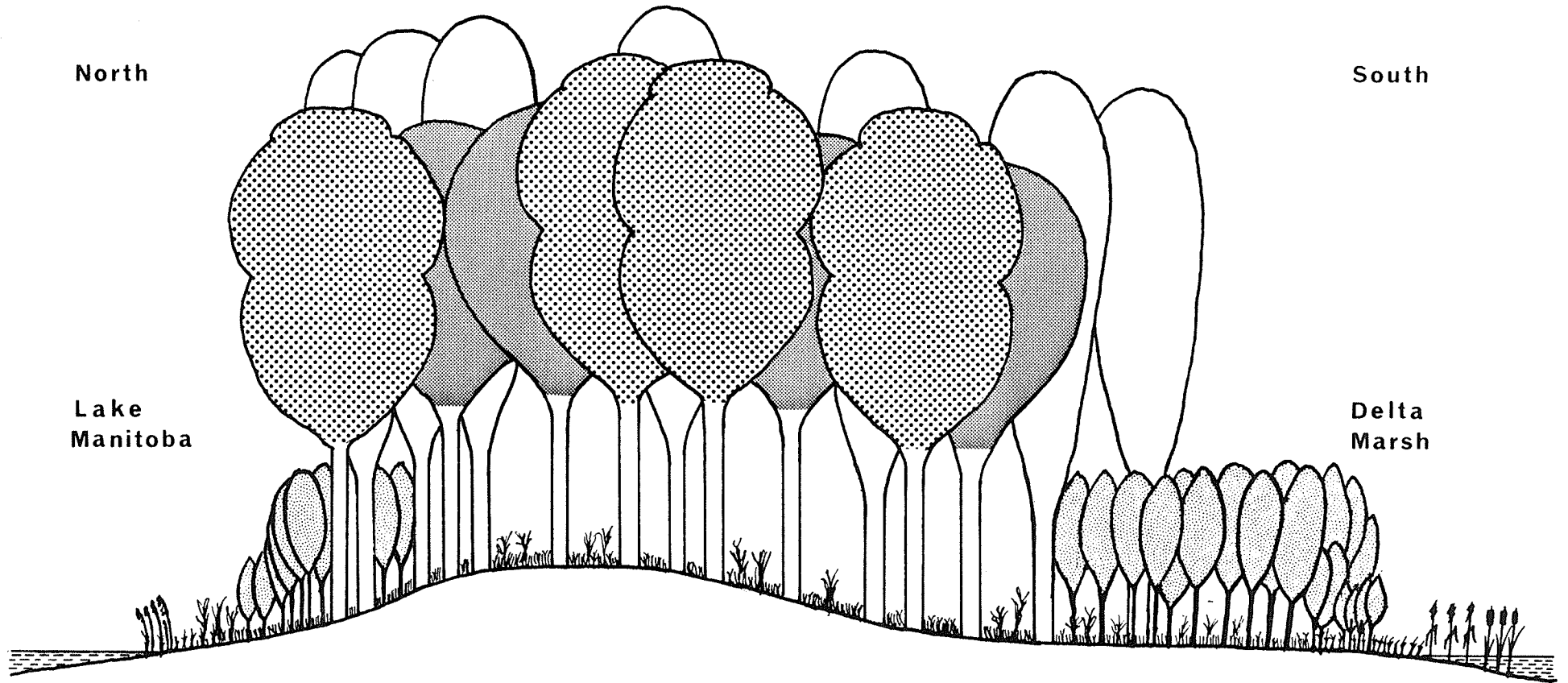
Horizontal Scale  
1cm = 4.5m

North

South

Lake  
Manitoba

Delta  
Marsh



Manitoba Maple



Peach-leaved Willow



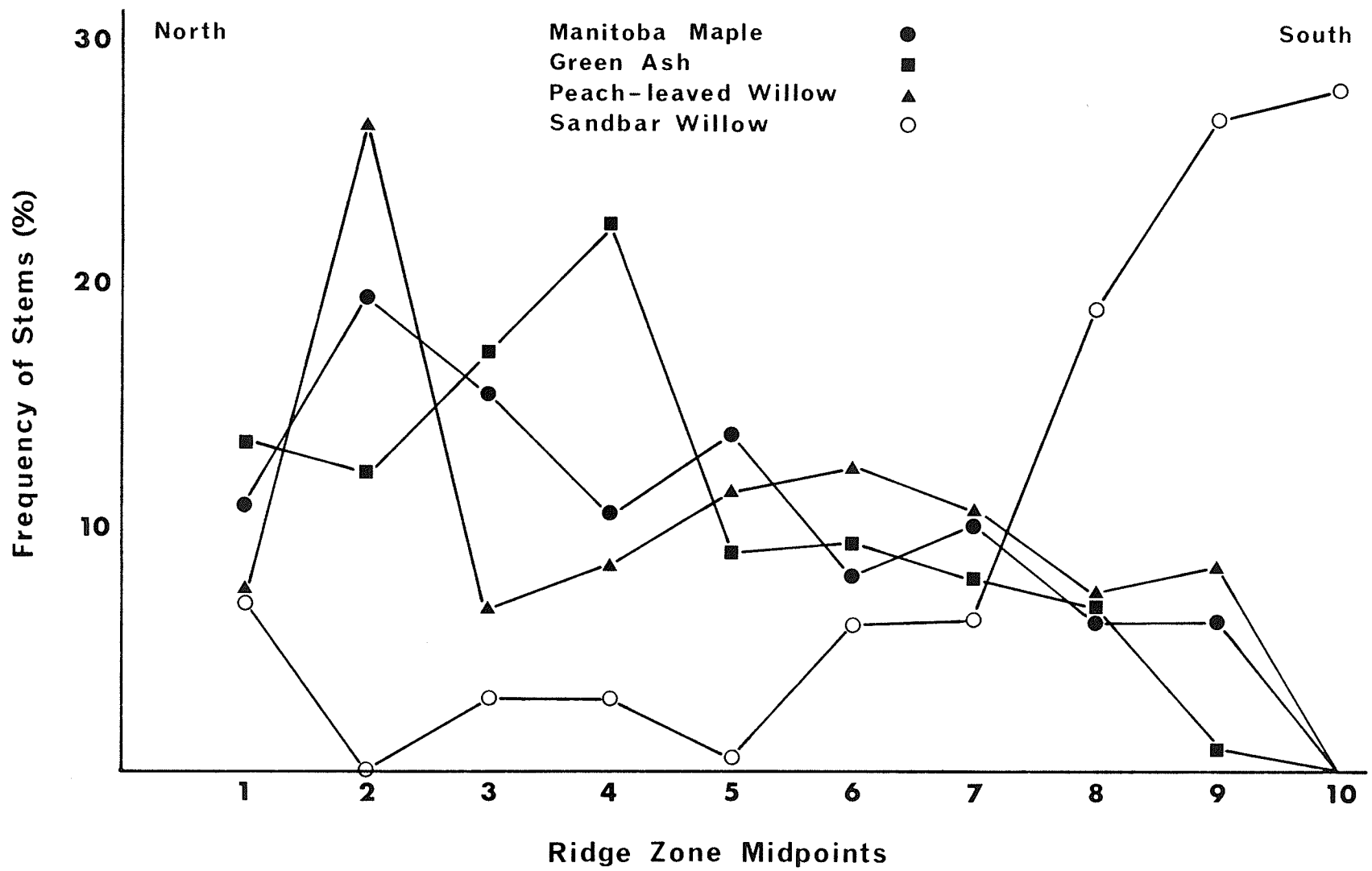
Green Ash



Sandbar Willow



Figure 11. Frequency distribution of the major tree species  
across the width of the ridge.



Peach-leaved willow, maple and ash all reach their maximum density in the north half of the ridge, while sandbar willow gradually reaches an appreciable tree density only in the south half of the ridge.

This vegetation gradient coincides with a topographical and edaphic gradient from north to south. The north zone, a forested dune, averages 2.4 m higher than the south zone which is at or near lake level for most of the length of the study area. The soil in the north zone is drier, sandier, and contains less organic material than the south zone. These environmental factors contribute, no doubt, to the floristic and structural heterogeneity of the ridge vegetation (see Löve and Löve 1954). Because of the rather abrupt change in topography south of the dune formation, the ridge forest appears to be characterized by a distinct north zone, corresponding to the forested dune, and a broader, more or less distinct, but still highly variable south zone, rather than by a gradual change in vegetation composition and structure from north to south.

The relatively greater variability of the south zone vegetation is due, in large part, to the occurrence of clumps of peach-leaved willow, conspicuous among the sandbar willow. This clumped distribution, due to the propensity of peach-leaved willow for vegetative reproduction, appears to coincide with southward extensions of the dune in the form of 'spits', notably, in cells 6 and 10. In cell 16, the existence of a broad blanket of sand, where the dune appears to have been

levelled off and the sand driven southward, may be responsible for the structurally homogeneous stand of mature ash and maple which extends virtually the full width of the ridge. One other notable departure from the general pattern in the south zone is the existence of a structurally homogeneous stand of cottonwood in the south portion of cell 8. The existence of mature trees of these species in the south half of the ridge distorts the floristic and structural pattern of the south zone, thereby contributing to its greater variability.

In summary, the most enlightening approach to the characterization of the ridge vegetation in terms of explaining the kingbird nest distribution has been to recognize floristically and, perhaps, structurally distinct north and south zones. Therefore, for the purpose of analysis, random plots were arbitrarily assigned to north or south groups on the basis of their distance from the north edge of the ridge. Of the original 100 plots, 14 contained no trees, and so were excluded from the random plot data set.

#### Analysis of Habitat Variables

Density of stems 10-15 cm dbh and density of maple, ash, and sandbar willow were significantly different between the north and south zones (Table 2). Peach-leaved willow distribution, predictably, was not significantly different between north and south zones. These results tentatively suggest that the basis of the difference between north and south



Table 2. Means, standard errors\*, and results of t-tests for habitat variables from random plot samples from the forested ridge, Delta Marsh.

Habitat variable	North zone (N=46)	South zone (N=40)	Significance ( $\alpha = .05$ )
Total stems	14.4 $\pm$ 1.19	14.9 $\pm$ 1.53	P=.812
Total basal area	0.2 $\pm$ 0.04	0.2 $\pm$ 0.03	P=.382
Stems 5-10 cm	9.2 $\pm$ 1.05	11.2 $\pm$ 1.60	P=.287
Stems 10-15 cm	2.6 $\pm$ 0.36	1.2 $\pm$ 0.26	P=.003
Stems 15-20 cm	1.1 $\pm$ 0.21	0.8 $\pm$ 0.17	P=.197
Stems 20-25 cm	0.5 $\pm$ 0.10	0.7 $\pm$ 0.20	P=.421
Stems 25-30 cm	0.3 $\pm$ 0.07	0.3 $\pm$ 0.10	P=.888
Stems 30-35 cm	0.3 $\pm$ 0.09	0.3 $\pm$ 0.14	P=.708
Stems > 35 cm	0.5 $\pm$ 0.15	0.3 $\pm$ 0.11	P=.410
Manitoba maple	4.6 $\pm$ 0.63	2.4 $\pm$ 0.55	P=.011
Green ash	3.3 $\pm$ 0.56	1.5 $\pm$ 0.42	P=.010
Peach-leaved willow	4.3 $\pm$ 0.89	3.2 $\pm$ 0.86	P=.371
Sandbar willow	1.4 $\pm$ 0.46	7.7 $\pm$ 1.62	P=.001

\*  $s/\sqrt{n}$



zones is primarily floristic.

Correlation coefficients calculated for all pairs of variables revealed a high degree of interrelationship (Table 3). Each of the variables was significantly correlated with at least one other variable, and many showed significant correlations with several other variables ( $P \leq .01$ ). This level of interrelationship indicated that the composite pattern of variation in the ridge vegetation was more complex than merely the sum of the contributions of the individual variables.

Hotelling's  $T^2$ -test, performed to test the null hypothesis of no difference between the group means of the 13 habitat variables analyzed simultaneously from north and south zones, indicated a highly significant difference between the zones ( $P = .005$ ).

Principal component analysis was employed to summarize the total variation in the random plot data in an ecologically meaningful number of factors (Table 4). The first principal component accounts for 22.8% of the total variance in the original data, and is highly correlated, positively, with total basal area, and negatively, with stems 5-10 cm dbh and sandbar willow. This component represents a broad continuum (from positive to negative) from areas with few but large stems to areas with many small stems, largely of sandbar willow. The amount of variation explained by the first component is not very large, suggesting that the choice of habitat variables was perhaps not optimal. Nevertheless,

Table 3. Correlation coefficients between 13 habitat variables from random plot samples from the forested ridge, Delta Marsh. Symbols represent the variables in their order of appearance in Table 2 (\*  $P \leq .01$ ).

	TST	TBA	ST1	ST2	ST3	ST4	ST5	ST6	ST7	MAP	ASH	PLW	SBW
TST	1.00												
TBA	.12	1.00											
ST1	.92*	-.13	1.00										
ST2	.37*	.08	.10	1.00									
ST3	.19	.22	-.08	.29*	1.00								
ST4	-.04	.41*	-.26*	.01	.31*	1.00							
ST5	-.09	.21	-.24	.03	.20	.26*	1.00						
ST6	-.03	.50*	-.15	-.16	.08	.17	.08	1.00					
ST7	-.07	.82*	-.19	-.10	-.09	.23	.03	.35*	1.00				
MAP	.28*	.06	.13	.55*	.27*	-.06	.02	-.02	-.14	1.00			
ASH	.01	.02	-.12	.40*	.19	.10	.18	-.11	-.07	.02	1.00		
PLW	.46*	.33*	.30*	.25*	.26*	.26*	.01	.18	.21	-.02	-.18	1.00	
SBW	.57*	-.18	.75*	-.26*	-.22	-.22	-.18	-.14	-.16	-.19	-.29*	-.16	1.00

Table 4. Correlations of the habitat variables with the four principal components extracted from the analysis of the random plot matrix.

Habitat variable	Component			
	I	II	III	IV
Total stems	-.52	.83	.10	.10
Total basal area	.64	.51	.40	-.11
Stems 5-10 cm	-.77	.56	.23	.08
Stems 10-15 cm	.01	.57	-.64	-.27
Stems 15-20 cm	.29	.48	-.37	.28
Stems 20-25 cm	.56	.27	.06	.46
Stems 25-30 cm	.40	.09	-.17	.56
Stems 30-35 cm	.46	.20	.43	-.17
Stems >35 cm	.57	.21	.56	-.27
Manitoba maple	-.05	.44	-.50	-.46
Green ash	.20	.10	-.57	.21
Peach-leaved willow	.13	.67	.21	.01
Sandbar willow	-.74	.13	.45	.28
% of total variance	22.8	20.5	16.2	8.8
Cumulative %	22.8	43.3	59.5	68.3

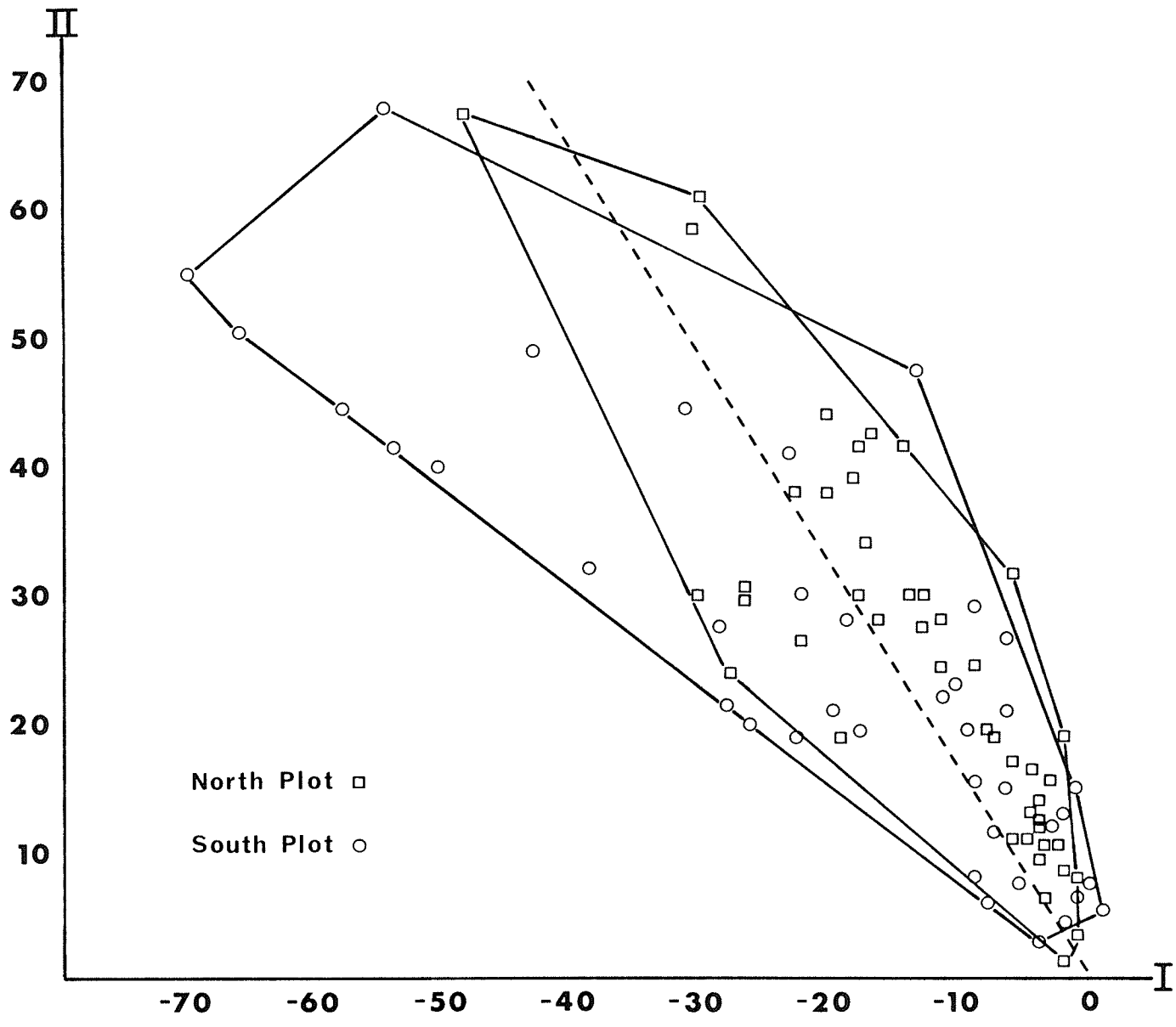
the first component identified objectively what appeared, on the basis of field observations, to be an important pattern of variation in the ridge vegetation.

The second principal component accounts for an additional 20.5% of the total variance. It is highly correlated with total density of stems and density of peach-leaved willow, and thus represents a gradient in density of stems (especially the smaller size classes) and density of peach-leaved willow.

The third and fourth components account for 16.2% and 8.8%, respectively. Their contribution in terms of ecological meaningfulness is ambiguous.

The first two components together account for 43.3% of the total variation, and can be used as axes of the habitat space of the ridge (Fig. 12). A straight line fitted by eye separates the scatter of points such that 80% of the plots occurring in the north zone of the ridge are located to the right of the line, and 60% of the plots occurring in the south zone are located to the left. The relatively greater distinctness of the north zone is indicated by the level of classification achieved, and also by the smaller space occupied in the ordination by the cluster of north points. Plots to the extreme left of the scatter are characterized floristically by sandbar willow almost exclusively, and structurally by a high number of small stems. Plots at the top extreme are dominated floristically by peach-leaved willow, and structurally by many small stems.

Figure 12. Ordination of random plots along the first two principal components of the random plot analysis. Polygons surround the respective scatters of north and south plots. Straight line fitted by eye through the origin maximizes the separation between north and south plots.



Plots near the origin are characterized by ash and maple, and by few but large stems. Predictably, many of the south plots which were misclassified as north (i.e., located to the right of the line) show the influence of the dune substrate, and contain a peach-leaved willow component.

PCA has identified two important trends in the variation of the ridge vegetation. The first emphasizes the structural dichotomy of the north and south zones: large stems in the north zone, and small stems with a strong sandbar willow component in the south zone. The second trend emphasizes density of stems, and identifies a strong peach-leaved willow influence.

DFA was performed on the random plot data to achieve the maximum separation possible between north and south zones, and to evaluate the relative power of each of the variables to achieve discrimination between the groups. The analysis identified density of stems 5-10 cm dbh, total density of stems, density of sandbar willow, and stems 10-15 cm dbh as, respectively, the most important contributors to separation of the zones (Table 5). Note the similarity between this discriminant function and the first principal component.

A frequency distribution of discriminant scores was obtained by multiplying the original values of the random plot variables by the discriminant function coefficients and summing the values to produce a discriminant score for each plot (Fig. 13). The distribution can be considered an

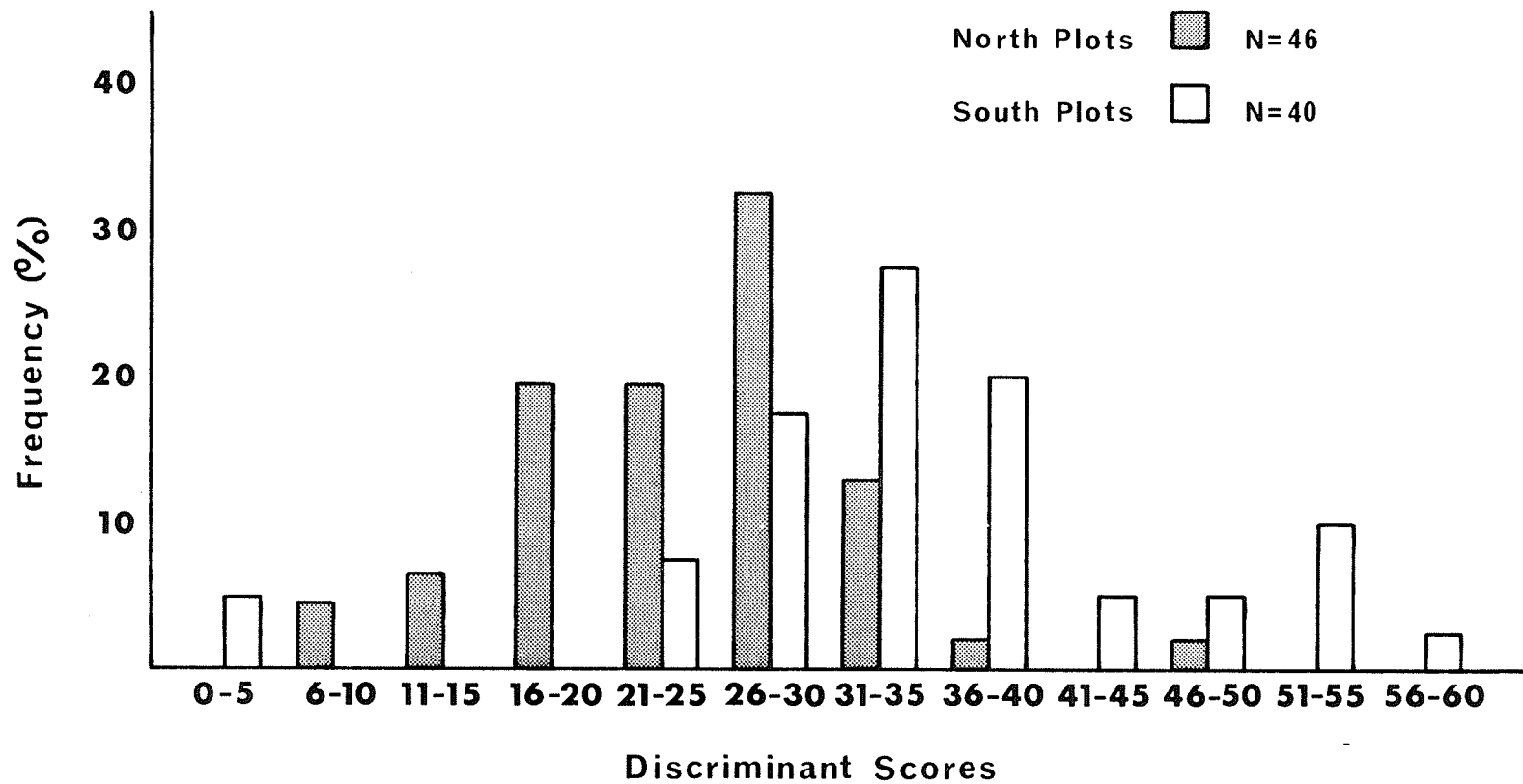
Table 5. Standardized discriminant function coefficients from the analysis of the random plots.

Habitat variable	Coefficient <sup>1</sup>
Total stems	5.672
Total basal area	-0.170
Stems 5-10 cm	-7.023
Stems 10-15 cm	-1.658
Stems 15-20 cm	-1.060
Stems 20-25 cm	-0.469
Stems 25-30 cm	-0.389
Stems 30-35 cm	-0.360
Stems > 35 cm	-0.809
Manitoba maple	0.247
Green ash	0.152
Peach-leaved willow	0.775
Sandbar willow	1.902

<sup>1</sup> The absolute value of each coefficient represents the relative contribution of its associated variable to the discriminant function



Figure 13. Frequency distribution of discriminant scores  
obtained from analysis of the random plot data.



ordination of the plots from north to south (i.e., from left to right) across the width of the ridge. Note that, consistent with the pattern established in the PCA ordination, the south zone shows more variability than the north zone. Both this ordination and that produced by PCA will be particularly useful reference models in comparing the results of the nest site analyses.

### Characteristics of the Nest Sites

#### Importance Values of the Tree Species

An examination of the importance values of the major tree species around the kingbird nest sites revealed some interesting differences in the two species (Table 6).

At the macrosite level, the values for peach-leaved willow and green ash were much higher around western kingbird nests than around eastern nests. The most striking difference, however, was in the importance of sandbar willow which had a value around eastern kingbird nests 4.3 times the value it achieved around western nests. A large sandbar willow component appeared in only 25% of eastern kingbird macrosites, reflecting their location in the extreme south portion of the ridge.

At the microsite level, the difference between the two kingbird species with respect to peach-leaved and sandbar willow importance values was still obvious. However, the importance value of ash around eastern nests increased relative to its value at western sites.

Table 6. Importance values of the major tree species at kingbird nest sites on the forested ridge, Delta Marsh.

Tree species	Eastern kingbird		Western kingbird	
	Macro-site	Micro-site	Macro-site	Micro-site
Manitoba maple	23.6%	19.2%	21.2%	22.4%
Green ash	24.6	28.7	32.0	27.0
Cottonwood	7.3	6.6	5.5	1.6
<u>Prunus</u> spp.	0	0	0	0
Peach-leaved willow	28.9	32.0	37.7	49.0
Sandbar willow	15.6	13.5	3.6	0
Total	100.0	100.0	100.0	100.0

## Analysis of Individual Variables

### i) Macrosite Variables

Total density of stems, stems 5-10 cm dbh, and sandbar willow density were all highly significantly different between the kingbird species (Table 7). Density of stems > 35 cm dbh and average tree height were also significantly different.

### ii) Microsite Variables

A pattern of differences similar to that observed at the macrosite level was observed in the microsites (Table 8). The significant difference for stems 10-15 cm dbh and the absence of a significant difference in maximum tree height represent the major departures from the macrosite pattern. This latter variable is not really comparable with average tree height, and given the small sample size of trees measured, the non-significance of maximum tree height is not surprising.

### iii) Nest Tree Variables

All nest tree variables except relative nest tree height were significantly different between the species (Table 9). Nest tree height and dbh, and nest height were highly significantly different. Western kingbirds chose, on the average, larger, taller nest trees than easterns, and nested higher, not only in absolute terms, but also in terms of relative position in the nest tree. Predictably, western kingbird nests, situated on the dune, for the most part, were located significantly closer to the north edge of the ridge.

Table 7. Means, standard errors, and results of t-tests for habitat variables from eastern and western kingbird macrosites.

Habitat variable	Eastern (N=58)	Western (N=22)	Significance ( $\alpha = .05$ )
Total stems	75.2 $\pm$ 4.06	53.1 $\pm$ 3.96	P<.001
Total basal area	1.3 $\pm$ 0.09	1.6 $\pm$ 0.13	P=.071
Stems 5-10 cm	45.1 $\pm$ 4.28	23.1 $\pm$ 3.01	P<.001
Stems 10-15 cm	11.4 $\pm$ 0.90	8.9 $\pm$ 1.18	P=.098
Stems 15-20 cm	7.2 $\pm$ 0.59	5.5 $\pm$ 0.70	P=.074
Stems 20-25 cm	4.4 $\pm$ 0.57	5.4 $\pm$ 0.95	P=.383
Stems 25-30 cm	3.3 $\pm$ 0.42	4.1 $\pm$ 0.85	P=.397
Stems 30-35 cm	1.9 $\pm$ 0.27	2.6 $\pm$ 0.37	P=.146
Stems > 35 cm	1.9 $\pm$ 0.35	4.1 $\pm$ 0.71	P=.008
Manitoba maple	17.8 $\pm$ 2.02	12.5 $\pm$ 1.83	P=.057
Green ash	16.7 $\pm$ 2.02	16.9 $\pm$ 2.59	P=.943
Peach-leaved willow	19.1 $\pm$ 3.05	20.3 $\pm$ 4.72	P=.830
Sandbar willow	18.6 $\pm$ 3.98	1.8 $\pm$ 1.37	P<.001
Canopy cover %	60.6 $\pm$ 2.72	56.4 $\pm$ 3.29	P=.328
Mean tree height m	10.3 $\pm$ 0.38	12.3 $\pm$ 0.51	P=.003

Table 8. Means, standard errors, and results of t-tests for habitat variables from eastern and western kingbird microsites.

Habitat variable	Eastern (N=58)	Western (N=22)	Significance ( $\alpha = .05$ )
Total stems	15.9 $\pm$ 1.18	10.1 $\pm$ 0.96	P<.001
Total basal area	0.3 $\pm$ 0.03	0.4 $\pm$ 0.05	P=.060
Stems 5-10 cm	9.1 $\pm$ 1.16	3.2 $\pm$ 0.77	P<.001
Stems 10-15 cm	2.9 $\pm$ 0.42	1.6 $\pm$ 0.29	P=.011
Stems 15-20 cm	2.4 $\pm$ 0.88	1.1 $\pm$ 0.31	P=.161
Stems 20-25 cm	1.3 $\pm$ 0.30	1.0 $\pm$ 0.32	P=.465
Stems 25-30 cm	0.8 $\pm$ 0.16	1.1 $\pm$ 0.26	P=.366
Stems 30-35 cm	0.4 $\pm$ 0.10	0.6 $\pm$ 0.19	P=.421
Stems > 35 cm	0.7 $\pm$ 0.22	1.6 $\pm$ 0.33	P=.030
Manitoba maple	3.0 $\pm$ 0.62	2.5 $\pm$ 0.71	P=.567
Green ash	4.4 $\pm$ 0.64	2.9 $\pm$ 0.68	P=.120
Peach-leaved willow	5.4 $\pm$ 1.48	4.6 $\pm$ 1.08	P=.680
Sandbar willow	3.2 $\pm$ 0.87	0.0	P<.001
Canopy cover (%)	75.4 $\pm$ 2.57	79.0 $\pm$ 2.36	P=.297
Maximum height (m)	13.6 $\pm$ 0.59	15.8 $\pm$ 0.92	P=.054

Table 9. Means, standard errors, and results of t-tests for variables associated with eastern and western kingbird nest trees.

Variable	Eastern (N=58)	Western (N=22)	Significance ( $\alpha = .05$ )
Distance to north edge (m)	41.2 $\pm$ 2.63	30.5 $\pm$ 2.71	P=.006
Nest tree height (m)	12.1 $\pm$ 0.55	15.3 $\pm$ 0.59	P<.001
Relative nest tree height	1.2 $\pm$ 0.47	1.3 $\pm$ 0.52	P=.232
Nest tree dbh (cm)	24.6 $\pm$ 1.59	36.2 $\pm$ 1.97	P<.001
Nest tree crown volume (m <sup>3</sup> )	87.3 $\pm$ 10.89	142.6 $\pm$ 20.69	P=.024
Nest height (m)	6.8 $\pm$ 0.33	9.6 $\pm$ 0.43	P<.001
Relative nest height	0.57 $\pm$ 0.02	0.64 $\pm$ 0.02	P=.028

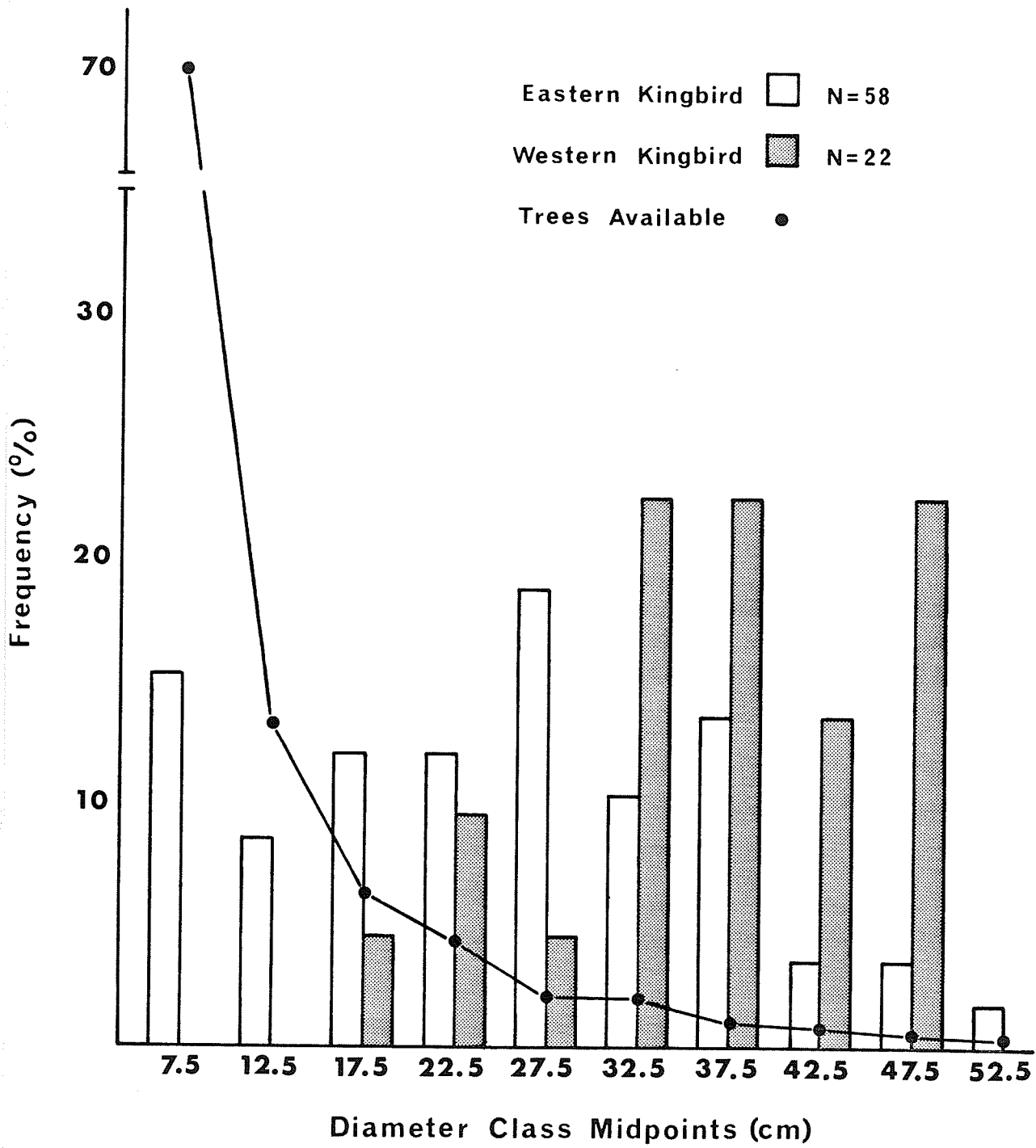


Ash and peach-leaved willow were selected as nest trees most frequently by both species (Table 10). The frequency of selection of these tree species was not significantly different between the kingbird species, using the  $\chi^2$ -test on the combined yearly samples ( $P > .05$ ). The frequency of selection of tree species was not consistent from year to year for either kingbird species. Eastern kingbirds selected ash significantly less frequently ( $P < .05$ ) and sandbar willow much more frequently in 1977 than in 1976. Western kingbirds selected ash less frequently and peach-leaved willow much more frequently in 1977 than in 1976, but the differences were not significant.

Structurally, the difference between the nest trees of each kingbird species was quite marked (Table 9). Eastern kingbirds selected nest trees from virtually the entire range of tree sizes, while most western kingbird nest trees were selected from the largest size classes (Fig. 14). Trees larger than 30 cm dbh represent only 4.6% of the trees on the study area (as deduced from the analysis of the random plots). Yet, 33% of eastern nests and 82% of western nests were selected from this range of sizes. A  $\chi^2$ -test indicated that both these frequencies of selection represented significant deviations from expectation ( $P < .005$ ). Also, the frequency of selection by western kingbirds from this range of tree sizes was significantly higher than that by eastern kingbirds ( $P < .005$ ).



Figure 14. Frequency distribution of tree size classes (all species) selected as nest trees by eastern and western kingbirds, in relation to their relative availability on the study area.



## Multivariate Analysis of Combined Data Sets

### i) Macrosite and Nest Tree Variables

A correlation matrix calculated for the combined macrosite and nest tree data sets indicated a high degree of interrelationship among the variables (Table 11). Each variable was significantly correlated with at least one other variable ( $P \leq .01$ ), and some variables were highly correlated with several variables. Total density of stems, for instance, was highly correlated, positively with the smallest size classes, maple, and both willow species, and distance to the north edge, and negatively with most nest tree variables.

Hotelling's  $T^2$ -test indicated a significant difference between eastern and western kingbird nest sites using the combined macrosite and nest tree data set ( $P = .018$ ). Results of the same test performed on the data sets separately indicated a significant difference between the macrosites ( $P = .035$ ) and a highly significant difference between the nest trees of the two species ( $P < .001$ ).

### ii) Microsite and Nest Tree Variables

An examination of the correlation matrix for the combined microsite and nest tree data sets indicated, again, a high degree of interrelationship among the variables (Table 12). But, while the pattern of correlations between the microsite and nest tree variables was much the same as between the macrosite and nest tree variables, the pattern

Table 11. Correlation coefficients between 22 habitat variables from the combined kingbird macrosite and nest tree data sets. Symbols represent the variables in their order of appearance in Tables 7 and 9.

	TST	TBA	ST1	ST2	ST3	ST4	ST5	ST6	ST7	MAP	ASH	PLW	SBW	CAN	THT	DNE	NTH	RNT	NTD	NTC	NHT	RNH	
TST	1.00																						
TBA	.04	1.00																					
ST1	.88*	-.33*	1.00																				
ST2	.46*	.21	.17	1.00																			
ST3	.21	.37*	-.14	.39*	1.00																		
ST4	.01	.61*	-.36*	.15	.46*	1.00																	
ST5	.01	.64*	-.33*	.04	.44*	.83*	1.00																
ST6	-.28*	.59*	-.48*	-.13	.21	.43*	.35*	1.00															
ST7	-.22	.69*	-.33*	-.04	-.12	.01	.08	.39*	1.00														
MAP	.30*	-.03	.21	.36*	.18	-.01	-.04	-.12	-.11	1.00													
ASH	.04	.05	-.09	.43*	.09	.14	.13	.03	-.11	.13	1.00												
PLW	.29*	.37*	.11	.25	.29*	.24	.17	.12	.16	-.28*	-.33*	1.00											
SBW	.63*	-.42*	.85*	-.15	-.36*	-.41*	-.33*	-.43*	-.30*	.03	-.17	-.17	1.00										
CAN	.18	.47*	-.09	.24	.49*	.45*	.45*	.18	.15	.36*	.19	-.07	-.16	1.00									
THT	-.23	.77*	.07	.07	.36*	.59*	.59*	.64*	.50*	-.13	.19	.17	-.58*	.42*	1.00								
DNE	.36*	-.15	.41*	-.01	.01	-.13	-.04	-.20	-.23	-.06	-.21	.04	.41*	-.04	-.28*	1.00							
NTH	-.42*	.60*	-.63*	.01	.19	.44*	.44*	.53*	.45*	-.16	.11	.13	-.59*	.20	.66*	-.20	1.00						
RNT	-.40*	-.06	-.37*	-.06	-.09	.01	-.01	-.01	-.01	-.09	-.07	-.01	-.29*	-.21	-.17	-.08	.51*	1.00					
NTD	-.49*	.36*	-.60*	-.05	.04	.24	.22	.31*	.36*	-.08	.02	.02	-.58*	.06	.44*	-.35*	.70*	.48*	1.00				
NTC	-.35*	.09	-.40*	.04	.01	.13	.10	.08	.10	.20	.17	-.21	-.40*	.19	.28*	-.25	.46*	.32*	.76*	1.00			
NHT	-.41*	.50*	-.60*	.02	.14	.43*	.42*	.35*	.36*	-.09	.11	.15	-.60*	.06	.57*	-.17	.78*	.32*	.61*	.42*	1.00		
RNH	-.09	-.02	-.10	.04	-.01	.10	.07	-.11	-.03	.07	.02	.13	-.20	-.23	.04	-.05	-.08	-.13	.03	.04	.53*	1.00	

\*  $P \leq .01$

Table 12. Correlation coefficients between 22 habitat variables from the combined kingbird microsite and nest tree data sets. Symbols represent the variables in their order of appearance in Tables 8 and 9.

	TST	TBA	ST1	ST2	ST3	ST4	ST5	ST6	ST7	MAP	ASH	PLW	SBW	CAN	MHT	DNE	NTH	RNT	NTD	NTC	NHT	RNH	
TST	1.00																						
TBA	.15	1.00																					
ST1	.77*	-.28*	1.00																				
ST2	.39*	.06	.40	1.00																			
ST3	.08	.03	.28*	.72*	1.00																		
ST4	.16	.45*	-.05	.42*	.53*	1.00																	
ST5	.13	.61*	-.29*	.00	-.02	.55*	1.00																
ST6	-.01	.43*	-.17	-.11	-.10	.15	.21	1.00															
ST7	-.23	.52*	-.06	.28*	.50*	.22	.00	.03	1.00														
MAP	.35*	-.13	.39*	.20	-.14	-.18	-.17	-.09	-.12	1.00													
ASH	.08	-.08	-.01	.17	-.11	-.04	.01	-.08	-.15	-.12	1.00												
PLW	.22	.26	.27*	.59*	.83*	.48*	.08	.14	.47*	-.24	-.27*	1.00											
SBW	.53*	-.32*	.74*	-.08	-.12	-.23	-.22	-.20	-.23	.20	-.15	-.16	1.00										
CAN	.02	.51*	-.23	.01	.01	.31*	.45*	.31*	.21	.09	.17	.03	-.37*	1.00									
MHT	-.20	.67*	-.45*	-.02	.06	.38*	.48*	.27*	.47*	-.21	.02	.15	-.51*	.53*	1.00								
DNE	.43*	.04	.33*	.21	.15	.28*	.20	-.08	-.14	.01	-.14	.17	.30*	.00	-.20	1.00							
NTH	-.38*	.55*	-.54*	.06	.20	.34*	.37*	.25	.51*	-.27*	.02	.23	-.60*	.45*	.65*	-.20	1.00						
RNT	-.20	.12	-.21	.10	.15	.02	.07	.16	.17	-.03	-.11	.17	-.28*	.04	-.01	-.08	.51*	1.00					
NTD	-.52*	.37*	-.51*	-.13	.03	-.01	.05	.15	.49*	-.10	-.08	.04	-.54*	.35*	.40*	-.35*	.70*	.48*	1.00				
NTC	-.45*	.09	-.40*	-.09	-.06	-.11	-.04	-.09	.24	.02	.11	-.18	-.38*	.27*	.16	-.25	.46*	.32*	.76*	1.00			
NHT	-.31*	.45*	-.51*	.06	.13	.27*	.35*	.09	.36*	-.11	.01	.16	-.58*	.37*	.56*	-.17	.78*	.32*	.61*	.42*	1.00		
RNH	.06	-.01	-.06	.10	-.02	.00	.05	-.18	-.10	.25	.00	-.01	-.15	-.06	.02	-.05	-.08	-.13	.03	.04	.53*	1.00	

\*  $P < .01$

of interrelationships within the microsite matrix itself was different from that among the macrosite variables.

Hotelling's  $T^2$ -test, performed on the combined microsite and nest tree data sets, revealed, quite surprisingly, no significant difference between the species ( $P = .063$ ).  $T^2$ -test on the microsite data alone indicated a very non-significant difference ( $P = .255$ ). This suggests that the size of the microsite plot was simply too small to incorporate enough variation in the vegetation surrounding the nests, upon which to discriminate between the species.

### Principal Component Analysis

#### i) Macrosite Variables

Five principal components were extracted from PCA of the combined kingbird species macrosite data matrix, accounting for 81.8% of the total variance of the original data (Table 13).

The first principal component accounts for 30.3% of the total variance, and is highly correlated, positively with total basal area and the larger stem size classes, and negatively with sandbar willow and stems 5-10 cm dbh. Thus, it represents the same structural dichotomy explained by the first principal component of the random plot PCA. This similarity is surprisingly strong, in view of the difference in plot size, and consequently in the amount of information gathered.

The second principal component accounts for 20.5% of



Table 13. Correlations of the habitat variables with the five principal components extracted from the analysis of the combined kingbird species macrosite matrix.

Habitat variable	Component				
	I	II	III	IV	V
Total stems	-.43	.85	.22	.04	.17
Total basal area	.78	.30	.31	.26	.30
Stems 5-10 cm	-.77	.53	.25	.00	.17
Stems 10-15 cm	.10	.71	-.28	.45	-.29
Stems 15-20 cm	.45	.59	-.11	-.19	-.28
Stems 20-25 cm	.70	.38	-.04	-.40	.18
Stems 25-30 cm	.67	.33	-.09	-.46	.30
Stems 30-35 cm	.68	-.17	.12	.05	.23
Stems > 35 cm	.42	-.20	.44	.66	.27
Manitoba maple	-.14	.37	-.47	.25	.21
Green ash	.13	.19	-.71	.27	.10
Peach-leaved willow	.24	.42	.65	.02	-.49
Sandbar willow	-.81	.20	.24	-.16	.41
% of total variance	30.3	20.5	13.3	9.8	7.9
Cumulative %	30.3	50.8	64.1	73.9	81.8

the total variance. It is highly correlated with total stems and with the smaller size classes, and as such represents a gradient from less dense to denser areas. Again, the similarity with the second component of the random plot PCA is quite close, with the exception that the strong influence of peach-leaved willow in the latter is reduced compared to that of maple in both. The difference in the influence of peach-leaved willow may reflect the difference in size of the sampling units.

The third component, accounting for an additional 13.3% of the variance, appears to represent a contrast between plots having an ash and maple component and those with a peach-leaved willow component. The fourth and fifth components account for 9.8% and 7.9%, respectively. The contribution of the former is ambiguous, while the latter appears to represent a contrast between plots dominated by peach-leaved willow and those influenced by sandbar willow.

A plot of the scores of the macrosite plots along the first two principal components of the combined species analysis (Fig. 15) resembles the ordination of the random plots (Fig. 12) in both shape and position of the scatter. An ordination (Fig. 16) obtained by weighting the macrosite plots with the principal component weights derived from the analysis of the random plots (Table 4) matches very closely the ordination of the combined species macrosite plots (Fig. 15). This would suggest that the distribution of nests represents a response by each species to certain aspects of

Figure 15. Ordination of kingbird macrosite plots along the first two principal components extracted from the analysis of the combined species macrosite matrix. Straight line through the random plot scatter (Fig. 12) is superimposed on the macrosite ordination.

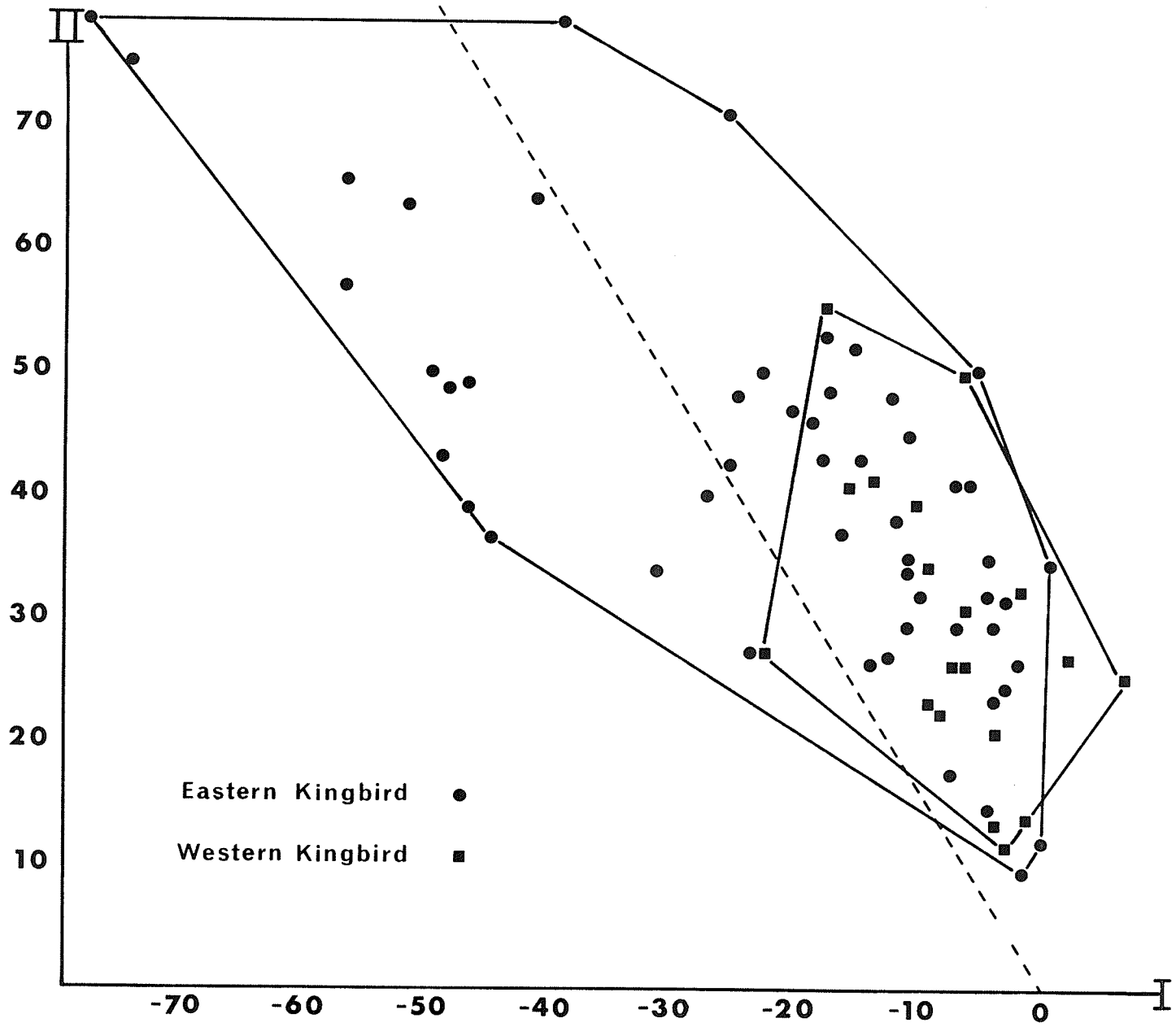
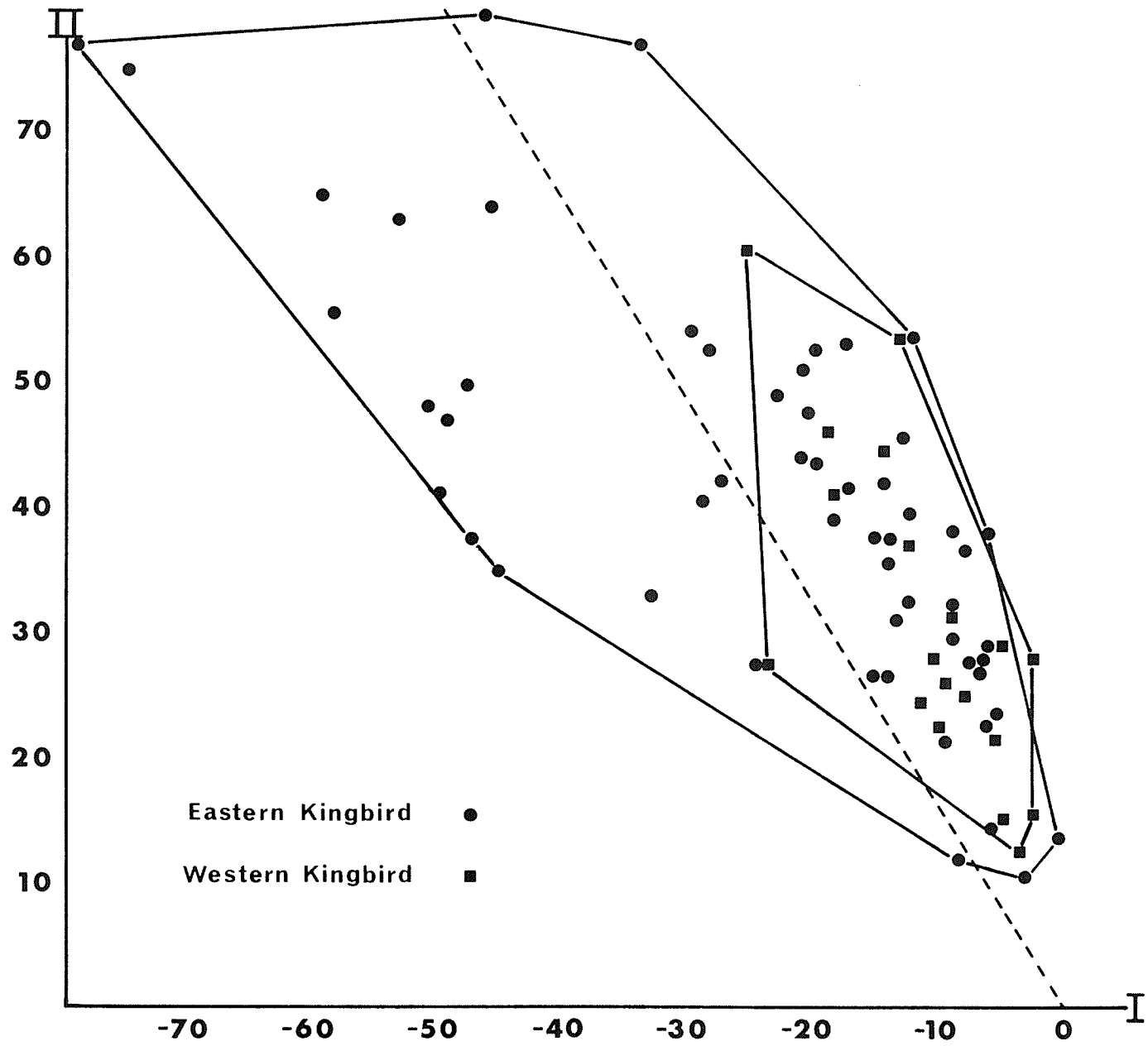


Figure 16. Ordination of the kingbird macrosite plots obtained by weighting the macrosite data with the principal component weights derived from the analysis of the random plots.



the north-south pattern of variation in the ridge vegetation.

A notable difference appears, however, when the straight line fitted to the random plot ordination is superimposed on the macrosite ordinations. Predictably, almost all of the western kingbird plots fall to the right of the line (analogous to the north zone of the random plot ordination), but surprisingly, 75% of the eastern plots also fall to the right of the line. This latter observation is higher than expected on the basis of the microgeographical distribution of eastern kingbird nest sites, and suggests that those eastern nest sites which occur in the south zone of the ridge do not all reflect, in their composition, the type of habitat believed to characterize the south zone in general. In other words, the ordinations suggest that some eastern kingbird nest sites may, in fact, be situated in islands of 'north-zone type' habitat occurring in the south zone of the ridge.

The narrowness or stenotypy of the western kingbird response to the vegetation pattern is indicated by the concentration of the points in a relatively small portion of the habitat space depicted in the macrosite ordination. This portion of the space also contains most of the eastern kingbird points, suggesting, tentatively at least, that this space could describe the set of habitat characteristics preferred by both species.

A separate PCA was performed on the macrosite data of each species individually, in order to identify the features

of each species' realized habitat niche (i.e., habitat component of the realized niche — see Smith 1977). Separate PCA's can be used to investigate how each species responds to the characteristics of the habitat without the influence of the other species' responses on the analysis.

The results of the separate PCA's (Table 14) indicate that the two species respond quite differently to the pattern of vegetation. In fact, their responses as summarized in the first two principal components of each analysis are virtually orthogonal to each other (Fig. 17). The eastern kingbird ordination is very similar to that of the combined species ordination, indicating that the two major trends in the vegetation pattern of the ridge are represented in the first two principal components of the eastern kingbird PCA. The same two trends are represented in the western kingbird ordination, except that their order of importance is reversed. The western kingbird response on the first component resembles the eastern response on the second component, the major exceptions being the replacement of maple by peach-leaved willow as the important floristic influence, and the influence of larger stems. The pattern of correlations on the second component of the western kingbird PCA resembles the pattern on the first component of the eastern PCA, with the addition of a stronger correlation with ash, and weaker correlations with the largest size classes.

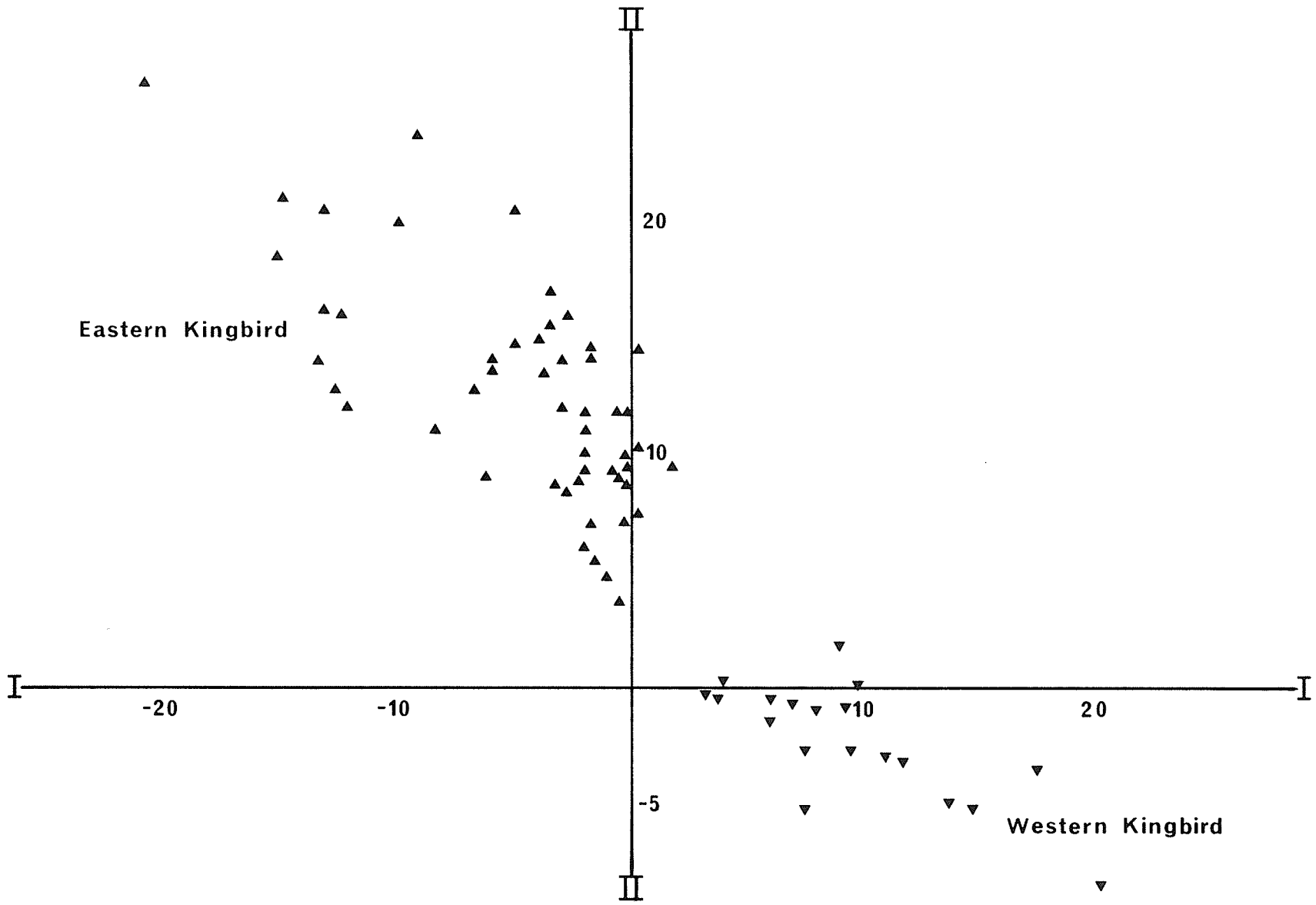
In both species the first two components account for approximately half of the total variance. The two species



Table 14. Correlations of the habitat variables with the first two principal components extracted from the analysis of the individual species macrosite matrices.

Habitat variable	Component			
	Eastern		Western	
	I	II	I	II
Total stems	-.34	.88	.94	-.22
Total basal area	.84	.30	.39	.58
Stems 5-10 cm	-.72	.59	.53	-.77
Stems 10-15 cm	.19	.72	.59	-.14
Stems 15-20 cm	.63	.40	.78	-.03
Stems 20-25 cm	.78	.24	.61	.63
Stems 25-30 cm	.74	.20	.55	.71
Stems 30-35 cm	.75	-.12	-.14	.41
Stems > 35 cm	.50	-.07	-.24	.18
Manitoba maple	-.07	.43	.19	.01
Green ash	.13	.33	-.16	.48
Peach-leaved willow	.31	.26	.78	-.26
Sandbar willow	-.79	.26	-.16	-.56
% of total variance	34.3	18.7	28.6	20.7
Cumulative %	34.3	53.0	28.6	49.4

Figure 17. Ordinations of eastern and western kingbird macrosite plots along the first two principal components extracted from each of the separate species analyses.



differ primarily in the order in which they respond to the major trends in the pattern of variation on the ridge. The eastern kingbird nests are distributed more evenly over the total range of variation in the ridge habitat; therefore, the eastern ordination reflects that of the random vegetation ordination more closely than does the western. The western kingbird nest distribution is restricted largely to the north zone of the ridge; therefore, the major trend in the ridge variation, i.e., the north-south dichotomy, is reflected in the western ordination only secondarily.

ii) Microsite Variables

Four principal components were extracted from the PCA of the combined species microsite matrix, accounting for 73.2% of the total variance in the original data (Table 15).

The first principal component accounts for 26.8% of the variance. It is highly correlated with peach-leaved willow, medium sized stems, stems > 35 cm dbh, and total basal area. The trend here is not clear, but may reflect the presence or absence of peach-leaved willow in a microsite, and the corresponding structural influence of this variable.

The second principal component, accounting for 23.1% of the total variance, is highly positively correlated with stems 5-10 cm dbh, total stems, and sandbar willow, and shows negative correlations with total basal area and the large stem sizes. Clearly, this component represents the same continuum that characterizes the structural difference

Table 15. Correlations of the habitat variables with the four principal components extracted from analysis of the combined kingbird species microsite matrix.

Habitat variable	Component			
	I	II	III	IV
Total stems	.17	.72	.60	.09
Total basal area	.57	-.42	.52	-.17
Stems 5-10 cm	.06	.95	.14	-.08
Stems 10-15 cm	.66	.49	-.14	.35
Stems 15-20 cm	.80	.31	-.42	.05
Stems 20-25 cm	.76	-.10	.25	.19
Stems 25-30 cm	.39	-.39	.64	.17
Stems 30-35 cm	.21	-.34	.42	-.30
Stems > 35 cm	.62	-.14	-.32	-.30
Manitoba maple	-.21	.47	.22	-.12
Green ash	-.12	-.03	.04	.86
Peach-leaved willow	.85	.22	-.20	-.17
Sandbar willow	-.32	.71	.24	-.27
% of total variance	26.8	23.1	13.5	9.8
Cumulative %	26.8	49.9	63.4	73.2

between the north and south zones.

The third component is correlated with stems 25-30 cm dbh, total stems, and total basal area, and seems to represent plots having, at the same time, numerous and fairly large stems. The fourth component shows high correlation only with ash.

In summary, the combined species PCA using the microsite data does not give a meaningful summarization of the information contained in the original variables. Certainly, it does not suggest the close parallel with the random plot ordination that was observed with the macrosite PCA (Fig. 18). In contrast to the macrosite analysis, the microsite PCA suggests that the choice of nest sites is not determined by the obvious patterns of variation in the ridge vegetation. Nevertheless, the ordination of the microsites using the principal component weights derived from the analysis of the random plots is consistent with the pattern observed at the macrosite level (Fig. 19).

### Discriminant Function Analysis

#### i) Macrosite Variables

DFA was performed on the macrosite data to achieve the maximum separation possible between eastern and western kingbird nest sites, and to evaluate the contribution of each variable to discrimination. The analysis identified stems > 35 cm dbh, stems 5-10 cm, total stems, and sandbar willow as, respectively, the four most important contributors

Figure 18. Ordination of kingbird microsite plots along the first two principal components extracted from the analysis of the combined species microsite matrix.

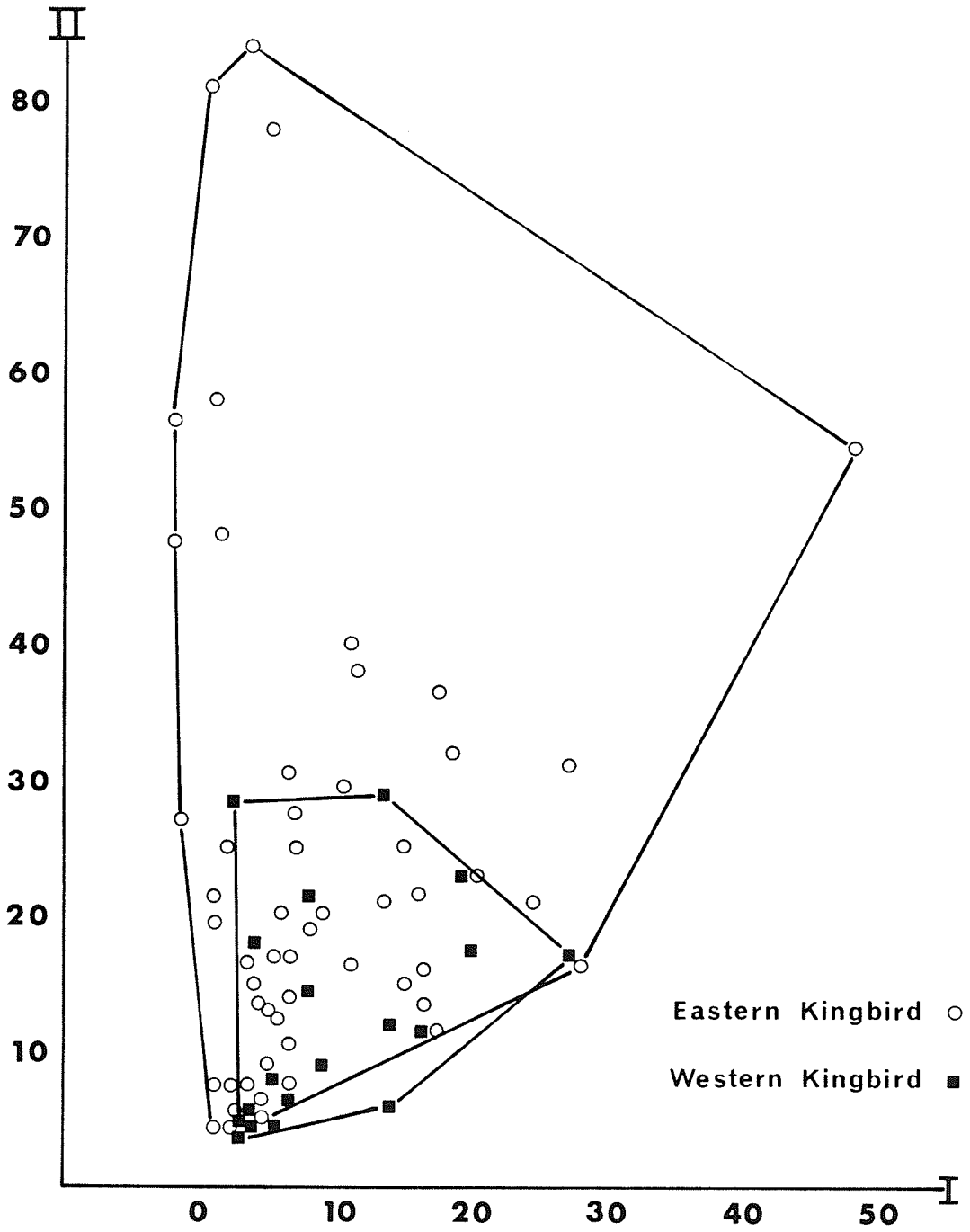
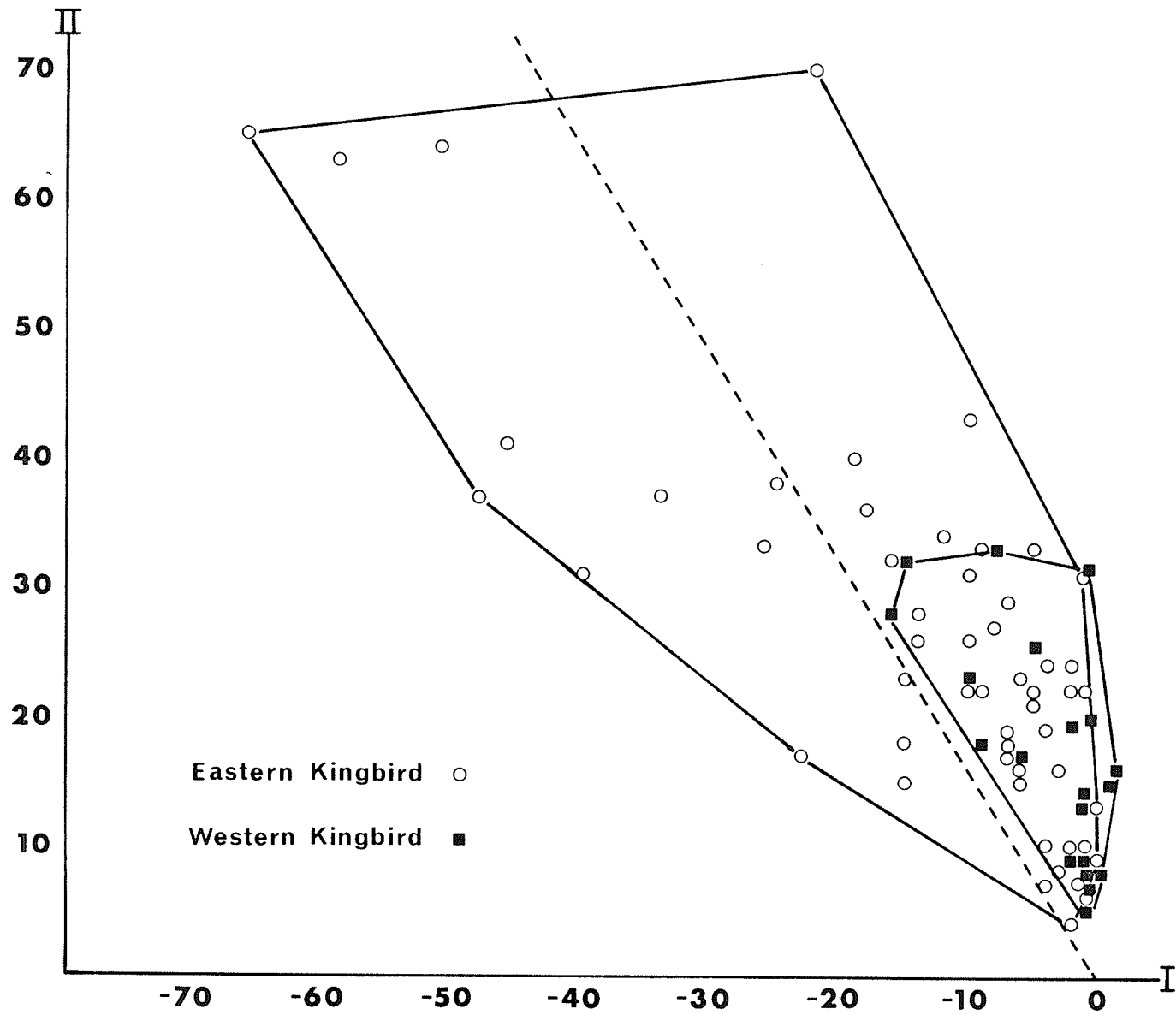




Figure 19. Ordination of the kingbird microsite plots obtained by weighting the microsite data with the principal component weights derived from the analysis of the random plots.



to the separation of the species (Table 16).

A plot of the frequency distribution of the discriminant scores obtained from the macrosites graphically depicts the separation of the two species along the discriminant axis (Fig. 20). Eastern and western kingbird nest sites show a pattern of separation similar to that of the separation between the zones of the ridge, with western sites and north plots at the left end, and eastern sites and south plots at the right end of their respective ordinations.

To test the hypothesis that the factors separating north and south zones were also important in the separation of the kingbird species, discriminant scores were derived by multiplying the scaled macrosite data by the discriminant function coefficients from the random plot DFA. These discriminant scores reflect the response of the kingbird macrosite data to the factors important in the north-south separation (Fig. 21). Student's t-test indicated that the mean discriminant scores were not significantly different between the species ( $P = .216$ ). This result is interpreted to mean that although the nest sites show the same pattern of separation as the random plots, other factors are also influencing the distribution of the nest sites, to the extent that the factors responsible for separating north and south zones are not sufficient to achieve a significant separation of the species.

Table 16. Standardized discriminant function coefficients from the analysis of the kingbird scaled macrosite data

Habitat variable	Coefficient <sup>1</sup>
Total stems	0.528
Total basal area	0.472
Stems 5-10 cm	-0.533
Stems 10-15 cm	0.256
Stems 15-20 cm	0.399
Stems 20-25 cm	-0.258
Stems 25-30 cm	-0.472
Stems 30-35 cm	0.130
Stems > 35 cm	-0.852
Manitoba maple	-0.025
Green ash	-0.252
Peach-leaved willow	-0.254
Sandbar willow	0.526

<sup>1</sup> The absolute value of each coefficient represents the relative contribution of its associated variable to the discriminant function

Figure 20. Frequency distribution of discriminant scores obtained from the analysis of the kingbird scaled macro-site data.

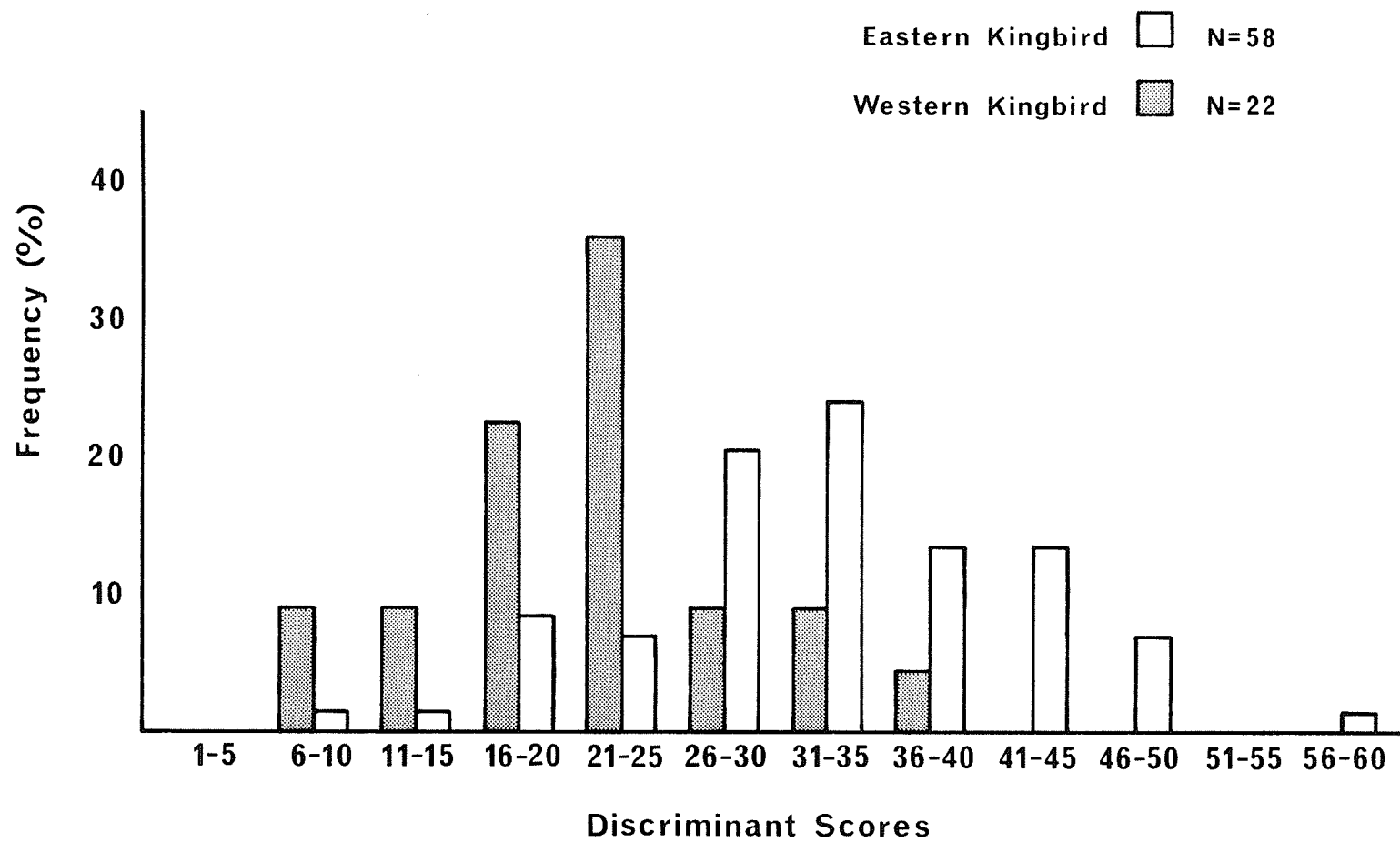
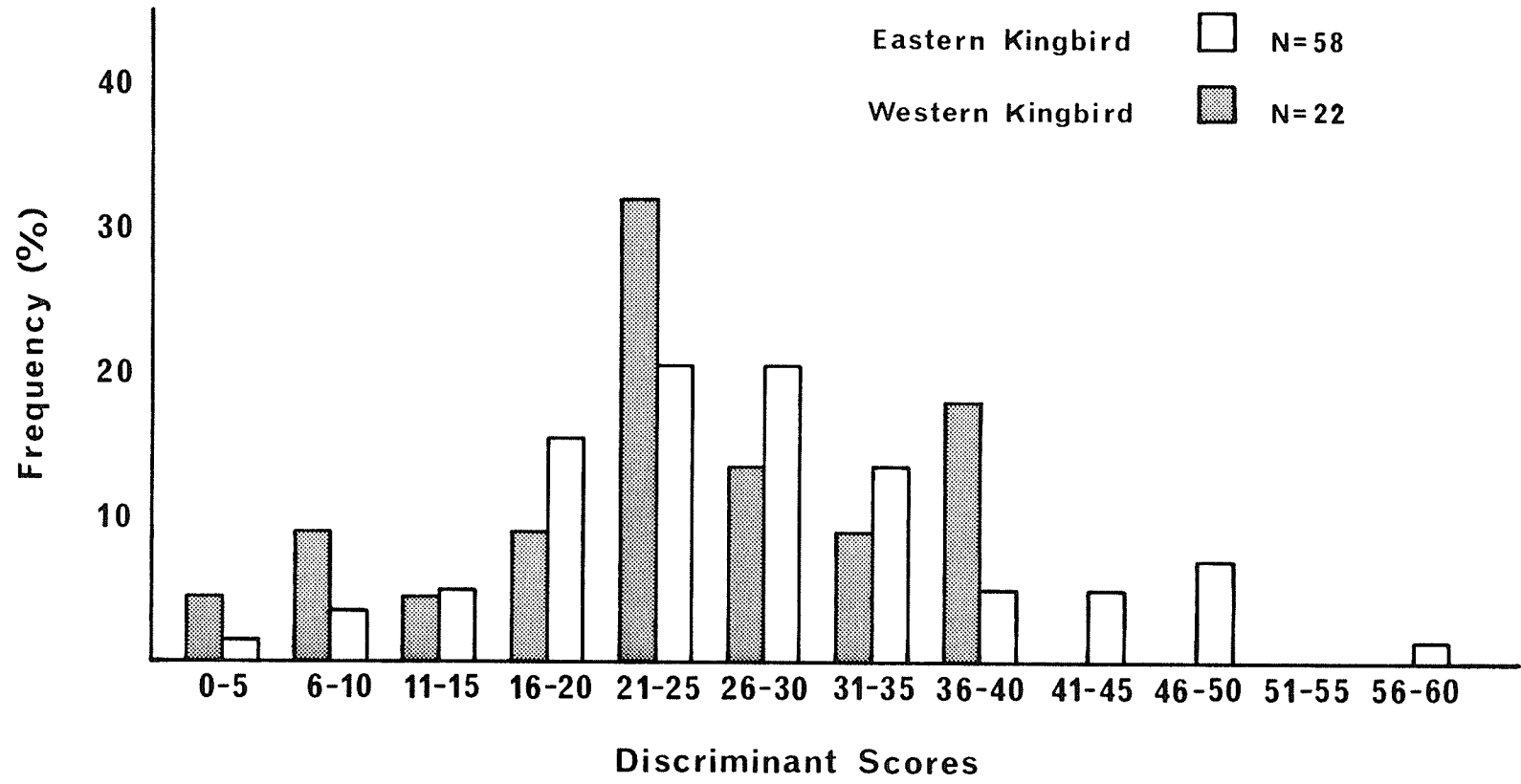


Figure 21. Frequency distribution of discriminant scores obtained by weighting the kingbird scaled macrosite data with the discriminant weights derived from the analysis of the random plots.





ii) Microsite Variables

DFA performed on the microsite plots identified stems > 35 cm dbh, peach-leaved willow, stems 15-20 cm, and stems 5-10 cm as, respectively, the four most important contributors to separation of the species (Table 17).

A plot of the frequency distribution of discriminant scores from the microsite analysis shows a pattern of species separation similar to the pattern observed in the macrosite DFA, although the separation between the species is not as great (Fig. 22). Predictably, a t-test for the significance of mean discriminant scores derived from the discriminant coefficients of the random plot DFA applied to the microsite data indicated a highly non-significant difference ( $P = .491$ ). This supports further the contention that the differences between north and south zones identified in the analysis are not sufficient to account for the observed difference in the distribution of nest sites of the two kingbird species.

Hotelling's  $T^2$ -test revealed that microsites of the kingbird species combined were significantly different from the random plots ( $P < .001$ ). Kingbirds selected sites with fewer small stems and more large stems, and more green ash and less sandbar willow than in random plots (Table 18). The highly significant difference in total basal area together with a highly non-significant difference in the total number of stems, further suggests a preponderance of large stems around kingbird nest sites.

Hotelling's  $T^2$ -test indicated that eastern kingbird

Table 17. Standardized discriminant function coefficients from the analysis of the kingbird microsite data.

Habitat variable	Coefficient <sup>1</sup>
Total stems	0.275
Total basal area	0.011
Stems 5-10 cm	0.337
Stems 10-15 cm	0.308
Stems 15-20 cm	0.353
Stems 20-25 cm	0.280
Stems 25-30 cm	-0.311
Stems 30-35 cm	0.013
Stems > 35 cm	-0.548
Manitoba maple	-0.302
Green ash	0.070
Peach-leaved willow	-0.455
Sandbar willow	0.079

<sup>1</sup> The absolute value of each coefficient represents the relative contribution of its associated variable to the discriminant function

Figure 22. Frequency distribution of discriminant scores  
obtained from the analysis of the kingbird microsite data.

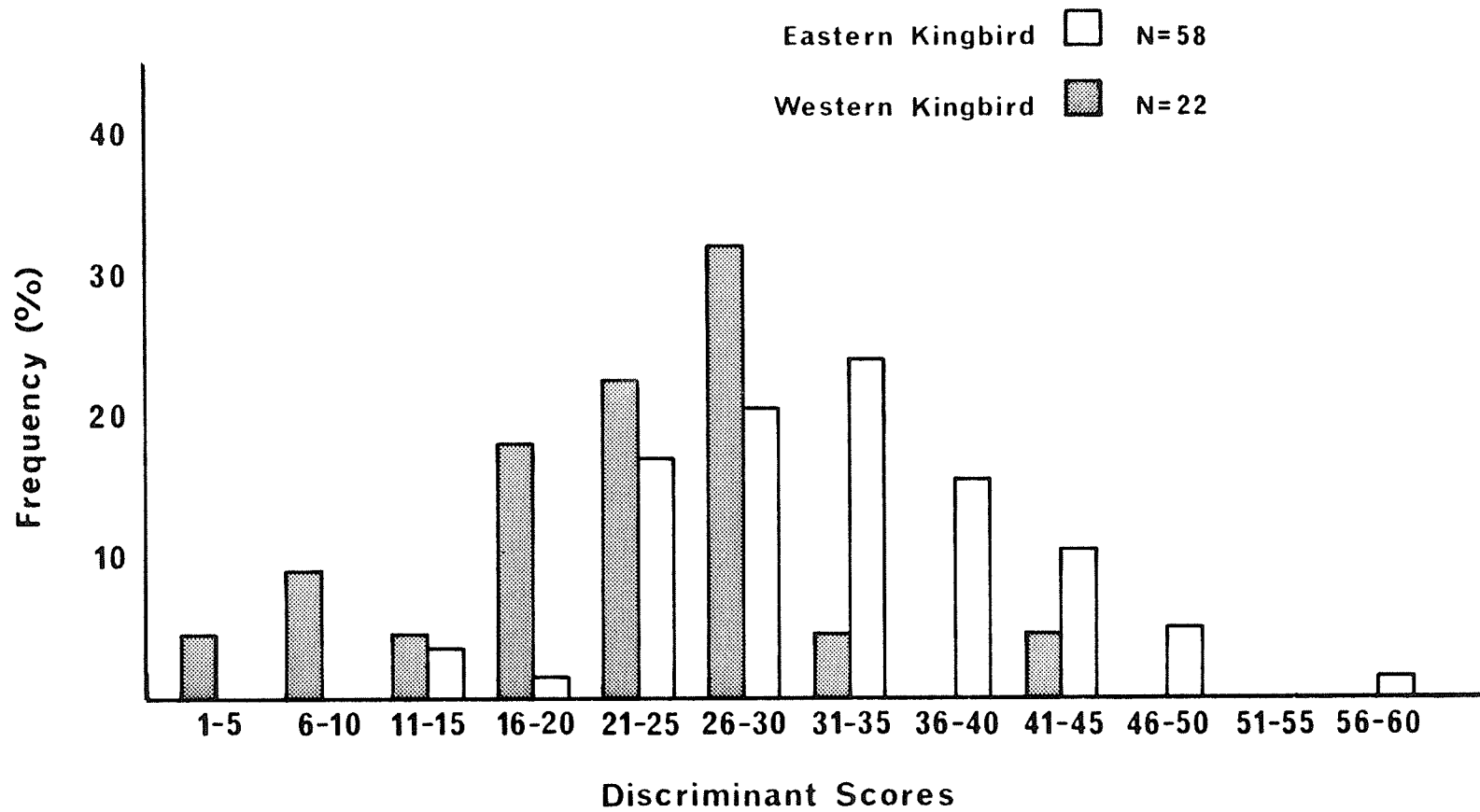


Table 18. Means, standard errors, and results of t-tests of comparisons of habitat variables from kingbird microsites with those from random plots on the forested ridge, Delta Marsh.

Habitat variable	Combined microsites (N=80)	Random vs plots (N=86)		Eastern kingbird microsites (Table 8)	Random vs plots (N=86)	Western kingbird microsites (Table 8)	North vs random plots (Table 2)
Total stems	14.3±0.94	14.6±0.95	P=.813		P=.403		P=.005
Total basal area	0.3±0.03	0.2±0.02	P=.001		P=.025		P=.004
Stems 5-10 cm dbh	7.1±0.87	10.1±0.93	P=.020		P=.304		P<.001
Stems 10-15 cm	2.3±0.24	1.9±0.24	P=.228		P=.074		P=.043
Stems 15-20 cm	1.5±0.23	0.9±0.14	P=.042		P=.032		P=.804
Stems 20-25 cm	1.1±0.20	0.6±0.11	P=.055		P=.079		P=.223
Stems 25-30 cm	0.9±0.14	0.3±0.06	P<.001		P=.003		P=.006
Stems 30-35 cm	0.5±0.09	0.3±0.08	P=.158		P=.340		P=.082
Stems > 35 cm	0.9±0.15	0.4±0.10	P=.007		P=.258		P=.003
Manitoba maple	2.8±0.49	3.6±0.44	P=.261		P=.438		P=.027
Green ash	4.0±0.50	2.5±0.37	P=.017		P=.011		P=.402
Peach-leaved willow	4.4±0.75	3.7±0.62	P=.502		P=.621		P=.687
Sandbar willow	2.4±0.65	4.3±0.86	P=.066		P=.370		P=.006

microsites were significantly different from random plots ( $P = .01$ ). The tendency to larger stems observed in the comparison using the combined species above is less obvious here, but present, nevertheless, and ash was significantly more abundant around eastern sites (Table 18).

Hotelling's  $T^2$ -test also indicated that western kingbird microsites, located almost exclusively in the north zone, were significantly different from north random plots ( $P = .008$ ). Western sites contained fewer small stems, more large stems, less maple, and, of course no sandbar willow (Table 18). The highly significantly greater total basal area combined with the highly significantly fewer total stems, emphasizes the importance of large stems around western kingbird sites.

Thus, both species appear to select nest sites non-randomly, at least at the microsite level, even though the difference between them is not significantly different.

### iii) Nest Tree Variables

DFA performed on the variables associated with the nest tree identified nest height, nest tree height and relative nest height as, respectively, the three best discriminators of kingbird nest trees (Table 19). This emphasis on height as a basis for separation of the species is enlightening, because it provides a partial explanation, at least, for the inability of the factors characterizing north and south zones to account for the significant difference in the distribution of the nests of the two species. A variable

Table 19. Standardized discriminant function coefficients from the analysis of the kingbird nest tree data.

Nest tree variable	Coefficient <sup>1</sup>
Distance to north edge	0.273
Nest tree height	1.379
Relative nest tree height	0.116
Nest tree dbh	-0.536
Nest tree crown volume	0.153
Nest height	-2.109
Relative nest height	0.858

<sup>1</sup> The absolute value of each coefficient represents the relative contribution of its associated variable to the discriminant function

representing height was not included in the random plot data set, and thus the response of the kingbird data matrices to a height component could not be evaluated.

Nest height was the most important discriminator of the two species at the level of nest tree. To determine if nest height was an important contributor to the vertical separation of these two species elsewhere, the frequency distribution of nest heights on the ridge (Fig. 23) was compared with that of 231 eastern and 103 western kingbird nests from Manitoba, Saskatchewan, and Alberta which were reported to the Prairie Nest Records Scheme (Fig. 24). A t-test indicated that western kingbird nests were again significantly higher than eastern kingbird nests ( $P < .001$ ). Thus, the observations on the ridge are consistent with the pattern of vertical separation shown by these species elsewhere in sympatry, and probably reflect an innate preference in western kingbirds for higher nest sites, at least in the sympatric portions of their range.

#### iv) Combined Macrosite and Nest Tree Variables

DFA performed on the combined data sets identified stems 5-10 cm, total stems, nest height, nest tree height, and stems  $> 35$  cm as, respectively, the five best discriminators of eastern and western kingbird nest sites (Table 20). A  $T^2$ -test indicated a highly significant difference ( $P < .001$ ) using just these five variables.

Figure 25 represents a parsimonious summarization of the



Figure 23. Frequency distribution of eastern and western kingbird nest heights on the forested ridge, Delta Marsh.

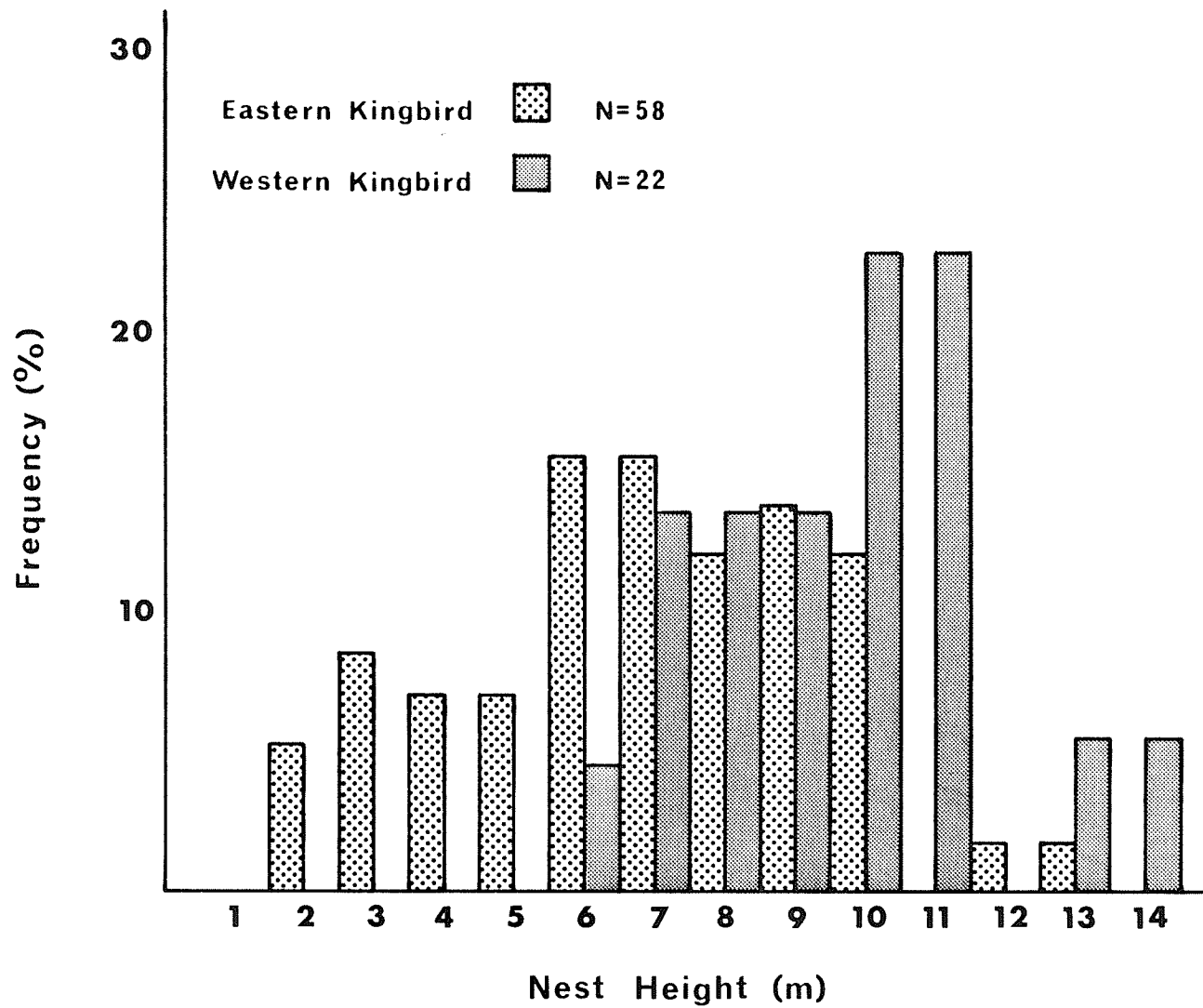


Figure 24. Frequency distribution of eastern and western kingbird nest heights recorded in the Prairie Nest Records Scheme.

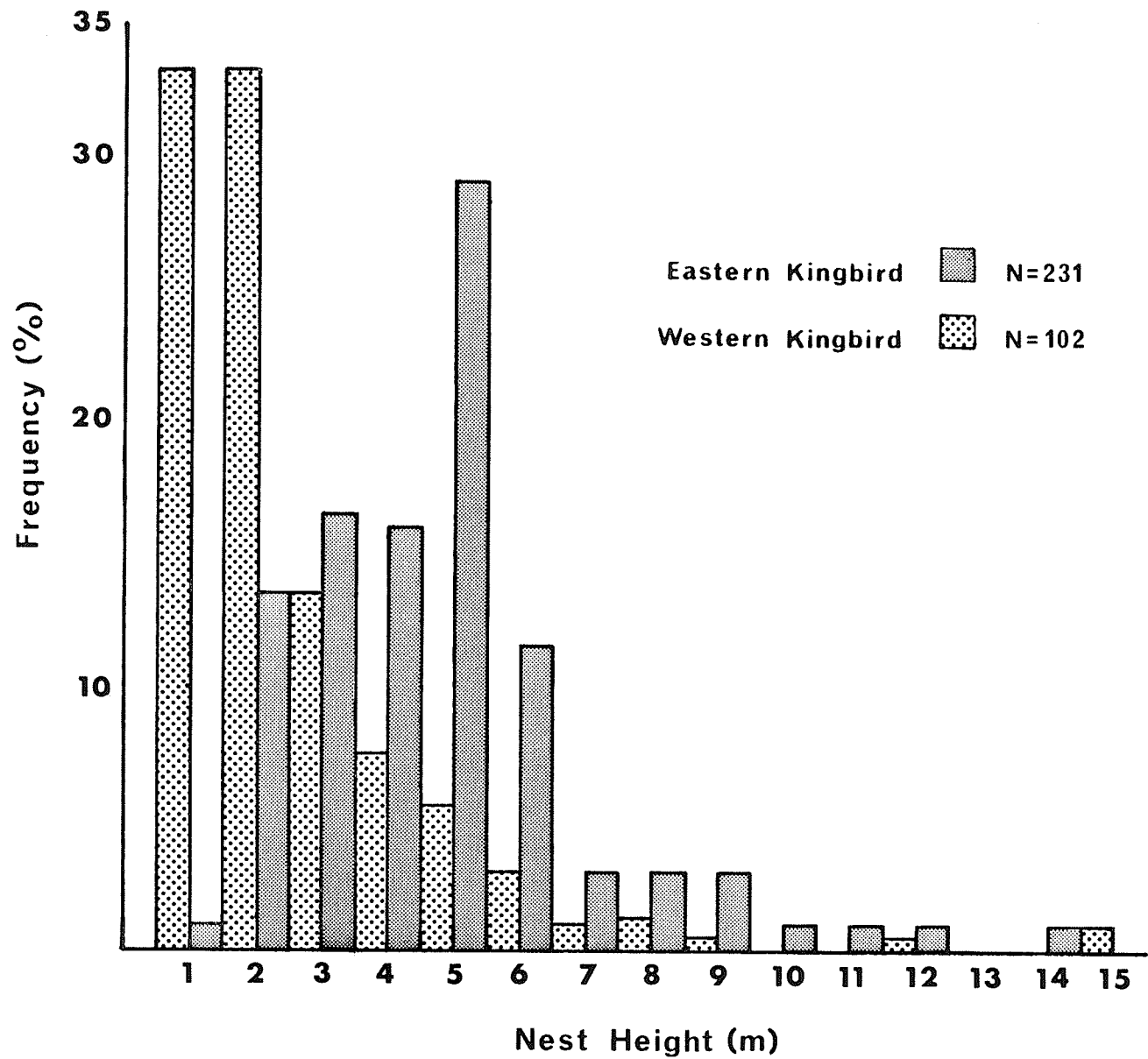
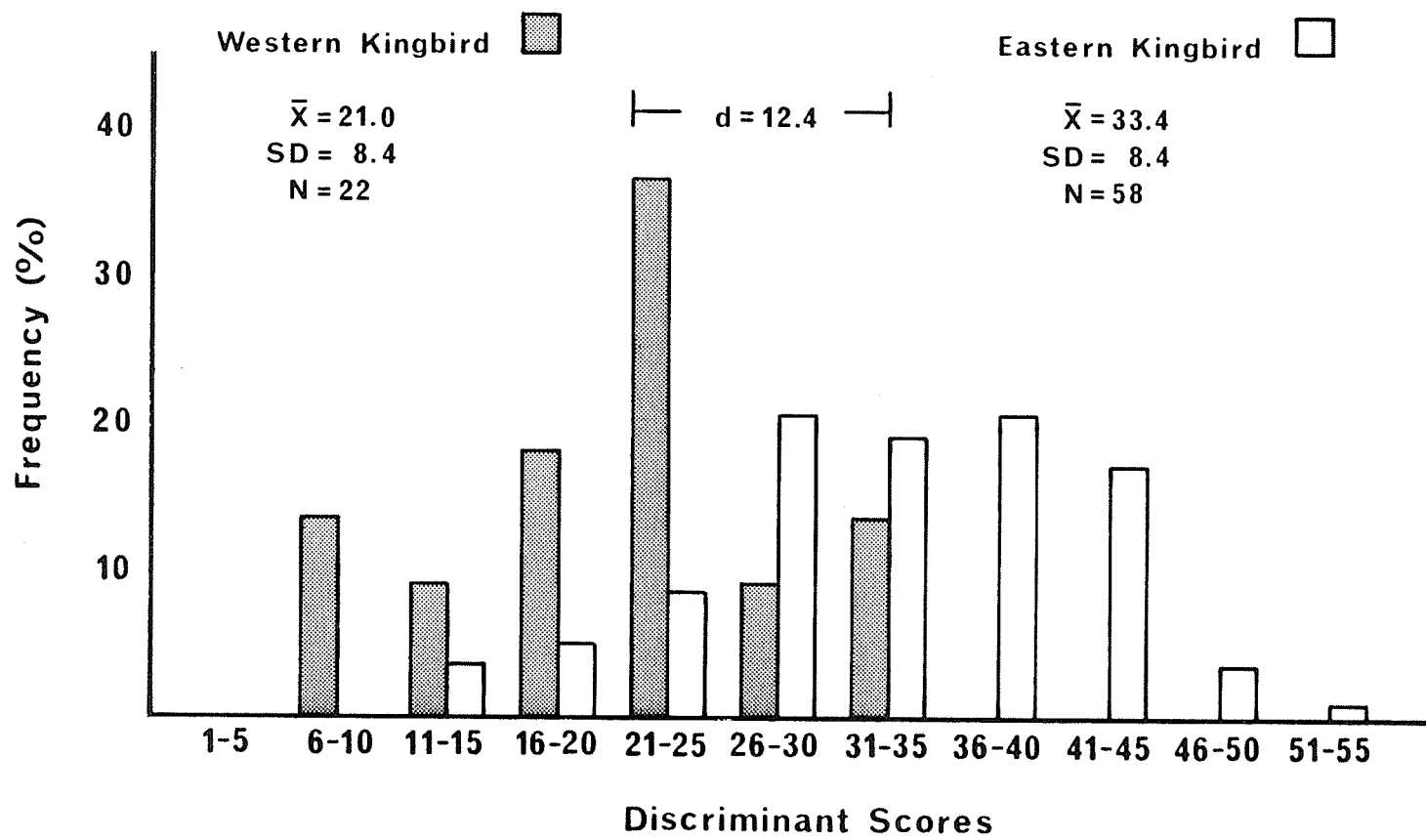


Table 20. Standardized discriminant function coefficients from the analysis of the combined macrosite and nest tree data sets.

Variable	Coefficient <sup>1</sup>
Total stems	5.885
Total basal area	0.733
Stems 5-10 cm	-6.392
Stems 10-15 cm	-1.203
Stems 15-20 cm	-0.741
Stems 20-25 cm	-1.076
Stems 25-30 cm	-0.904
Stems 30-35 cm	-0.406
Stems > 35 cm	-1.260
Manitoba maple	0.038
Green ash	-0.023
Peach-leaved willow	-0.031
Sandbar willow	0.122
Canopy cover (%)	0.197
Mean tree height	-0.352
Distance to north edge	0.188
Nest tree height	1.428
Relative nest tree height	-0.030
Nest tree dbh	-0.313
Nest tree crown volume	-0.033
Nest height	-1.968
Relative nest height	0.928

<sup>1</sup> The absolute value of each coefficient represents the relative contribution of its associated variable to the discriminant function

Figure 25. Frequency distribution of discriminant scores obtained from the analysis of the five best discriminating variables from the combined macrosite and nest tree data set.



use of available nest site resources by both species. In this respect it is analogous to a plot of resource utilization functions, and hence serves as a model of resource partitioning between the kingbird species. Recalling the model of May and MacArthur (1972), the extent to which these species approach limiting similarity, in terms of the nest site resource, can be calculated by dividing the distance between the species' means by their standard deviations. The value obtained (1.5) is above the value indicated by the model (i.e.,  $d/w \approx 1$ ). In other words, the distance between the means along the resource axis is greater than the dispersion of either species around its own mean. Therefore, following the model of May and MacArthur, the species have not reached the level of limiting similarity (or maximum tolerable overlap) along this resource axis. If nest site availability is the most critical factor regulating the populations of these species, they will probably be able to coexist indefinitely.

#### Intraspecific Variation in Eastern Kingbird Nest Sites

The observation that most eastern kingbird nests appeared to be located in the same portion of the habitat space as the western nests (Figs. 16, 19) led to the hypothesis that the basis for the significant differences between the two species was simply a greater variability in the eastern kingbird sites, due to the greater population size. In other words, would a smaller population of eastern



kingbirds still have exhibited significant nest site differences when compared to western kingbirds, especially if the distribution of the former had been restricted to the north zone of the ridge?

The following hypotheses were tested using Hotelling's  $T^2$ -test on the various nest site data sets:

- 1) eastern kingbird nest sites in the north zone were not different from eastern kingbird sites in the south zone;
- 2) eastern kingbird sites in the north zone were not different from western kingbird sites;
- 3) eastern kingbird sites in the south zone were not different from western kingbird sites.

Eastern kingbird nest sites in the north zone were not significantly different from those in the south zone at the level of the nest tree, but very nearly significantly different at the other two levels (Table 21). At the macrosite level, south zone sites had significantly more total stems, stems 5-10 cm, and sandbar willow, and significantly fewer stems 20-25 cm and 30-35 cm, and fewer green ash. North zone sites had significantly higher trees on average. At the microsite level south zone sites had significantly more total stems, stems 5-10 cm, and sandbar willow, and significantly fewer stems > 35 cm and green ash. At the nest tree level, south zone nests had significantly smaller nest trees.

Eastern kingbird nest sites in the north zone were not significantly different from western kingbird sites at the macrosite and microsite level, but were significantly

Table 21. Results of  $T^2$ -tests for all levels of resolution using north-zone eastern kingbird, south-zone eastern kingbird, and western kingbird nest sites.

Groups	Significance						
North-zone eastern kingbird <u>vs</u> South-zone eastern kingbird	<table border="0"> <tr> <td data-bbox="792 596 967 623">Macrosite</td> <td data-bbox="1040 596 1195 623">P = .065</td> </tr> <tr> <td data-bbox="792 659 967 686">Microsite</td> <td data-bbox="1040 659 1195 686">P = .052</td> </tr> <tr> <td data-bbox="792 722 967 749">Nest tree</td> <td data-bbox="1040 722 1195 749">P = .124</td> </tr> </table>	Macrosite	P = .065	Microsite	P = .052	Nest tree	P = .124
Macrosite	P = .065						
Microsite	P = .052						
Nest tree	P = .124						
North-zone eastern kingbird <u>vs</u> Western kingbird	<table border="0"> <tr> <td data-bbox="792 848 967 875">Macrosite</td> <td data-bbox="1040 848 1195 875">P = .529</td> </tr> <tr> <td data-bbox="792 911 967 938">Microsite</td> <td data-bbox="1040 911 1195 938">P = .772</td> </tr> <tr> <td data-bbox="792 974 967 1001">Nest tree</td> <td data-bbox="1040 974 1195 1001">P = .025</td> </tr> </table>	Macrosite	P = .529	Microsite	P = .772	Nest tree	P = .025
Macrosite	P = .529						
Microsite	P = .772						
Nest tree	P = .025						
South-zone eastern kingbird <u>vs</u> Western kingbird	<table border="0"> <tr> <td data-bbox="792 1106 967 1134">Macrosite</td> <td data-bbox="1040 1106 1195 1134">P = .005</td> </tr> <tr> <td data-bbox="792 1169 967 1197">Microsite</td> <td data-bbox="1040 1169 1195 1197">P = .020</td> </tr> <tr> <td data-bbox="792 1232 967 1260">Nest tree</td> <td data-bbox="1040 1232 1195 1260">P &lt; .001</td> </tr> </table>	Macrosite	P = .005	Microsite	P = .020	Nest tree	P < .001
Macrosite	P = .005						
Microsite	P = .020						
Nest tree	P < .001						

different at the nest tree level. At the macrosite level, western sites had significantly fewer total stems and stems 15-20 cm. At the microsite level, western nest sites had significantly fewer stems 10-15 cm and green ash. At the nest tree level, western nest trees were significantly taller and larger, and western nests were significantly higher.

South zone eastern kingbird nest sites were significantly different from western nest sites at all three levels. At the macrosite level, eastern nest sites had significantly more total stems, stems 5-10 cm, and sandbar willow, and significantly less total basal area, and fewer stems 30-35 cm and > 35 cm. Western nest sites had significantly taller trees. At the microsite level, eastern sites had, again, significantly more total stems, stems 5-10 cm and sandbar willow, and significantly less total basal area and fewer stems > 35 cm. Western nest trees were significantly taller and larger, and western nests were significantly higher, both absolutely and relatively.

It would appear, then, that even if the eastern kingbird population were much smaller, and perhaps restricted to the north zone as a consequence, the nest sites of the two species would still be different in some respects, and probably sufficiently different to avoid competition.

## DISCUSSION

## Pattern of Variation in the Ridge Vegetation

Multivariate analyses of the random plot data revealed the existence of two types of microhabitat, corresponding roughly to the north and south halves of the ridge forest. Principal component analysis identified two major trends in the variation of the ridge vegetation (Table 4). The first emphasized the structural difference between the north and south zones, namely, large stems in the north zone, and small stems, largely of sandbar willow, in the south. The second trend emphasized total density of stems and identified a strong peach-leaved willow influence. The first component provided a more meaningful separation of the north and south zones, while the second component appeared to emphasize differences within each zone.

Discriminant function analysis identified stems 5-10 cm, total stems, sandbar willow, and stems 10-15 cm, as the variables most important in discriminating between the zones (Table 5). The similarity between the character loadings on the discriminant function and those on the first principal component underlines the importance of this major gradient in the ridge vegetation. Thus, although univariate tests of significance identified primarily floristic differences between the microhabitat types, multivariate analyses indicated that, in fact, the difference between the microhabitat types was best characterized by a combination of structural and

floristic influences, but primarily structural.

Discriminant analysis classified 74% of the north-zone plots, and also 42% of the south-zone plots, as having north-zone type vegetation. Thus, the north-zone microhabitat appears to be more abundant than the south-zone type, and perhaps the ridge vegetation may be more accurately described as a mosaic of microhabitat patch types.

#### Kingbird Species' Responses to the Pattern of Variation

Eastern and western kingbirds showed different patterns of response to the heterogeneity of the ridge vegetation in the distribution of their nest sites. Eastern kingbird nests were more abundant and more uniformly distributed on the ridge than were those of western kingbirds.

Principal component ordinations of the nest sites indicated that eastern kingbirds exploited a broader range of microhabitats than western kingbirds, at both the macro-site (Fig. 15) and microsite levels (Fig. 18). Eastern kingbird nest sites showed a more uniform distribution than western kingbird sites along both principal component axes. Western kingbirds showed a clumped distribution in both ordinations, particularly along the major gradient in the ridge vegetation (i.e., Fig. 15: PC I; Fig. 18: PC II).

Ordination of the nest sites on the first two principal components of the random plot analysis (Figs. 16, 19) showed a relationship between the two species' responses similar to that above. Predictably, the western kingbird habitat

space corresponded closely to that identified as having characterized the north-zone microhabitat (Fig. 12). Eastern kingbird nest sites were, however, less uniformly distributed, particularly along the first principal component (i.e., the north-south continuum), than would have been expected on the basis of their microgeographical distribution on the ridge. This suggests that most eastern kingbird nest sites were situated in patches of north-zone type microhabitat.

Projections of both macrosites and microsites along the discriminant axis of the random plot analysis revealed that, although the species' patterns of response were similar to those in the nest site discriminant ordinations, the projections resulted in far less pronounced separation of the species. At the macrosite level, the differences between the species was no longer significant, and at the microsite level, the difference became highly non-significant. Yet, analysis of the kingbird nest sites (Tables 16, 17) indicated that the differences between the species was best characterized by a set of variables similar to those which best characterized the difference between north and south microhabitats. The major exception to this general similarity was in the importance accorded stems > 35 cm, at both macrosite and microsite levels. The presence of significantly more stems > 35 cm around western kingbird nest sites appears to be an important difference between the species. At the microsite level, peach-leaved willow also played a more important role than it did in the random plot analysis.

Within the range of microhabitat types available on the study area, the eastern kingbird can be considered to show the fine-grained response of a generalist in its selection of nest sites. It exploits the two major microhabitat types roughly in proportion to their availability (see Wiens 1976). The western kingbird, on the other hand, exploits only the north-zone microhabitat type, and resembles a specialist in its coarse-grained response to the habitat heterogeneity (see Wiens 1976).

Rosenzweig (1974) proposed a theory for the evolution of habitat selection which predicts that in a habitat consisting of unequally abundant patch types, two phenotypes (here, congeneric species) will be able to coexist successfully if one, the specialist, exploits the more abundant patch type only, and the other, the generalist, exploits the given mixture of patch types (see also Dueser and Shugart 1978). Under these conditions the niche of the specialist will be nested within that of the generalist. The theory also predicts that intertypic (here, interspecific) territoriality may evolve, and intertypic (interspecific) competition should be substantial.

Nest site selection in eastern and western kingbirds is consistent with Rosenzweig's theory in most respects. Principal component ordinations of the microhabitats of the two species depict the western kingbird habitat niche as more or less a subset of the eastern kingbird habitat niche. Furthermore, the absence of a significant difference between

western kingbird nest sites and north-zone eastern kingbird sites at both the macrosite and microsite levels (Table 21) indicates that both sets of nest sites are similar subsets of the total eastern kingbird set.

Yet, contrary to the predictions of Rosenzweig's theory, field observations of the two species indicate very little interspecific interaction. The only form of interspecific aggression observed during the study involved the very infrequent intrusion of a bird of one species into the nest tree of the other species. This is in contrast to the strong intraspecific aggression involving members of either species in the general vicinity of a nest. Such a pattern of behaviour is inconsistent with interspecific territoriality, and certainly does not suggest substantial interspecific competition.

No other studies of nest site selection in sympatric eastern and western kingbirds are available for comparison with respect to the above observations. Hesperheide (1964) concluded that interspecific territoriality between western kingbirds and Cassin's kingbirds (*T. vociferans*) in Arizona apparently did not exist. Ohlendorf (1974), studying the same species in Texas, reported some interspecific aggression in defense of nest sites by both species, but more so by Cassin's kingbird. Both studies reported frequent intraspecific territorial interactions in western kingbirds. Davis (1941) observed that aggression between eastern kingbirds and other species, including western kingbirds,



occurred only in the immediate vicinity of the nest tree, and involved only birds entering or moving around within the nest tree. He also pointed out that interspecific encounters involving eastern kingbirds lacked the violence of intraspecific interactions of this species. The observations of the present study are consistent with those of Davis.

The emphasis on the importance of the nest tree per se suggests an explanation for the apparent lack of substantial interaction between the species, in spite of the overlap at the microhabitat level. Western kingbirds selected significantly different nest trees than eastern kingbirds, even if only the north-zone nesting eastern kingbirds are considered (Table 21). Western kingbird nest trees were taller and larger than eastern kingbird nest trees, and western nests were higher. The emphasis placed on height by discriminant analysis of both the nest tree and combined macrosite and nest tree data sets (Tables 19, 20) is given further support by the observation that across the prairies western kingbird nests are significantly higher than those of eastern kingbirds. It would appear then, that vertical separation is a major vehicle for nesting habitat resource partitioning between these species. Thus, at the level of the nest tree, the habitat niches of eastern and western kingbirds are not nested, and thus, only the occasional conflict would arise between the species at a nest site.

## Nest Site Selection and Coexistence in Kingbirds

Wiens (1973) pointed out that distinct bird-vegetation relationships can be discovered at the within-habitat level, but that these patterns may be of a very fine spatial scale. This is the case with eastern and western kingbird nest site selection on the forested ridge. The total range of variation in the vegetation, both structural and floristic, is small, and thus the differences in nest sites of congeneric species will be subtle, at best. Nevertheless, with a level of analysis that is sufficiently fine and detailed, differences are shown to exist.

The question remains whether the distribution of the nests of each species represents true nest site selection, or merely nest site correlation (see Wiens 1976). Does the distribution of nests represent an active preference on the part of either or both species, or is the correlation of a species' presence with certain habitat factors the result of the operation of external forces? If the former alternative applies, on what basis is the selection of nest sites made? The results of this study are only correlational, and such questions cannot be answered conclusively without experimental manipulation of the system. However, some evidence points toward true nest site selection.

Western kingbirds were observed on the ridge a few days earlier than eastern kingbirds each year. They thus had the advantage of a few days to select their microhabitats.

Since observations indicate that a nest is usually located where a pair was first observed, it appears that western kingbirds are not displaced from their preferred microhabitats by the later arriving eastern kingbirds. Western kingbirds on the ridge show the same tendency they show across the prairies to nest significantly higher than eastern kingbirds. Since the average tree height, nest tree height and nest height are significantly higher at western kingbird sites than at eastern kingbird sites, it would appear, again, that western kingbirds are not displaced by eastern kingbirds from their preferred sites.

The similarity of north-zone eastern kingbird and western kingbird microhabitats would suggest that the presence of western kingbirds in the north zone could result in the displacement of some eastern kingbirds from preferred microhabitats in the north zone, to south-zone type microhabitats. Yet, observations indicate that some of the earliest eastern kingbird nests were situated in south-zone type microhabitats in both years. These observations suggest that these sites were not exploited by late arrivers or by birds which were unsuccessful in obtaining north-zone type sites. In such a widely distributed species as the eastern kingbird (Fig. 1), exposed to a wide variation in habitats throughout its range, sufficient intrapopulational variation may exist that some individuals may demonstrate a preference for north-zone type sites and some for south-zone sites, totally independently of the presence of a

congener. In any case, the high degree of intraspecific aggression, compared with the infrequent instances of interspecific interaction, would suggest that the former is exerting a greater influence than the latter on the distribution of the nests of both species.

Assuming then, that nest sites are actively selected, the basis for differential selection would appear to be a combination of microhabitat and nest tree variables (Table 20). Western kingbird nest sites were characterized by fewer but larger trees than eastern kingbird sites, and western kingbird nest trees and nests were higher than those of eastern kingbirds. Given the emphasis that both species appear to place on defense of the nest tree, this may be the real basis for selection, in which case the microhabitat factors may simply be correlated with the nest tree factors. In any event, such a combination of variables is sufficient to characterize the nest sites of the two species, and to demonstrate separation of the species along the nesting habitat dimension, to the extent that competition for nest sites would not be substantial if this resource were, indeed, the limiting resource (Fig. 25).

## CONCLUSIONS

Eastern kingbird and western kingbird nests showed similar distributions over the length of the study area. Eastern kingbird nests were more uniformly distributed over the width of the study area than western kingbird nests which were situated almost entirely in the north zone.

Principal component analysis of the random plots defined the 'habitat space' of the study area in terms of the major components of variation in the vegetation. Discriminant function analysis of the random plots identified the major gradient in the variation of the vegetation. This gradient, corresponding roughly to a microgeographical gradient from north to south across the study area, was characterized by an increase in the number and a decrease in the size of trees across the ridge, and by an increase in the density of sandbar willow. The analysis recognized two microhabitat types, corresponding to the north and south zones of the ridge.

Principal component analysis of the kingbird nest sites at both macrosite and microsite levels determined the relative position of each species in the 'habitat space'. Projection of the nest site data onto the random plot ordination indicated that eastern kingbird nest sites were more uniformly distributed than those of western kingbirds along the major components of variation in the ridge vegetation.

Western kingbird nest sites were restricted to that portion of the habitat space identified as characterizing the north-zone type microhabitat. Most eastern kingbird nest sites also occupied this portion of the habitat space, suggesting that north-zone type microhabitat was preferred by both species.

Discriminant function analysis of the nest sites at all three levels of resolution identified the variables most important in characterizing the differences between the nest sites of the two species. At the macrosite level, stems > 35 cm, stems 5-10 cm, total stems, and density of sandbar willow were the most important contributors to the separation of the species. At the microsite level, stems > 35 cm, density of peach-leaved willow, stems 15-20 cm, and stems 5-10 cm were the most important discriminators. Western kingbird sites were characterized by fewer but larger trees than eastern kingbird sites at the microhabitat (macrosite and microsite) level. At the nest tree level, nest height, nest tree height, and relative nest height were the best discriminators. Western kingbird nest trees were larger and taller, and their nests were placed higher than those of eastern kingbirds.

Eastern kingbirds employed the fine-grained strategy of a habitat generalist in their selection of nest sites from both available microhabitat types, and in their selection of nest trees from a wide range of tree size classes. Western kingbirds exhibited the coarse-grained response of

a specialist, selecting sites in only the north-zone type microhabitat, and nest trees from the larger size classes.

A combination of macrosite and nest tree variables best characterized the differences in nest sites of the two species, and achieved the best statistical separation between them: stems 5-10 cm, total stems, nest height, nest tree height, and stems  $> 35$  cm. The degree of separation of the species along the resource dimension of nesting habitat, defined in terms of these five discriminating variables, is considered sufficient to permit coexistence of the species in the event nesting habitat should prove to be the resource limiting the population of either species.

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