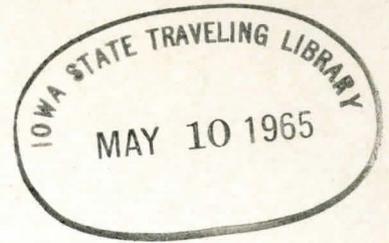


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Role of Habitat in the Distribution and Abundance of Marsh Birds



by Milton W. Weller and Cecil S. Spatcher

Department of Zoology and Entomology

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SUMMARY

Severe drouth during the 1950's produced dramatic changes in the vegetation of midwestern glacial marshes and in the abundance and distribution of marsh birds. Changes in marsh habitat quality and quantity were studied in relation to bird populations in two small central Iowa marshes, Little Wall and Goose lakes near Jewell. General observations also were made on several larger marshes in northwest Iowa near Ruthven.

These marshes were nearly dry in 1956 and became densely vegetated. With gradually rising water levels, plants flourished, and bird populations increased. Gross cover maps demonstrated the change in cover-water ratio and interspersion. Population estimates showed the changes in distribution and density of various species of marsh birds. During dry periods, only adaptable species such as redwinged blackbirds were present. As water levels increased, densely vegetated areas were opened up by muskrat cutting, and yellow-headed blackbirds, coots, pied-billed grebes and least bitterns became established and increased in numbers. Maximum bird numbers and diversity were reached when a well-interspersed cover-water ratio of 50:50 occurred. By 1962, muskrats and high water had eliminated virtually all emergent vegetation with the result that all species except redwings were eliminated. A similar pattern occurred on marshes throughout Iowa, and similar changes have been noted throughout the glacial marsh region during this and previous post-drouth periods.

Habitat changes permitted a measure of habitat preference and adaptability in several species. Populations shifted from area to area around the marsh as conditions changed because of muskrat cuttings. Redwings used shoreward vegetation and were the most tolerant of changing conditions. They utilized a higher percentage of brush and tree nest sites over land as emergent vegetation disappeared. Yellow-headed blackbirds were restricted to robust emergent vegetation standing in water but used only those areas adjacent to open water.

Coots and pied-billed grebes both nested over water in cover of medium density with sizable adjacent water openings. Both were quite toler-

ant of open-marsh stages, and nest losses in coots at that time often were due to wind damage.

Black terns selected low, natural nest sites or built nests low to the water in sparse emergent vegetation where they were protected from wave action. Forster's terns nested on higher sites, such as active muskrat houses, often in open-water areas, or built nests higher above the water than those of black terns.

The only competition noted was among shoreward nesting redwings and over-water nesting yellowheads. Some interspecific chases were observed; yellowheads dominated redwings in the ideal yellowhead habitat, but redwings occasionally nested in yellowhead territories in small patches of vegetation not used by yellowheads.

Evolution of nest-site selection seems to have been influenced by general habitat of the ancestral stocks (terrestrial versus aquatic), by mode of locomotion (perchers, walkers, swimmers and flyers) and by use of the major emergents (shoreward or water's edge). The vertical height and resulting "layers" of vegetation, their robustness and their relationship to water, influence species use and, thereby, species diversity.

Short-term fluctuations in marsh habitat conditions seem common in marshes as a result of change in rainfall and subsequent water level changes. The dry and wet, open stages are the least productive of birds, while the hemi-marsh is ideal. Marsh birds have adapted to these conditions, and marsh bird populations are characterized by pioneering ability and mobility. A variety of marsh types and sizes of marshes in a given area are essential to the preservation of marsh bird diversity.

Marshes are highly productive ecosystems characterized by dramatic short-term fluctuations. There are periodic invasions of terrestrial flora and fauna during dry years, while wet years produce a pond or lake-type community. The viewpoint of marshes as transient seral stages is challenged because of their duration of life and because of the equally dramatic changes that may occur in surrounding terrestrial biomes. It is suggested that a biome-type classification be applied to lakes, marshes, swamps and bogs.

Role of Habitat in the Distribution and Abundance of Marsh Birds¹

by Milton W. Weller² and Cecil S. Spatcher³

The recent drouth of the late 1950's and early 1960's produced some dramatic effects on the quality and quantity of emergent vegetation in glacial marshes of the central United States and Canada. These vegetative changes have had great impact on the distribution and size of marsh bird populations. Similar plant responses must have resulted from the dry years of the late 1800's and the 1930's, and intervening wet years produced opposite extremes on many marshes. Such habitat changes undoubtedly have occurred throughout the racial history of many marsh animals, and the maintenance of a species depended upon its adaptability.

Obviously, many factors other than habitat influence the size and species composition of a marsh bird population. Among these are geographic location (both continental and in relation to other water areas), competition, pioneering ability, population levels, habitat conditions in wintering areas, mortality in breeding and wintering areas, and climatic factors (see Kendeigh, 1934). No study could hope to measure all or even most of these influences, but habitat has a clear-cut impact on bird populations and is more readily measured.

The study of habitat change and its effects on birds involves long-term research with the usual problems of consistency of effort and method. This study is no exception and suffers from a necessary part-time and divided effort. Many observations are not as detailed as might be desired, and some facets — such as the determination of precise populations — were considered impractical to attain in the time available.

This work covers the history of vegetation and birds of two marshes for a 5-year period beginning in 1958 at the culmination of a series of drouth years in central Iowa. Additional observations on some other marshes near Ruthven, Iowa,

indicated that the phenomena viewed during more intensive study at Little Wall and Goose lakes were occurring there. Observational data from Iowa are integrated in the discussion with data from marshes in Utah and Texas and in Manitoba, Canada, to present a synthesis of ideas concerning evolution of habitat niches and ecosystem dynamics, productivity and succession in marshes.

The investigation was started by the senior author under a grant from the Iowa State University Alumni Foundation and was completed under Project 1504 of the Iowa Agricultural and Home Economics Experiment Station. The junior author was financed during 1960 and 1961 by the National Science Foundation Teacher's Research Participation Program.

We express our appreciation to many individuals for assistance. The late Professor Paul L. Errington and students Roger J. Siglin, John Bedish, David Waller and Robert Buckley made especially significant contributions.

STUDY AREAS

Intensive studies were made on two marshes, Goose and Little Wall lakes, located near the town of Jewell, Iowa (Hamilton County), approximately 20 miles north of Iowa State University. Both are natural, shallow, glacial marshes which may be classified as fresh deep marshes (Martin et al., 1953). Both have small watersheds, and their water levels closely parallel rainfall; they are virtually dry marshes in some years and open-water lakes in other years.

Goose Lake contains approximately 135 acres; Little Wall Lake includes nearly 275 acres. The areas are within 2 air miles of each other, and some birds, such as ducks and geese, often move between areas.

Following a series of years with below-normal rainfall in the mid-1950's, Goose Lake dried out in 1956. Mud cracks were conspicuous, and portions of the marsh formed an excellent site for the germination of many marsh emergents. Little Wall Lake also was dry except for about one-third

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TABLE 1. Some marshes near Ruthven, Iowa, observed during the period, 1958-63.

Northeastern Clay County:	
Dan Green Slough.....	340 acres
Trumbull Lake.....	1,190 acres
Smith's Slough.....	200 acres
Round Lake.....	425 acres
Barringer Slough.....	1,430 acres
Southwestern Palo Alto County:	
Rush Lake.....	460 acres

that had been dredged in 1953. Water returned gradually to both areas starting in 1957, and both were at full pool by 1962.

The dominant plants at both lakes were cattail (*Typha augustifolia*, *T. latifolia* and their hybrids), hardstem bulrush (*Scirpus acutus*), river bulrush (*Scirpus fluviatilis*) and sedges (*Carex* spp.). Emergents of lesser importance were reed (*Phragmites communis*), softstem bulrush (*Scirpus validus*), rice cut-grass (*Leersia oryzoides*), arrowhead (*Sagittaria* spp.), spikerush (*Eleocharis* spp.) and burreed (*Spartanium* spp.).

Additional observations were made at several marshes in the lake region near Ruthven, Iowa, where Bennett (1938), Low (1941; 1945), Provost (1947) and others have studied anatids and other marsh birds and where Hayden (1943) had surveyed marsh vegetation. Noteworthy areas and their sizes are listed in table 1.

METHODS

Vegetation

The dominant emergent vegetation of Little Wall and Goose lakes was mapped by using United States Air Force aerial photos as a base map and for an outline of water-cover areas during 1958. Annually in late winter, the vegetation was cover-mapped grossly by pacing on ice (see Mosby, 1963, for a general discussion of mapping techniques). Major emphasis was placed on determining the size and location of water areas and delineating the large areas of robust emergents. This system provided the easiest means of measuring the distribution of major emergent plants that would remain as potential nest sites during the spring. Because of the size of the areas, these maps are gross and do not provide precise measurements of the acreage of each plant species. They do, however, reflect approximate percentages of major emergents and open water. Density of the vegetation was not measured, but qualitative notes were made. The 1958 cover map of Little Wall Lake (fig. 1) and the 1959 cover map of Goose Lake (fig. 2) show the nature of the habitat at the beginning of intensive studies. Although a cover map of Goose Lake was made during the spring of 1958, less field work was done there than at Little Wall Lake until 1959; the cover during 1958 and 1959 differed only slightly.

A more detailed cover map was made on 13 quadrats, 100 feet square, which formed a belt transect 100 feet wide connecting the large island at Goose Lake to the southeastern shore. A tape was used to determine the distribution of vegetative zones and nests within these plots during 1960-62.

Aerial photographs were taken during several years, and both black and white and color photos were taken from several photo stations at each lake annually.

Bird Populations

Little work has been done on census methods for marsh birds, but several techniques commonly in use for terrestrial species were applied (Kendeigh, 1944). Because of the variety of species involved, no one technique proved satisfactory to provide population estimates for all species. The distribution and number of territorial males were the best indications of the location of nesting blackbirds as well as a crude index of their density. Three to five counts were made each spring on clear, quiet mornings. However, since both species are polygamous, nest locations and numbers also were quite important. Determination of the number of nests was the main method of population appraisal for other marsh birds. It was impractical to attempt to locate all nests of very abundant species, however, and population estimates of some species are qualitative, involving numbers of nests and territories and comparative observations from year to year. The accuracy of these may be low for some species for some years, and no measure of the variability is available. The population changes recorded were dramatic, however, and reduce the importance of errors of estimation. Moreover, the distribution of the nesting birds within the available habitat was considered of primary interest in measuring the responses of birds to changed conditions.

A minimal amount of nest-statistics was recorded: clutch size or number and age of young, water depth at the nest site, height of nest above soil or water, vegetation and location. Because of limited time, few nests were rechecked for nest success.

RESULTS

Species Composition and Chronology of Nesting

The species of birds that either nested or were thought to have nested at Goose and Little Wall lakes are listed in table 2. These constitute the usual avian fauna of prairie glacial marshes (Provost, 1947; Beecher, 1942), except that there were no nesting Forster's terns (*Sterna forsteri*), and there were relatively few anatids present.

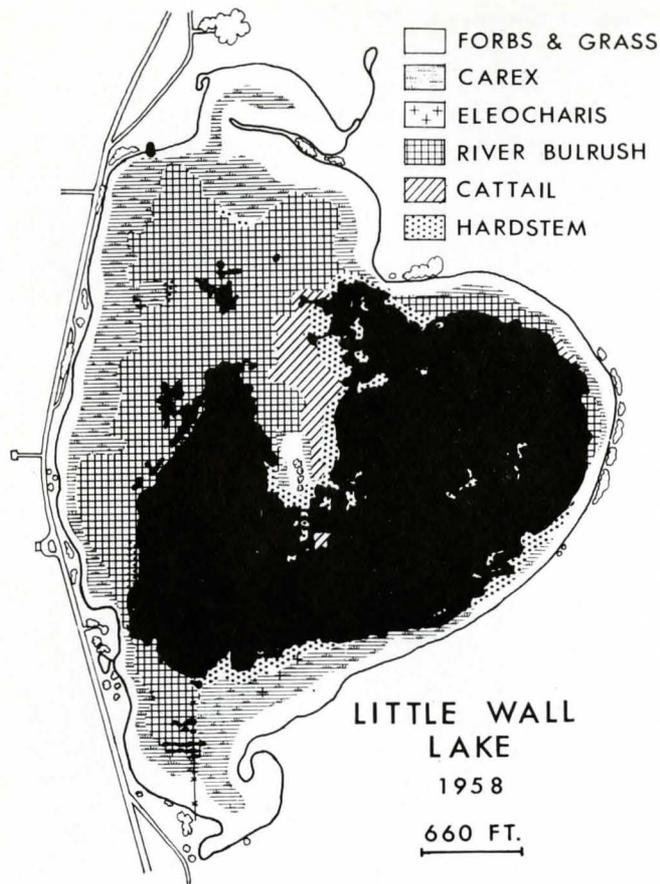


Fig. 1. The major emergent vegetation of Little Wall Lake at the initiation of the study. Hardstem, river bulrush and Carex in the southern, western, and extreme northern portions of the lakes were dry.

The isolation of these areas may have been responsible for the shortage of ducks, since these lakes are at the southern end of the Wisconsin glacial lobe, and the nearest large marsh is about 20 miles distant. A larger number and greater variety of species were present in the rich marshes of northwestern Iowa; these have been discussed by Bennett (1938), Provost (1947) and others.

TABLE 2. Some breeding birds of Little Wall and Goose lakes.

Pied-billed grebe (<i>Podilymbus podiceps</i>)
Least bittern (<i>Ixobrychus exilis</i>)
American bittern (<i>Botaurus lentiginosus</i>)
Mallard (<i>Anas platyrhynchos</i>)
Pintail (<i>Anas acuta</i>) ^a
Blue-winged teal (<i>Anas discors</i>)
Ring-necked duck (<i>Aythya collaris</i>)
Ruddy duck (<i>Oxyura jamaicensis</i>)
Virginia rail (<i>Rallus limicola</i>)
Sora (<i>Porzana carolina</i>)
Common gallinule (<i>Gallinula chloropus</i>)
American coot (<i>Fulica americana</i>)
Killdeer (<i>Charadrius vociferus</i>)
Spotted sandpiper (<i>Actitis macularia</i>) ^a
Black tern (<i>Chlidonias niger</i>)
Long-billed marsh wren (<i>Telmatodytes palustris</i>)
Yellowthroat (<i>Geothlypis trichas</i>)
Yellow-headed blackbird (<i>Xanthocephalus xanthocephalus</i>)
Redwinged blackbird (<i>Agelaius phoeniceus</i>)
Swamp sparrow (<i>Melospiza georgiana</i>) ^a
Song sparrow (<i>Melospiza melodia</i>) ^a

^aNo nests found during this study, but resident pairs were observed.

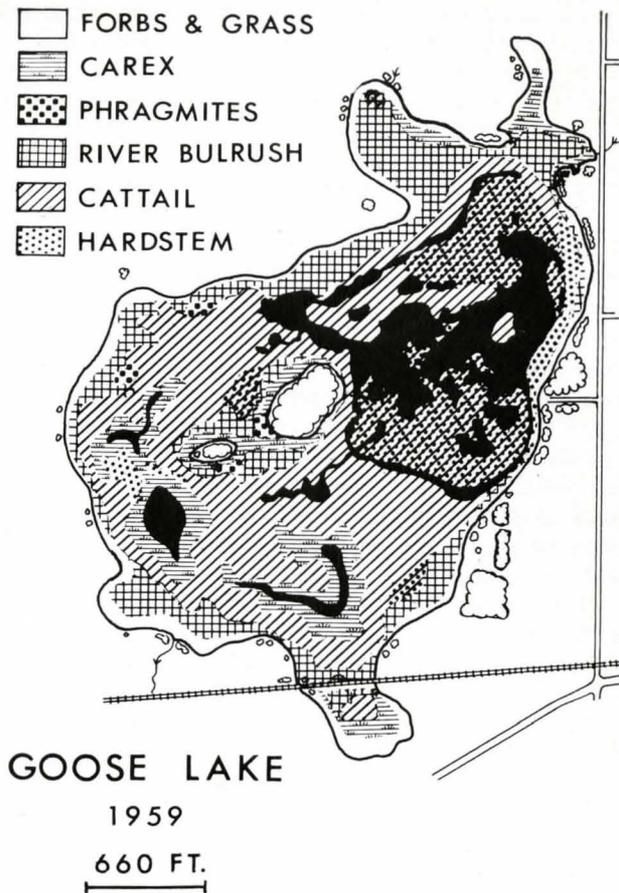


Fig. 2. The major emergent vegetation of Goose Lake when intensive observation began during 1959. Vegetation differed only slightly in 1958. Note two wooded islands.

The chronology of nesting is shown for nine common species of marsh birds in fig. 3. This chart was prepared by pooling nest records from both lakes for the 5-year period. Early dates are based on observations of nest building and records resulting from "back-dating" from the time the nest was found to the approximate time of nest establishment. Final dates include some nests that were still active, but no predictions of completion dates were made.

In general, nest initiation of most species, and especially of early nesting birds, preceded the maturation of green vegetation. Nests commonly

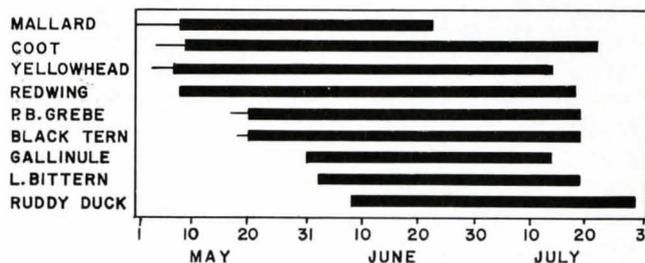


Fig. 3. Chronology of nesting of some species at Little Wall and Goose lakes, 1958-62. Thin lines indicate back-calculated dates of nest initiation.

were placed in stems of plants of the previous year; however, later nests were constructed in or of green vegetation, and blackbird nests often were tipped and their contents spilled because they were attached to one or more growing stems. Such losses might well lead to the evolution of use of old, tan vegetation as opposed to new, green vegetation.

Under extreme conditions of nearly complete absence of vegetation, some delay in nesting chronology was noted. At Goose Lake in 1962, following the nearly complete elimination of tall emergents by muskrats, yellow-headed blackbirds were few and did not seem to start nesting. However, following the growth of river bulrush in mid-June, a small population of birds appeared and initiated nests nearly 6 weeks later than normal. Meanley (1952) noted similar behavior in short-billed marsh wrens (*Cistothorus platensis*) nesting in cultivated rice.

Implications of similar responses to vegetation were noted in a non-passerine at Rush Lake in northwestern Iowa during 1963. Because of reduced water levels created by an intentional marsh "drawdown" designed to stimulate growth of vegetation, almost no emergent vegetation had sufficient water at its bases to be attractive as nesting cover for coots. In early June, when coot nests were near hatching at adjacent lakes, flocks of coots were still conspicuous at Rush Lake. Some pairs were seen, but territorial defense was not conspicuous. In late June, following the maturation of a bed of arrowhead in open water, only pairs and singles were seen, and fighting was common. Several broods were noted later.

Thus, despite unfavorable conditions, a few birds seem to remain on what probably were natal marshes and occasionally meet with suitable ecological changes which permit nesting — although delayed.

Another chronological variable not apparent in fig. 3 was noted among blackbirds. Redwings arrived on breeding areas in mid-March, and territories were occupied long before females arrived as also noted by Allen (1914) and others. However, the permanence of occupancy by these males is uncertain. Yellow-headed blackbirds arrived in late April with little differential migration of sexes (but, as with redwings, there was a clear-cut differential in age and time of migration, with young being considerably later than adults). The result was that both species began nesting concurrently, and, in a few cases, the highly social yellowheads actually preceded redwings. The termination of nesting by yellowheads also seemed more abrupt, and only a small number of females (yearlings or renesting birds?) were responsible for the nests found in the latter portion of June and early July.

Habitat Changes at Little Wall and Goose Lakes

Figures 1 and 2 demonstrate grossly the vegetation and also show the classical patterns of plant zonation, as outlined by Weaver and Clements (1929) and detailed for bird communities by Beecher (1942) and Aldrich (1943). The usual sequence of plants from shore to open water at these areas, as in other midwestern marshes, is: cottonwood (*Populus deltoides*), willow (*Salix* spp.), sedges and aquatic grasses, arrowhead, softstem bulrush, broad-leaved cattail, river bulrush, narrow-leaved cattail and hardstem bulrush. Not all these species were present in all areas, and the factors determining the species composition of any particular area are poorly understood.

In most cases, plant distribution followed the typical zonation dictated by tolerance of various plants to water depth. In a few cases, however, some variations were noted on sizable areas, especially at Goose Lake. Root systems of many emergents are established mainly during periods when marsh bottoms are exposed, and concentric zones of vegetation form that reflect the contour of the marsh bottom. At Goose Lake in 1958, several areas showed reversed plant zones, with bands of rice cut-grass, sedge, river bulrush or burreed in deep-water areas, and cattail or other plants, normally found in deep water, were in shallow areas. Presumably, such zones developed because of water level fluctuations that created suitable conditions for germination for various species at various levels of the marsh. In addition, large areas apparently were ideal for the germination of many species. In the level central basin of the lake, mixed stands of plants normally found in several zones had developed, and the large "islands" of emergents in Goose Lake contained cattail, hardstem and softstem bulrush, arrowhead, rice cut-grass, and willows and other marsh-edge plants.

The changes in vegetation that occurred at Little Wall and Goose lakes between 1958 and 1962 are shown in figs. 4 and 5 as a comparison of relative amounts of open water and dominant robust emergents such as river bulrush, cattail and hardstem bulrush. Sedges are included with upland plants or other low marsh-edge plants in these figures because sedges were little used by nesting birds. These figures, then, reflect the annual changes in available tall, robust emergents for use by nesting marsh birds.

Vegetation changes mainly were a product of muskrat cutting, often followed by inundation from the gradually rising water levels. However, flotation occurred, and soil-water conditions changed considerably along the shore zone.

In 1958, Little Wall Lake had a large water area, approximately 4½ to 5 feet deep, that re-

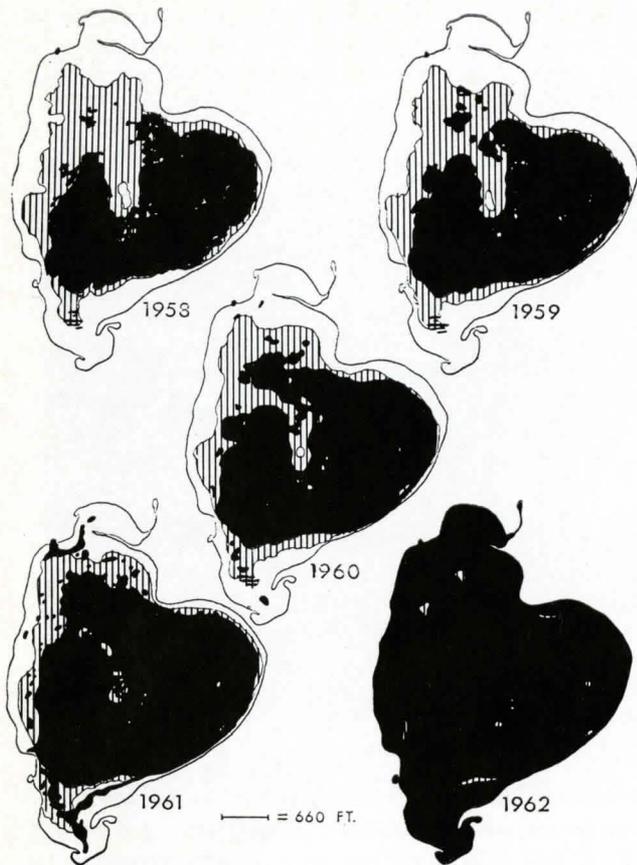


Fig. 4. Gross changes in the open water (black) in relation to robust emergent vegetation (pattern) and low *Carex*, grasses and forbs (white) at Little Wall Lake.

sulted from dredging before the study (1953). However, there was an abrupt edge between this water area and the non-dredged area. If an outline of water level were superimposed on fig. 1, it would not exceed greatly the open-water area except in a pocket in the northeastern portion of the lake. The edge was covered by thick rootstocks, and the only natural gradient between the water-plant edge was in the northeastern portion of the pool and along the eastern and southern edge of the "peninsula" or "island" formed by dredge deposits (fig. 1). Thus, despite the superficially good appearance of the plant-water edge, swimming birds met an abrupt change from water to virtually dry vegetation. The natural marsh edge attracted a few birds, but the general dryness of the marsh produced unattractive conditions. The entire southeastern shoreline was heavily grazed and lacked the dense emergent vegetation found in the ungrazed portion.

The unflooded portions of the lake bottom were sufficiently dry so that at least one pheasant nested in the south end of Little Wall Lake, and meadowlarks (*Sturnella neglecta*) and bobolinks (*Dolichonyx oryzivorus*) were common there. A meadowlark nest and nests of two ground-nesting

mourning doves (*Zenaidura macroura*) were recorded in the northern bay of the lake. Upland moist soil grass such as squirrel-tail grass (*Hordeum jubatum*) was common as were forbs like swamp milkweed (*Asclepias incarnata*) and goldenrod (*Solidago* spp.). The central "island" was sufficiently dry and grassy to attract swamp sparrows and spotted sandpipers.

As water levels increased gradually, muskrats spread into suitable areas and increased in numbers. Cutting of emergents by muskrats for food and lodge materials gradually created small open-water areas in the dense vegetation, and increased water levels created more suitable and natural marsh edges and bottom contours. Various areas of the lake reached ideal conditions at various times, but, by 1961, the remaining vegetation was broken by small water areas created by muskrats (fig. 6) and suitable for most birds; the lake achieved maximum bird production despite a reduced area of vegetation (fig. 4). Because of increased rainfall and an extremely high muskrat population (see Errington, Siglin and Clark, 1963, for a discussion of muskrat populations), it is doubtful that any significant amount of vegetation would have lasted into 1962. In the fall of 1961, however, pumps were installed in a nearby drainage ditch to pump water into Little Wall Lake. As a result, water levels increased by 5

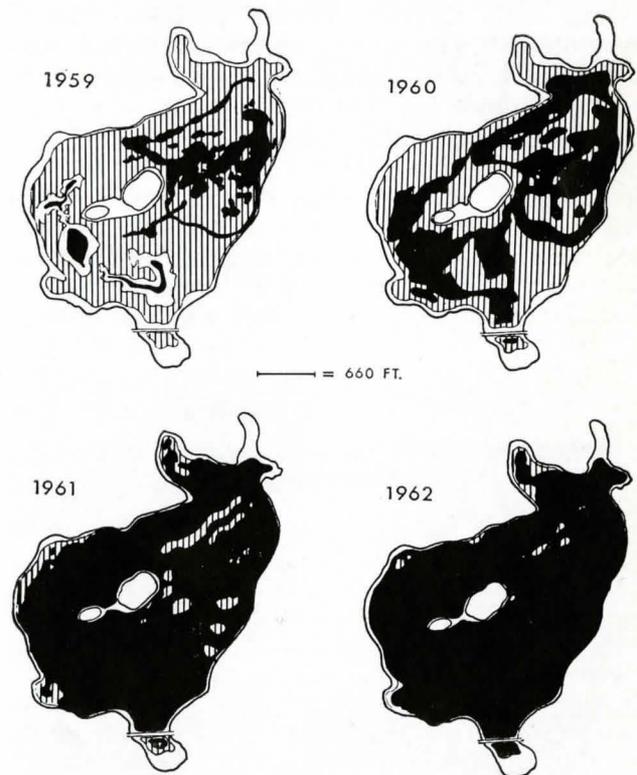


Fig. 5. Gross changes in the open water (black) in relation to robust emergent vegetation (pattern) and low *Carex*, grasses and forbs (white) at Goose Lake.



Fig. 6. Muskrat lodges and the resultant openings in river bulrush; west shore of Little Wall Lake, 1961.

feet, and no emergent vegetation suitable for nesting birds survived. Several patches of hardstem bulrush, one bed of narrowleaf cattail and some sparse river bulrush survived several years—but in stands too thin for nest sites (fig. 7).

A similar but more natural pattern was recorded at Goose Lake (fig. 5) where most vegetation already was reflooded by the time of the initial mapping in the winter of 1957-58. Vegetation was quite dense in some areas, and central "islands" of vegetation were characterized by complex mixtures of deep-water and marsh-edge

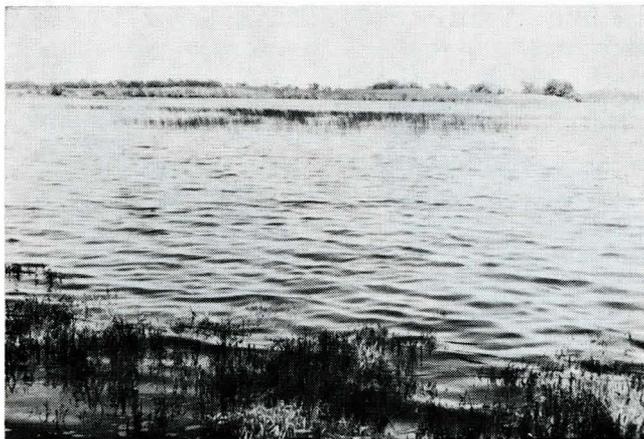


Fig. 7. Hardstem bulrush that persisted in water approximately 5 feet deep; northwest shore of Little Wall Lake, 1962.

plants. Despite a low muskrat population, several sizable pools of open water made portions of the lake highly suitable for most marsh birds. Thus, the number of bird species using the area at the beginning of the study was greater than at Little Wall Lake.

Conditions were ideal for muskrats at Goose Lake with dense emergents and water 2½ feet deep in some areas. Populations increased in a typical sigmoid fashion. Although careful territory counts are not available for each year, lodge-counts were made periodically and reflect the dramatic increase in muskrats and in construction of lodges which resulted in a dramatic decline in the percentage of emergents present and an "eat-out" of vegetation by 1961 (figs. 8 and 9).

Vegetative changes at these lakes demonstrated what seems a common pattern of short-term plant succession on such semipermanent water basins. The most dramatic invasions of plants occurred during periods when the marsh bottom was exposed or when water was very shallow. In general, established plants tended to persist in the same areas despite water fluctuations. Thus, hardstem bulrush stands were located in the same areas in Little Wall Lake despite complete drying or inundation with 6 feet of water. Both extremes seem to produce a small and sparse crop subject to disease, but the rootstocks were remarkably tolerant. The size and density of the stands,

therefore, changed much more than did their general location on the lake. Marsh-edge plants persisted for 2 or 3 years at Goose Lake. Some, such as willows, were known to persist in one marsh (Dan Green Slough) for 5 years, even in 2 to 3 feet of water. Cattail and hardstem bulrush were the only emergents to survive more than 3 years. Simultaneously, shoreward stands of sedges and river bulrush flourished as water levels increased, but increased density or spread of plants was mainly in areas of established rootstocks or seed plants.

One phenomenon associated with increased water levels was the change in the character of the marsh bottom. Early post-drouth flooding did not disturb the solid mat of rootstocks on the bottom, but continued submergence of 2 to 3 years, and perhaps muskrat activity, resulted in a softening and eventual flotation of the bottom rootstocks and mat of organic debris. Walking was difficult because of the submerged bog-like mat floating 6 to 12 inches above the basin. In some cases, mats floated to the surface and were broken up by wind action and probably became established in other areas of the marsh.

Bird Populations in Relation to Habitat

To appraise the impact of habitat changes on the bird population of these lakes, it is necessary to compare changes in numbers and locations of nests. Numbers are indicated by the number of nests found and by counts of territorial males.

TABLE 3. Numbers of nests found at Little Wall Lake, 1958-62.

Species	1958	1959	1960	1961	1962	Total
Yellowhead	111	59	71	151	0	392
Redwing	38	86	80	168	16	388
Coot	0	2	10	58	0	70
Black tern	12	5	8	36	0	61
Least bittern	0	0	10	11	0	21
P.-B. grebe	0	0	1	9	0	10
Gallinule	0	0	0	3	0	3
Mallard	2	1	1	2	1	7
Blue-winged teal	0	1	0	5	0	6
Ring-necked duck	0	0	0	1	0	1
L. B. marsh wren	1	—	2	—	0	3
Virginia rail	0	0	1	0	0	1
Pheasant	0	1	0	0	0	1

TABLE 4. Numbers of nests found at Goose Lake, 1958-62.

Species	1958 ^a	1959	1960	1961	1962	Total
Yellowhead	1	138	255	28	1	423
Redwing	7	123	140	80	18	368
Coot	4	49	19	16	1	89
Black tern	10	24	42	8	8	92
L. bittern	5	7	62	2	2	78
P.-B. grebe	3	8	38	26	5	80
Gallinule	0	3	5	7	0	15
Mallard	0	2	3	6	1	12
Blue-winged teal	1	0	1	3	0	5
Ruddy	0	2	1	1	0	4
Ring-necked duck	0	0	0	1	0	1
American bittern	0	0	0	1	0	1
Sora	0	0	0	0	1	1
Pheasant	0	1	0	0	1	2

^aData for 1958 are not complete.

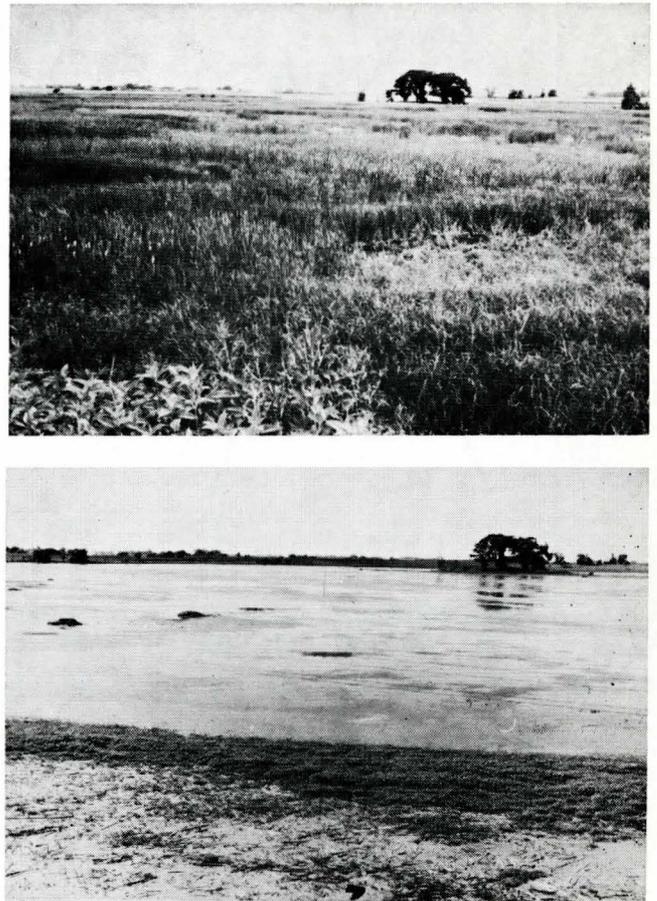


Fig. 8. Views of the southern end of Goose Lake and the small island in the summer of 1959 (upper) and in early summer 1962 after the severe muskrat eat-out.

The total number of nests found are shown in tables 3 and 4, and habitat use and other nest-statistics gathered from some of these nests are shown in table 5. Figures 10 and 11 summarize population changes as shown by nests or territorial males. There is undoubtedly some bias because of variations in nest hunting effort in different years, but it is believed that the intensity

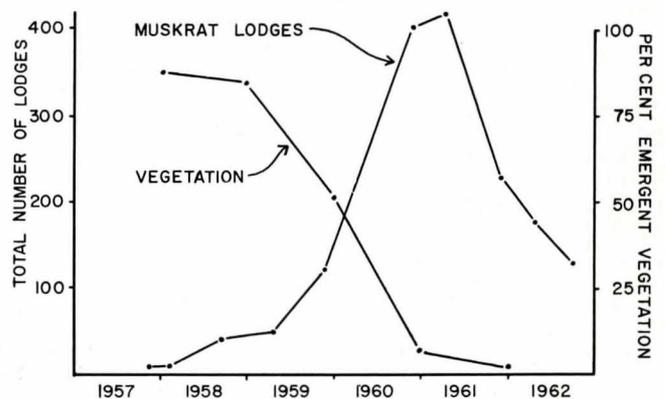


Fig. 9. The relationship, as suggested by muskrat house counts, between the percentage emergent vegetation at Goose Lake and the muskrat population.

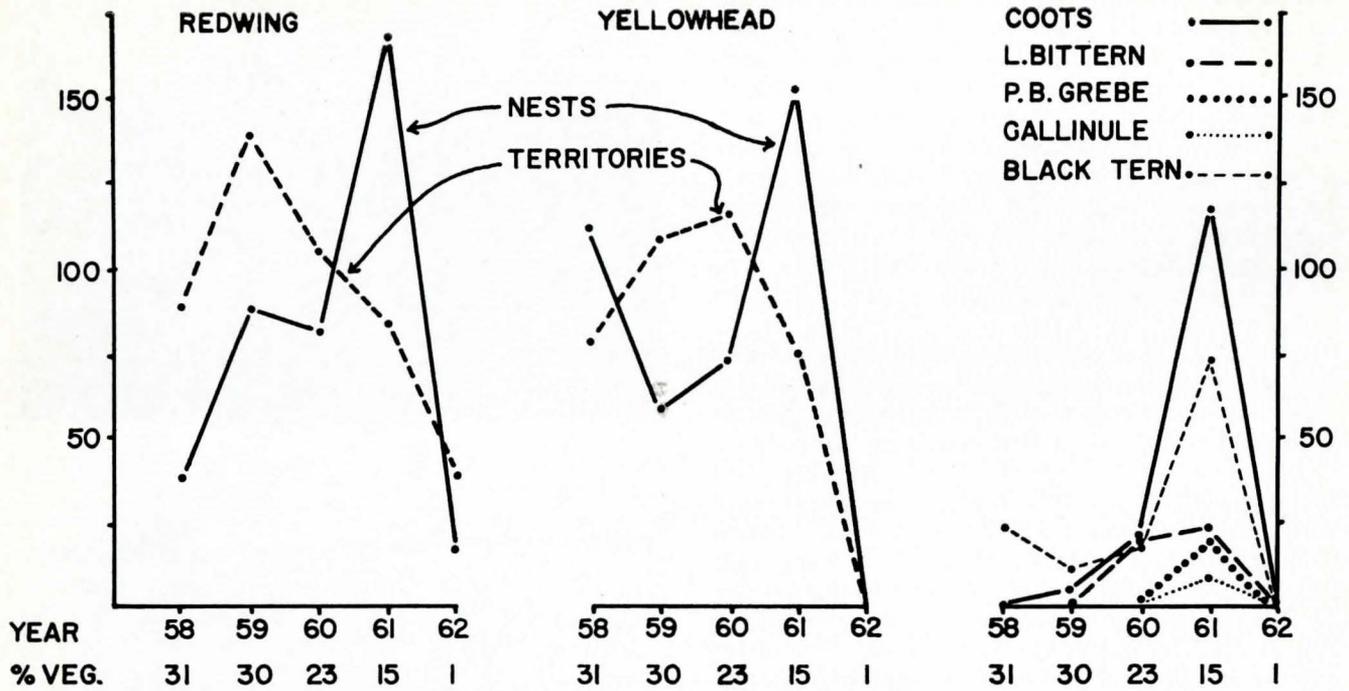


Fig. 10. Populations of seven species of birds at Little Wall Lake, 1958 to 1962. Peak population was reached in 1961 when the percentage of emergent vegetation was approximately half that of when the study started.

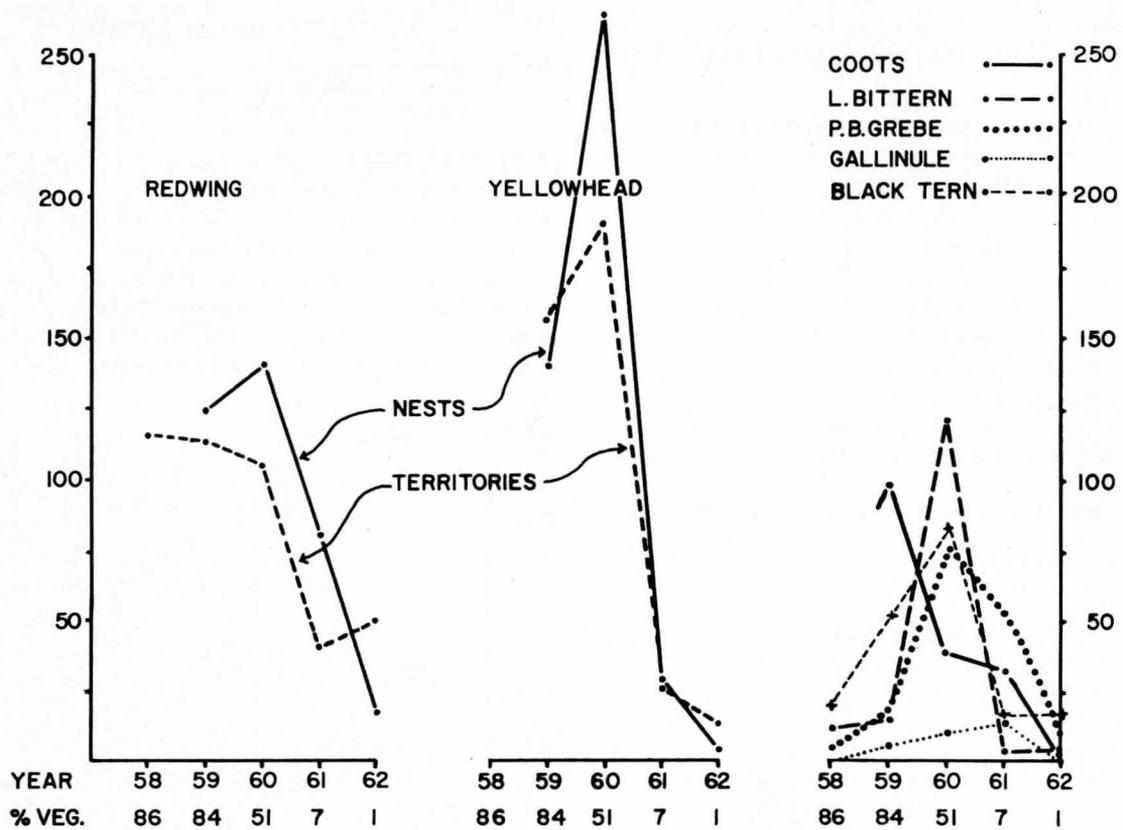


Fig. 11. Populations of seven species of birds at Goose Lake, 1958 to 1962. Peak populations were reached in 1960 when the cover-water ratio was approximately 50:50.

TABLE 5. Data on nest position and vegetation in which nest was constructed — Goose Lake, 1959 to 1962, and Little Wall Lake, 1958 to 1962.

Year, location and kind of nest	No. nests measured	Average water depth below nest	Average height of nest above substrate	Percentage of nests over land (no water)	Sedge	Sedge and river bulrush	River bulrush	River bulrush and cattail	Cattail	Cattail and hardstem	Hardstem bulrush	Phragmites	Mixed emergents	Forbs	Low trees and bushes
LITTLE WALL, 1958															
Yellow-headed blackbird	102	10.0 (5)	-----	0	0	0	1	0	31	1	69	0	0	0	0
Redwinged blackbird	23	4.2 (16)	-----	16	1	0	7	0	0	0	12	0	0	1	2
GOOSE LAKE, 1959															
Yellow-headed blackbird	138	24.5 (67)	8.8 (62)	0	0	0	34	3	62	0	14	0	25	0	0
Redwinged blackbird	113	13.3 (63)	10.5 (58)	5	12	4	26	8	29	0	8	2	21	3	0
Least bittern	5	17.0 (2)	8.0 (4)	0	0	0	1	1	0	0	2	0	1	0	0
Coot	49	28.0 (27)	-----	0	2	0	5	2	21	0	6	0	13	0	0
LITTLE WALL, 1959															
Yellow-headed blackbird	57	13.4 (20)	12.8 (19)	0	0	0	15	0	8	0	23	0	11	0	0
Redwinged blackbird	86	7.5 (40)	9.1 (37)	9	2	1	63	0	2	0	13	4	0	0	1
GOOSE LAKE, 1960															
Yellow-headed blackbird	255	22.4 (255)	11.3 (255)	0	0	0	25	20	114	85	2	0	9	0	0
Redwinged blackbird	140	13.6 (140)	12.9 (140)	0	5	14	37	20	22	4	2	0	36	0	0
Least bittern	61	19.5 (61)	6.9 (61)	0	0	0	9	2	8	21	6	0	15	0	0
Coot	17	23.2 (17)	-----	0	0	0	1	0	10	4	0	0	2	0	0
P.-B. grebe	26	-----	-----	0	0	0	0	0	18	5	0	3	3	0	0
LITTLE WALL, 1960															
Yellow-headed blackbird	64	14.8 (64)	10.5 (64)	0	0	0	31	4	9	11	5	0	4	0	0
Redwinged blackbird	74	10.0 (74)	10.0 (74)	15	12	6	38	0	0	2	5	0	11	0	0
Least bittern	10	13.5 (10)	8.5 (10)	0	0	0	5	0	0	0	0	0	5	0	0
Coot	10	13.6 (10)	-----	0	0	0	6	0	0	0	3	0	1	0	0
GOOSE LAKE, 1961															
Yellow-headed blackbird	16	21.7 (16)	10.3 (16)	0	0	0	6	0	9	0	1	0	0	0	0
Redwinged blackbird	60	8.2 (43)	13.4 (62)	3	17	0	25	0	6	0	0	0	12	0	0
Coot	16	20.6 (16)	-----	0	0	0	7	0	8	0	1	0	0	0	0
P.-B. grebe	26	-----	-----	0	0	0	4	0	21	0	1	0	0	0	0
LITTLE WALL, 1961															
Yellow-headed blackbird	151	16.3 (151)	7.2 (151)	0	0	0	79	0	6	0	47	0	19	0	0
Redwinged blackbird	168	11.5 (151)	12.4 (166)	10	41	21	72	0	1	0	12	0	9	0	12
Least bittern	11	17.5 (11)	5.3 (11)	0	0	0	2	0	0	0	9	0	0	0	0
Coot	58	16.9 (58)	-----	0	0	0	38	1	1	0	14	0	4	0	0
P.-B. grebe	9	-----	-----	0	0	0	5	0	0	0	4	0	0	0	0
GOOSE LAKE, 1962															
Redwinged blackbird	18	1.0 (10)	31.7 (10)	94	2	0	1	0	0	0	0	0	0	3	12
LITTLE WALL, 1962															
Redwinged blackbird	16	12.0 (9)	51.2 (15)	44	0	0	0	0	0	0	0	0	0	2	14

of searching adequately measured abundant species, whereas chance played a large part in the location of nests of less common birds. For common species, changes were sufficiently dramatic that errors of estimate were negligible.

These data show a general post-drouth upsurge as the dense vegetation was reduced to an attractive interspersion of cover and water openings. A 1-year difference in peaks of bird numbers at Goose Lake (1960) and Little Wall Lake (1961) was due to the more rapid increase in water level and cover-water interspersion at Goose Lake and, subsequently, to a more rapid elimination of cover.

Although no data were available for Goose Lake in 1957 and little were recorded in 1958, the recorded data from both lakes can be pooled to show a typical population change in reflooded marshes and to express the pioneering ability of the various bird species involved. In general, species sufficiently adaptable to move into new areas during the first year of reflooding seem to be redwinged blackbirds, yellow-headed blackbirds, black terns, mallards, blue-winged teal and, possibly, coots. Least bitterns, pied-billed grebes, gallinules and diving ducks, like the ring-necked duck and ruddy duck, probably require 2 or more years after the marsh opens up. In the cases of grebes and bitterns, fish and amphibian populations may be important factors in the suitability of an area for rearing young.

Some species were not recorded in sufficient numbers to significantly show any influence of habitat on populations. Pheasant nests were recorded only when in the dry lake bed or in emergent vegetation at the shoreline. Sora and Virginia rails were common in 1958 and 1959, but their nests were rarely found. Marsh wrens were abundant from 1958 to 1960, but little time was devoted to searching for their nests. Duck populations were low in all years, but the peak for all species was 1961, during the peak production period of Little Wall Lake and following the peak production at Goose Lake. Duck numbers were lowest in 1962 when virtually all brood cover had been eliminated.

An approximate ratio of emergent vegetation to water is recorded for each year for each lake (figs. 10 and 11). Peak populations were reached at Goose Lake when the ratio of emergent vegetation to water was 50:50. The pattern at Little Wall Lake is complicated by the fact that a large lake area was present which was of little significance in attracting birds. However, there was a drop in emergent vegetation-water ratio of from 31 to 15 percent, reflecting mainly additional openings created by muskrats. Because the emergents were virtually dry and unattractive in 1958, the change by 1961 reflected approximately a 50:50 ratio of cover and water area, exclusive of the main lake.

Distribution of Nests in Relation to Vegetative Changes

The drastic vegetative changes at Goose and Little Wall lakes produced not only conspicuous changes in bird populations but also dramatic spatial shifts in area use. Reduction in plant density or elimination of cover forced birds to select new nesting areas in subsequent years and provided a measure of the limits of their adaptability. These spatial changes are shown in figs. 12 to 20. These maps show location of nests, not density, and demonstrate typical patterns of habitat utilization, such as the shoreward location of redwings as opposed to nesting of yellowheads near the water's edge. In addition, the maps show annual changes in the total area of nesting and shifts in nest locations. Collectively, the maps demonstrate a shoreward shift in area use concurrent with the elimination of nesting cover—first in the center of the marsh and later toward the periphery of the marsh. In the extreme condition, nesting areas were eliminated for most marsh species, while more adaptable forms shifted to terrestrial or marsh-edge vegetation. When compared with population data (figs. 10 and 11), the nest location maps indicate periods of ideal



Fig. 12. Distribution of nesting redwinged blackbirds at Little Wall Lake, 1958-62. Note gradual peripheral shift from emergent (median zone) to upland vegetation (outer zone).

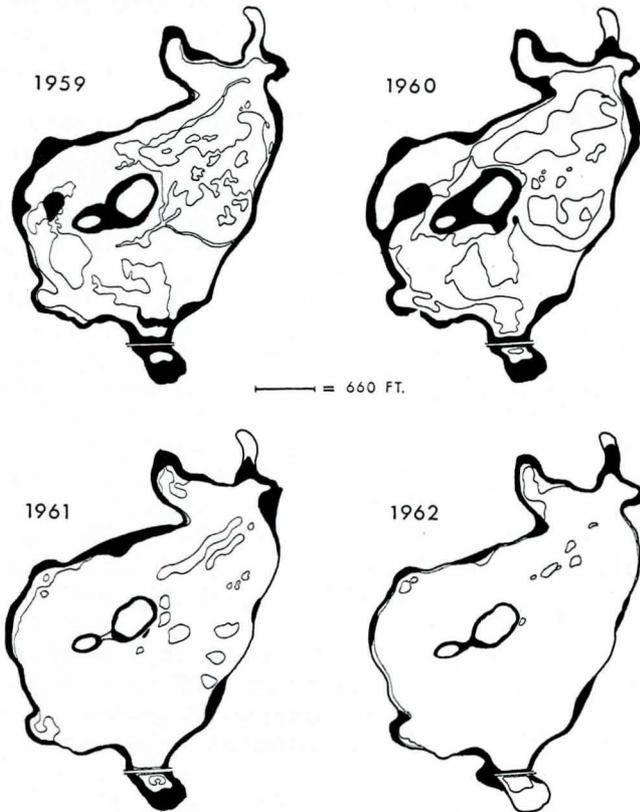


Fig. 13. Distribution of nesting redwinged blackbirds at Goose Lake, 1959-62. Note population along island edge and small areas in the emergent vegetation (*Carex*) that were used for several years.

cover-water interspersed when maximum numbers of birds found ideal conditions.

These responses vary considerably in some species or ecologically associated species, and species discussions will help to clarify these differences.

Redwinged and Yellow-Headed Blackbirds. The amazingly adaptable redwing fared best of all marsh birds in locating suitable nest sites, but even this species was reduced in numbers during the early, dry and the late, open-water stages of the habitat cycle. When the extensive stands of emergent vegetation in Little Wall Lake were nearly dry, redwings nested well out from shore in areas little used by yellowheads (figs. 12 and 14), but numbers were low. Redwings also utilized the dry emergent vegetation on the central peninsula where they found willows for song perches and emergents for nest sites. The Goose Lake population was more typical in that redwings formed a peripheral band around the lake and around the island (fig. 13). Only in the western and southern portions in low sedge and sparse cattail unused by yellowheads did redwings nest in the emergents away from the shore.

A gradual shoreward shift in nest sites of redwings is apparent in figs. 12 and 13. Although a

few redwings nested in low trees in all years, tree nests increased markedly in numbers and in the percentage of the total nests found as the emergent vegetation was eliminated from 1958 to 1962: 2 (5%), 1 (1%), 0, 12 (7%), 14 (87%), respectively.

There was relatively little overlap in habitat utilization of redwings and yellowheads (figs. 12, 13, 14 and 15). Yellowheads favored emergents standing in water adjacent to water openings, while redwings utilized emergents, shrubs and trees without regard to the presence of water at the bases of the plants. No yellowheads nested over land, in trees or in low sedges as did redwings. This lack of flexibility eliminated the species from Little Wall Lake and dramatically lowered their numbers at Goose Lake.

Especially noteworthy changes in areas used by yellowheads at Little Wall Lake were caused by the elimination of nest sites by the muskrat cutting of bulrush "islands" and the increase in use of newly flooded hardstem bulrush in the southern bay. At Goose Lake, the northern inlet and the south bay became populated in 1959 as water levels increased and muskrats created small openings. Neither area was used in 1958.

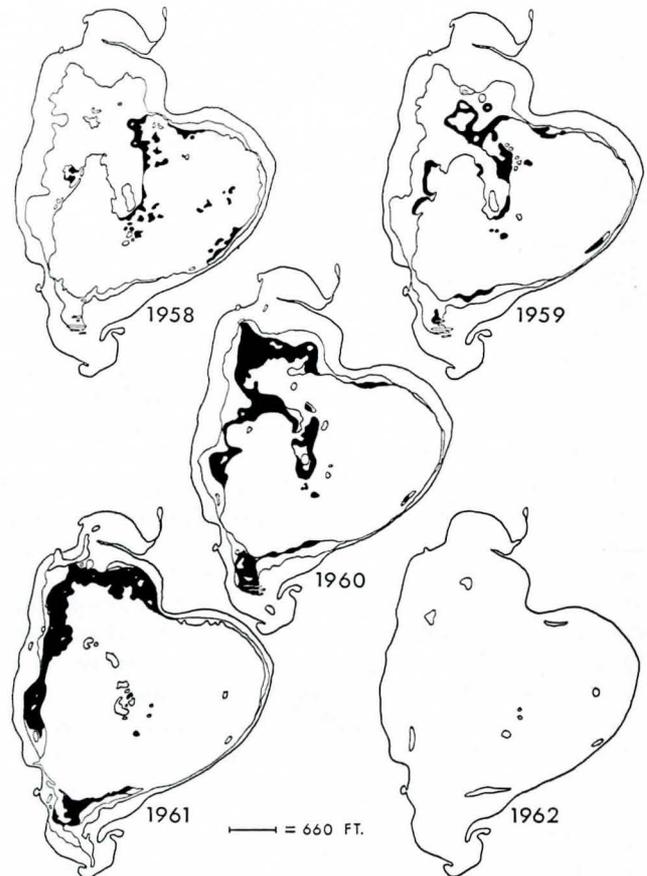


Fig. 14. Distribution of nesting yellow-headed blackbirds at Little Wall Lake, 1958-62. Note preference for the water's-edge zone of emergents and compare with the peripheral distribution of redwings (fig. 12).

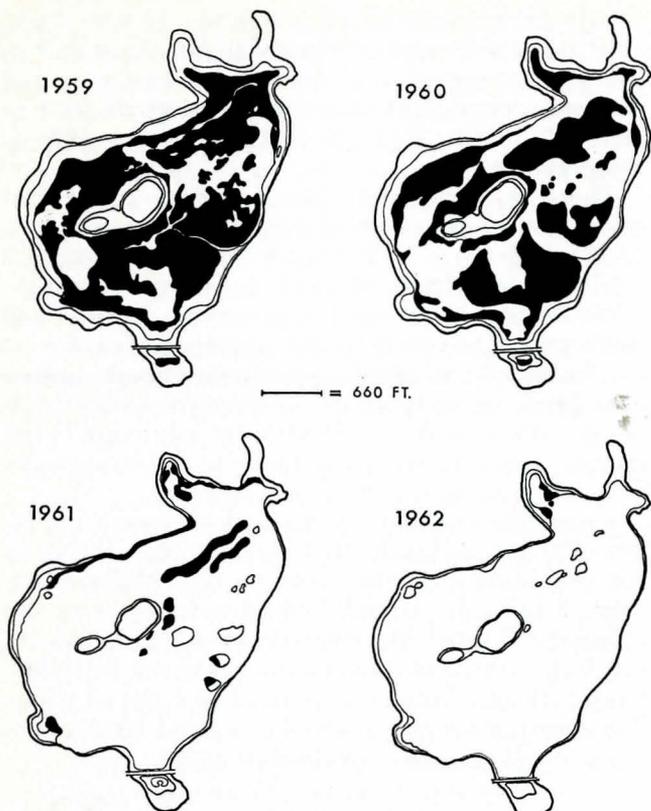


Fig. 15. Distribution of nesting yellow-headed blackbirds at Goose Lake, 1959-62. Yellowheads were restricted to emergent vegetation, although they gradually shifted shoreward.

Occasionally, flocks of yearling yellowheads were seen at Little Wall Lake. These arrived several weeks after nesting started, and such yearlings were pursued intensively by adult males. During the drier years, yearling yellowheads were forced into poor-quality emergents — usually of low density and dry at the bases — and did not really establish territories. Observations on flocks elsewhere indicated a similar situation; vegetation was inferior because it was not flooded, lacked water openings or was too sparse to be utilized by adults.

Coot and Common Gallinule. Both species nested only in emergent vegetation standing in water where they could swim to the nest. Coots and gallinules were similar to yellowheads in that certain areas were much used while others were not. Favored areas were of moderate plant density in adequate water and with adjacent open pools. Coots used much of Goose Lake in 1958 in its second year after reflooding (fig. 17). At this time, there were several sizable bodies of water interspersed in the dense emergent vegetation. At Little Wall Lake, however, the abrupt cover-water edge and the dryness of the emergents were unattractive to swimming waterbirds. Several coots nested at Little Wall Lake in 1959, but the population flourished in 1960 and 1961 as the last dense stands of emergents were opened (fig. 16).

Common gallinules nested in the same general areas as did coots and built similar nests. Common gallinules, however, were never numerous at either lake.

Black Tern. Terns shifted locations dramatically at Little Wall Lake as muskrats cut wave-slowing vegetation and opened pools in dense vegetation (fig. 18). Since terns are social birds, their nests tended to be in groups in especially suitable areas.

At Goose Lake, a less open situation existed, and partial cutting by muskrats had less influence than it did at Little Wall Lake. Nests at Goose Lake were often in open areas but were usually protected from wave action. The nests were on muskrat feeder stations or were built up in floating plant debris or dense beds of submerged, rooted aquatics. A gradual decimation of the population was apparent at Goose Lake (fig. 19), and a build-up and decline was noted at Little Wall Lake as habitat conditions first improved and then deteriorated.

Pied-Billed Grebe. The general dryness of the emergent vegetation at Little Wall Lake during 1958 to 1960 was unattractive to grebes. The large open-water area attracted large numbers

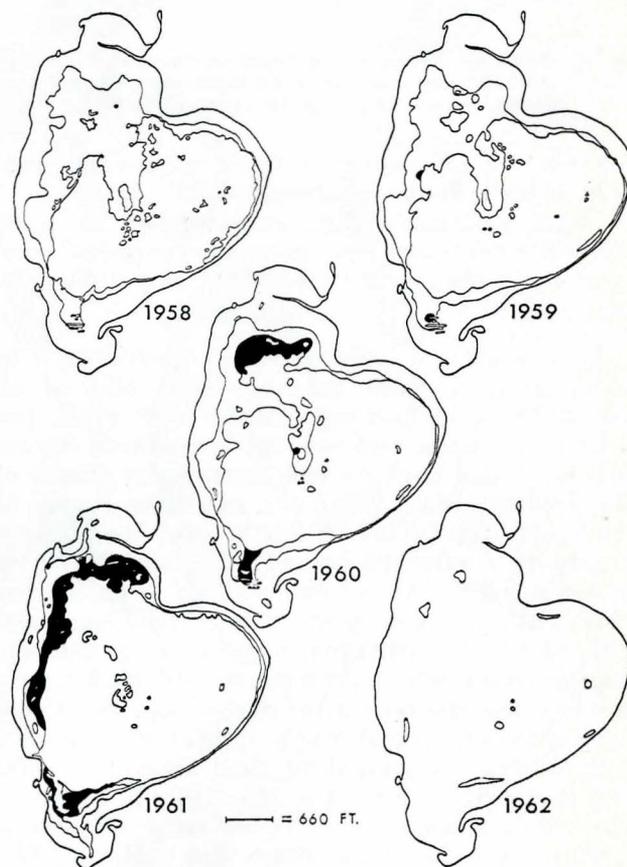


Fig. 16. Distribution of nesting coots at Little Wall Lake, 1958-62. Lack of coots during 1958 probably resulted from the abrupt edge between dry emergents and open water.

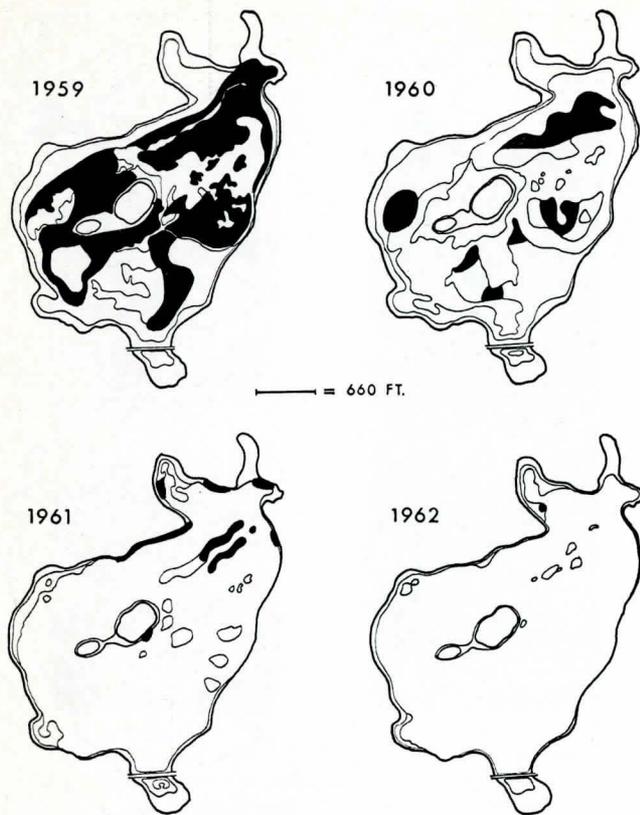


Fig. 17. Distribution of nesting coots at Goose Lake, 1959-62. The decline in area use and in numbers occurred in 1960 when other species reached their peak.

during spring migration, but none remained to nest until the cover was reduced in density and well interspersed with water areas.

At Goose Lake, grebes moved in during the year following flooding (1958) and found much of the central portion of the lake suitable for nesting (fig. 20). Grebes were surprisingly tolerant of open water, and their buoyant nests were found in sites only slightly protected from waves and open to view in all directions. Nevertheless, there was little evidence of nest damage.

Changes in Bird Populations and Vegetation on Goose Lake Transect

More precise data were recorded on a belt transect 1,300 feet long extending from the large island to the southeastern shore of Goose Lake. Part of the area was ideal cover in 1960, when the belt was established, but nearly 900 feet already showed signs of over-cutting by muskrats, and some cattail had been uprooted by flooding. The first 300 feet near the island are shown in fig. 21. Species composition and nest numbers are shown in table 6. The drastic decline in 1961 from the peak of 1960 is clearly shown. The reduction in cover was reflected in an almost complete elimination of nesting birds by 1961 (mainly because of

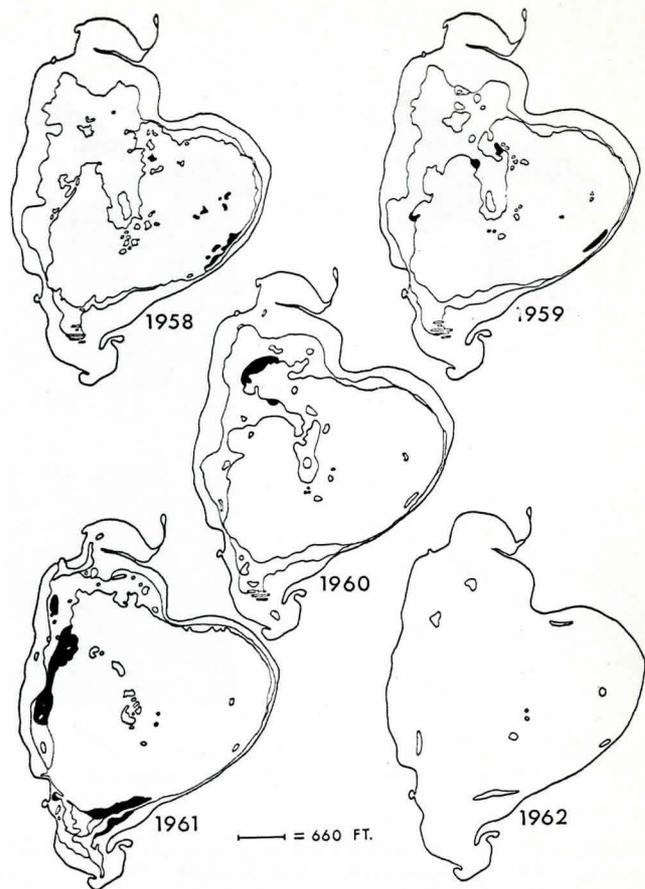


Fig. 18. Distribution of nesting black terns at Little Wall Lake, 1958-62. In 1958, populations were restricted to hardstem "islands" which were virtually destroyed by muskrats in the fall of 1958. All suitable emergents were eliminated by 1962.

muskrat cutting), and no nests were found in 1962. Again, the redwing adapted best, although a few terns constructed nests on the abundant floating debris.

These diagrams show clearly the "edge" concept as detailed by Beecher (1942). Nests were placed at the edges of plants of different physiognomy and at cover-water edges. Redwings, for example, flew from song-posts on land over *Carex* beds to nest in river bulrush, which was more robust and apparently provided more suitable nest sites. Figure 21 (1960) also clearly shows the usual situation in distribution of blackbird nests, with redwings close to shore and yellowheads near open water. Note especially, however, that one redwing nest was found a long distance from shore in some short, thin cover, apparently unattractive to yellowheads.

Habitat Selection and Adaptability

Although many generalizations have been made on habitat selection in birds, the precise environmental factors that influence the suitability of habitat for nest sites are little understood. Some of these features can be appraised by examination

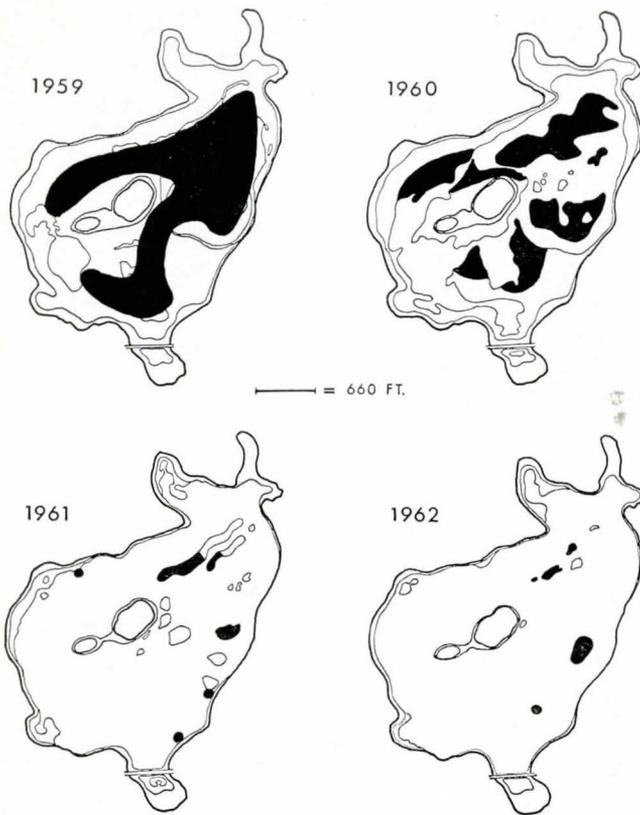


Fig. 19. Distribution of nesting black terns at Goose Lake, 1959-62. Central emergent cover seemed preferred.

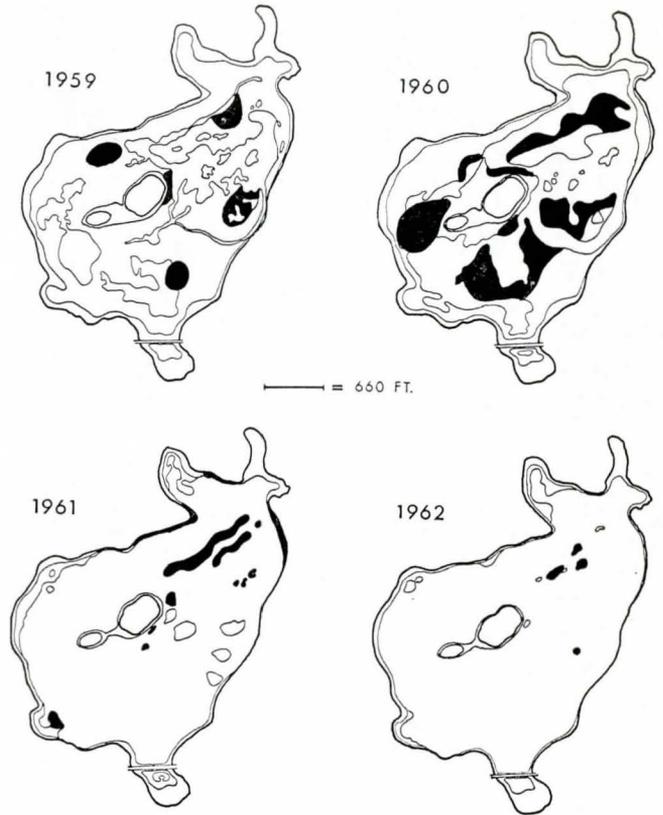


Fig. 20. Distribution of nesting pied-billed grebes at Goose Lake, 1959-62. As with black terns, vegetation in the central portion of the marsh seemed preferred.

and measurement of the characters of the nest site—especially in areas of high density of nests of any species. Moreover, observation of nests of a single species over a variety of habitats reflects the tolerance or adaptability of the species. In addition to measurements of these factors, the drastic habitat changes at Goose and Little Wall lakes permitted appraisal of the limits of adaptability to nest site selection.

Habitat selection is generally regarded as a response to certain environmental stimuli which fulfill a set of innate psychological requirements (Lack, 1933). This is usually a species-constant character (but not without variability) which thereby results in an attraction of sufficient individuals of the same species in the same area so that pairing and reproduction can occur. The presence of members of the same species is, there-

fore, an essential psychological element of the environment which varies in importance with the social tendencies of the species. Other influences are habitat factors, such as the physical characters of the vegetation for song perches and nest sites, the presence of water and the general aspect of the surrounding community (Svårdson, 1949). In many cases, a particular locale is well suited for many species which, presumably, do not compete seriously. In a few instances, there seem to be actual interspecific species attractions for at least some members of a species, as noted by the concentration of duck nests in gull nesting-islands (Koskimies, 1957).

Some qualitative generalizations derived from this and other studies are shown in fig. 22. Species discussions will help to clarify the usual nest sites, the limits as observed in this study and some unknowns which need experimental testing.

Beecher (1942) and other workers have shown that innate requirements for nest sites are satisfied by plants of many species as long as they are similar in life form. Some species of marsh birds favor tall, coarse emergents, while other species utilize short and less robust plants.

Redwinged and Yellow-Headed Blackbirds. The general distribution of these two blackbirds is

TABLE 6. Nests found in belt transects at Goose Lake, 1960-62.

Species	Total nests			Nests per 100 ² ft. quadrat		
	1960	1961	1962	1960	1961	1962
Redwinged blackbird	21	3	0	1.61	0.23	0
Y.-H. blackbird	28	0	0	2.15	0	0
P.-B. grebe	3	0	0	0.23	0	0
Coot	3	0	0	0.23	0	0
Least bittern	5	0	0	0.39	0	0
Black tern	3	3	0	0.23	0.23	0
Total	63	6	0	4.84	0.46	0

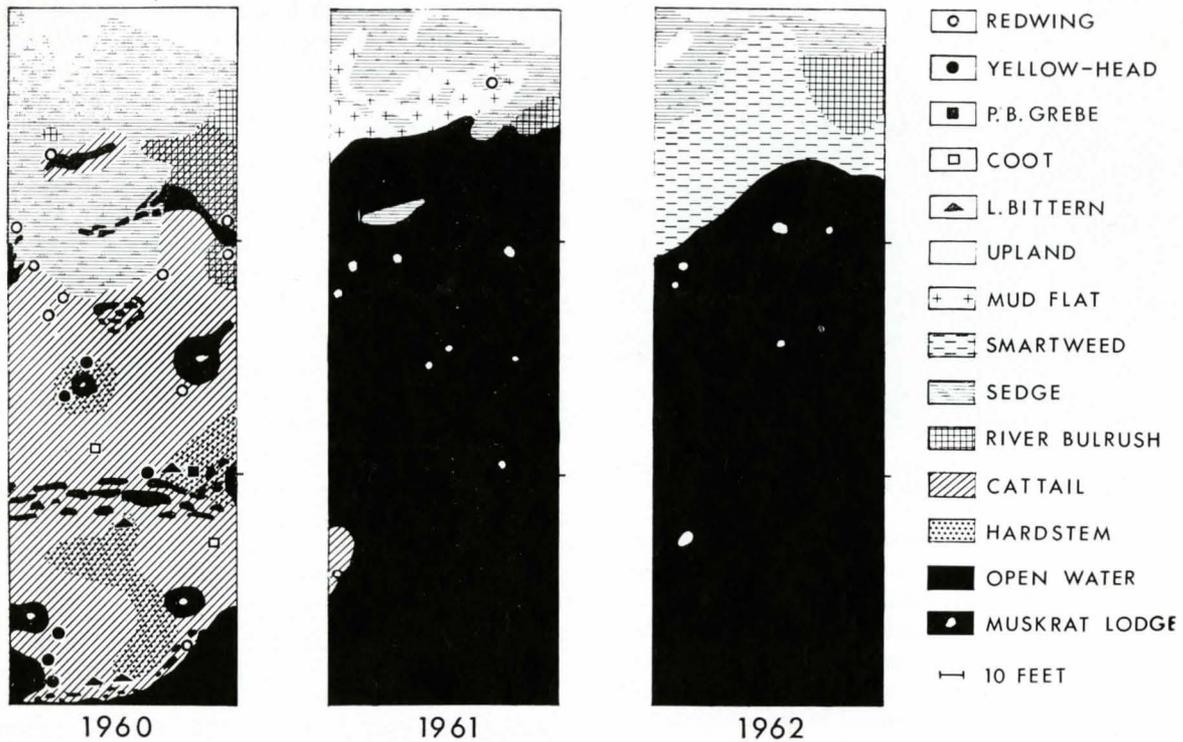


Fig. 21. Detailed cover maps of three quadrats at Goose Lake. Nest locations demonstrate the preference for cover-water edge or the edge between two cover-types. The decline in emergent vegetation eliminated all species of nesting birds.

well known; the precise habitat stimuli that bring about this distribution are less well understood.

In general, the redwing is the more terrestrial of the two, and nests in forbs, grasses, cultivated crops and trees are common (Case and Hewitt, 1963). However, the redwing's great density in marshes and its response to any body of water implies an original evolution to marsh habitat. Changes in land-use and the elimination of bobolinks in many areas may have influenced a recent spreading into available niches.

Redwing nests are similar to nests of other

terrestrial birds in being constructed of grasses and other fine vegetation and, even if built quite some distance from shore, being lined with fine plant material or hair (fig. 23). Mud is common in the nest bottom. The young have dark plumage.

Nests of yellowheads are typically of coarse material throughout and only rarely are lined with finer material. Nest material is usually wet, old, plant debris that can be easily woven. The young are light-colored as are most true marsh birds.

Records of nests of both species indicate a

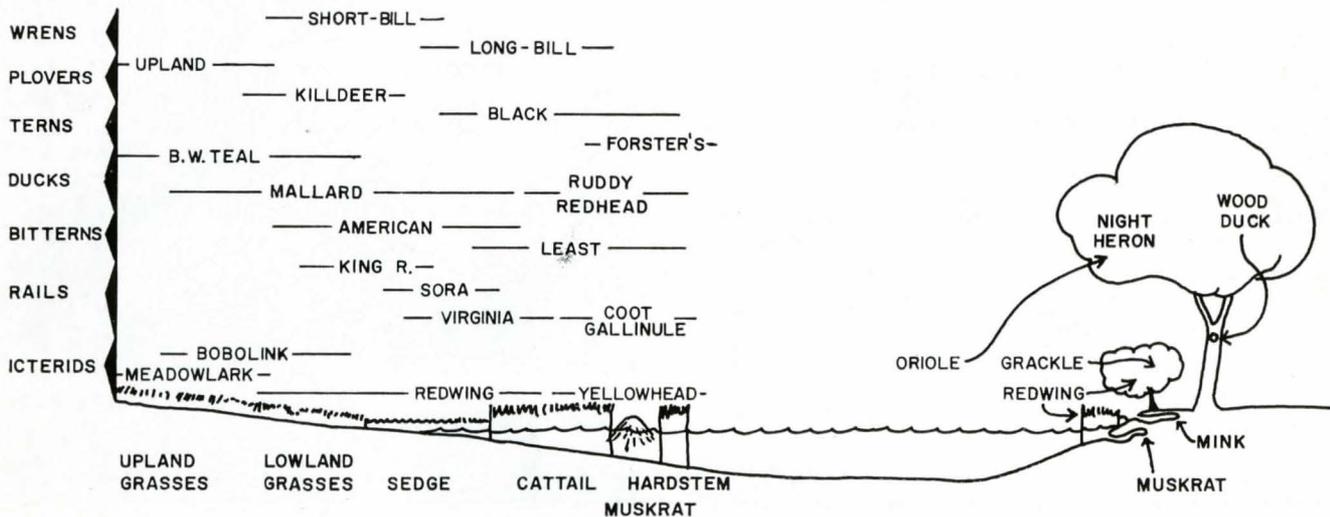


Fig. 22. A schematic drawing of the habitat selection by several groups of marsh and marsh-edge birds.

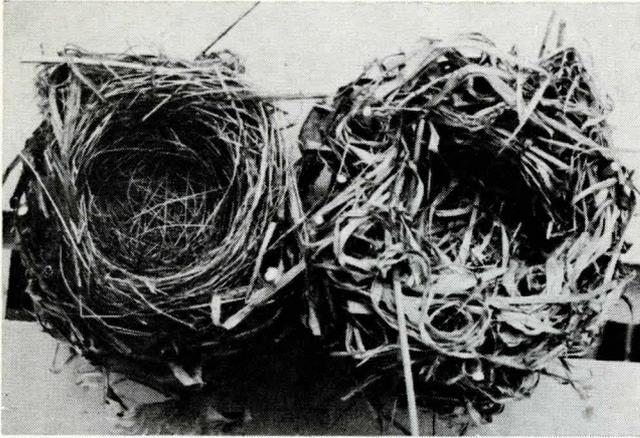


Fig. 23. Redwinged blackbird (left) and yellow-headed blackbird nests showing typical difference in construction materials.

greater adaptability of the redwing to supporting structures. Redwing nests were found in low sedge and in trees 20 feet above ground or water. No yellowhead nest was found over land in this study, but the depth of water was insignificant as shown by annual and geographic variation (table 5). Moreover, yellowheads were found only in tall and coarse emergents, such as river and hardstem bulrush and cattail, and use of these varied annually because of availability in relation to open water (table 5). Several nests were found in willows standing in water at Dan Green Slough (fig. 24), and use of willows also was noted by Linsdale (1938).

Statistics on height of the nest above water or land (table 5) indicate that the height of redwings' nests is greater than that of yellowheads'. Possibly this is related to redwings' contact with terrestrial predators, as is other nest-defense behavior of redwings (Siglin and Weller, 1963).

The major factors that influence the presence or absence of yellowheads can be analyzed grossly by using nest statistics in a comparative form similar to the model prepared by Svårdson (1949) for pipits (genus *Anthus*). Our comparison differs from Svårdson's in that our model (table 7) compares the significance of an optical stimulus to two species rather than evaluating the relative

TABLE 7. A comparison of key habitat stimuli in nest-site and territory selection by redwinged and yellow-headed blackbirds.

	Nests showing character			
	Yellow-headed blackbird		Redwinged blackbird	
	Percent	Range	Percent	Range
Water under nest.....	100	(-)	88	(0-98)
Tall robust emergents.....	100	(-)	86	(0-100)
Open water near nest.....	100	(-)	75 ^a	(0-100)
Conspecific males near.....	100	(-)	80 ^a	(0-100)
Open country.....	100 ^a	(-)	75 ^a	(0-100)
High song posts.....	5 ^a	(0-10)	75 ^a	(20-100)

^aEstimates

importance of several characters in a single species. Table 7 compares percentages of all nests found that displayed a certain character. Estimates were necessary in some cases, but this type of summary clearly demonstrates the greater specificity of yellowheads to certain environmental stimuli. These data suggest that the important factors limiting the nest site selection of yellowheads are: (1) water at the base of the nest, (2) tall, robust emergents, (3) nest site adjacent to or near open water and (4) the presence of other yellowheads.

Observations of shifting populations and distribution of nests support these generalizations. During 1958 and 1959 at Little Wall Lake and 1958 at Goose Lake, the north ends of the lakes were dry and densely vegetated. Neither area was used by yellowheads until flooded and opened by muskrat cutting. However, redwings used the area in small numbers.

In another case, at Round Lake near Ruthven, Iowa, redwings nested in dense shoreline cattail and used trees as song posts. A linear opening (created artificially by tractor cutting on ice) located 100-200 feet from shore was much used

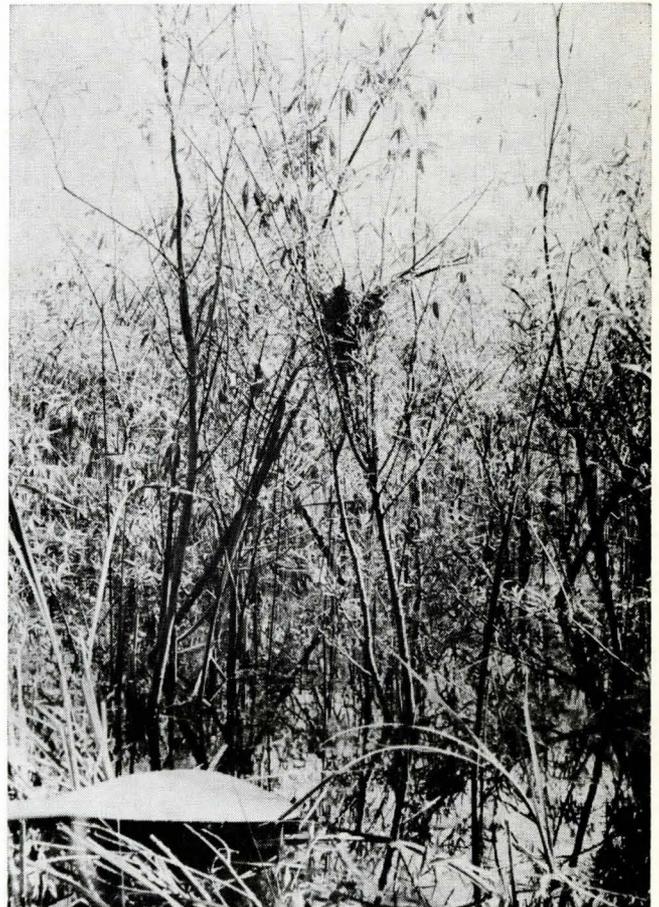


Fig. 24. Yellow-headed blackbird nest in willow tree standing in water, Dan Green Slough, 1961.

by yellowheads. But beyond this artificial opening, the dense cattail beds lacked openings and were used sparsely only by redwings. In this case, the redwings established territories several hundred yards from shore. A third, more complex, case was noted at Dan Green Slough near Ruthven. A bed of willows had developed in the center of the marsh during a dry period. The zonation was, therefore, the reverse of the usual with willows on the shore, a band of cattail, and then a bed of willows in deep water. Yellowheads were dominant in the central cattail belt, while redwings dominated the willows and cattail near shore. But both species nested in the central willow bed, although the redwing seemed present in greatest numbers. Apparently, the willows were not ideal for yellowheads, and redwings utilized all sites not occupied by yellowheads despite distance from shore.

While it is clear that yellowheads do not need a high song post (cattail or muskrat houses are used regularly), the importance of the song post to the redwing is uncertain. Redwings can and do establish territories in the absence of taller posts but seem to prefer tall structures in the area. Tests with cut trees indicate that the presence of perches in the absence of nesting cover does not produce an area suitable for a territory. How-

ever, redwings immediately use any perches placed in or near their territory.

Interspecific aggression also plays an important role in the selection of nest sites by redwings. Interspecific chases between redwings and yellowheads are common during a short period following the arrival of yellowheads. During this time, changes in redwing territories seem to occur, as noted in fig. 25 showing early spring territory counts. Counts of aggressive actions showed that male yellowheads chased both male and female redwings and that chases by male yellowheads sometimes were as common as intraspecific chases. The brief duration of this readjustment may explain why it has not been reported by other observers.

In general, yellowheads dominated redwings within territory that was marginal for redwings (some distance from shore) and preferred by yellow-headed blackbirds. However, neither species seems to be chased from a well-established territory, and, occasionally, a redwing seems to maintain a territory in an area which yellowheads dominate. Often, there seems to be minor habitat differences, such as height or density of the vegetation, which may influence this tolerance.

During this study, redwings used a greater variety of habitat types and tolerated changed

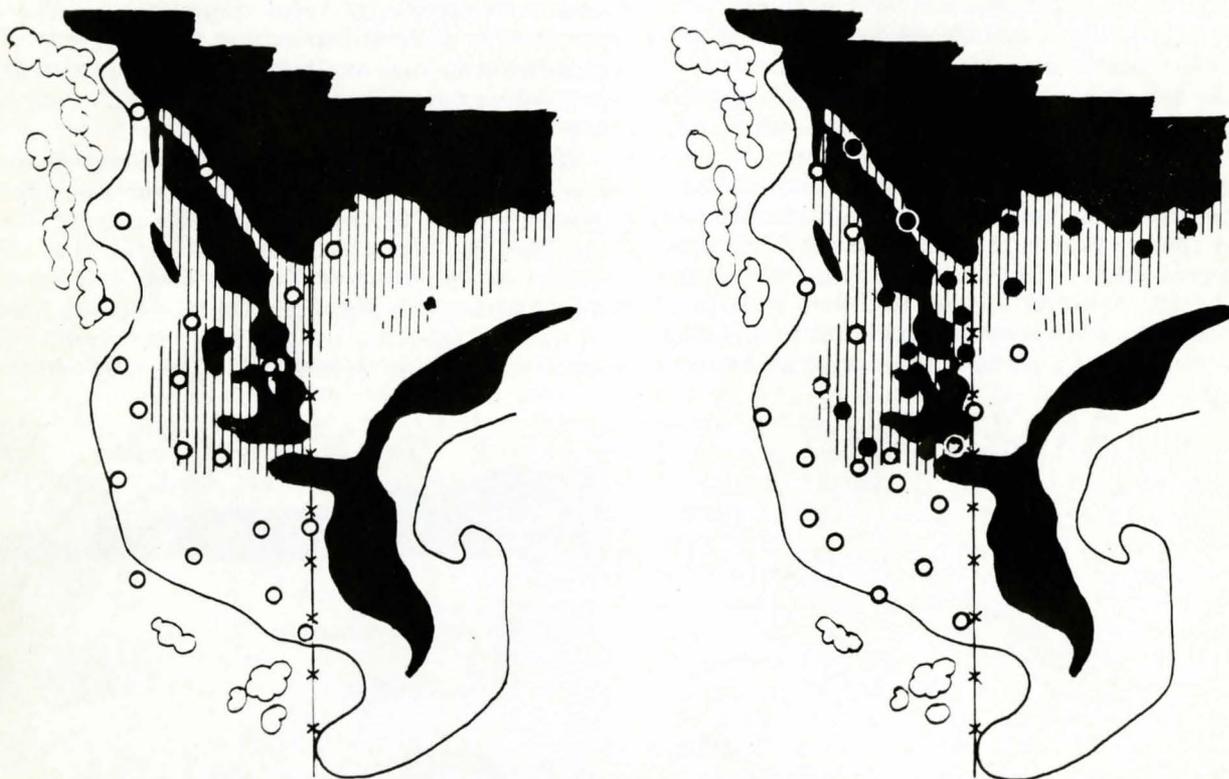


Fig. 25. Figure at left shows the distribution of territorial male redwinged blackbirds (circles) at the south end of Little Wall Lake before the arrival of yellow-headed blackbirds in the spring. Note partial occupancy of emergents (pattern) near open water (black). Figure at right shows the location of territorial male redwings (circles) and yellow-headed blackbirds (dots). Note yellowhead dominance of central area of emergents adjacent to open water.

conditions more readily than did yellowheads. The highly specific habitat and social requirements of yellowheads are responsible for what is virtually an all-or-none response to marsh areas, while redwings persist in small numbers even under extreme conditions.

Coot and Common Gallinule. Coots and gallinules invariably selected over-water nest sites; nests were attached to vertical stalks of emergents. The height of the emergents usually was tall, but muskrat-chewed cattail "stubble" was used by both species during the years when few emergents were present. As with other marsh birds, the species of plant was irrelevant (table 5) as long as it was standing in water, but robust emergents seemed favored. Willow trees were used as a structure to bind to at Rush Lake and as a total support structure for one nest at Dan Green Slough. Because the nest was bound between stalks of emergents, little substrate was necessary, especially for coots. In some cases, nests of both species were floating and barely attached to prevent drifting. Unlike most other species studied, coots seemed to carry vegetation quite some distance because nests were occasionally constructed of materials that did not occur within 25 feet of the nest.

Coots seem to pioneer newly flooded areas more quickly than do gallinules, but both were extremely tolerant of "open" conditions despite an obvious danger to the nests.

Because both male and female incubate and are highly aggressive and broody, coots seem to suffer little egg loss from aerial predators. Numerous investigators have commented on their nest success and dense populations. Kiel and Hawkins (1953) found 99 percent egg success of 1,304 eggs in 380 coot nests in Manitoba, Canada. Miller and Collins (1954) noted 95 percent nest success of 140 coot nests in California, and Hunt and Naylor (1955) reported 95 percent success of 20 nests in 1951 and 97 percent of 143 nests in 1953 in the same state. At Dan Green Slough in northwest Iowa, Sooter (1941) found 91 percent success of 104 nests in 1936 but only 77 percent success of 347 nests in 1937. The latter occurred during both high-water conditions and dense coot populations. Harris and Marshall (1957) reported a case in which 63 percent of 30 nests located in sparse cover were lost because of a wind storm. Wolf (1955) reported only 72 percent success of 10 nests, 73 percent of 8 nests and 95 percent of 63 nests in several Utah lakes. Lower success was due to drying of areas rather than to flooding. Thus, nest success can be reduced significantly by environmental influences. Several examples of this were noted in the Iowa studies, but nest success data were not recorded regularly. However,

some general observations and limited data are worthy of note.

At Rush Lake, observations began after most vegetation had been reduced to "stubble" by muskrats and ice action. Birds nested in quite exposed positions (fig. 26), and nests were in very poor condition. Similar observations were made at Goose Lake during 1961 and in the Delta marshes of Manitoba during 1956. Nest success seemed unusually low for coots, mainly as a result of desertion. The opposite extreme also was noted at Rush Lake when water levels declined during the period when most coots were incubating. The result was mass desertion (only 5 of 14 nests under observation hatched) and flocking of coots. A lowering of water levels before nest initiation produced the same effects: flocking and reduced nesting as discussed in connection with chronology of nesting.

It appears that coots are much bound to nesting areas (perhaps "natal" marshes) and that they must be virtually forced to leave by extreme habitat conditions of very dry or open conditions. The recent drouths throughout the prairies, and as shown in the population data here, give proof of the impact of drouth on coots, and the wet part of the water cycle is equally influential. Coots do not seem to recognize the inadequacy of the habitat. It is probable that habitat quality is a major regulator of coot populations. Various marshes in different areas are in peak production at different times and tend to maintain a uniform population over a wide area, but local fluctuations are violent.

Gallinules were not sufficiently common to allow much analysis of habitat preference. Nests generally were constructed slightly above the water level, as is characteristic of some other rails, while the bases of coot nests usually were well under water. No significant difference was noted in habitat selection by gallinules and coots. Gallinule nests often were found in more dense cover

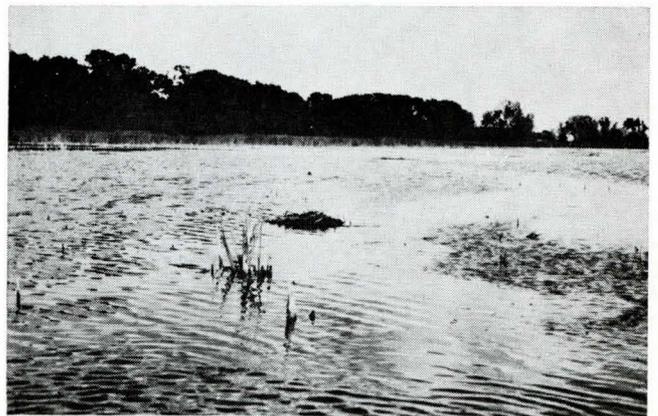


Fig. 26. Coot nest in open water at Rush Lake. Only cattail stubble held the nest in place, and the nest eventually was destroyed.

close to shore, but several very exposed nests were noted at both Goose and Rush lakes.

Black and Forster's Terns. Nest sites of black terns were typically on some low and wet substrate in water. Low and deteriorated muskrat houses were common sites, but any pile of vegetable debris or floating rootstocks was used. Occasionally, nests were found on floating boards. Construction was simply a gathering of local debris in most cases, but nests several inches high occasionally were made of green grass or cattails, with only submerged vegetation as a base.

There is no real evidence that lack of a substrate prevents nesting, but substrates are used regularly where available. Some general correlation exists between the numbers of muskrat houses on Goose Lake (though these counts do not include feeding platforms, they reflect muskrat activity) and the percent of black tern nests found which were on muskrat houses or feeders (fig. 27). The lack of agreement for 1961 probably is because, although the muskrat houses remained, there was little emergent vegetation surrounding these houses, and they were generally less attractive to terns than were houses surrounded by emergents.

Emergent vegetation — even though sparse — seems preferred by black terns. Emergent vegetation probably reduces wind action and seems an innate optical requirement. Cattail debris, which seemed ideal for nest sites, did not attract nesting birds where there were no adjacent emergents. Also, a large floating mass of rootstocks at Goose Lake did not induce nest sites, presumably because it was similar to a mud flat and lacked water surrounding the nest.

In general, peak numbers of terns were present when there was good interspersed of water and emergents. When cover was reduced, most terns nested in or near the sparse clumps of cattail and bulrush.

In comparison with black terns, Forster's terns were species of larger and more open marshes. None nested at Goose or Little Wall lakes, but Forster's terns were common at Rush Lake and Barringer Slough in northwestern Iowa. The most clear-cut difference in nest-site selection of these two species was the obvious preference of Forster's terns for higher and drier sites than used by black terns. Forster's terns used high, fairly new and often active muskrat houses (which does not seem true of black terns). Nests of 21 Forster's terns on muskrat houses at Rush Lake averaged 14.5 inches above the water level, while those of 146 black tern nests on old muskrat houses at Goose and Little Wall lakes averaged only 2.8 inches above water level, and seven black tern nests at Rush Lake were an average of 3.4 inches above the water. Of 156 black tern nests

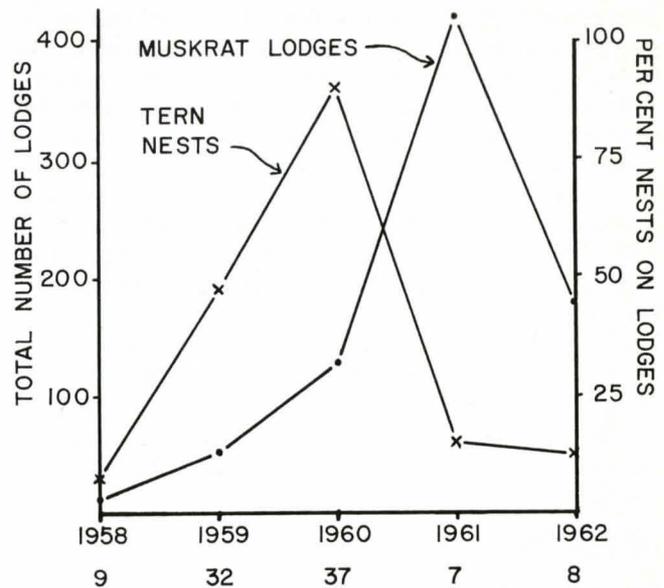


Fig. 27. Gross relationship between the number of muskrat lodges and the use of feeder stations by nesting black terns. Numbers of tern nests found are shown under each year.

and 39 Forster's tern nests observed during this study, 53 percent of the Forster's tern and 72 percent of the black tern nests were on muskrat houses. This is a minimal figure, since it is not always possible to determine the origin of the substrate of the nest.

The general difference in height of nests above water was evident in nests not constructed on muskrat houses but built on floating rootstocks, debris, boards, etc. Thirteen such Forster's tern nests at Rush Lake averaged 5.3 inches above water level, while 21 black tern nests at Goose and Little Wall lakes were only 2.3 inches above water.

In general, these two species were ecologically separated on the areas where both occurred, with black terns using mainly marginal areas of marshes and Forster's terns using cattail islands or lake edges. Occasionally, however, nests were found as close as 25 feet.

Pied-Billed Grebe. Like the coot and gallinule, the pied-bill seemed present in greatest numbers when dense emergents were well interspersed with open pools. However, the pied-bill is quite tolerant of open areas if considerable floating debris is present. A few vertical stalks of cattail stubble often hold completely exposed nests. Because the nest is entirely floating and buoyant, it is less subject to wave damage than are many nests. Pied-bills pioneer more slowly than do coots, possibly because animal foods of importance to grebes first must repopulate the marshes.

Least Bittern. This species seems to nest only over water in sturdy emergents and seems to pioneer at about the same rate as do grebes (i.e., about the second or third year after flooding).

Nests are almost always over water. Peak populations were reached in 1960 at Goose Lake, when all other species reached their peak, and in 1961 at Little Wall Lake, when cover-water interspersions were best there. The densities recorded at that time have exceeded any previously reported (Weller, 1961). Bitterns did not use the dense vegetation in the north end of Little Wall Lake until it was opened by muskrats. Because the nest is elevated in emergents, the presence of tall plants usually was essential. Dense vegetation seemed preferred, but a few tolerant individuals nested in isolated small clumps of cattail at Goose Lake in 1961.

Like grebes, bitterns undoubtedly are influenced by populations of frogs, fish and invertebrates.

DISCUSSION

Evolution of Habitat Niches

Although most species observed during this study found the median cover-water interspersions stage ideal and many species nested in the same areas, there was a distinct lack of competition for nest sites in several groups of closely related species. Other cases were less clear-cut and may reflect a situation in which nest sites are not limiting. When additional data are available, some definite pattern in habitat selection may be found for most species. Presumably, these species evolved and exist now with fairly distinctive preferences (fig. 22). Only one case of apparent competition (redwing-yellowhead) occurred, and the significance of this is unmeasured.

In the present study, as well as in those of other workers (Beecher, 1942, for example), the importance of physiognomy of the nesting cover to birds selecting nest sites has been shown quite clearly. A sound ecological classification of marsh birds must, then, be based primarily on life-form of plants, rather than on purely taxonomic categories. This also simplifies discussions of similar habitats involving different species in different parts of the world. Beecher (1942) has pointed out some of the problems associated with a classification based on life-form, but the shifting use of different plant species by birds limits a simple taxonomic description. Birds not limited by plant species do seem limited by plant life-form. In comparing populations of long-billed marsh wrens in this and previous studies, such populations could fall in any of these community names: lake sedge-marsh wren, phragmites-marsh wren, hardstem bulrush-marsh wren or cattail-marsh wren. All represent the same basic life-form, but the availability of the plants and ecological conditions at the time created different selections of plants.

Marsh birds are characterized by a response to

water and to a vegetative substrate near water. All demand plants of sufficient density to support the nest and, in some species, to hide it as well. Some birds clearly are more adaptable and are more difficult to classify than others. At least four categories are recognizable: (1) birds that select nest sites in marsh-edge low trees and shrubs, (2) birds that utilize short and delicate edge or shallow-water emergents such as low sedges and grasses, (3) species that prefer tall and robust emergents standing in water, such as cattails and bulrushes and (4) species that use low mats of vegetation, often in open areas. Not all species are limited to one life-form zone (the redwing, for example), but the greatest density of nests often occurs in one. Other species, such as the yellow-headed blackbird, are quite specific in habitat choice and, thus, have a low adaptability. Some marsh birds seem to vary in site selection with availability, possibly because of annual changes or geographic location tied to subspecific variations as discussed by Miller (1942). For example, great-blue herons commonly nest in tall trees in the Midwest but nest in marsh emergents in the western United States and in cactus and other low plants in coastal Texas.

These various habitat niches regulate the presence or absence of bird species — the greater variety of plant life-forms, the greater the bird variety. This clue to bird-species diversity agrees generally with the concepts of vegetation "layers" in deciduous woods as described by MacArthur and MacArthur (1961). However, other factors seem strongly influential since the mechanical access to plants via open water areas or similar edges seems important to most marsh birds.

The evolution of nest site selection involves the habitat preferences and the mode of locomotion of the parent stock. Most species seem either to utilize the "robust emergent zone" or to be influenced by it. Some approach this important zone either from the shoreward side or from open water — either for nesting or for general activities such as feeding and rearing of young. "Shoreward-marsh" species are redwings, swamp sparrows, yellowthroats, soras, Virginia rails and American bitterns. Mallards are flexible in selection but often use the sedge-grass zone. "Water's-edge" species are yellow-headed blackbirds, gallinules, coots, least bitterns, ruddy ducks and redheads.

Of the birds of terrestrial ancestry, several species have become highly specialized and nest only in marshes and in tall emergents. Species such as the yellow-headed blackbird and the long-billed marsh wren use uplands little during nesting and favor vegetation adjacent to open water.

Locomotory habits also are influential. "Perching marsh birds," such as redwings, have gripping

feet, are good short-distance flyers and are the least specialized in morphology or in behavior. As Beecher (1942) noted, specialization reduces adaptability. Perching marsh birds are, therefore, most likely to use a variety of vegetative types for nesting and feeding. "Walking marsh birds," such as bitterns and rails, have adaptations of bills and feet and behavioral characters that more nearly limit them to marsh life. The chief foods of adults and young are dominantly aquatic forms. The "swimming marsh birds" are, of course, the most highly specialized in morphology and behavior, but some forms, like dabbling ducks, have adapted to nesting on land. Coots, grebes and inland diving ducks (*Aythya* spp.) are more restricted to permanent water areas and emergent vegetation. Certain terns and gulls may be considered "marsh-flyers," because they are specialized for hovering and diving and do not swim regularly. Their nests are often in the open, and the adults land directly on the nest. The young are well adapted to marsh life by being capable swimmers and by a camouflage of light tan common to marsh birds.

The specialization of yellowheads probably represents both a long-term evolution and some ecological or behavioral force which induced a habitat limitation. Evolution in arid regions of the western United States may have produced a response to the tall emergents characteristic of arid-land marshes. Competitive action between two species may have been involved. An example of more recent evolution of different nest site selection in closely related species would be the redwing and the tri-colored blackbird (*Agelaius tricolor*) (Orians, 1961). In the latter species, many characters of the yellowhead are apparent; territorial behavior more closely associated with nesting, nests dominantly in emergent vegetation (but they will nest in uplands) and more dense populations which are well synchronized in chronology of nest-building. Tri-colored blackbirds seem more flexible in nest site selection than are yellowheads, however, and this may reflect a recent or less specialized evolution.

Factors other than nest site selection may be involved in the apparent lack of competition among some of the shoreward nesting rails. Data from Tanner (1953) and Beecher (1942) show little habitat selection according to plant species. General observations of feeding and nesting habitat suggest, however, that soras prefer shallow or mainly moist shoreward sites in short, fine and dense vegetation, while Virginia rails favor deeper water and commonly will nest in robust plants over water several feet deep. This conclusion is supported by apparent preference of soras for seeds, while Virginia rails favor aquatic invertebrates (Horak, 1964). It seems probable that

soras are more common in the drier marsh stages and that Virginia rails do best under wet-marsh conditions.

The coot and gallinule are species closely related to the "walkers" but are "swimmers" and approach the vegetation from the water side. Nest sites seem similar in both species, and other factors may play a role in their ability to utilize the same areas without apparent competition.

Among swimming birds, the evolution of nest site selection in ancient forms like the pied-billed grebe is uncertain. Its present limiting specializations are clear-cut, however.

It is among ducks that the greatest adaptability is shown, and this is, in part, why anatids are a dominant group throughout the world. All clearly show a highly aquatic adaptation by ancestral forms but recent (?) adaptation to upland areas. Mallards, blue-winged teal and other members of the genus *Anas* are so adapted. As their present preferences imply, they probably evolved in connection with somewhat temporary shallow-water areas. Despite high nest losses on shore, the flexibility in choice of nest site and the mobility of flightless young undoubtedly have real advantages in using available water areas. Even these are limited by a necessity of water for the young. Some geese have achieved a remarkable freedom from the water, while many ducks of the genera *Aythya* and *Oxyura* clearly demonstrate the evolution of marsh-adapted species that do poorly under dry conditions.

Dynamics of Habitat and Animal Populations in Marshes

Marshes are a common and well-accepted example of long-term plant succession, but the ever-present short-term fluctuations often are ignored. These fluctuations may be anywhere from 4 or 5 to 35 years in duration and may represent extremes in numbers and species of both plants and animals. These variations may be regarded as fluctuating around a mean representing the water area "type." These types have been classified according to permanence of water and vegetation (Martin *et al.*, 1953). However, all types of these shallow water areas may, in their fluctuations around the mean, duplicate in part the floral and faunal characteristics of the other types. Thus, each type may undergo a short-term succession which may shift toward more mesic or more hydric situations.

In the semipermanent marshes observed during this study, a pattern of fluctuation occurred that seemed sufficiently regular and predictable to be termed a "marsh habitat cycle" and to be divided into stages. This fluctuation was, of course, continuous, but artificial divisions (based on water

level, vegetation and vertebrate populations) are useful in discussions. Suggestions for such stages are shown in table 8, with comments on the usual vertebrate fauna. When sufficient data are available, the stages may be used in the estimation of production of muskrats, waterfowl and other marsh species. Moreover, conspicuous forms may serve as "indicator species" or conditions by which qualitative estimates of productivity can be made. For some species, such a system may provide an index with an accuracy as great as that of censuses.

Causes and Length of the "Cycle." The usual fluctuations in marshes in the midwestern United States are a function of water depth, muskrat populations and the responsiveness of plants and animals to changing environmental conditions.

Glacial basins are characterized by shallowness and by uniformity of depth. Thus, changes in water level influence a major portion of the basin simultaneously. In addition, the rolling terrain in which potholes are found results in a relatively small run-off area so that potholes vary directly with the amount of rainfall. In temporary-water areas, a late summer drying is characteristic, and quick-responding plants such as smartweeds (*Polygonum* spp.), millet (*Echinochola* spp.) and

other mud-bar species are regular. In semi-permanent waters, a late summer decline is common owing to lack of rainfall as well as to evaporation and plant transpiration. Smartweeds and millets find suitable bars for germination along the edges and may cover much of the marsh bottom during drouth (or as a result of artificial "drawdowns" for the production of waterfowl foods). Seasonal fluctuations in water levels also may be of value to aquatic emergents which tolerate higher water levels for only short periods and which reproduce vegetatively or germinate best at low water levels.

Annual and longer-term variations in rainfall are primary causes in the dynamics of marsh habitat. Several years of below-average rainfall may reduce water levels to a point where revegetation of the marsh bottom may occur. The rate at which water returns to the area determines the rate and direction of changes in marsh stages. In the midwestern glacial potholes, increased rainfall has moved like a "wave" from south to north, and potholes in Iowa and the Dakotas have undergone a transition from dry-marsh to open-water areas.

Rate of change also is a function of muskrat populations which, in many cases, may be the immediate cause of the elimination of vegetation. Muskrats cannot precede the return of water but

TABLE 8. Stages of the typical habitat cycle in semipermanent marshes.

Stage name	Water in relation to basin capacity	Vegetation	Muskrat populations	Bird populations	Conspicuous indicator conditions
A. Dry marsh	Absent or low; emergents dry or nearly dry at base	Dense revegetation; most species find a suitable seedbed	Low to absent; populations centrally located	Redwings sparse; some use by upland birds	Redwings; few muskrat lodges; low water
B. Dense marsh: more vegetation than open water	Increasing water levels; emergents flooded	Very dense; rate of opening dependent upon muskrat populations and influence of flooding on certain species	Increasing	Numbers and variety increasing	Redwings increase; first yellowheads adjacent to sparse open pools; few coots and grebes
C. Hemi-marsh: open water and vegetation are equal	Median to near maximum	Muskrat eat-out; flotation and death; decline in shallow-water species. Veg. propag. by deep-water species	Increasing rapidly; well distributed	Maximum species diversity and production for most species	Many redwings; yellowheads uniformly distributed; coots and pied-billed grebes abundant
D. Open marsh: more open water than vegetation	Maximum	Submergents and deep-water species persist; others gone or going	Maximum or declining	Most species declining; a few swimming species tolerate as long as some vegetation persists	Sparse bird populations and emergents
E. Open water marsh (virtually an eutrophic lake)	Maximum or as low as median	Hardstem bulrush may persist in sparse populations	Sparse; bank dense common	Redwings use shoreline vegetation; other species virtually absent except as migrants	Redwings use shoreline shrubs and trees

respond quickly to the newly formed niche. When the muskrat population is on the increase, the water openings surrounding lodges form an ideal interspersions of cover-water area for most marsh birds. However, an uncontrolled population soon reaches a stage where all vegetation is used for food and lodges (the "eat-out"). Trapping commonly limits the population before the "eat-out" and, thereby, preserves the length of the period of ideal cover-water interspersions.

Elimination of vegetation may be due to direct mortality or to flotation caused by flooding, a method somewhat slower than muskrat action where narrow-leaved cattail and hardstem bulrush are dominants. However, plants less tolerant of deep water, such as rice cut-grass, broad-leaved cattail and sedges, disappear more rapidly.

Variations in this pattern also may result from a stabilizing of water at a below-average level or a reduction of water level following original inundation. At such stages, vegetative propagation may cause extensive re-invasion of already opened areas, but the rate seems far slower than that achieved through seeding. Whether such propagation could keep pace with cutting by even a small muskrat population is questionable. The marsh manager may utilize water level controls to lengthen the duration of this cycle, but it is doubtful that it can or should be maintained indefinitely.

Regardless of these variations, the long-range weather cycles produce conditions which eventually bring marshes to one extreme or the other. These are times of crisis for all marsh animals, but it is obvious that similar crises have been faced by each species throughout its racial history and that they have become amazingly adaptable.

Muskrat Populations. Although subject to many complex population variables (see Errington, 1963), the controlling factor in muskrat population abundance observed in this study seemed primarily habitat. Although data were not recorded during the drouth period, the late Dr. Paul L. Errington maintained some notes on the area and found a drastic decline to virtual absence when the lakes went dry. Presumably, population declines were due to the same factors as in other areas; reduced water level caused a reduction in habitat and, thereby, increased social pressures (Errington, 1939) and vulnerability to predation (Errington and Scott, 1945).

Reflooding produced ideal breeding conditions and, presumably, high reproductive success and excellent survival and spread of offspring. Major utilization seemed to start in central deep-water areas and spread peripherally as vegetation in the center was cleared. Relatively little trapping per-

mitted an almost undisturbed population growth which eventually resulted in the stripping of most vegetation for food and, especially, for lodge construction. At the peak of numbers when old rootstocks were scarce, muskrats utilized old tubers in the lodges which actually were torn apart. This food shortage resulted in at least delayed production, and little production probably would have occurred if muskrats had not used upland corn fields for food (Errington, Siglin and Clark, 1963). The high population also experienced considerable disease which contributed significantly to the decline — but only after vegetation had been eliminated.

This pattern of sigmoidal growth and rapid decline seemed common to most midwestern water areas during the post-drouth periods of the early 1960's. Many variations undoubtedly occur, but this contracted situation dramatized what appears to be a regular situation in muskrat populations.

Bird Populations. The rapid pioneering by marsh birds to newly created habitat reflects considerable evolutionary adaptation to fluctuating environments. However, limitations are quite clear, and the rate of population establishment is dependent on specific requirements. Few of these are understood but involve such factors as suitable substrates for nests and the presence of food organisms as well as the total complex of habitat stimuli to which each species reacts.

The general patterns of utilization and population growth as observed in Iowa marshes is summarized schematically in fig. 28. This figure shows the importance of habitat in determining the abundance and species composition of a marsh bird population. Numerous approximations were necessary but were deemed essential for a work-

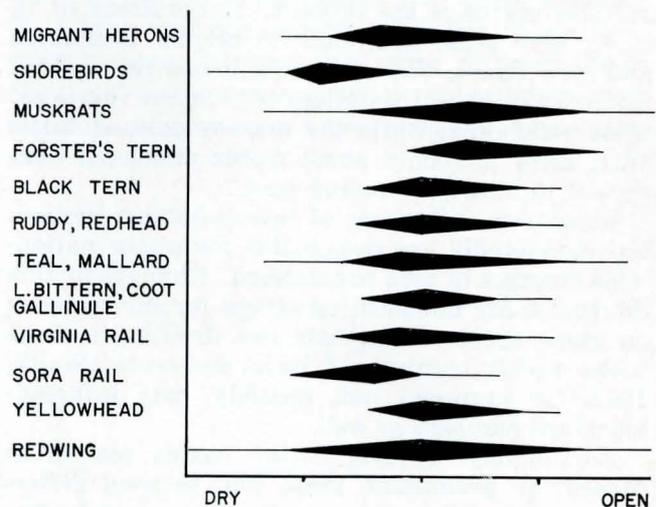


Fig. 28. Schematic presentation of the change in abundance of marsh birds in relation to the extremes in habitat conditions of semi-permanent marshes.

ing hypothesis. Noteworthy among these are those concerning shorebirds and herons. Observations of shorebirds were much more common during the drier stages than the wet periods. Presumably, this was due to the extensive mud flats, especially at Little Wall Lake. Such mud bars were at one time common at Goose Lake because of intensive grazing, and shorebirds apparently were common then (Scott and Sooter, 1937). Herons, especially migratory great blue herons (*Ardea herodias*) and black-crowned night herons (*Nycticorax nycticorax*), were most common as migrants during the early stages of reflooding.

It is apparent from fig. 28 that half vegetation and half open water produced the most suitable conditions for most species and that the habitat extremes were tolerated by a few forms but were not ideal for any marsh species. However, several species seemed to prefer the drier (soras) or wetter (Forster's terns) stages. None preferred the extremes. At the peak period, nests per acre were about two for yellowheads, one for redwings, one-half for least bitterns, one-fifth for coots and one-fourth for grebes.

Of perhaps greater significance than ratio of cover to water is the interspersion and water area size. Small openings created by muskrats (approximately 0.01 to 0.03 acre) seemed ideal for many species, but grebes, ducks and, perhaps, coots found the area more satisfactory when interconnecting waterways developed between pools. Experimentally cut areas of one-fortieth acre (33x33 feet square) in a large dense stand of cattail at Round Lake proved unattractive to most species except redwings. Such areas, presumably, were too small for "take-off" and landing areas and too few to give the impression of interspersion. They also lacked interconnecting trails. It appears that "edge" alone is unattractive unless suitable openings are present. Large areas of $\frac{1}{4}$ to $\frac{1}{2}$ acre seem necessary to attract swimmers and slow flyers. This probably is one reason that Goose Lake had an excellent population very soon after reflooding, while the marshy part of Little Wall Lake had only small water areas not connected to a large "landing pool."

Long-term influences of marsh-habitat dynamics undoubtedly are responsible for major nationwide changes in bird populations. Changes of this dimension are unmeasured except for survey work on game species. Not only can drouths in large areas modify numbers of ducks and coots (Smith, 1962, for example) but, possibly, may influence blackbird numbers as well.

Fortunately, several water basins are often present in production areas and respond differently to rainfall and muskrats. Some may be improved, while others become less satisfactory. Thus, in all but extreme climatic conditions, pop-

ulations of birds must be adapted to shifting from marsh to marsh and area to area. Over-all population levels may be maintained in this manner despite sub-optimal conditions. In extreme cases, however, most marsh bird populations must be affected. Iowa has experienced two such extremes of drouth, and the immediate post-drouth period has been reflected in remarkably large bird populations. Marshes eventually reached an open-water stage which resulted in many fewer species and individuals. Undoubtedly, this has been the pattern of marsh bird populations in the Midwest since at least post-glacial times.

Productivity of Marshes

Aquatic ecosystems are known for their productivity (Odum, 1959), and some represent maximum complexity, efficiency and diversity ("maturity" of Margalef, 1963). However, aquatic systems vary, and marshes are, by physical limitation, the least stable (i.e. "immature") of water areas. They have low lake-area/watershed ratios, and water levels vary markedly. At times they have ideal light, temperature and soil relationships and hence can achieve high production and efficiency. As measured in terms of emergent vegetation and vertebrates, both diversity and density vary dramatically from the peak to poor production years. In a sense, these changes are successional stages leading toward but rarely achieving "maturity" or equilibrium.

In general, a deep, fresh marsh is a basin of considerable permanence with a life certainly numbering in thousands of years. Regardless of their long-term "directions" in succession, such basins undergo oscillations resulting from instability of rainfall at periods of several to many years. In each "cycle," there is a successional change from a near-terrestrial community to a near-stable eutrophic lake with a complex fauna and flora. A complete drying of the marsh converts the basin to a nearly terrestrial fauna although marsh plants still may dominate. At this time, there is considerable animal movement from the terrestrial ecosystem. This drying apparently revitalizes a basin in which nutrients no longer are available and in which plant toxins have concentrated (Cook and Powers, 1958); ideal growth conditions for plants result. The eventual return of water eliminates terrestrial forms and attracts semi-aquatic and aquatic forms. The composition of this biota probably influences the stability and efficiency of the resultant marsh ecosystem. It may remain sometime in this stage, and the energy flow may: (1) be less or (2) take place in aquatic forms, such as invertebrates, fish and amphibians, rather than in the surface semi-aquatic or water-associated food webs of the

marsh stage. A change in water level (and possibly internal biotic factors) may reduce production or change the organisms involved. Occasionally, a biotic maladjustment (such as a surge in populations of muskrats) disrupts other biotic components, such as nesting birds. However, it seems more common to find external forces, such as climate, playing the regulatory role on marsh stability.

The energy wealth of the marsh at its peak of productivity (at least the visible surface fauna) is remarkable and may be due to the high waste of energy characteristic of immature ecosystems as discussed by Margalef (1963). This energy, according to water levels and other factors, may be poured into emergent plants which are then used by muskrats in a direct and simple chain that may end in disbalance of muskrats in numbers and in social structure. Possibly, the cutting of emergents yields a vast energy supply to the truly aquatic forms which flourish in a "lake" after the marsh vegetation has been reduced.

Although primary production of marshes is rivaled by few communities (Odum, 1959), it is uncertain if this production is limited to periodic "surges" or if such a peak production can be maintained in a state of equilibrium if marsh water levels are constant. The "balance" of species interactions necessary to maintain this equilibrium seems delicate. Too little is known of seasonal and annual dynamics of marsh animals to evaluate this. It is possible that balance or stability of marshes is impossible and, perhaps, undesirable and that peak production can only be achieved periodically. The "balance" may be an average of extremes, both of which are functional and which maintain an average production that might not be realized if a marsh is stabilized at either very low or very high water levels.

Marshes and Concepts of Succession

Marshes long have been considered as stages of succession in terrestrial communities (Reed-swamp stage of Weaver and Clements, 1929; the "marsh-associations" of Beecher, 1942; the

Telmatodytes-Podilymbus "marsh biocies" of Kendeigh, 1948; seral stages of various communities in Shelford, 1963; lentic series of Welch, 1935). Others have viewed marshes more as entities—but still clearly regarded as a transient stage leading toward more mesic conditions (the pond succession of Buchsbaum and Buchsbaum, 1957). These concepts imply a brief period of life comparable to secondary succession in prairie or woods, yet data to support such a transitory stage are scarce. Most basins are of glacial origin and thus are several thousand years old, and, although most become increasingly shallow, the rate of this fill-in must be measured nearly by geologic time-scale. Moreover, there are forces, such as wave and ice action, which deepen basins. Is, then, a marsh community truly more temporary than any dynamic terrestrial biome under the influence of major climatic changes? Is it justifiable to consider a marsh as a "dying lake" when it was never deep enough to be considered a lake—or to call it a seral stage eventually to join the terrestrial surroundings when several thousand years may be required for this process to occur? Moreover, it is probable that these basins were formed in the Pliocene period and have been in some bog or marsh state ever since the ice retreated. At the same time, the surrounding terrestrial vegetation in some areas may have changed just as dramatically.

No one can doubt the advantages of this concept to dramatize the dynamics of succession, but the temporal limits of the successional concept and of biome permanence are vague. It seems reasonable to recognize lakes, marshes and bogs as biomes. The resultant problems of terminology and limitations of major, as well as of minor, subdivisions differ little from the problems associated with terrestrial communities and their ecotones. It is true that the spatial relationships and geographic area involved are quite different from the usual biome concept, but no more unique than the concentric biome zones proposed for oceans (see Kendeigh, 1961).

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