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

by

DAVID I. MacKENZIE

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DAVID I. MacKENZIE

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

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

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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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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 (Svärdson 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.

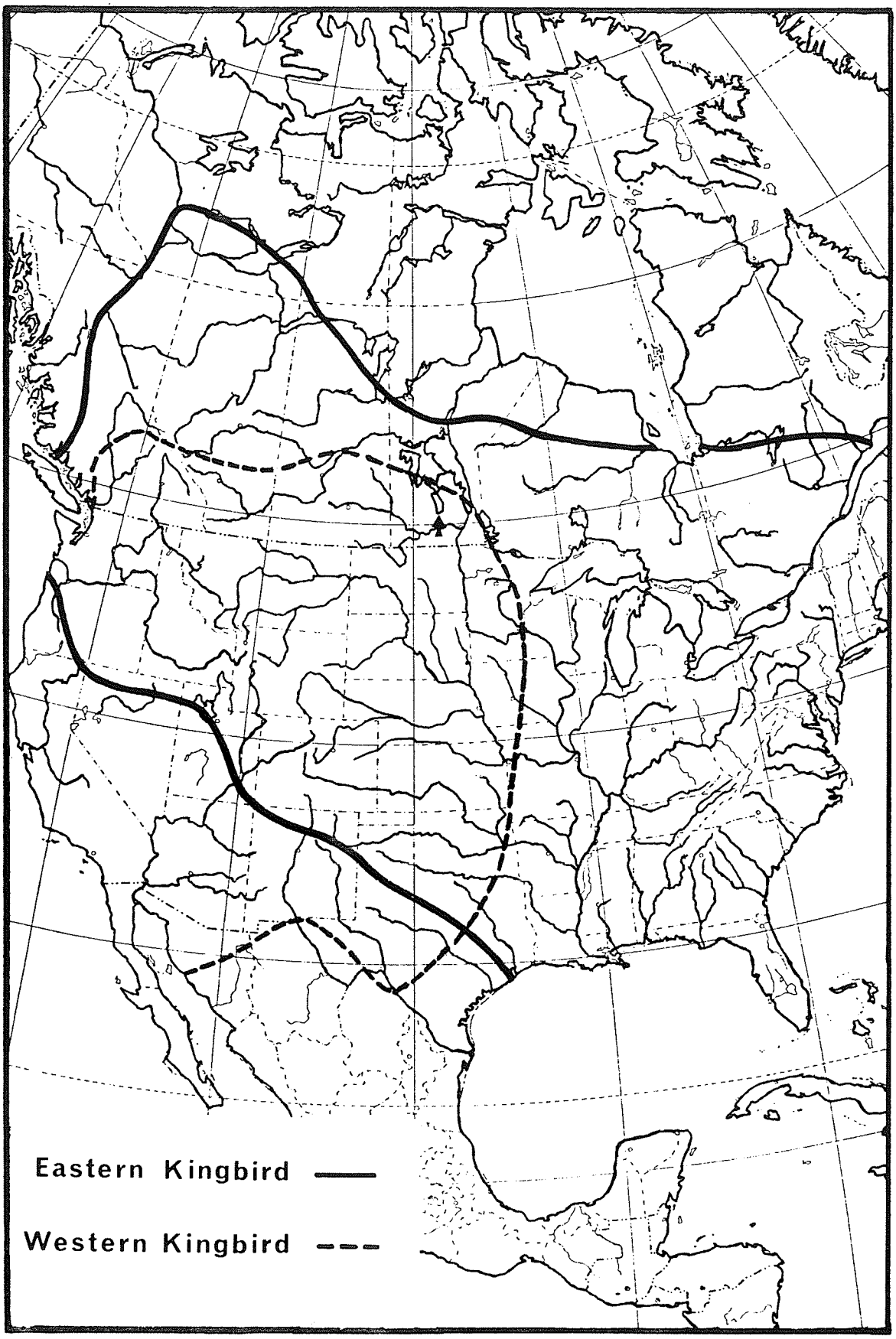
The Species

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.).


Eastern Kingbird
Western Kingbird

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°11'N, 98°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.

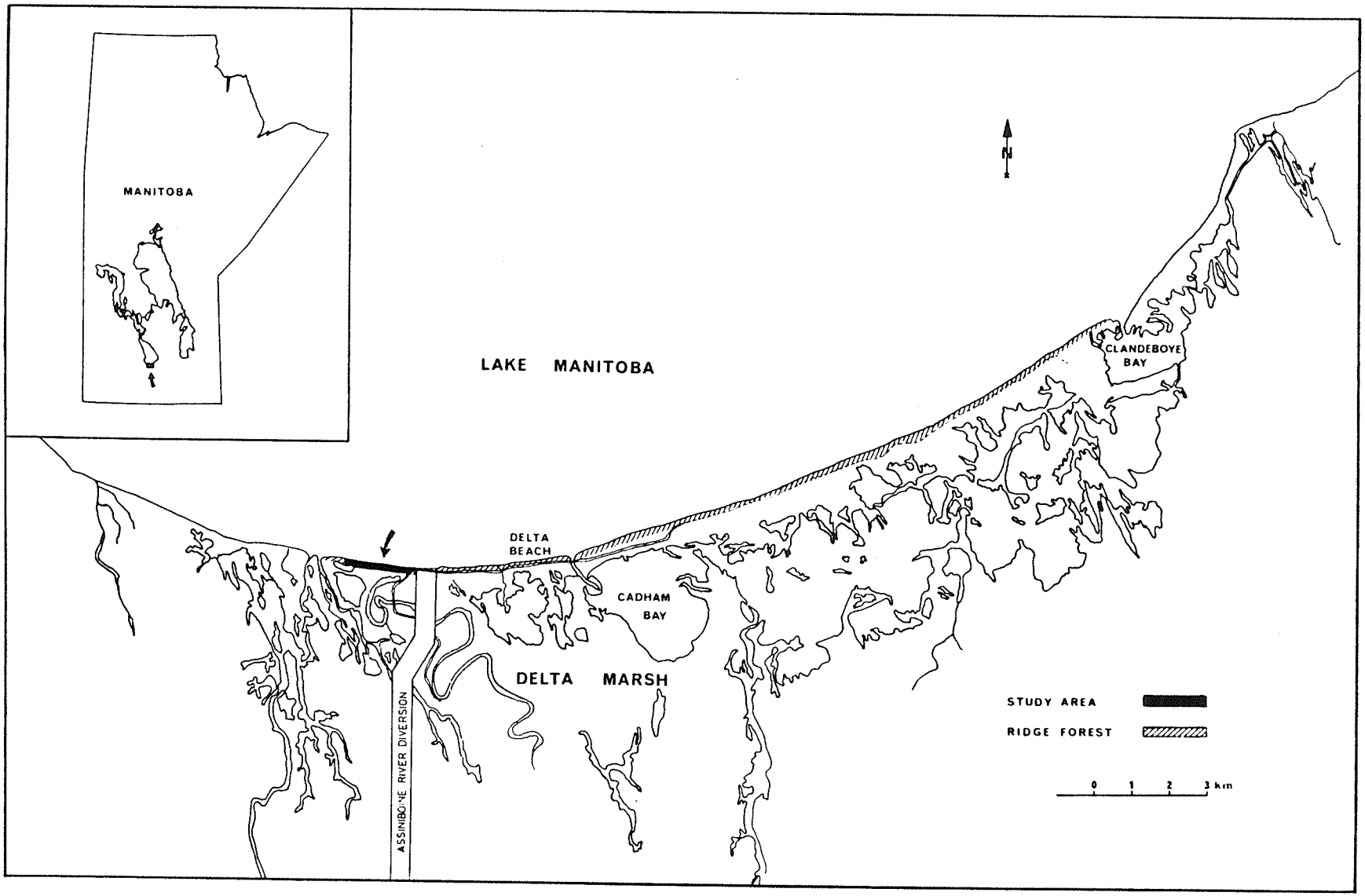
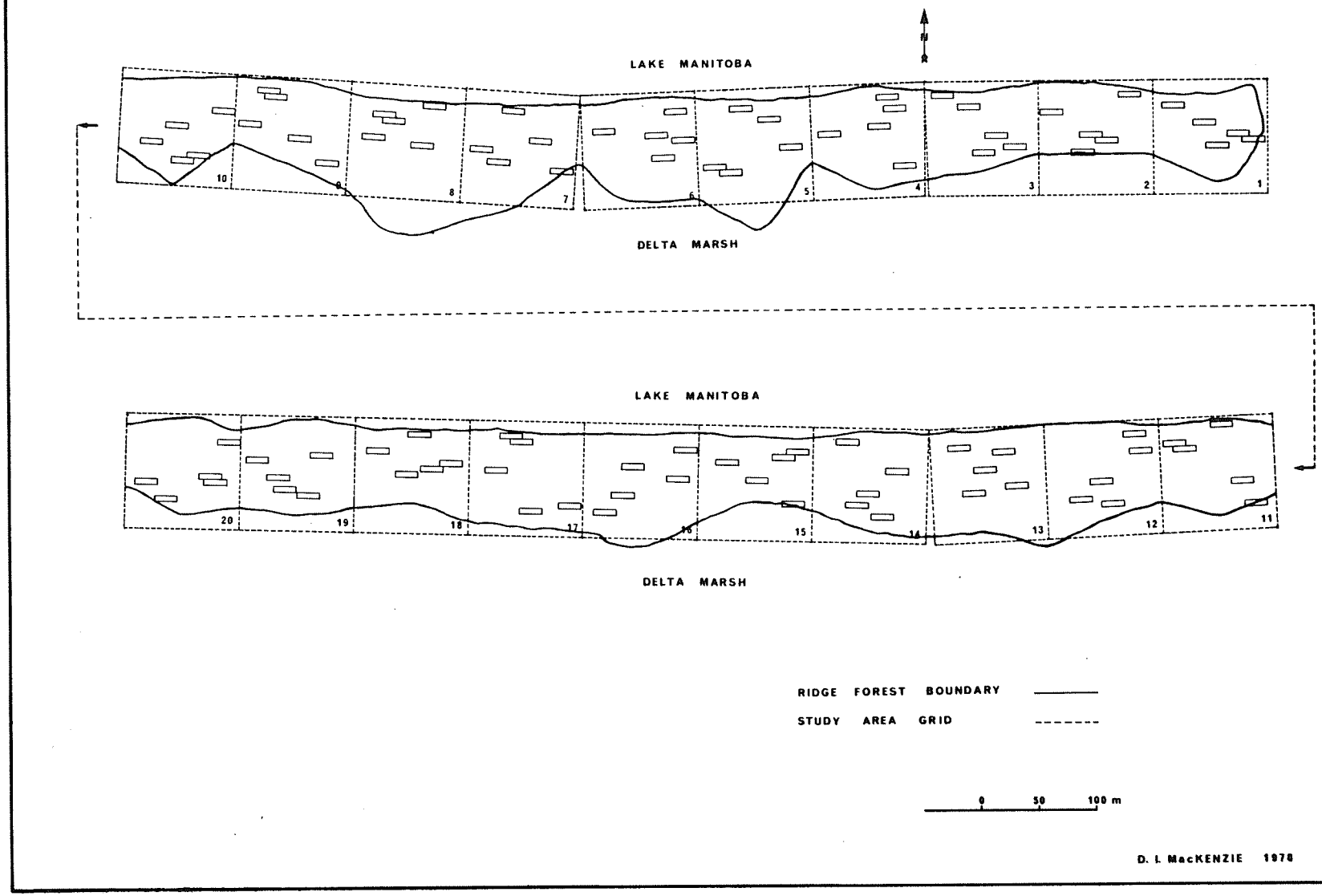

MANITOBA
LAKE MANITOBA
N
CLANDEBOYE BAY
DELTA BEACH
CADHAM BAY
DELTA MARSH
ASSINIBOINE RIVER DIVERSION
STUDY AREA
RIDGE FOREST
0 1 2 3 km

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


LAKE MANITOBA
10
9
8
7
6
5
4
3
2
1
DELTA MARSH
LAKE MANITOBA
20
19
18
17
16
15
14
13
12
11
DELTA MARSH
RIDGE FOREST BOUNDARY
STUDY AREA GRID
0
50
100 m
D. I. MacKENZIE 1978

(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