HABITAT SELECTION AND SPECIES INTERACTIONS OF SOME MARSH PASSERINES

by

DeVere Eugene Burt

A Thesis Submitted to the

Graduate Faculty in Partial Fulfillment of

The Requirements for the Degree of

MASTER OF SCIENCE

Major Subject: Zoology (Animal Ecology)

Approved:

Signatures have been redacted for privacy

ersity
Of Science and Technology
Ames, Iowa

1970

TABLE OF CONTENTS

INTRODUCTION

The non-passerine marsh nesting avifauna of the owrld is a diverse complex of species consisting of six cosmopolitan families (Darlington 1957). Morphological and behavioral specialization cause severe habitat limitations and restrict the group to marshes. Yet as a specialized non-passerine element, they are very successful, and capable of rapid pioneering into available habitats.

North American marsh nesting passerines have little in common with non-passerine marsh birds. For example, there are no marsh passerine genera with cosmopolitan distributions: Mayr (1946) feels 80-100% of the North American forms originated as species in North America. Udvardy (1958) has pointed out that there is no close phyletic relationship between the 12 North American forms and the 12 marsh nesting passerines of the western Palearctic. Furthermore morphological and behavioral specialization is rare in the passerine group. Two exceptions are yellow-headed blackbirds (Xanthocephalus xanthocephalus) and long-billed marsh wrens (Telmatodytes palustris). But North American marsh nesting passerines have been categorized by Udvardy (1958) as "recent offshots of typical arboreal families and genera".

Yellow-headed blackbirds, red-winged blackbirds (Agelaius phoeniceus), and long-billed marsh wrens are the major passerines of Iowa marshes. Although other songbirds utilize marsh borders as breeding areas in the state, none regularly breeds in marshes.

The yellow-headed blackbird and long-billed marsh wren are restricuted to marshes during nesting; the red-winged blackbird uses a broad range of habitats for nest sites, but concentrates at marsh edges. All are polygamous, sympatric over much of their ranges, and hold mutually exclusive territories.

The red-winged blackbird and long-billed marsh wren occur throughout much of North America. The yellow-headed blackbird is a species of the marshes of desert and grassland areas of western North America. The Mississippi River roughly denotes the eastern border of the range of the yellow-headed blackbird.

Breeding ranges of the blackbirds are of particular interest because the southeastern boundary of the range of the yellow-headed blackbird occurs in Iowa. Large breeding populations of X. xanthocephalus in Iowa are found within the boundaries of the Des Moines lobe of the Wisconsin glacial moraine and in the Missouri River marshes (Fig. 1), and it rarely nests outside these limits (Weller, 1969). Red-winged blackbirds nest throughout the state. Hence, studies on the blackbirds in this geographic area provide data on interactions of two ecologically similar species near the distributional limits of one.

The three-species complex offers an excellent opportunity for the study of habitat selection and species interaction in a relatively simple ecosystem. Such a study was conducted during the breeding seasons of 1967 and 1968 at Elk Creek Marsh in north-central Iowa. The project considered the following factors of the nesting ecology of the three species: habitat selection, nest-site selection, nest-defence behavior, social systems, and morphological adaptations. Data obtained were integrated with that from the literature to consider the hypothetical evolutionary relationships of the three species.

STUDY AREAS

Elk Creek Marsh is a state-owned unit located in Worth County, Iowa. The study area (includes) 7.5 miles of Elk Creek bottomland, and contains a total of 1,646 acres. The management unit is divided into four segments (A, B, upper C, and lower C) (Fig. 1). Two dams constructed in the western 3.5 miles of Elk Creek form segments A and B. During 1968, the segment A and B impoundments were maintained at 83 and 135 acres, respectively. The majority of the area is upland, but ten small natural and artificial marshes are located close to the stream and in the uplands.

Most data were collected in Segment B (Fig. 2), especially in Bergo's Slough, potholes 4 and 10 and the western end of impoundment B. These areas were selected because of large breeding blackbird populations.

Bergo's Slough provided data on red-winged blackbirds nesting in association with yellow-headed blackbirds and long-billed marsh wrens. It is a 33 acre sedge marsh formed from a natural oxbow of Elk Creek. Distribution of vegetation in Bergo's Slough during 1968 is shown in Fig. 3. Lake sedge (see Table 1 for scientific names of plants) and bur-reed were co-dominants and formed fairly closed communities. Bur-reed occurred in the deeper sections of the marsh (12 to 18 inches of water). Lake sedge occupied the shallow flats of the eastern end and partially surrounded the bur-reed. Lake sedge was important habitat for long-billed marsh wrens. Isolated clumps of broad-leafed cattail

Figure 1. Elk Creek Marsh. Boundaries are stipiled. Black Areas within the boundaries are open water of the impoundments.

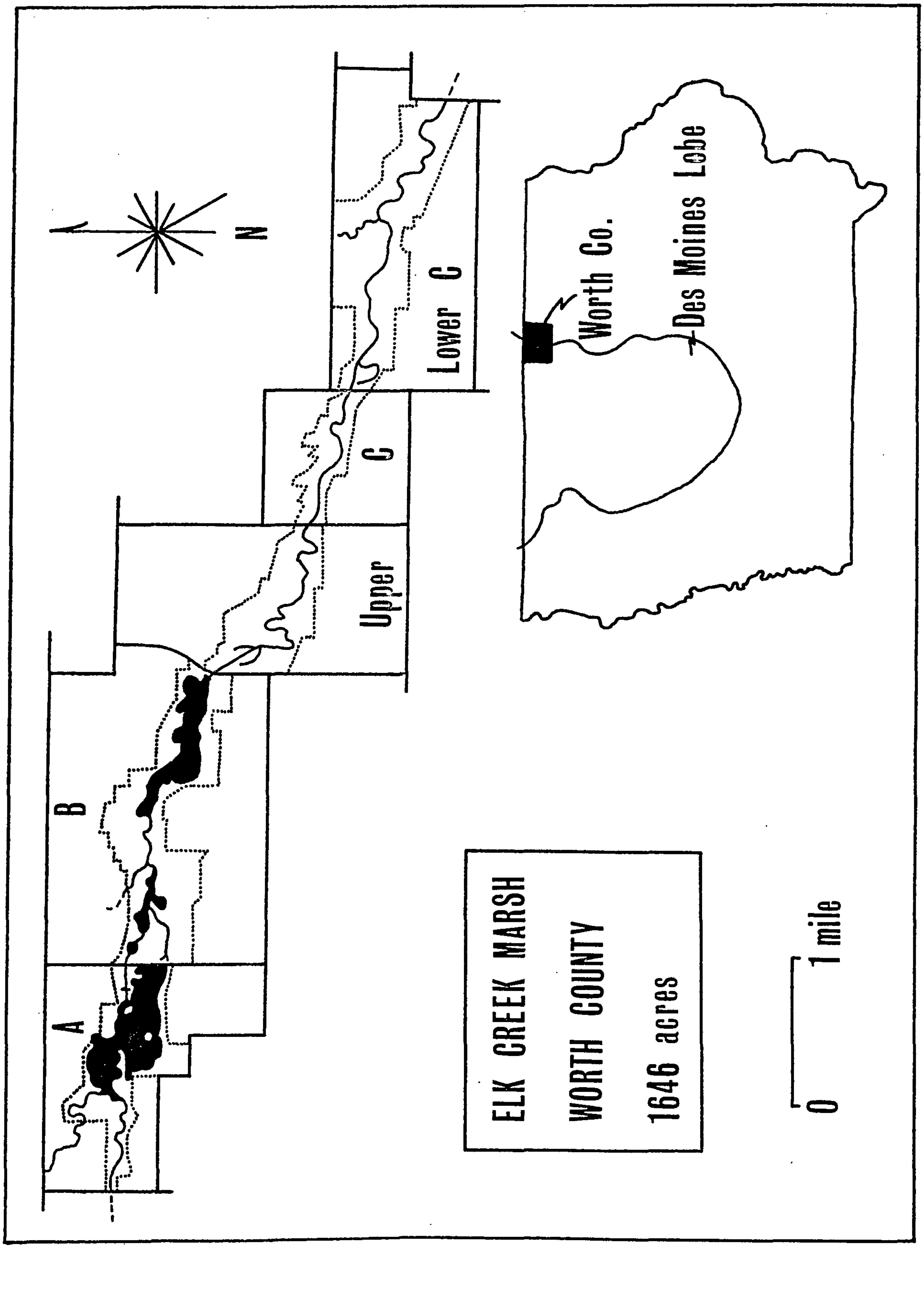

ELK CREEK MARSH
WORTH COUNTY
1646 acres
0
1 mile
A
B
Upper
C
Lower C
N
Worth Co.
Des Moines Lobe

Figure 2. Segment B at Elk Creek Marsh.
Study areas are numbered.

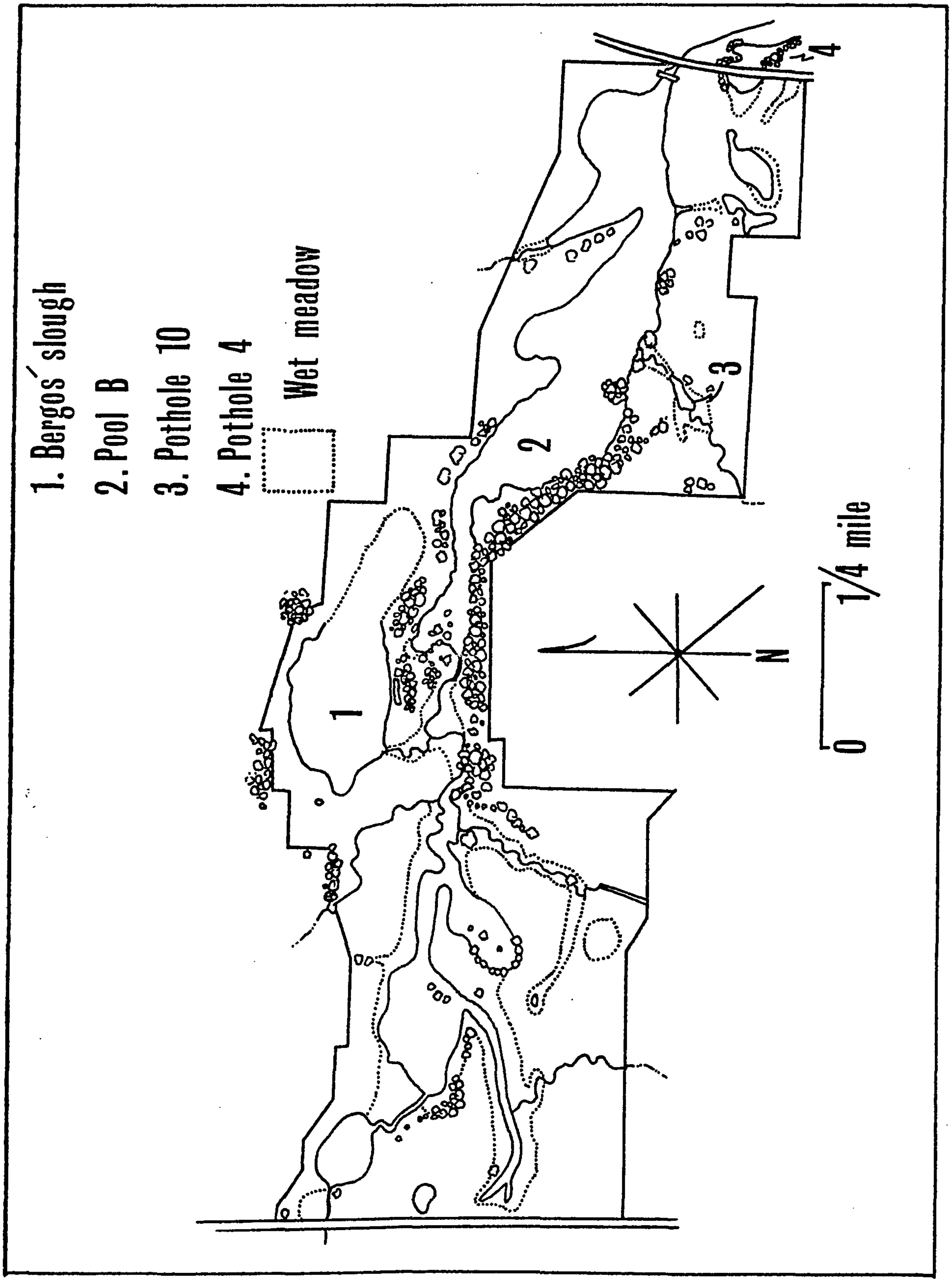
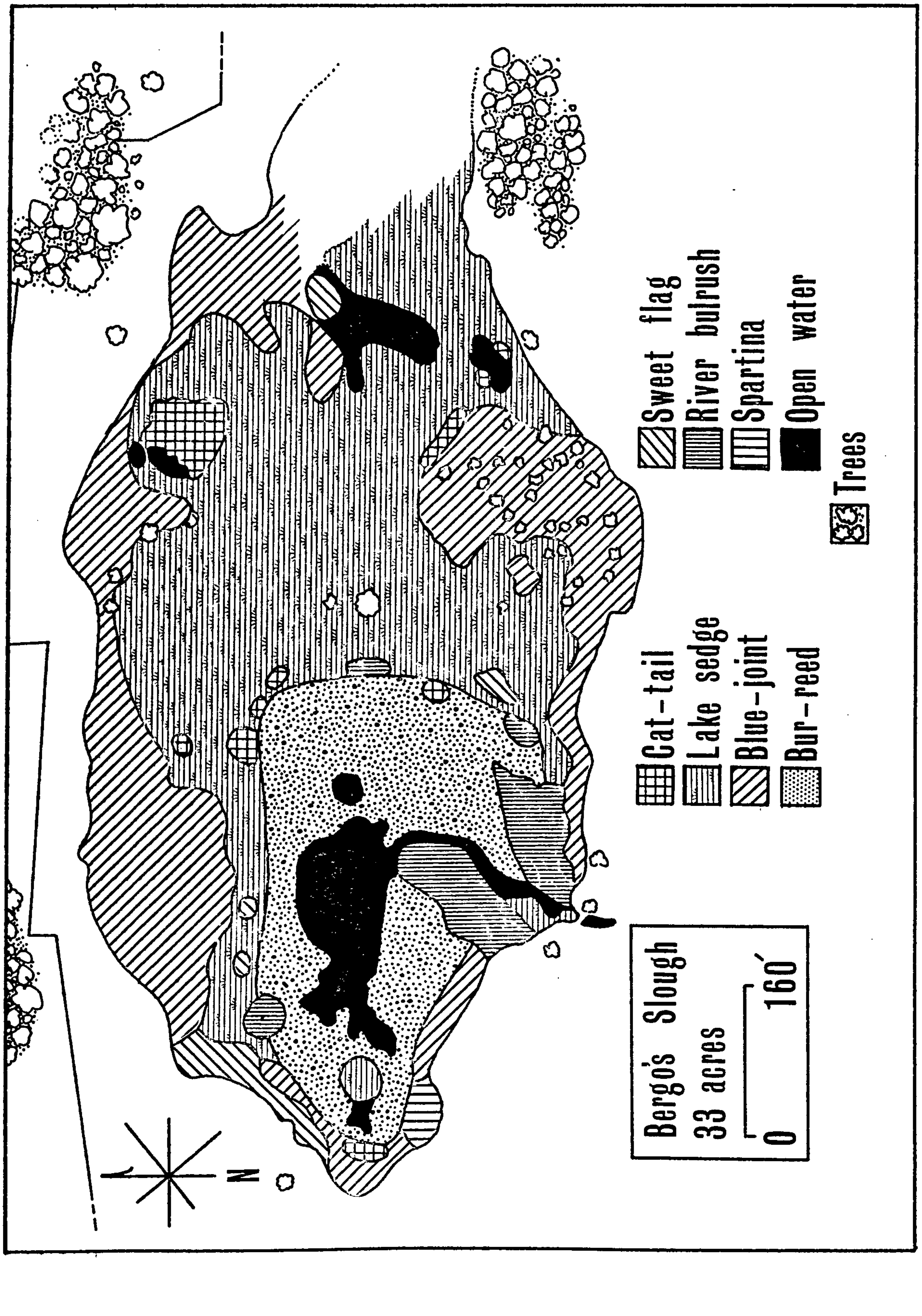

1. Bergos´ slough
2. Pool B
3. Pothole 10
4. Pothole 4
Wet meadow
1
2
3
4
N
0
1/4 mile

Figure 3. Bergo's Slough. Distribution of vegetation during 1968.


Bergo's Slough
33 acres
0 160´
N
Cat-tail
Lake sedge
Blue-joint
Bur-reed
Sweet flag
River bulrush
Spartina
Open water
Trees

were scattered about the more shallow areas, and were used by large numbers of nesting yellow-headed blackbirds and red-winged blackbirds.

Construction of the B impoundment was completed in 1965. A study area of approximately 63 acres was selected at its west end in 1967 (Fig. 4). Prior to inundation, the study area contained a complex of wet meadow plants. Most plants requiring more mesic conditions were eliminated the first growing season following inundation. Tussock sedge and sparse beds of lake sedge remained as co-dominants in 1967. Approximately 38 male red-winged blackbirds held territories in the densest beds of lake sedge.

Habitat conditions deteriorated in pool B in autumn 1967 and it was not used as a study area in 1968. Potholes 4 and 10 then were selected to replace the B impoundment to provide nesting data on red-winged blackbirds in habitats where yellow-headed blackbirds were not present.

Pothole 4 is a man-made oxbow, an acre in size, formed during channel straightening by the Corps of Engineers (Fig. 5). It contains a flora more similar to Bergo's Slough than to that of the B impoundment. Dominant plants include soft-stem bulrush, bur-reed and tussock sedge.

Pothole 10 (Fig. 6) was constructed by land fill and completed in autumn of 1967. Its early vegetational history following inundation parallels the B impoundment. Mesic species disappeared the first growing season following inundation, leaving tussock sedge as a dominant.

Table 1. Species of plants* used as nesting substrate by blackbirds and marsh wrens at Elk Creek Marsh study areas

Species	Scientific Name
Broad-leafed cat-tail	*Typha latifolia*
Bur-reed	*Sparganium eurycarpum*
Common reed	*Phragmites phragmites*
Blue-joint	*Calamagrostis canadensis*
Reed canary grass	*Phalaris arundinacea*
Slough-grass	*Spartina pectinata*
Hard-stem bulrush	*Scirpus acutus*
River-bulrush	*Scirpus fluviatilis*
Soft-stem bulrush	*Scirpus validus*
Carex sp.	*Carex*
Lake sedge	*Carex lacustris*
Tussock sedge	*Carex tuckermanni*
Sweetflag	*Acorus calamus*
Willow	*Salix* sp.

*Scientific names from Fernald (1950)

Figure 4. West B pool study area. Distribution of vegetation during 1967.

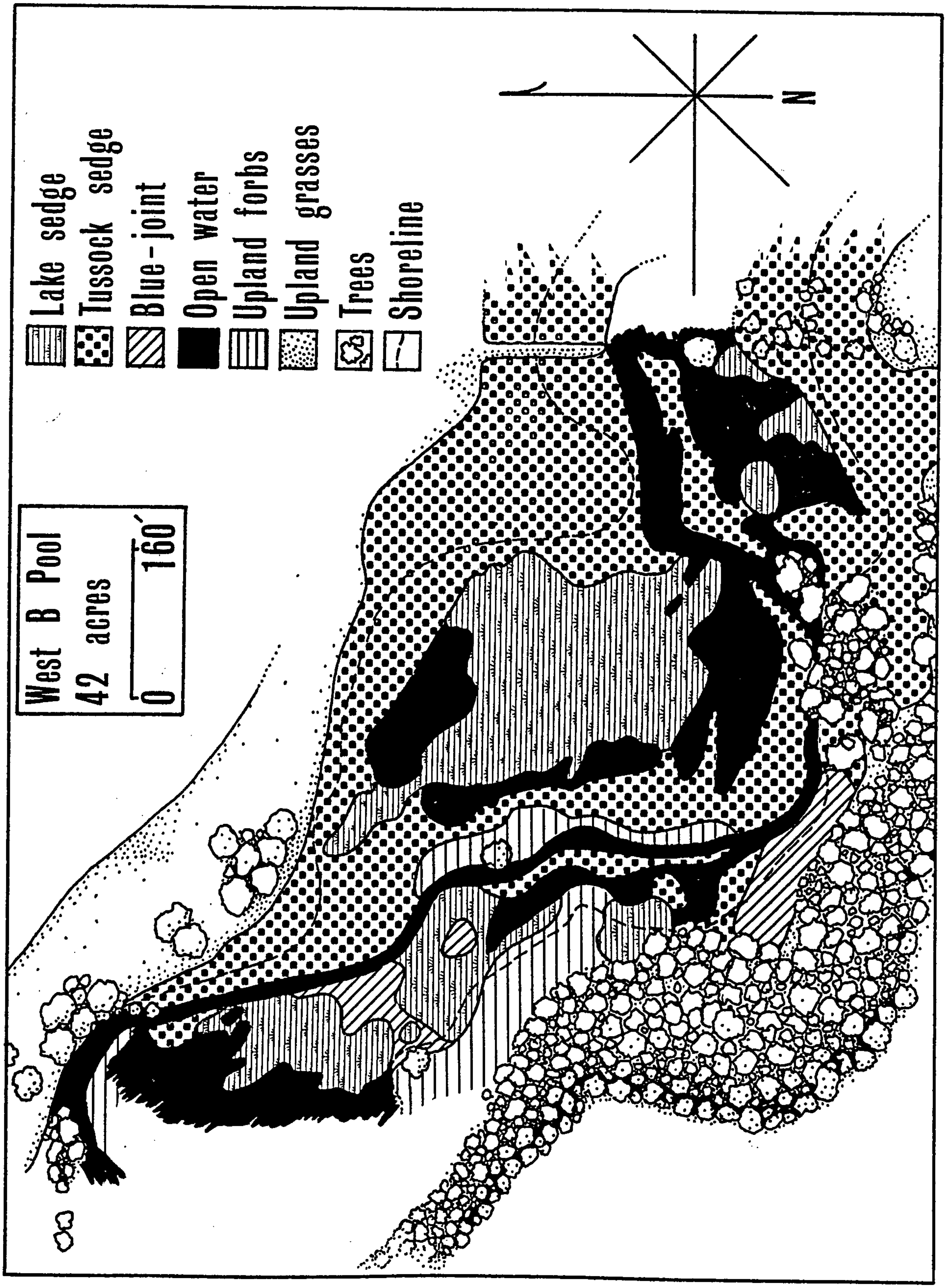

West B Pool
42 acres
0
160'
Lake sedge
Tussock sedge
Blue-joint
Open water
Upland forbs
Upland grasses
Trees
Shoreline
N

Figure 5. Pothole 4. Distribution of vegetation during 1968.

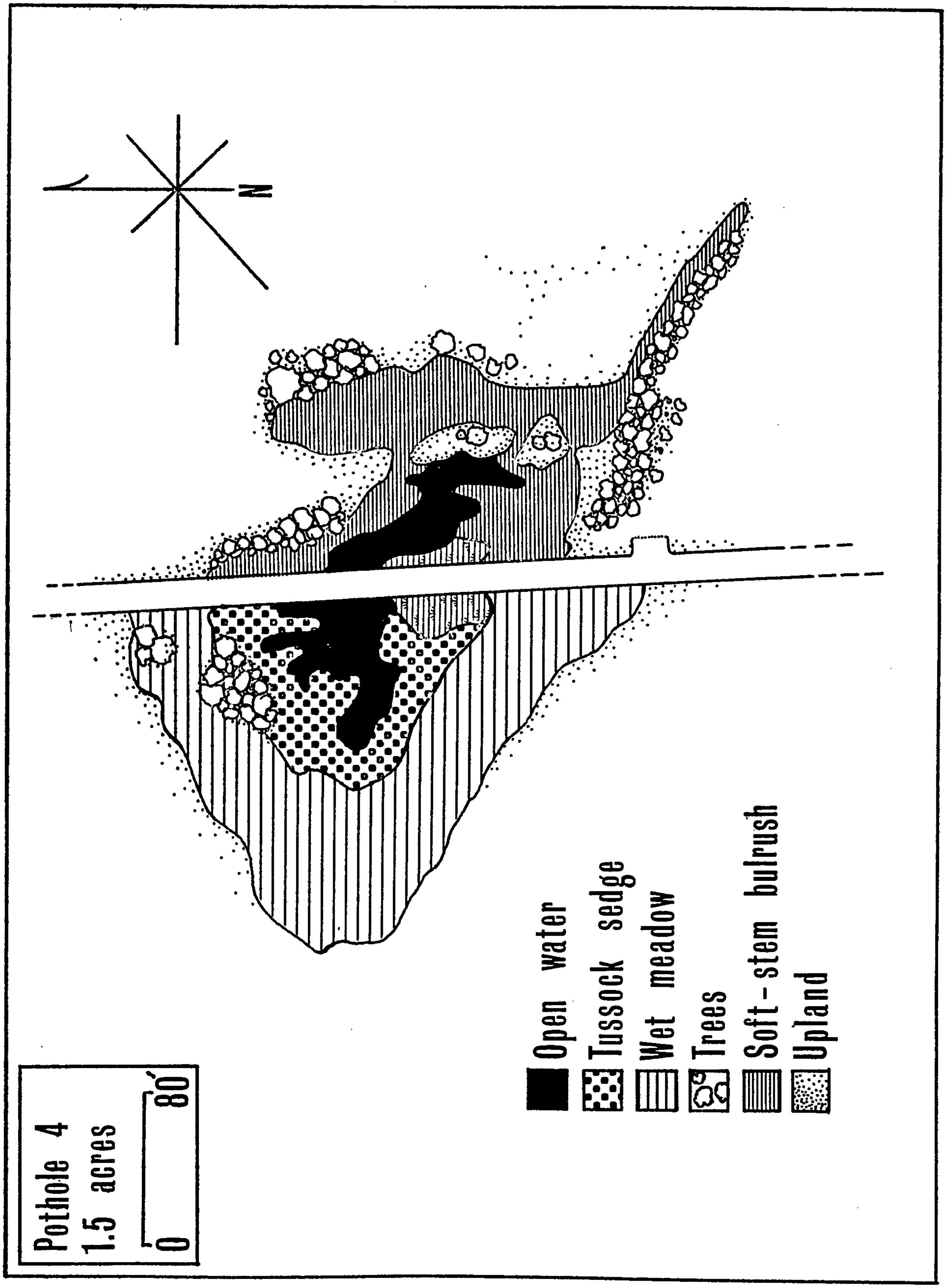
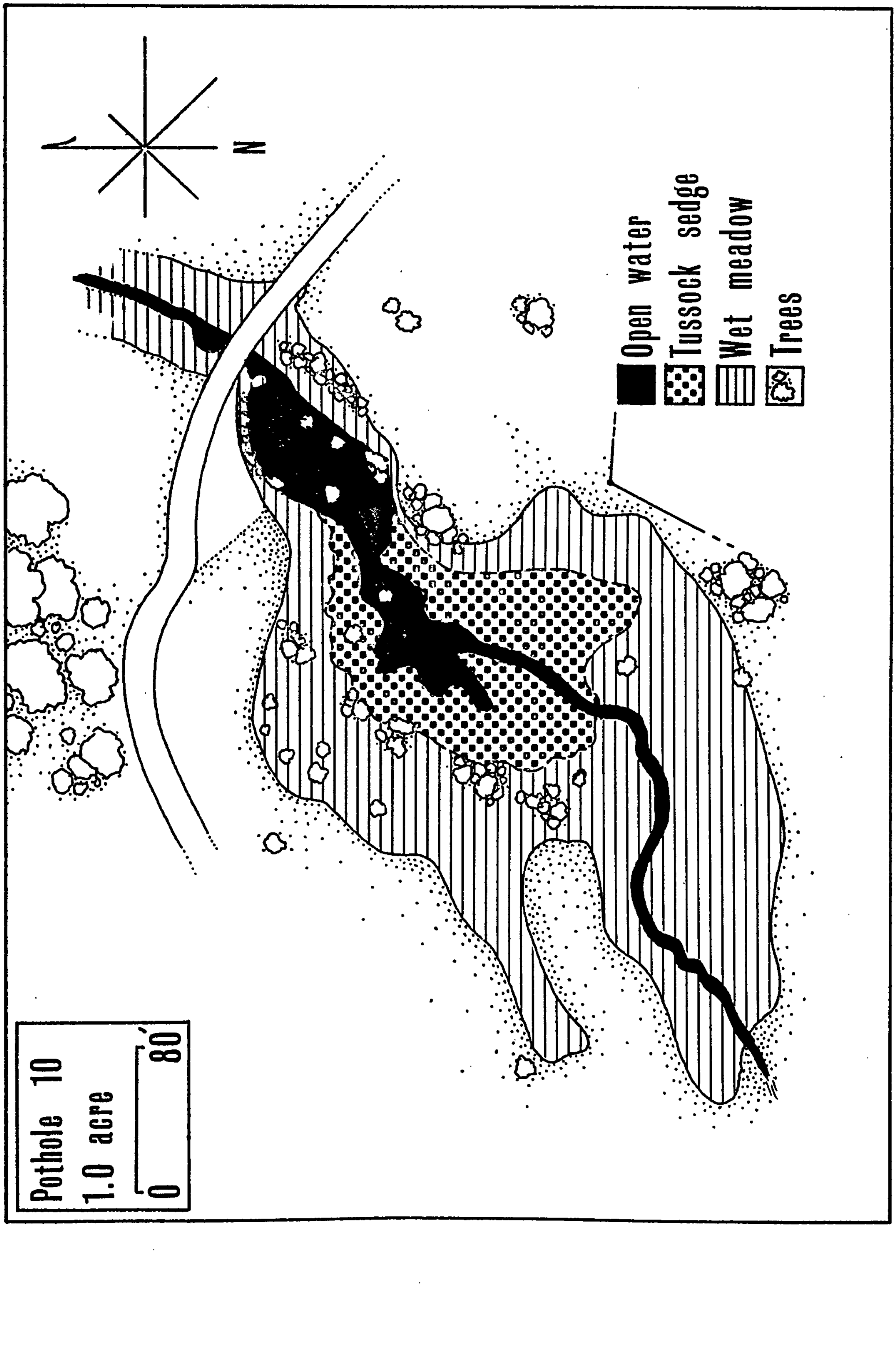

N
Pothole 4
1.5 acres
0
80'
Open water
Tussock sedge
Wet meadow
Trees
Soft-stem bulrush
Upland

Figure 6. Pothole 10. Distribution of vegetation during 1968.


Pothole 10
1.0 acre
0
80'
N
Open water
Tussock sedge
Wet meadow
Trees

METHODS

Cover maps of study areas were prepared by tracing shore lines and other conspicuous features from aerial photos. The areas were then cover mapped during the winter on the ice, using a compass and pacing. As reported by Weller and Spatcher (1965), this system provides a gross but easy means of measuring the distribution of those marsh plants that remain as potential nest sites in the spring. Aerial photos would have been more accurate but cost was prohibitive. Two areas in Bergo's Slough used for intensive studies were mapped by the intersection method (Mosby, 1963) and nests were plotted. This allowed greater detail and accuracy (Fig. 10 and 14).

Blackbird populations were estimated by nest counts, and the standard procedure of repeated observations of singing males (Kendeigh, 1944). Marsh wren populations also were determined by singing male counts.

Bird territories were recorded on the cover maps. Blackbird territories were mapped by observing individual males on song perches and plotting their positions on the cover map. The bill-up display of the red-winged blackbird and the bill-down (nodding) posture of the yellow-headed blackbird have been used to denote territorial boundaries (Nero, 1963, Orians and Christman, 1968), but too many individuals were present to accurately map all territories in this study. Methods used in mapping blackbird and marsh wren territories were not accurate enough to give respective territory size.

All nests were assigned a number and marked with strips of flagging tape. The nest number was written on the flagging tape with a waterproof felt-tip marker. The tape then was tied to vegetation within three feet of the nest. Certain statistics were collected at each nest and recorded on data sheets. Nest positions were plotted on a cover map. An attempt was made to record fates of all nests, but nests were difficult to relocate and many marked nests were not found again. Whenever possible, nests were checked every three days, but sometimes duties elsewhere interfered with this routine.

RESULTS

Physical Features of Nest Sites

It has been noted by Fautin (1940), Weller and Spatcher (1965) and Miller (1968) that yellow-headed blackbirds always build their nests over water. By contrast, the versatile red-winged blackbird builds on a variety of substrates, many of which are terrestrial. The yellow-headed blackbird normally nests in emergent vegetation, but Roberts (1909), Linsdale (1938), Fautin (1941) and Weller and Spatcher (1965) have recorded nests in flooded willows (Salix sp.) in central marsh areas. Red-winged blackbirds frequently nest in trees and even have been recorded nesting in tree holes (Campbell, 1948), and bird houses (Nero, 1950). Versatility in the type of nest attachment described by Nickell (1958) probably contributes to the wide range of nest sites used by red-winged blackbirds.

Data on nesting substrates used by red-winged blackbirds, yellow-headed blackbirds and long-billed marsh wrens at Elk Creek are presented in Table 2. Yellow-headed blackbirds used only five species of vegetation typical of deep marsh habitats. Red-winged blackbird nests were found in 11 plant species representing all seral stages of the hydrosere. Four of the 12 plant species involved were used by both species of blackbirds. Seventy-seven per cent of all red-winged blackbird nests were built in four of the plant species in which 99% of the yellow-headed blackbird nests were found.

Marsh wrens also used five different plant species, but 96% of all nests were located in lake sedge. Beecher (1942) and Welter (1935) believed that lake sedge was optimal habitat for the long-billed marsh wren, although Bent (1958a) reported that marsh wrens on the east coast used many species of emergents, trees, and shrubs. Marsh wren nesting substrates overlapped with three used by yellow-headed blackbirds. Competition, as defined by Mayr (1963), was lessened between nesting marsh wrens and yellow-headed blackbirds because of differences in nest-site selection (i. e., small overlaps in nest substrates)(Table 2). All nesting substrates used by long-billed marsh wrens also were used by red-winged blackbirds. Of particular importance was the high percentages of nests of marsh wrens and red-winged blackbirds in lake sedge. Approximately 52% of the red-winged blackbird nests in Bergo's Slough (1968) were built in areas of potential competition with marsh wrens.

Heights of nests of the red-winged blackbird have been studied by Meanley and Webb (1963), Weller and Spatcher (1965), Taylor (1965) Goddard and Board (1967) and Holcomb and Twiest (1968). Meanley and Webb (1963), and, Holcomb and Twiest (1968) correlated increasing nest success with increasing nest height but data on fate of nests are too limited in this study for meaningful comparative analysis. Nest heights of the three species above the (water or ground) are presented in Table 3. Yellow-headed blackbirds nested lower in the vegetation than did red-winged blackbirds in all plant species except lake sedge. The difference in average blackbird nest heights was caused by the low profile of dead bur-reed stalks, used for nest attachment. The total height of bur-reed used for nest attachment by yellow-headed blackbirds averaged about 10 inches above the water.

Table 2. Nest substrates used by red-winged blackbirds, yellow-headed blackbirds, and long-billed marsh wrens at Bergo's Slough 1967 and 1968

Plant Species	Yellow-headed blackbird %	Sample	Red-winged blackbird %	Sample	Long billed marsh wren %	Sample
Bur-reed	58.3	74	15.8	22	0.4	1
River bulrush	6.3	8	3.6	5	0.8	2
Lake sedge	22.0	28	52.5	73	96.0	218
Broad-leafed cat-tail	12.5	16	5.0	7		
Hard-stem bulrush	0.9	1				
Soft-stem bulrush			0.7	1		
Tussock sedge			9.4	13	0.8	2
Carex sp.			1.4	2		
Sweet flag			1.4	2	1.7	4
Reed canary grass			3.6	5		
Blue-joint			4.3	6		
Willow			2.2	3		
Total		127		139		227

Old bur-reed stalks were not as strong as were cat-tail stalks and did not provide comparable nest support. Blackbird nests placed high in vegetation are more secure from flooding than those placed lower, such as yellow-headed blackbird nests in bur-reed. Analysis of nest height data on 681 yellow-headed blackbird nests from two central Iowa cat-tail marshes by Weller and Spatcher (1965) reflect the marginal nature of Bergo's Slough to nesting yellow-headed blackbirds. A great majority of the yellow-headed blackbird nests they observed were built in cat-tail and bulrushes (Scripus spp.)(Bur-reed and lake sedge were not present). The 681 nests averaged 10.2 inches above the water, as compared to 6.3 inches above the water for yellow-headed blackbird

Table 3. Height in inches, of nests above the substrate in Bergo's Slough 1968

Plant Species	Sample size	Mean	Range
YELLOW-HEADED BLACKBIRD			
River-bulrush	4	6.7	4-10
Broad-leafed cat-tail	16	11.1	8-18
Bur-reed	65	4.6	2-7
Hard-stem bulrush	1	15.0	----
Lake sedge	9	9.3	4-14
Total	95	6.3	
RED-WINGED BLACKBIRD			
Broad-leafed cat-tail	6	20.0	12-32
Bur-reed	12	8.3	3-10
Lake sedge	29	8.9	6-17
Tussock sedge	10	18.5	5-36
Sweetflag	2	7.0	4-10
Red-canary grass	4	22.5	19-27
Blue-joint	5	16.8	10-23
Total	68	12.4	
LONG-BILLED MARSH WREN			
Bur-reed	1	16.0	----
Lake sedge	86	11.9	7-21
Tussock sedge	1	18.0	----
Sweetflag	4	13.5	6-20
River-bulrush	1	44.0	----
Total	93	12.4	

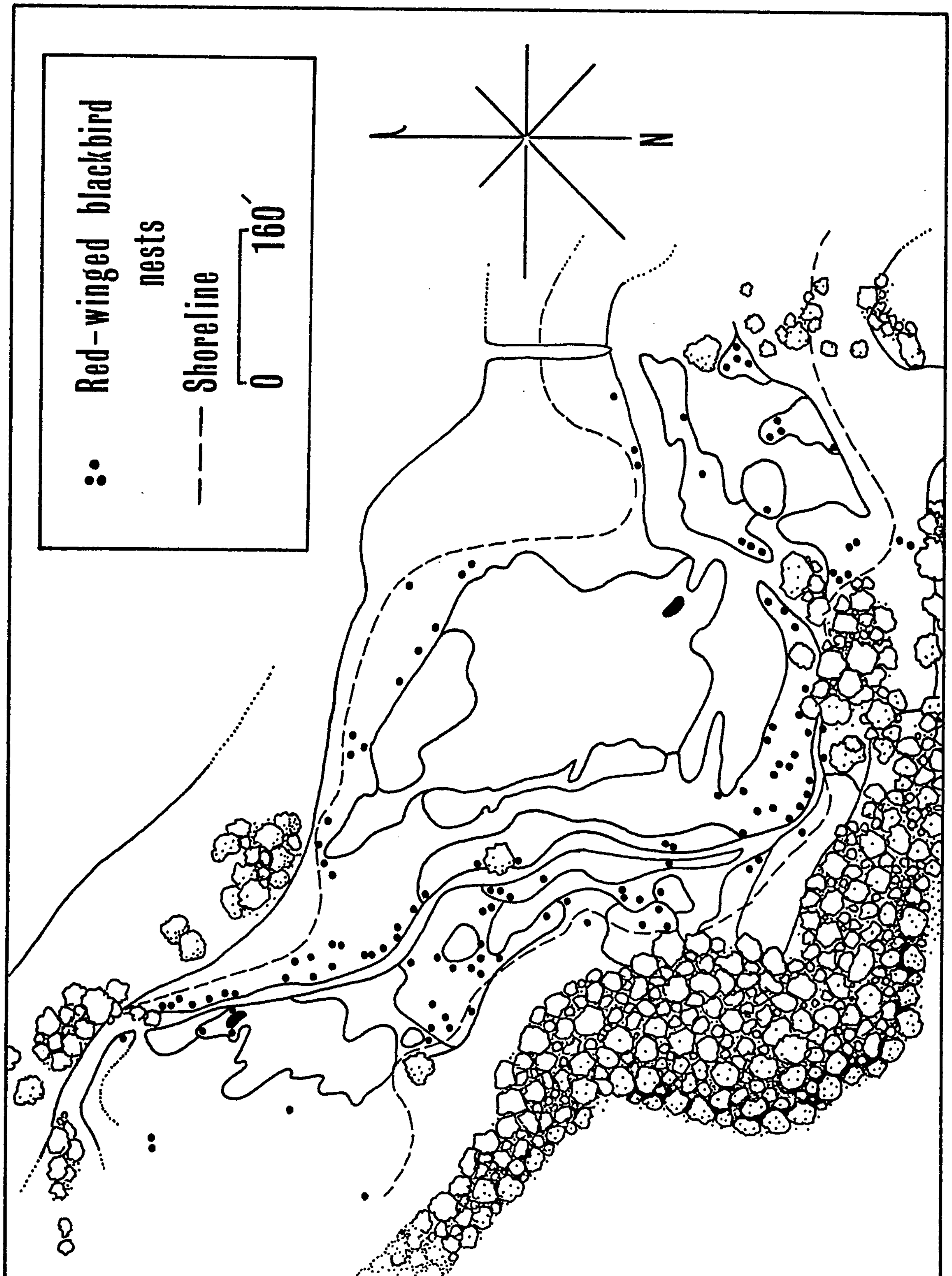
nests at Elk Creek. Of interest is the similarity of nest heights of Elk Creek red-winged blackbirds nesting in cat-tail and 138 red-winged blackbird nests examined by Wien (1965) at Madison, Wisconsin. Red-winged blackbird nest heights averaged 20 inches in cat-tail at Elk Creek while the 138 Madison nests in cat-tail averaged 23.7 inches.

Distances from nests to cover-water edge or edge of two different cover types are shown in Table 4. Seventy per cent of all yellow-headed blackbird nests were found within 20 feet of open water. Red-winged blackbirds also displayed a high response to water-vegetation edge, while nest site selection of marsh wrens did not appear to be affected by the presence of open water as measured in this study.

Nests of marsh wrens and yellow-headed blackbirds appear to be randomly distributed with respect to the edge of two different cover types. By comparison, over 65% of the red-winged blackbird nests were within 20 feet of a vegetational edge.

An influence by yellow-headed blackbirds on nest site selection of red-winged blackbirds is suggested in Table 5. Over 73% of the yellow-headed blackbird nests in Bergo's Slough in 1968 were within 20 feet of open water. Only 36% of the red-winged blackbird nests in Bergo's Slough (1968) were found within 20 feet of open water. By contrast, 54% of the red-winged blackbird nests in potholes 4 and 10 (yellow-headed blackbirds not present) were less than 20 feet from open water. Fig. 7 shows the nesting distribution of red-winged blackbirds in relationship to open water-vegetation edge, in habitat without a large breeding population of X. xanthocephalus. Nero (1956) and Wien (1965) also noted that red-winged blackbirds at Madison Wisconsin usually nested on the edges of cat-tail clumps bordering areas of open water in a marsh where yellow-headed blackbirds did not occur. Percentages of red-winged blackbird nests in the potholes and in Bergo's Slough within 20 feet of a boundary between two cover types are similar (65 and 66% respectively).

Figure 7. Nesting distribution of red-winged blackbirds in relation to open water.



Red-winged blackbird nests
Shoreline
0
160'
N

Table 4. Distance from open water and vegetation edge of red-winged blackbird, yellow-headed blackbird and long-billed marsh wren nests in natural and impounded habitats, 1967-1968

Species	Distance in feet 0-20	21-40	41+	Sample
	Distance of nest from vegetative edge			
Yellow-headed blackbird	69.7%	15.5%	14.7%	(129)
Red-winged blackbird	57.6%	16.8%	25.4%	(326)
Long-billed marsh wren	35.1%	20.4%	44.1%	(179)
	Distance of nest from open water edge			
Yellow-headed blackbird	41.1%	27.2%	31.6%	(136)
Red-winged blackbird	61.2%	25.4%	13.1%	(366)
Long-billed marsh wren	36.0%	29.9%	34.0%	(247)

This may mean the presence of yellow-headed blackbirds has little affect on this aspect of red-winged blackbird nest site selection.

Nesting distribution of yellow-headed blackbirds, red-winged blackbirds and long-billed marsh wrens in Bergo's Slough in 1967 and 1968 is presented in Fig. 8 and 9. All of the marsh was not used by the three species; rather all three tended to occur in small groups of 2-10 males with females, leaving vacant areas between given groups.

Most yellow-headed blackbird nests in Bergo's Slough were situated in bur-reed close to small open water areas but the maps lack the detail to show this. Certain species of emergent vegetation with similar life-form (i.e., bur-reed and cat-tail) in association with adjoining areas of

Figure 8. Nesting distribution at Bergo's Slough during 1967. Eleven yellow-headed blackbird males and 23 red-winged blackbird males held territories within the given areas. No census data were collected on long-billed marsh wrens.

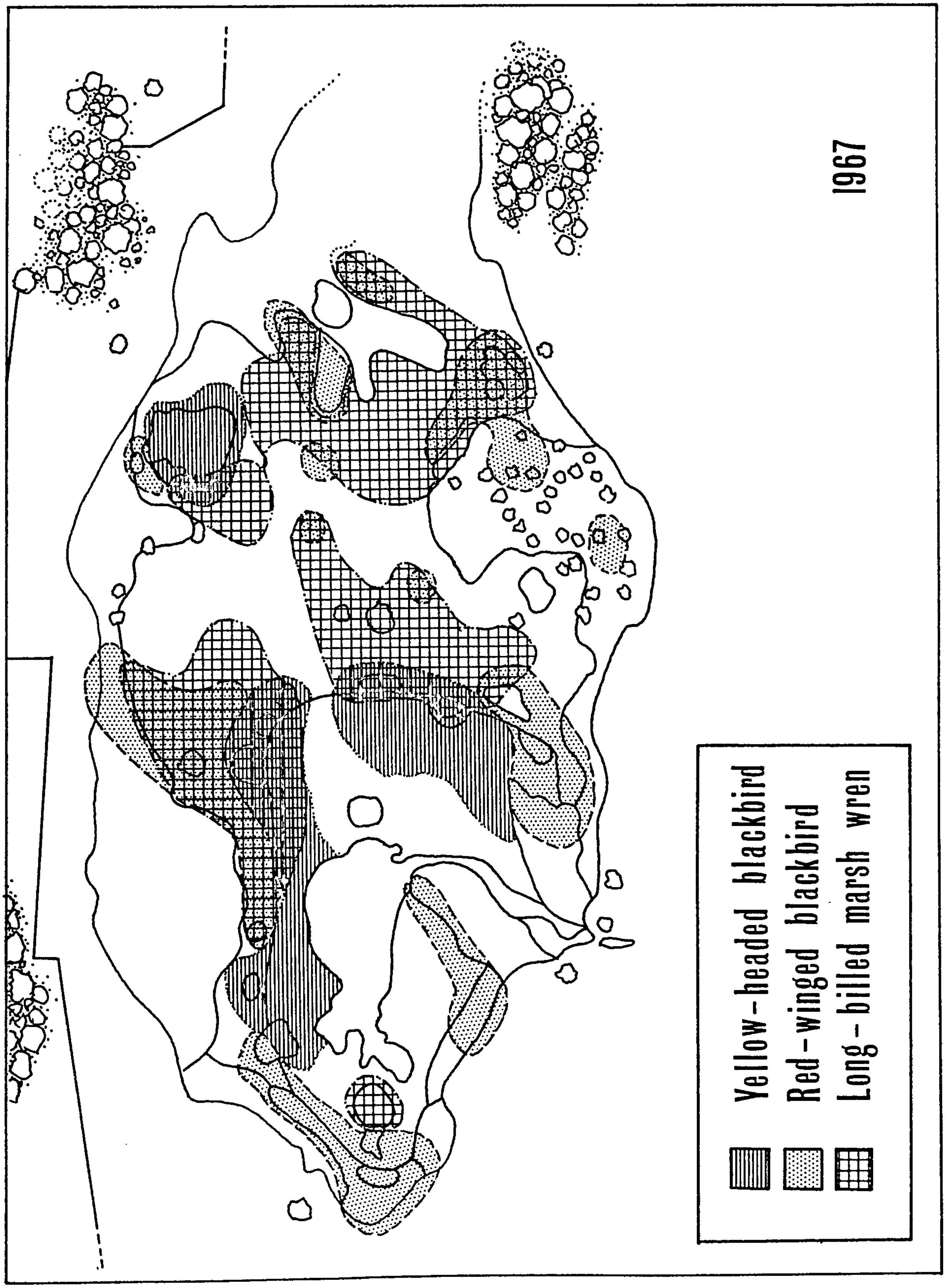

1967
Yellow-headed blackbird
Red-winged blackbird
Long-billed marsh wren

Figure 9. Nesting distribution at Bergo's Slough during 1968. Forty-two yellow-headed blackbird males, 52 red-winged blackbird males, and 42 long-billed marsh wren males held territories within the given areas.

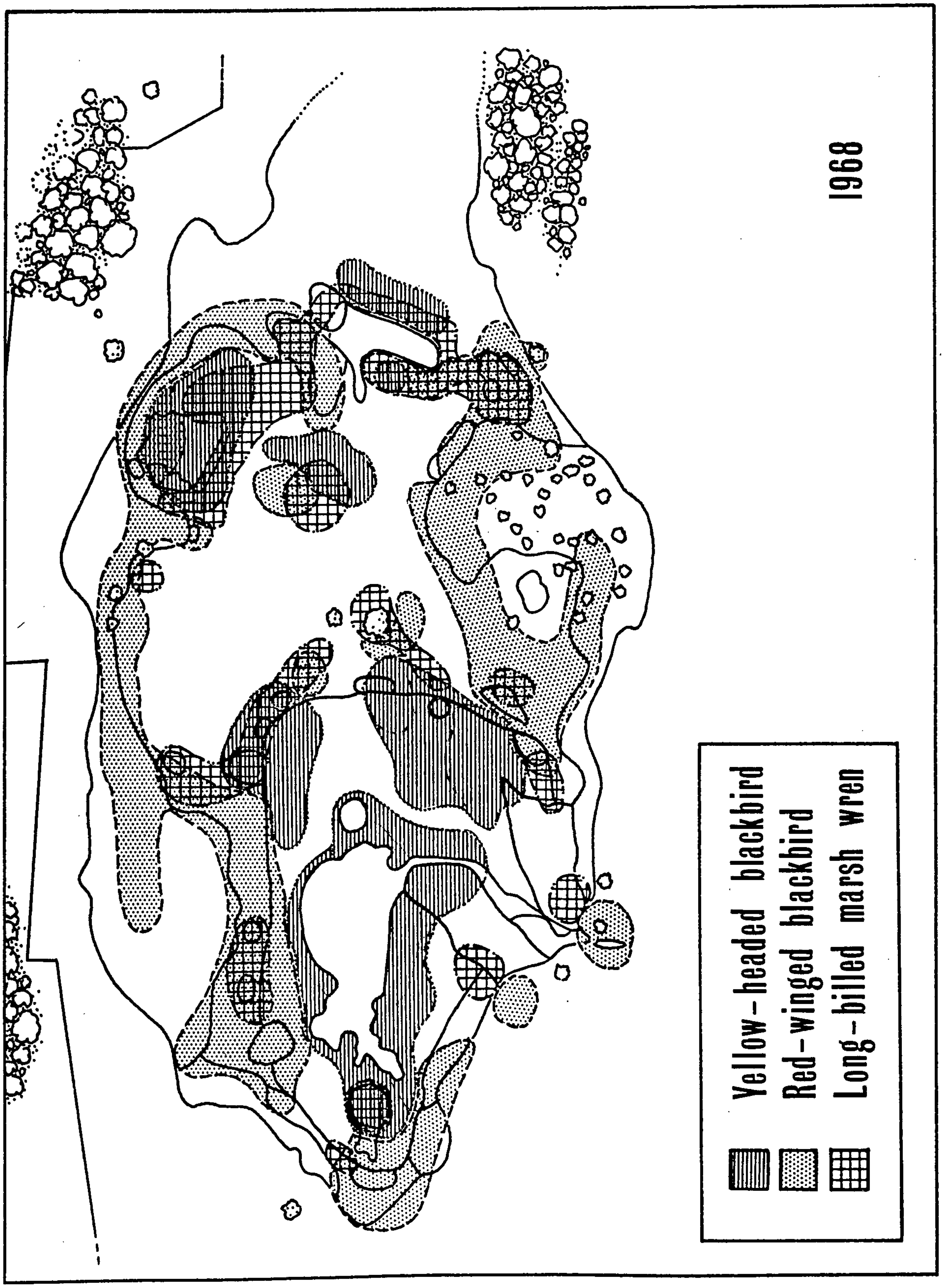

1968
Yellow-headed blackbird
Red-winged blackbird
Long-billed marsh wren

Table 5. Distance from open water and vegetation edge of red-winged blackbird, yellow-headed blackbird and long-billed marsh wren nests (1968)

Species	Distance in feet 0-20	21-40	41+	Sample
	Distance from vegetative edge			
Yellow-headed blackbird				
Bergo's 1968	35.7%	26.5%	37.7%	98
Red-winged blackbird				
Bergo's 1968	66.6%	21.3%	12.0%	75
Potholes 1968	65.9%	31.9%	2.1%	45
Long-billed marsh wren				
Bergo's 1968	40.8%	38.5%	30.6%	98
	Distance from open water edge			
Yellow-headed blackbird				
Bergo's 1968	73.4%	14.2%	12.2%	98
Red-winged blackbird				
Bergo's 1968	36.6%	9.8%	53.5%	71
Potholes 1968	54.3%	8.6%	36.9%	46
Long-billed marsh wren				
Bergo's 1968	39.8%	10.2%	49.9%	98

open water seemed to influence yellow-headed blackbird nest site selection and densities. Also see Ellarson, 1950, Weller and Spatcher, 1965 and Willson, 1966. Yellow-headed blackbirds seldom used lake sedge for nesting substrate; however, those nesting in the "B" impoundment in 1967 were exceptions. All nests were in the densest stands of lake sedge bordering open water areas.

Temporal and Spatial Relationships of Nests

Nest site locations of the three species were related temporally and spatially. Birds nesting in isolated cat-tail and lake sedge beds in Bergo's Slough demonstrated these relationships. The isolated cat-tail bed shown in Fig. 10 occupied approximately 10,000 square feet and was used extensively by nesting yellow-headed blackbirds. Seven males established territories which included small portions of the cat-tail. All but one of 15 nests were built in the cat-tail (Fig. 11). Intraspecific clashes were frequent. Fourteen of the nests were abandoned, possibly because of frequent aggressive interaction between pairs.

By June 14, yellow-headed blackbirds had left the cat-tail bed and, by June 18, red-winged blackbirds had moved into the cat-tail and started nest building (Fig. 12). On July 9, a total of 8 red-winged blackbird nests was present in the cat-tail bed, all of which were successful (Fig. 13). Marsh wrens also moved to the perimeter of the cat-tail bed after the yellow-headed blackbirds departed, and nested in close proximity to red-winged blackbirds (Fig. 11, 12 and 13). Three marsh wren nests with eggs and young were located within 10-75 feet of active red-winged blackbird nests.

Roberts' (1909) description of the fate of a small Minnesota yellow-headed blackbird colony in common reed is very similar to that of the group nesting in cat-tail at Elk Creek. Both involved small tracts of tall, robust emergents selected for nest sites by yellow-headed blackbirds and surrounded by open water and low uniform stands of vegetation. In both instances, large numbers of males established territories including parts

Figure 10. Distribution of vegetation around the isolated cat-tail bed in Bergo's Slough 1968.

Code: (1) Cat-tail, (2) Lake sedge, (3) Blue-joint, (4) *Carex* spp., (5) Sweet flag, (6) Soft-stem bulrush, (7) Tussock sedge

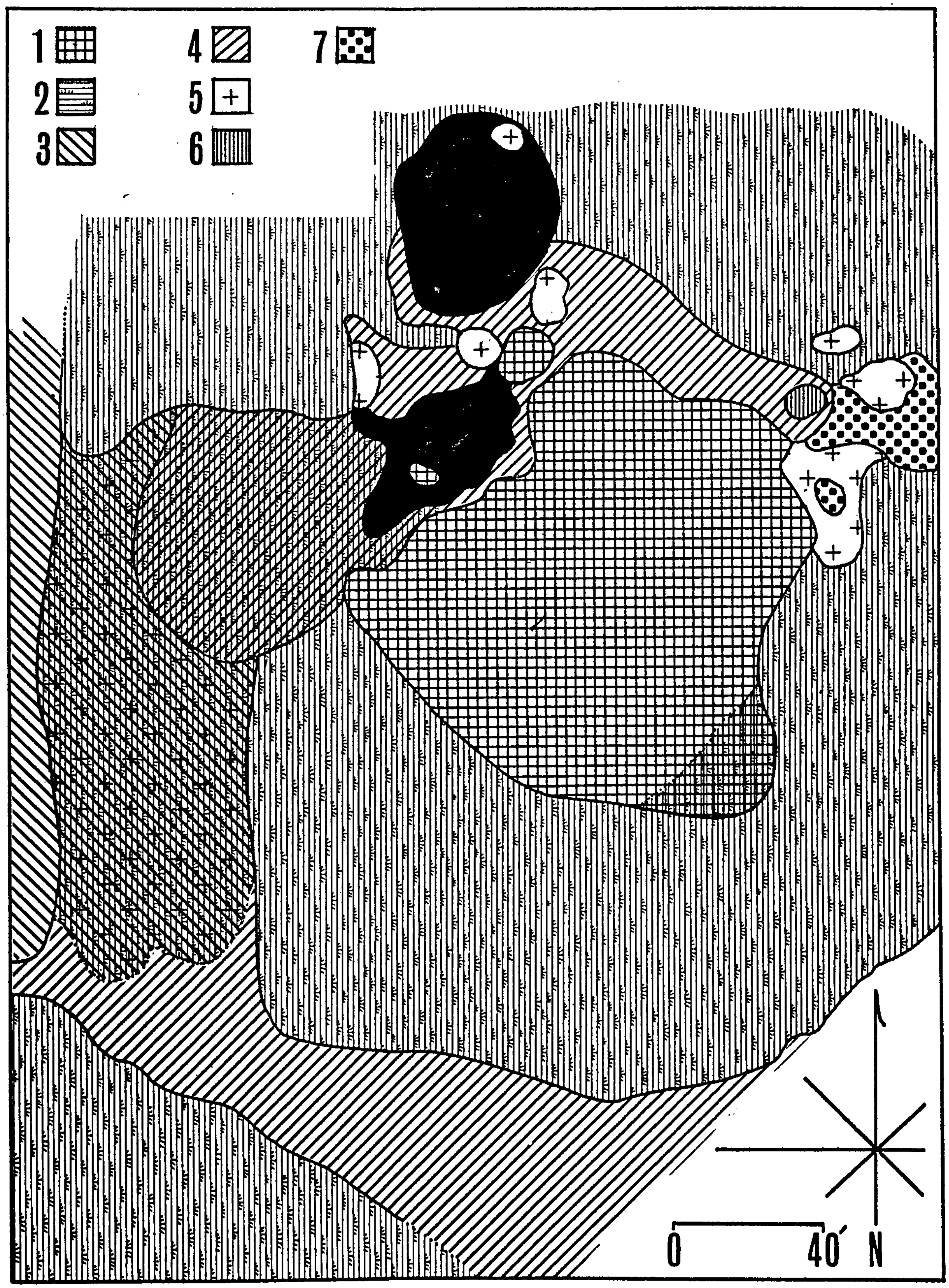

1
2
3
4
5
6
7
0
40′
N

Figure 11. Nest site locations of yellow-headed blackbirds, red-winged blackbirds, and long-billed marsh wrens in the area of the isolated cattail bed on June 3.

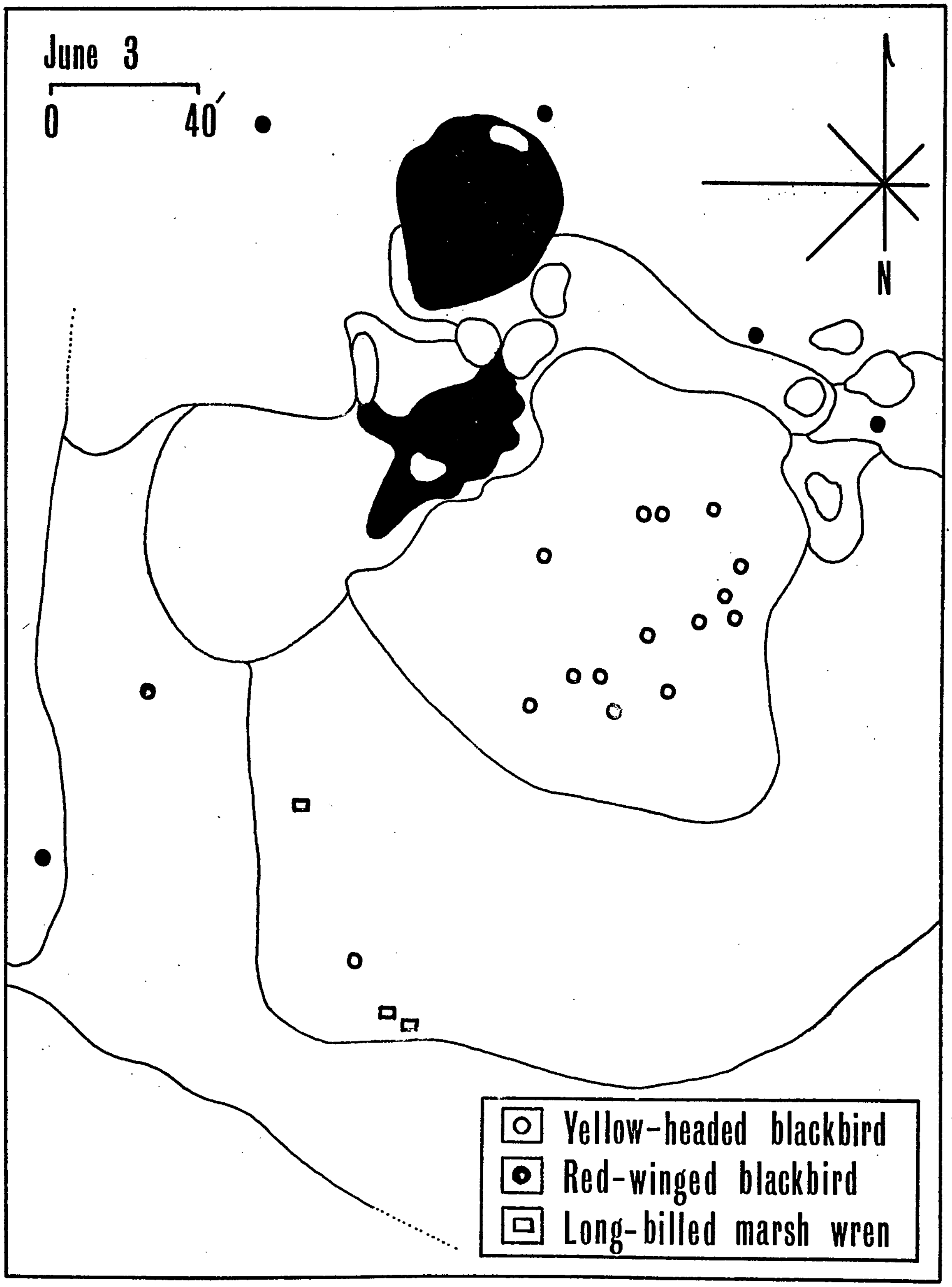

June 3
0
40'
N
Yellow-headed blackbird
Red-winged blackbird
Long-billed marsh wren

Figure 12. Nest site locations of yellow-headed blackbirds, red-winged blackbirds, and long-billed marsh wrens in the area of the isolated cattail bed on June 18.

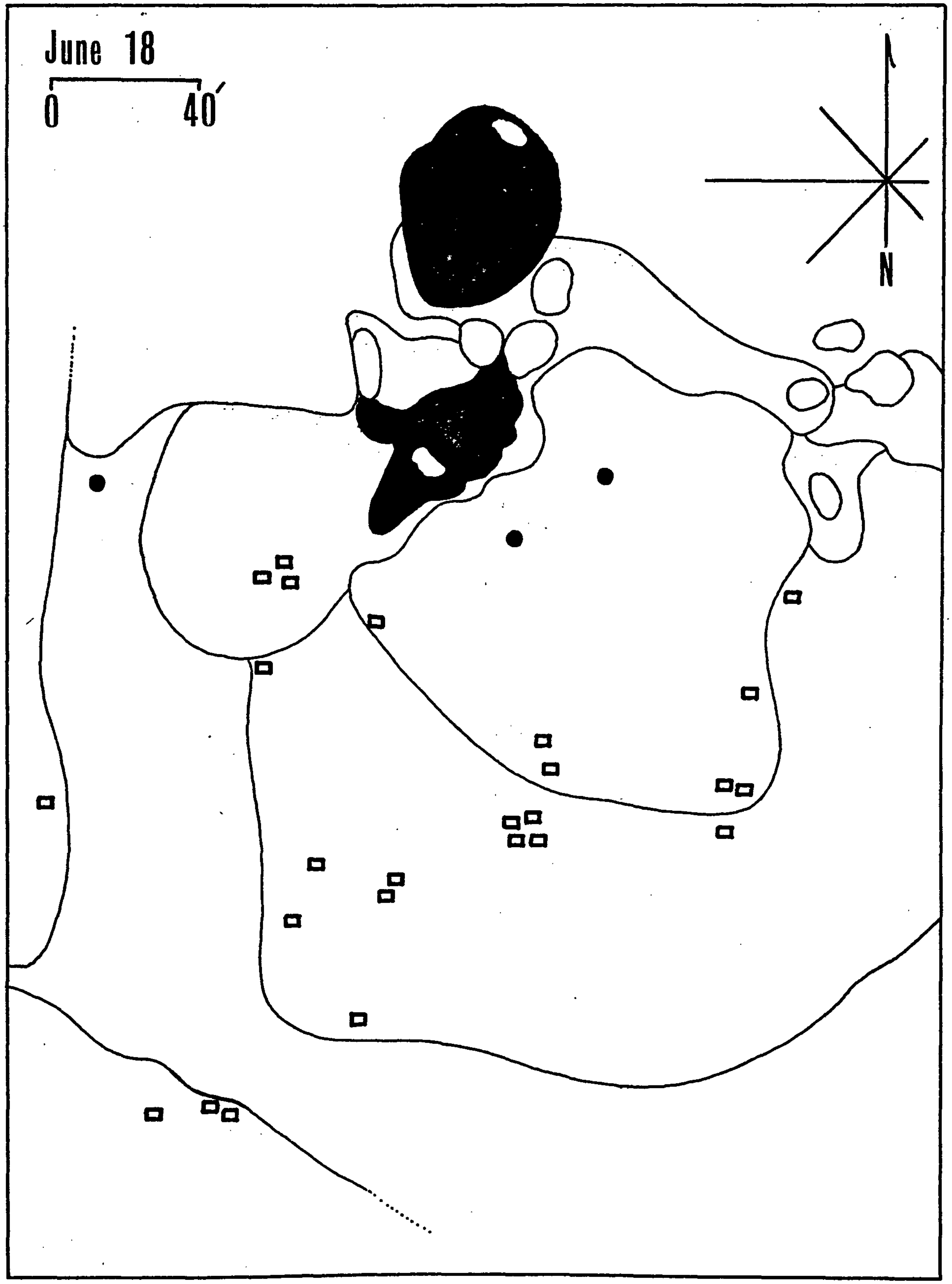
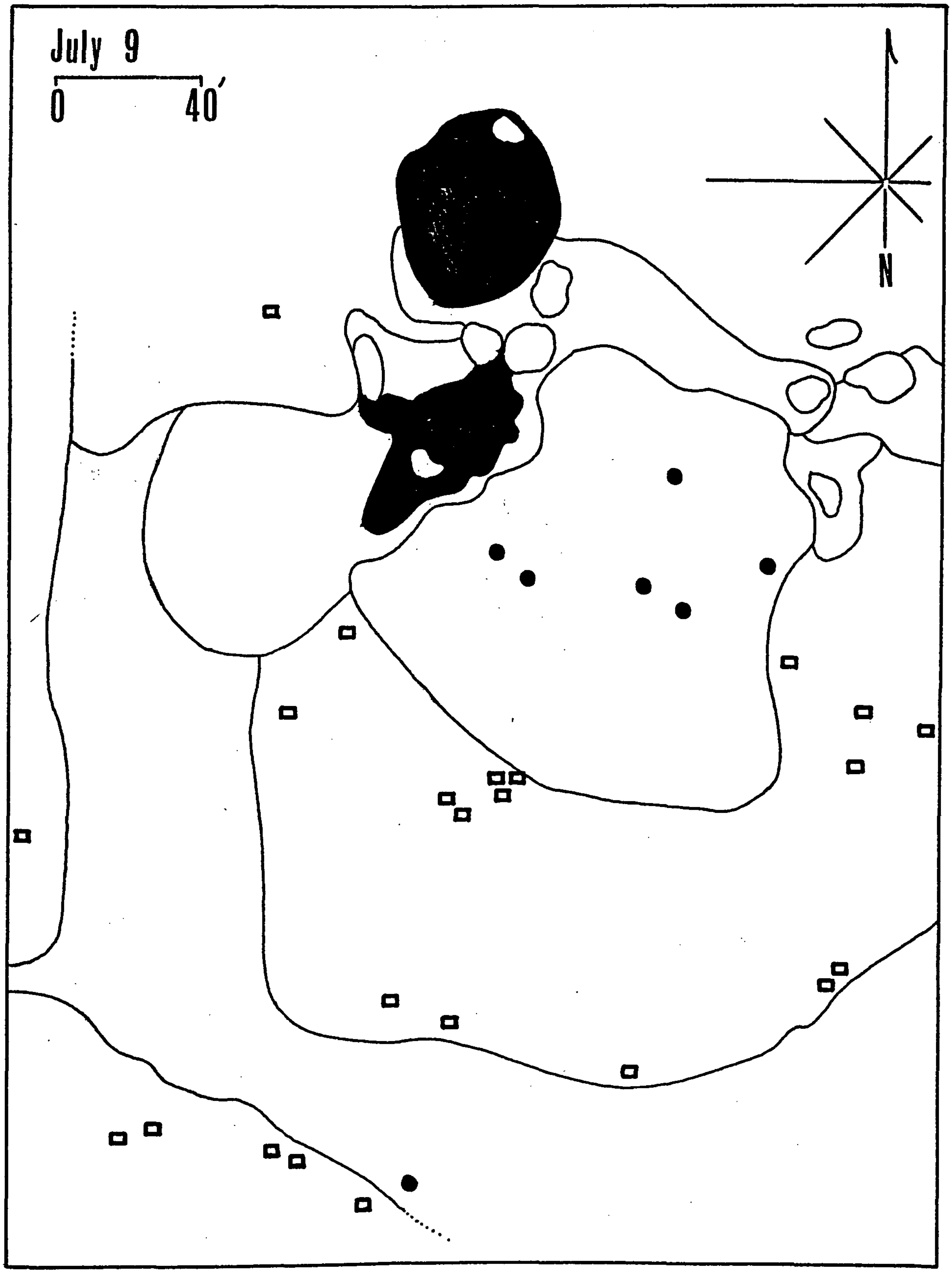

June 18
0
40'
N

Figure 13. Nest site locations of yellow-headed blackbirds, red-winged blackbirds, and long-billed marsh wrens in the area of the isolated cattail bed on July 9.


July 9
0
40'
N

of the tall robust emergent bed. Almost all nests were constructed within the tall vegetation, resulting in high densities. The cat-tail bed at Elk Creek contained 14 yellow-headed blackbird nests, or a density of about one nest per 714 square feet of cat-tail. Roberts' (1909) birds were nesting in approximately one acre of common reed where he found 62 nests, or a density of approximately one nest per 702 square feet. Twenty-eight of the 62 nests were never completed and only 17 females hatched eggs. Of the 17, one fledged offspring. All 14 of the Elk Creek nests were completed, but eggs were laid in only one, which was successful. Roberts (1909) was unable to identify the agent causing the desertion and or (destruction) of the nests, but intraspecific competition may have been a factor.

Whereas the cat-tail used was isolated among shorter emergents, a bed of lake sedge in Bergo's Slough was conspicuous by its low profile, dense stand and isolation in taller emergents (Fig. 14). The distribution of blackbird nests around the lake sedge bed is typical (Fig. 15). Red-winged blackbird nests were close to land and yellow-headed blackbirds were located closer to open water. Figure 15 shows that marsh wren nests built early in the season, were all located in the lake sedge bed. No wren nests were built outside the sedge area until June 18. This behavior suggests that marsh wren distribution was restricted by the presence of the blackbirds prior to mid-June. Yellow-headed and red-winged blackbirds which had nested around the sedge bed were still feeding large nestlings or fledglings by mid-June, and inter- and intraspecific territorial aggression was nearly absent. This also is indicated by the

Figure 14. Distribution of vegetation in the area of the isolated lake sedge bed of Bergo's Slough 1968.

Code: (1) Cat-tail, (2) Lake sedge, (3) Bur-reed, (4) River bulrush, (5) Sweet flag, (6) Soft-stem bulrush, (7) *Spartina sp.* (8) Tussock sedge.

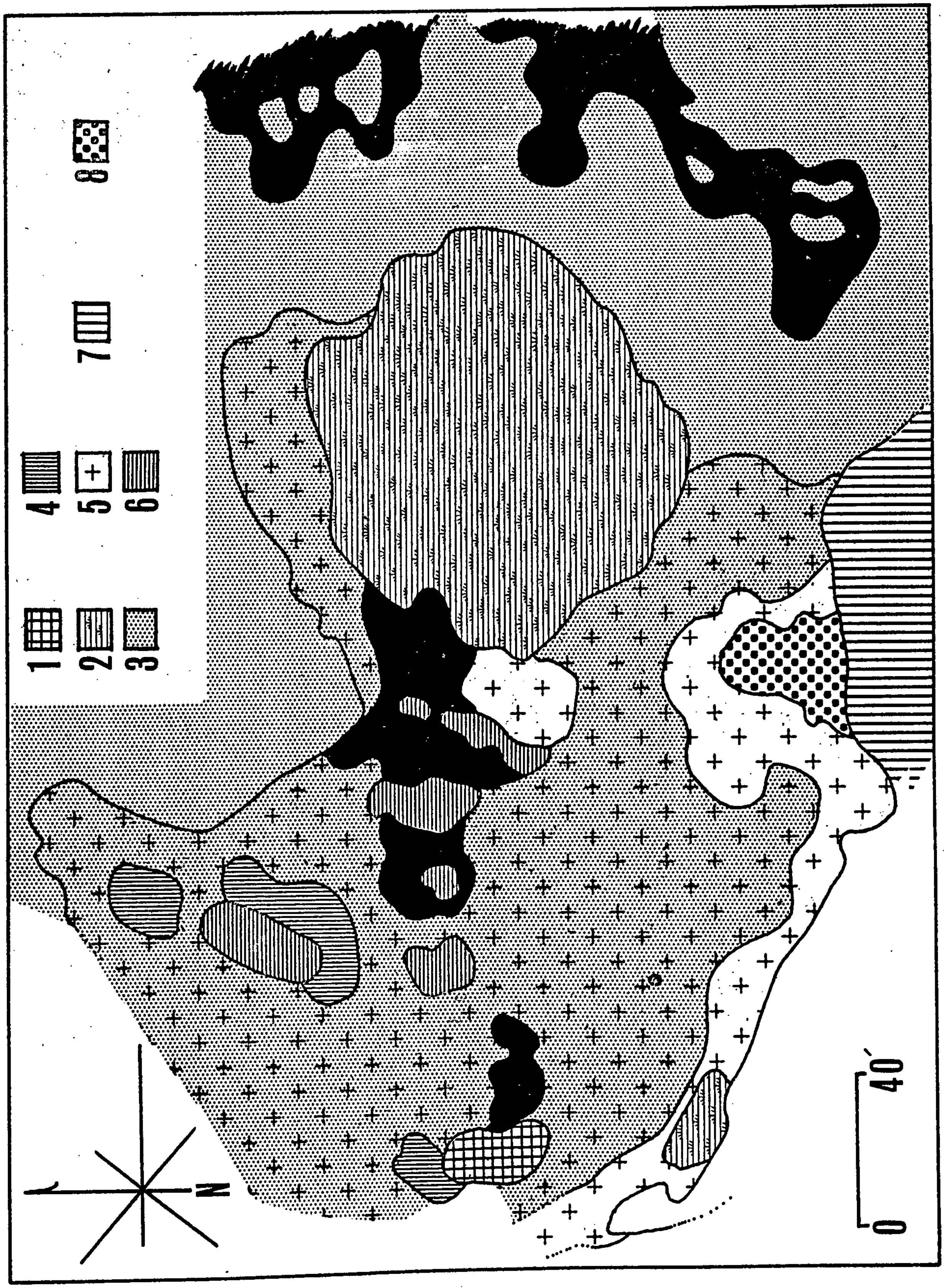
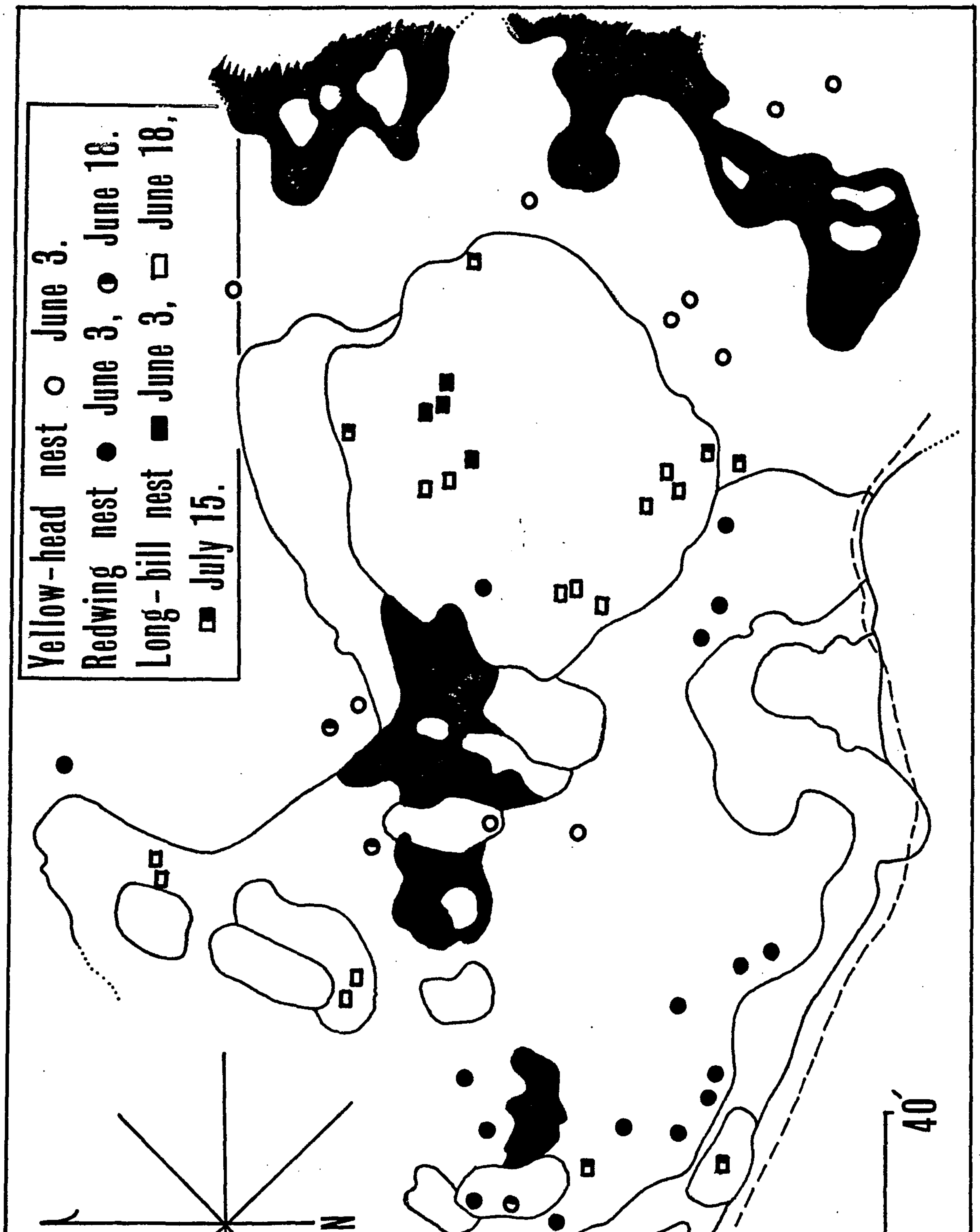

1
2
3
4
5
6
7
8
N
0
40´

Figure 15. Distribution of nests from June 3 to July 15 in the area of the isolated lake sedge bed, Bergo's Slough 1968.


Yellow-head nest ○ June 3.
Redwing nest ● June 3, ◐ June 18.
Long-bill nest ■ June 3, □ June 18,
▣ July 15.
N
0
40'

proximity of wren and red-winged blackbird nests in the cat-tail bed discussed earlier, (see Fig. 13). Yellow-headed blackbirds were probably responsible for the restricted distribution of both red-winged blackbirds and marsh wrens in the sedge bed area during early June.

Wren-Blackbird Interactions

The egg-breaking behavior of long-billed marsh wrens was noted by Allen (1914), Welter (1935), Ammann (1938), and Orians and Willson (1964). The seriousness of this behavior in egg loss probably depends upon population densities of wrens and blackbirds. Allen (1914) felt it was serious. He found 28% destruction by marsh wrens of eggs in 51 red-winged blackbird nests. In comparison, Welter (1935) didn't feel marsh wren predation on blackbird eggs was significant. Orians and Willson (1964) noted blackbird aggression directed at marsh wrens and emphasized its survival value in that it prevented some egg loss. They also noted that both red-winged and yellow-headed blackbirds were aggressive toward marsh wrens, but they did not indicate any differences in intensity of aggression by the two species.

At Elk Creek Marsh, three direct red-winged blackbird/marsh wren interactions were observed. No body contact was made, and the wren was chased from the area of the blackbird nest by the male red-winged blackbird. Yellow-headed blackbird attacks on long-billed marsh wrens were much more intense. Five different encounters between male yellow-headed blackbirds and marsh wrens were observed. During each encounter, marsh wrens were chased by male yellow-headed blackbirds into dense vegetation, captured and pecked vigorously. In four instances, numerous feathers were plucked from the wren. On two occasions, male yellow-headed blackbirds released the wrens, only to recapture them and resume their attacks a short distance away. No marsh wren mortality was observed as a result of the attacks.

Long-billed marsh wrens build numerous nests during a breeding season. Verner (1963) reported up to 20 per male and Kale (1965) up to 27 per male. Nests usually are located in groups called courting centers (Verner, 1964). Courting centers function as song and display areas from which males advertise for mates. Males which fail to construct such nests seldom obtain a mate (Verner, 1964). Most male activity in the early part of the breeding season (late May and early June) in Iowa is restricted to the courting center area. During this period at Elk Creek, no males were observed over an estimated 100 feet from their respective courting centers, and most were observed well within 50 feet of their respective center. In my experience blackbird nests built early in the season and located close to marsh wren courting centers are more likely to be found and preyed upon by patroling male marsh wrens. Later in the season, some male marsh wrens help feed their young (Verner, 1965) and have less time for territorial activity as do the blackbirds. As a result, less interspecific conflict occurs.

Data from 108 blackbird nests (52 yellow-headed blackbird and 56 red-winged blackbird) tend to substantiate the above observations. Data on blackbird nests were divided into two groups based upon the proximity of the nests to wren courting centers. An arbitrary distance of 100 feet was used to divide the sample. Egg fates of the groups were compared.

Because predation by the marsh wren is restricted to eggs, blackbird nests referred to as successful in this discussion are those which hatched one or more eggs.

Data from the 108 blackbird nest sample are summarized in Table 6. Differential nest success believed related to distances from courting centers in red-winged blackbird nests was observed. Thirty-three per cent of the red-winged blackbird nests within 100 feet of marsh wren courting centers hatched eggs, while 53% outside the 100 foot distance hatched their clutches. The 56 red-winged blackbird nests used in this sample were early nests (started between 28 May and June 5). Hatching success of late red-winged blackbird nests (following June 18) within 100 feet of courting centers appear to be much higher than the early nests. Although a small sample size is involved (9 nests), all 9 nests hatched eggs even though some were within 10 feet of wren courting centers, indicating reduced wren-blackbird aggression by mid June.

A greater percentage of yellow-headed blackbird nests within 100 feet of wren courting centers hatched eggs than did those over 100 feet. If the 14 nests from the cat-tail bed are removed from the overall yellow-headed blackbird sample, 58.8% of their nests outside 100 feet hatched eggs. It appears from Table 6 that proximity to wren courting centers has no effect on hatching success of yellow-headed blackbirds.

Only five cases of blackbird egg destruction directly attributable to wren predation were observed at Elk Creek; all were red-winged blackbird eggs. In each nest, eggs were found with small round punctures, and some eggs in the same nest disappeared. Allen (1914) reported that

Table 6. Hatching success of red-wings and yellowheads related to the distance of their nests from marsh wren courting centers

	Within 100 feet		Outside 100 feet		
	% Successful	Sample	% Successful	Sample	Total
Yellow-headed blackbird	79.5	(21)	54.8	(31)	61.5 (52)
Red-winged blackbird	33.3	(24)	53.1	(32)	44.6 (56)

marsh wrens sometimes carry off the punctured egg after "drinking" its contents. This could account for the lost eggs observed in many of the deserted or destroyed blackbird nests. Entire clutches disappeared in 13 unsuccessful nests. Plains garter snakes (Thamnophis radix) were seen in Bergo's Slough on several occasions and may have accounted for some blackbird egg loss.

Renesting

Renesting in yellow-headed blackbirds is considered rare in Minnesota (Roberts, 1909), north-eastern Iowa (Ammann, 1938), and Washington as cited by Willson (1966). Some yellow-headed blackbird renesting was believed to have occurred at Elk Creek, but was not proven. Fautin (1940) reported second and third attempts by female yellow-headed blackbirds in Utah, and Young (1963) in Wisconsin also reported common renesting in the species, but neither author used marked birds. I have no evidence that north-central Iowa yellow-headed blackbirds are multi-brooded.

An example of low-renesting tendencies in yellow-headed blackbirds was recorded in the "B" impoundment in 1967. Fifteen nests had been found in lake sedge with long-billed marsh wren nests and numerous red-winged blackbird nests. Seven inches of rain over a two-day period raised water levels over 18 inches. Yellow-headed blackbirds and marsh wrens suffered 100% loss of nests, eggs and young. Water levels receded rapidly, and reached pre-rain levels within three days following the peak. However, yellow-headed blackbirds and marsh wrens abandoned their territories and no renesting attempts in the impoundment were recorded. The same behavior has been reported in marsh wrens by Welter (1935) and in yellow-headed blackbirds by Fautin (1940). Contrary behavior was observed in the long-billed marsh wren by Kaufmann and Ivins (1965) following a flood at Elk Creek in 1963. They noted little territorial abandonment by marsh wrens and that most of the population renested following the flood. Timing of the floods relative to the breeding cycle were the same in 1963 and 1967.

Many red-winged blackbirds also abandoned their territories following the 1967 flood. Census data indicated a minimum of 38 territorial males in the "B" pool study area prior to the flood. Sixteen (42.1%) remained on shoreline territories following the high water. Of 116 red-winged blackbird nests observed in the impoundment, 107 (92.2%) were destroyed by high water.

The red-winged blackbird's ability to utilize trees as a nesting substrate following removal of emergent vegetation within the same breeding season was observed at Elk Creek. A total of 39 red-winged blackbird nests were found throughout the upper floodplain of Elk Creek following the flood. Twenty-five of the 39 (64.1%) were built in trees. It is not known whether the tree nests were built by late nesters or by females that had lost the first nest to the flood. However, it has been demonstrated by Fankhauser (1964), using marked red-winged blackbird females, that some may select different habitat types for each nest during the season. He described one marked female that built two nests on the upland and a third in a marsh 600 yards from the first two.

Annual changes in nesting habitat also may influence site selection (Weller and Spatcher 1965). They found a correlation between the gradual elimination of emergent vegetation over a period of four years and a gradual increase in numbers and percentages of nests built in marsh-edge trees and shrubs by red-winged blackbirds.

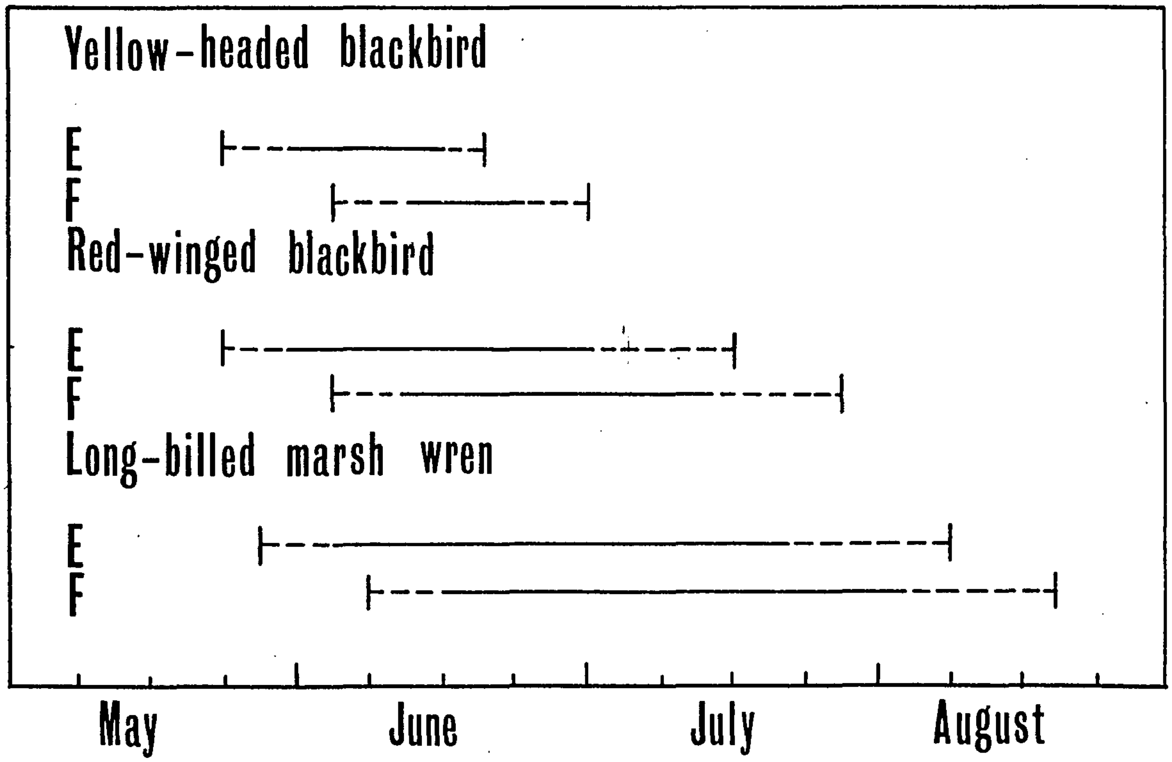
The survival value of the tree nesting habit in red-winged blackbirds is obvious, and probably developed in relation to repeated contacts with floods by stream edge nesting populations.

Breeding Synchrony

In Iowa, the yellow-headed blackbird population completes its breeding cycle in approximately a month (June), with egg laying lasting about two or three weeks (Fig. 16). Exceptions have been noted by Weller and Spatcher (1965).

Red-winged blackbirds in Iowa can be found feeding offspring in late July and egg laying may last for a period of approximately 7 weeks (Fig. 16). The literature indicates that lack of synchrony in the timing of egg laying by red-winged blackbirds is typical. For example, Strosnider

Figure 16. Chronology of reproduction at Elk Creek Marsh 1967-1968. E = on eggs, F = feeding young.


Yellow-headed blackbird
E
F
Red-winged blackbird
E
F
Long-billed marsh wren
E
F
May
June
July
August

(1960) noted that four females mated to one male, were 22 days out of phase on fledging dates of their offspring, and Nero (1956) reported similar findings on Madison area red-winged blackbirds. Smith (1943) observed slight differences in timing of egg laying within large and small populations of red-winged blackbirds. Small populations tended to be more synchronous. Case and Hewitt (1963) noted that terrestrial nesting red-winged blackbirds were a week to 10 days later than marsh nesting red-winged blackbirds in New York. No differences were observed at Elk Creek between Bergo's Slough and the pothole populations.

The long-billed marsh wren population completed its breeding cycle by August 1 at Elk Creek (Fig. 16). Although length of the breeding period indicates little synchrony within the population, Verner (1964) has found good synchronization of breeding marsh wren females paired to the same male, with less than two days overlap in egg laying.

The relatively synchronous timing of egg laying by local populations of yellow-headed blackbirds and long-billed marsh wrens is typical of most species of marsh nesting birds.

DISCUSSION

In his classic paper on blackbird behavior, Allen (1914) suggested that the red-winged blackbird was a "recent" member of the marsh avifauna. He listed numerous habitat-related behavioral responses of red-winged blackbirds to substantiate his observation. Data obtained in this study generally agree with Allen's thesis. Many of the behavioral responses of red-winged blackbirds described by Allen also were observed in Iowa. In addition, observations of interactions between red-winged blackbirds and other marsh-nesting species provide further support to this theory.

Species Interaction

Mayr (1963) lists two sets of biological characteristics that permit sympatry between closely related species: 1) mechanisms that guarantee reproductive isolation; and 2) the ability to resist competition from other species that utilize the same or similar resources.

Interspecific aggression culminating in mutually exclusive territories may be necessary to prevent hybridization in closely related congeners. However, it is not important in the yellowhead-redwing situation, because hybridization between the two has never been reported.

As for Mayr's second point, Cody (1968) lists the five ways that grassland nesting avian species can co-exist through resource division: 1) differences in foraging behavior; 2) food specialization; 3) differences in breeding periods; 4) horizontal habitat selection; and 5) vertical habitat selection.

Differences in Foraging Behavior

Because closely related species are more likely to draw upon the same resources, the most stringent test of ecological compatibility would be whether populations of the forms concerned could utilize the same space in a horizontal plane in periods of critical need, such as when nestlings are being fed (Dixon, 1961). Ecological compatibility has been observed in many co-existing congeners: Parus (Dixon, 1961), Dendrocia (MacArthur, 1958), Phalacrocorax (Lack, 1945), and North American Ardeidae (Meyerriecks, 1962). All of these authors stress foraging differences as the factor allowing horizontal overlap in the respective congeners.

Food habits of marsh nesting red-winged blackbirds have been studied by Bird and Smith (1964) and Snelling (1968) but quantitative comparative food habit studies of yellow-headed and red-winged blackbirds nesting on the same marsh have not been documented. Willson and Orians (1963) reported briefly on the subject, but presented no data. They observed that there were differences in feeding areas and food items. The Washington yellow-headed blackbird is a food specialist, and the red-winged blackbird is more versatile. Orians (1966) noted great overlap in the food taken by both species and differences in gross productivity of breeding lakes used by yellow-headed and red-winged blackbirds in the northwest corner of their ranges; yellow-headed blackbirds were restricted to the more productive lakes. Willson and Orians (1963) postulated that the larger yellow-headed blackbird would be a more efficient forager in the sparse vegetation of marsh centers, and conversely, that the smaller red-winged blackbird would be more efficient in the denser vegetation of the marsh edge. In my experience, the red-winged blackbird should be as efficient a forager in marsh centers as yellow-headed blackbirds (smaller size should enhance its efficiency) and selection should work accordingly, reinforcing competition for central areas.

Chronology of Nesting

Differences in the chronology of nesting between the three species may reduce competition, although nesting periods overlap considerably (Fig. 16). Staggered breeding periods allow less competition between congeners in the tropics (Ricklefs, 1966) and are aided by longer favorable periods for breeding. In North America, potential competition is reduced by staggered nesting seasons in the following marsh-edge species; yellow warbler (Dendroica petechia), Traill's flycatcher (Empidonax traillii) and the American goldfinch (Spinus tristis)(Nickell, 1958), and in marsh-nesting common grackles (Quiscalus quiscula) and red-winged blackbirds (Wien, 1965 and Snelling, 1968).

The red-winged blackbird renests readily and utilizes central marsh areas when the yellow-headed blackbird has departed. If late nesting red-winged blackbirds are successful in marsh centers, this could be another factor reinforcing competition with Xanthocephalus for central areas.

The long-billed marsh wren is multi-brooded (Verner, 1965). At Elk Creek, fresh clutches have been found as early as June 1 and as late as the first week in August. Thus, the wrens can and do take advantage of the yellow-headed blackbirds' absence later in the season, and along with Agelaius use the vacant habitat for nesting.

Habitat Requirements

In an analysis of habitat requirements and competition between red-winged and yellow-headed blackbirds, Miller (1968) noted the following points.

1. "The habitat requirements of breeding populations of redwings and yellow-headed blackbirds describe a niche relationship governed by 2 primary variables, water depth (including presence or absence of water) and nest height."

2. "Where both species occupy emergent vegetation in marshes, they require approximately the same structural features of the habitat and use them in almost identical ways."

3. "Where the two species are sympatric, redwings seek to establish territories in the deeper parts of a marsh and are subsequently excluded from this niche space by the dominant yellowhead, but there is only indirect evidence that it is preferred by redwings as well as yellowheads."

Data from red-winged blackbirds at Elk Creek nesting in potholes indicate the same nest site response to open water edge as in yellow-headed blackbirds (Table 4). Red-winged blackbirds did move into central marsh areas when yellow-headed blackbirds departed from Elk Creek. However, this is not offered as conclusive evidence that redwings prefer central marsh areas over marsh borders.

Evolutionary Implications

Aggressive interaction between *X. xanthocephalus* and *A. phoeniceus* may be a result of their similar nesting ecology, which in turn is probably related to great similarities in ancestral habitats. Factors believed to be important in the historical development of interactions between the three species are: (1) habitat and nest site selection; (2) nesting behavior, (3) social systems, and (4) morphological adaptation.

Habitat and Nest Site Selection

Data obtained in this study agree with that of others and indicate yellow-headed blackbird nest site selection is strongly influenced by open water edge (Table 4). Red-winged blackbirds in potholes nested nearer open water edge than did red-winged blackbirds in Bergo's Slough which were nesting in association with yellow-headed blackbirds. I think there probably is a positive response to open water edge by red-winged blackbirds nesting in Iowa, but the behavior is subordinate when yellow-headed blackbirds are present. Yellow-headed blackbirds do not appear to respond to vegetation edge (Table 4) but red-winged blackbirds nested in close proximity to cover boundaries in both the potholes and Bergo's Slough (Table 4). The red-winged blackbirds of Elk Creek seemed to prefer a nest site within 20 feet of open water and 20 feet of a major vegetation edge (Table 4). In marshes, this site is rare other than along shore zones during the "open marsh" stage of Weller and Spatcher (1965). It would be much more common along stream margins, characterized by narrow bands of cover types close to open water. Generally the vegetation suitable for nesting in marshes occurs in relatively homogenous stands. The ability of red-winged blackbirds to use trees as nesting substrates following nest loss in low herbaceous vegetation has been shown by this and other studies. Allen (1914) believed this habit indicated a recent breeding association with marshes by red-winged blackbirds.

Orians (1961b) states that peripheral territories are occupied first and are more strongly contested by red-winged blackbirds than are central marsh areas. I would suspect this in areas of sympatry because of displacement by yellow-headed blackbirds, but Orians gave no evidence, and I have none. Willson and Orians (1963) and Miller (1968) reported that, in areas of sympatry, when one species was absent on a marsh, the other normally nested from shore zone to marsh center. This study supports their findings as far as red-winged blackbirds are concerned (Fig. 7). However, Hardy and Dickerman (1965) and Hardy (1967) have demonstrated that habitat selection can be rigid in red-winged blackbirds. They have shown that two subspecies of red-winged blackbirds (A. p. nelsoni and A. p. gubernator) in Mexico are living essentially side by side without significant interbreeding because of rigid habitat selection. One subspecies nests in sedge, the other in robust emergents.

Nest Defence Behavior

In an extensive survey of avian social systems, Crook (1965) concluded that the social system of a given species is a joint adaptation to food distribution, and the kind and degree of safety from predators afforded by available nest sites. The behavioral responses to predators differ significantly between the two blackbirds during the nesting season. Siglin and Weller (1963) have shown that marsh nesting red-winged blackbirds respond more vigorously to terrestrial predators than do yellow-headed blackbirds. Behavior of females on nests are strikingly different upon human approach. Most yellow-headed blackbird females at Elk Creek quietly left the nest and crept off, keeping low in the vegetation. Ammann (1938) reported the same behavior, and it is similar to the behavior of most marsh birds. Red-winged blackbird females generally flew directly from the nest, and would hover over it calling vigorously, a trait associated with terrestrial birds. Long-billed marsh wren females behaved in the same manner as did yellow-headed blackbird females. Nests with eggs or young were left quietly and wren females always stayed low in the vegetation.

These factors imply specialization to marsh habitats by yellow-headed blackbirds and marsh wrens, and a closer relationship to terrestrial environments by the red-winged blackbird.

Social Systems

Orians (1961a) has suggested that polygamy is a more successful means of reproduction in red-winged blackbirds than monogamy. Case and Hewitt (1963) have shown that marsh nesting red-winged blackbirds generally have more females per male than do upland nesters. Other studies have shown that increasing nest success can be correlated with increasing water depth (Young 1963, and Goddard and Board 1967) and increasing nest height (Meanley and Webb 1963, and Holcomb and Twiest

1968). These data indicate strong selective pressures favoring marsh nesting red-winged blackbirds.

As noted earlier a given species social system is related to food distribution as well as response to predation (Crook 1965). Horn (1968) has shown this relationship in colonial nesting Brewer's blackbirds (Euphagus cyanocephalus). He postulated that "selection for efficiency of exploitation of a food supply that is variable in space and time led to an initial concentration of nests rather than to territoriality." Horn's (1968) reasoning also should apply to yellow-headed and red-winged blackbird nesting distributions, although Lack (1968: 54) does not consider them colonial. Polygamy probably evolved following contact with a food-rich environment by the ancestral forms of the blackbirds.

Morphological Adaptations

A measure of a species antiquity in a given environment is better correlated with its morphological specialization to the environment, than behavioral specialization, because behavioral changes normally precede morphological changes in the evolution of a species (Mayr, 1963: 604).

Data presented in this study and from the literature clearly show the behavioral specializations of the yellow-headed blackbird that restrict it to fresh water marsh habitats. In addition, Miller (1956) has pointed out that ecological tolerance in habitat selection of a species may be estimated in part by the degree to which it has become polytypic. The yellow-headed blackbird is monotypic (A.O.U., 1957) and has a narrow range of ecological tolerance. By contrast, the very generalized red-winged blackbird has diverged into 11 subspecies (A.O.U., 1957).

The yellow-headed blackbird is a generalized passerine. However, its feet are relatively large with long, strong toes, believed to be of aid in maneuvering in emergent vegetation and walking on floating vegetation or soft mud (Wetmore, 1920). The long-billed marsh wren also shows morphological specialization suggesting a long association with marshes. The bill is more elongate and there is a tendency toward reduction in use of the wings (Welter, 1935). Shortened wings are common in congeners which fly in or about dense vegetation (Hamilton, 1961). The red-winged blackbird is unspecialized morphologically.

The natal down of both species of blackbirds is light colored, in comparison to other blackbirds. In addition, the lining of the nest is light colored. These are believed to be adaptations of value in reflecting sunlight and probably the result of an evolution in open habitats (Linsdale 1936).

The juvenile plumage of the red-winged blackbird is dark, dull brown, which is characteristic of the more arboreal North American blackbirds. By contrast, the yellow-headed blackbird's juvenile plumage is tan, as are the terrestrial nesting icterids of North America, meadowlarks (Sturnella sp.) and the bobolink (Dolichonyx oryzivorus). Tan colored juvenile plumage also is characteristic of true marsh birds (Linsdale 1938).

The eggs of the yellow-headed blackbird and other ground nesting North American icterids have been described in Bent (1958b) as having the same basic ground colors. The red-winged blackbird has an egg ground color described as pale bluish green. It is characteristic of the arboreal orioles and blackbirds.

The morphological characters of the yellowhead indicate ecological similarities with other open low nesting icterids. By contrast the same characters in the red-winged blackbird suggest strong ecological ties to arboreal relatives.

Proposed Evolutionary Sequence

The successive thrusts of Pleistocene ice must have played a dominant role in recent speciation of many North American birds. This has been demonstrated by numerous authors and is summarized by Rand (1948) and Selander (1965).

The fossil record provides little information on the evolution of North American Icteridae (Wetmore, 1959). Four of the nine known Pleistocene icterids are extinct. Fossil locations have been of little aid in determining ranges or habitats as most have been found in two sites, the famous Rancho La Brea in California, and in Florida.

As shown by many studies, morphological and behavioral specialization in the yellow-headed blackbird have induced strong habitat limitations, characteristics common to all true marsh birds. However, the red-winged blackbird is unspecialized and displays broad ecological valence.

Responses of nesting red-winged blackbirds to water certainly indicate an original evolution involving water, but not necessarily marshes. Speculations on the ancestral habitat of the red-winged blackbird based upon behavior and morphology point to an eastern North

American origin. Natal down and nest lining indicate evolution in open areas. Egg color, juvenileplumage, and the general tendency to nest in low trees suggest an original arboreal substrate. The combined response to vegetation and open water edge in nest-site selection may indicate stream and lake margins or bogs were important ancestral habitats.

Wetmore (1959) felt that wintering areas of migratory species may reflect their Pleistocene (Wisconsin) distributions. This, of course, is speculative, as present wintering distributions may be affected by agricultural, and other man influenced factors. However heaviest concentrations of wintering red-winged blackbirds occur in the southeastern United States (Seubert, 1963). Abundant evidence of a southeastern glacial refugia during the Pleistocene has been shown by Blair (1958); (1965). Thus habitat was available for the red-winged blackbird during this period. Their range probably extended northward during the interglacial periods , and contact may have occurred with yellow-headed blackbird populations during the times of range extensions. Orians and Christman (1968) suggested the presence of pan-continental populations of red-winged blackbirds as early as ten-thousand years ago. They propose that the tri-colored blackbird (Agelaius tricolor) is a recent species developed from A. phoeniceus stock during the Pleistocene and that their period of sympatry could be as little as ten-thousand years.

Willson and Orians (1963) and Weller and Spatcher (1965) felt the yellow-headed blackbird probably evolved in marshes of arid and semi-arid regions of the western United States, and Beecher (1951) suggests, an agelaiine ancestor. Martin (1958) has pointed out that the pluvial lakes of the Great Basin region during the late Wisconsin period were productive aquatic environments. These were probably valuable refugia for yellow-headed blackbirds and many aquatic birds during a time when glacial ice covered most of North America.

Further evidence of recent contact between yellow-headed and red-winged blackbirds include interactions of the two species with long-billed marsh wrens. The red-winged blackbirds inability to prevent egg predation by marsh wrens plus a broad overlap in nest site selection indicate insufficient time has elapsed for mechanisms of behavioral compatibility to evolve.

Much work remains to be done with these ecologically similar blackbirds. Of primary importance are studies of comparative food habits, and territorial establishment. Data on marked birds of known age of both species are critical for an understanding of the displacement of red-winged blackbirds by yellow-headed blackbirds from marsh centers.

SUMMARY

1. Habitat selection, nest-site selection, and interactions of red-winged blackbirds, yellow-headed blackbirds, and long-billed marsh wrens were studied in north-central Iowa during the summers of 1967-1968.

2. Two populations of red-winged blackbirds were studied. One population nested in association with yellow-headed blackbirds and long-billed marsh wrens in an oxbow marsh. The other population occupied two upland potholes where breeding yellow-headed blackbirds and long-billed marsh wrens did not occur.

3. Data on the three species were compared with respect to physical features, temporal, and spatial relationships of nest site selection, and interactions of nesting birds.

4. There was little overlap in nesting substrates between yellow-headed blackbirds and long-billed marsh wrens. However nesting substrates used by red-winged blackbirds overlapped greatly with both yellow-headed blackbirds (77%), and long-billed marsh wrens (100%).

5. Yellow-headed blackbirds generally excluded red-winged blackbirds and long-billed marsh wrens from the marsh center where yellow-headed blackbirds tended to nest in groups. These areas were occupied by red-winged blackbirds and long-billed marsh wrens following the post-breeding departure of yellow-headed blackbirds.

6. Red-winged blackbird nests located within 100 feet of long-billed marsh wren courting centers suffered higher egg mortality then those red-winged blackbird nests over 100 feet from wren courting centers.

7. Yellow-headed blackbird success was not related to distances of nests from wren courting centers.

8. Red-winged blackbirds responded to flooding of sedge nesting areas by nesting in trees, an adaptation which probably developed in relation to repeated contacts with flooding by stream edge nesting populations.

9. Foraging behavior, chronology of nesting, and habitat requirements are important factors influencing species interactions in the redwing-yellowhead-marsh wren complex.

10. On the basis of habitat and nest-site selection, nesting behavior, social system development, and morphological adaptations, yellow-headed blackbirds and long-billed marsh wrens display specializations suggesting a long association with marshes. Red-winged blackbirds are considered more recent members of the mid-western marsh avifauna.

LITERATURE CITED

Allen, A. A. 1914. The red-winged blackbird: a study in the ecology of a cattail marsh. Linnaean Soc. N. Y., Proc. Nos. 24-25: 43-128.

Ammann, G. A. 1938. The life history and distribution of the yellow-headed blackbird. Unpublished Ph.D. Thesis, Univ. Mich. Library, Ann Arbor, Mich. 277 p.

American Ornithologists' Union, 1957. Check list of North American birds. Fifth Ed. Union, Baltimore, Md. 691 p.

Beecher, W. J. 1942. Nesting birds and the vegetation substrate. Chicago Ornithol. Soc., Chicago, Ill. 76 p.

Beecher, W. J. 1951. Adaptations for food getting in the American blackbirds. Auk. 68: 411-440.

Bent, A. C. 1958a. Life histories of North American nuthatches, wrens, thrashers and their allies. U. S. Nat. Mus., Bull. 195. 475 p.

Bent, A. C. 1958b. Life histories of North American blackbirds, orioles, tanagers and allies. U. S. Nat. Mus., Bull. 211. 549 p.

Bird, R. D., and Smith, L. B. 1964. The food habits of the red-winged blackbird (Agelaius phoeniceus) in Manitoba. Can. Field-Natur. 78: 179-186.

Blair, W. F. 1958. Distributional patterns of vertebrates in the southern United States in relation to past and present environments. In C. L. Hubbs (ed.) Zoogeography. Amer. Assoc. Adv. Sci. Symp. 51: 375-420.

Blair, W. F. 1965. Amphibian speciation, p. 543 to 556. In H. E. Wright, and D. G. Frey (eds.) The Quaternary of the United States. Princeton Univ. Press, Princeton, New Jersey.

Campbell, L. W. 1948. Nest-building adaptability of the eastern redwing. Wilson Bull. 60: 244.

Case, A., and Hewitt, H. O. 1963. Nesting and productivity of the red-winged blackbird in relation to habitat. Living Bird 2: 7-20.

Cody, M. L. 1968. On the methods of resource division in grassland bird communities. Amer. Natur. 102: 107-148.

Crook, J. H. 1965. The adaptive significance of avian social organization. Zool. Soc. London Symp. 14: 181-218.

Darlington, P. J. 1957. Zoogeography: The geographical distribution of animals. John Wiley and Sons., New York. 675 p.

Dixon, K. L. 1961. Habitat distribution and niche relationships in North American species of (Parus), p. 179-216. In W. F. Blair (ed.) Vertebrate speciation. Univ. Texas Press, Austin, Texas.

Ellarson, R. S. 1950. The yellow-headed blackbird in Wisconsin. Pass. Pigeon 12: 99-109.

Fankhauser, D. P. 1964. Renesting and second nesting of individually marked red-winged blackbirds. Bird-Banding 35: 119-121.

Fautin, R. W. 1940. The establishment and maintenance of territories by the yellow-headed blackbird in Utah. Great Basin Natur. 1: 75-91.

Fautin, R. W. 1941. Development of nestling yellow-headed blackbirds. Auk 58: 215-232.

Fernald, M. F. 1950. Gray's manual of botany. Eighth Edition. Amer. Book Co., New York. 1631 p.

Goddard, S. U., and Board, V. V. 1967. Reproductive success of red-winged blackbirds in North Central Oklahoma. Wilson Bull. 79: 283-289.

Hamilton, T. H. 1961. The adaptive significance of intraspecific trends of variation in wing length and body size among bird species. Evolution 15: 180-195.

Hardy, J. W. 1967. Evolutionary and ecological relationships between three species of blackbirds (Icteridae) in central Mexico. Evolution 21: 196-197.

Hardy, J. W., and Dickerman, R. W. 1965. Relationships between two forms of the red-winged blackbird in Mexico. The Living Bird 4: 107-130.

Hildon, O. 1965. Habitat selection in birds. Ann. Zool. Fennici 2: 53-75.

Holcomb, L. C., and Twiest, G. 1968. Ecological factors affecting nest building in red-winged blackbirds. Bird Banding 39: 14-22.

Horn, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's blackbird (Euphagus cyanocephalus). Ecology 49: 683-694.

Kale, H. W., II. 1965. Ecology and bioenergetics of the long-billed marsh wren in Georgia salt marshes. Nuttall Ornith. Club, Pub. No. 5, 142 p.

Kaufmann, G. W., and Ivins, R. 1965. The effects of a flood on nesting Iowa marsh birds. Iowa Bird Life 35: 9-11.

Kendeigh, S. C. 1944. Measurement of bird populations. Ecol. Monogr. 14: 67-106.

Lack, D. 1945. The ecology of closely related species with special reference to cormorant (Ph. carbo) and shag (Ph. aristotelis). J. Anim. Ecol. 14: 12-16.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co. Ltd., 11 New Fetter Lane, London. 409 p.

Linsdale, J. M. 1936. Coloration of downy young birds and of nest linings. Condor 38: 111-117.

Linsdale, J. M. 1938. Bird life in Nevada with reference to modifications in structure and behavior. Candor 40: 173-180.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.

Martin, P. S. 1958. Pleistocene ecology and biogeography of North America. In C. L. Hubbs (ed.) Zoogeography. Amer. Assoc. Adv. Sci. Symp. 51: 375-420.

Mayr, E. 1946. History of the North American bird fauna. Wilson Bull. 58: 1-68.

Mayr, E. 1963. Animal species and evolution. Belknap Press, Cambridge, Mass. 797 p.

Meanley, B., and Webb, J. S. 1963. Nesting ecology and reproductive rate of the red-winged blackbird in tidal marshes of the upper Chesapeake Bay region. Chesapeake Sci. 4: 90-100.

Meyerriecks, A. J. 1962. Diversity typifies heron feeding. Natur. Hist. 71: 48-61.

Miller, A. H. 1956. Ecological factors that accelerate formation of races and species of terrestrial vertebrates. Evolution 10: 262-277.

Miller, R. S. 1968. Conditions of competition between redwings and yellowheaded blackbirds. J. Anim. Ecol. 37: 43-62.

Mosby, H. S. 1963. Wildlife Investigational Techniques. Edwards Brothers, Inc., Ann Arbor, Mich. 419 p.

Nero, R. W. 1950. Red-wing nesting in bird house. Auk 73: 284.

Nero, R. W. 1956. A behavior study of the red-winged blackbird. I. mating and nesting activities. Wilson Bull. 68: 5-37.

Nero, R. W. 1963. Comparative behavior of the yellow-headed blackbird, red-winged blackbird, and other Icterids. Wilson Bull. 75: 376-414.

Nickell, W. P. 1958. Variations in engineering features of the nests of several species of birds in relation to nest sites and nesting materials. Butler Univ. Bot. Stud. 13: 121-139.

Orians, G. H. 1961a. The ecology of blackbird (Agelaius) social systems. Ecol. Monogr. 31: 285-312.

Orians, G. H. 1961b. Social stimulation within blackbird colonies. Condor 63: 330-337.

Orians, G. H. 1966. Food of nestling yellow-headed blackbirds, Cariboo Park Lands, British Columbia. Condor 68: 321-337.

Orians, G. H., and Christman, G. M. 1968. A comparative study of the behavior of the red-winged, tricolored, and yellow-headed blackbirds. Univ. of Calif. Pub. in Zool. 84. 81 p.

Orians, G. H., and Willson, M. F. 1964. Interspecific territories of birds. Ecology 54: 736-745.

Rand, A. L. 1948. Glaciation, and isolating factor in speciation. Evolution 2: 314-321.

Ricklefs, R. E. 1966. The temporal component of diversity among species of birds. Evolution 20: 235-242.

Roberts, T. A. 1909. A study of a breeding colony of yellow-headed blackbirds: including an account of the destruction of the entire progeny of the colony by some unknown natural agency. Auk 26: 371-389.

Selander, R. K. 1965. Avian speciation in the Quaternary, p. 527 to 542. In H. E. Wright, and D. G. Frey, (eds.) The Quaternary of the United States. Princeton Univ. Press, Princeton, New Jersey.

Seubert, J. L. 1963. Research on methods of trapping the red-winged blackbird (Agelaius phoeniceus). Angew. Ornith. 2: 163-169.

Siglin, R. J., and Weller, M. W. 1963. Comparative nest defense behavior of 4 species of marsh birds. Condor 65: 432-437.

Smith, H. M. 1943. Size of breeding population in relation to egg laying and reproductive success in the eastern redwing. Ecology 24: 183-207.

Snelling, J. C. 1968. Overlap in feeding habits of red-winged blackbirds and common grackles nesting in cattail marsh. Auk 85: 560-585.

Stronsider, R. 1960. Polygyny and other notes on the red-winged blackbird. Wilson Bull. 72: 200.

Taylor, W. K. 1965. Nesting heights of some Louisiana birds. Wilson Bull. 77: 147-150.

Udvardy, M. F. 1958. Ecological and distributional analysis of North American birds. Condor 60: 50-66.

Verner, J. 1963. Song rates and polygamy in the long-billed marsh wren. Intern. Ornith. Congr., Proc. 13: 299-307.

Verner, J. 1964. Evolution of polygamy in the long-billed marsh wren. Evolution 18: 252-261.

Verner, J. 1965. Breeding biology of the long-billed marsh wren. Condor 67: 6-30.

Weller, M. W. 1969. Distribution of the yellow-headed blackbird in Iowa. Iowa Bird Life 39: 3-5.

Weller, M. W., and Spatcher, C. E. 1965. Role of habitat in the distribution and abundance of marsh birds. Iowa State Univ., Agric. and Home Econ. Exper. Station, Spec. Rept. No. 43. 31 p.

Welter, W. A. 1935. The natural history of the long-billed marsh wren. Wilson Bull. 47: 3-34.

Wetmore, A. 1920. Observations on the habits of birds at Lake Burford, New Mexico. Auk 37: 393-412.

Wetmore, A. 1959. Birds of the Pleistocene in North America. Smithsonian Misc. Collection 138: 1-24.

Wien, J. A. 1965. Behavioral interactions of red-winged blackbirds and common grackles on a common breeding ground. Auk 82: 356-375.

Willson, M. F. 1966. Breeding ecology in the yellow-headed blackbird. Ecol. Monogr. 36: 51-77.

Willson, M. F., and Orians, G. H. 1963. Comparative ecology of red-winged and yellow-headed blackbirds during the breeding season. Int. Zool. Congr., Proc. 16(3): 342-346.

Young, H. 1963. Age specific mortality in the eggs and nestlings of blackbirds. Auk 80: 145-155.

ACKNOWLEDGMENTS

My sincere thanks to Dr. Milton W. Weller for his liberal guidance, patience, and friendship. Loren Bates and Steve Beyers assisted with the field work and offered valuable suggestions. The Iowa State Conservation Commission provided funds and lodging during the course of the study. Tom Whitaker, Unit Game Manager, was always available for help and loaned equipment when needed. State employee, Simon Winden, and his wife were especially helpful and provided much information on the history of the study area.

Finally, special thanks is due to many students who offered criticism, advice and suggestions on the manuscript.