A comparison of blackbird reproductive success

in natural and restored Iowa wetlands

by

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GENERAL INTRODUCTION

Wetlands have long been recognized for their importance as habitat for waterfowl (Batt et al. 1989). However, their importance as habitat for other nongame species (Weller 1986) and their overall importance as a functioning ecosystem has only recently received widespread recognition. Because of this increasing concern, pressures calling for draining wetlands have slightly lessened. In response to this, a recent cooperative effort, the North American Waterfowl Management Plan, has helped reverse this trend of wetland loss. Iowa is part of the plan's Prairie Pothole Joint Venture with a goal to acquire 30,000 acres of wetland habitat in 15 years and to restore 700 acres of wetlands on private land each year (Gladfelter 1990). Iowa has made substantial progress toward this goal since 1986 (Zohrer 1996).

While the loss of wetlands and its wildlife and vegetation have been studied extensively, overall wetland function has not been considered until recently. Several studies have evaluated the success of Iowa wetland restorations by examining species richness and abundance measures of invertebrates, birds, and plants.

This paper compares natural and restored wetlands using nest-site, wetland habitat, and landscape variables to explain nesting productivity of red-winged blackbirds (Agelaius phoeniceus) and yellow-headed blackbirds (Xanthocephalus xanthocephalus).

Thesis Organization

This thesis consists of one paper intended for publication in the Journal of Wildlife Management. The daily survivorship rates and nest densities of red-winged blackbirds and yellow-headed blackbirds on natural and restored wetlands are compared. These values are then explained in relation to nest-site variables, wetland habitat variables, and surrounding landscape variables. A literature cited section for the general introduction and general summary, which follows the paper, is included after the appendices. Jeannette Schafer designed the study, conducted the field work, and is the principal author of the paper. Dr. James J. Dinsmore assisted in the studies completion through advising and obtaining funding for Jeannette Schafer, and edited this paper.

BLACKBIRD REPRODUCTIVE SUCCESS AND HABITAT RELATIONSHIPS IN RESTORED AND NATURAL WETLANDS IN NORTHWESTERN IOWA

A paper to be submitted to the Journal of Wildlife Management

Jeannette L. Schafer

Abstract: I evaluated the habitat quality of natural and restored wetlands by comparing red-winged (Agelaius phoeniceus) and yellow-headed (Xanthocephalus xanthocephalus) blackbird daily survival rates (DSR) and nest densities in 3 wetland categories. I then related these population parameters to habitat variables at 3 spatial scales: nest-site, wetland, and landscape. DSRs were not different between the three categories of wetlands, but natural wetlands had higher nest densities than wetlands restored in complexes for red-winged blackbirds. At the nest-site scale, red-winged blackbirds in 1994 were more likely to be successful if nests were built in live cattails (Typha spp.), over deeper water farther from shore, and higher in the vegetation. Yellow-headed blackbirds in 1994 were more successful in nests built over deeper water farther from shore and higher in the vegetation. In 1995, red-winged blackbirds nesting on shore were more successful in higher nests while yellow-headed blackbirds were more likely to survive in nests built lower in the vegetation. Red-winged blackbird nestling DSRs in 1995 were lower in wetlands with larger areas. In 1994, yellow-headed nestling DSRs were higher in isolated restored wetlands. Red-winged

blackbird nest densities were lower in vegetation patterns 1 and 3 (1994), isolated restored

wetlands (1995), and restored wetlands in complexes (1994 and 1995). Yellow-headed

blackbird nest densities were lower with the absence of nesting marsh wrens (1994) and

lower in isolated restored wetlands (1995). At the landscape scale, red-winged blackbird

nests were more successful when the habitat was more fragmented with a great variety of

habitats available. Yellow-headed blackbirds were more successful when habitats were more

evenly distributed between wetlands, other habitats, and agriculture. Habitat generalists (red-

winged blackbirds) and specialists (yellow-headed blackbirds) respond differently to

changing breeding habitat conditions. Managing to have a wide diversity of habitats

available is important to support the greatest variety of species possible in a given year.

Since the 1780s, more than half of the original wetlands in the United States have been

drained or altered (Dahl 1990). Recently, increasing recognition has been given to their

importance as habitat for waterfowl and nongame species (Weller 1986, Batt et al. 1989)

along with a multitude of other values (Greeson et al. 1979). As a result, political and

economic pressures calling for wetland drainage have somewhat diminished. Iowa, in which

about 90% of the original wetlands have been lost, has had some of the most extensive

drainage of any state (Bishop 1981, Dahl 1990). A recent cooperative effort, the North

American Waterfowl Management Plan, has helped reverse this. Iowa is part of the plan's Prairie Pothole Joint Venture with a goal to acquire 30,000 acres of wetlands and associated upland habitat in 15 years and to restore 700 acres of wetlands on private land each year (Gladfelter 1990). More than 5,400 acres of wetlands in 1,147 basins in Iowa have been restored since 1986 (Zohrer 1996).

This loss of wetlands and its fauna and flora has been studied extensively. Whereas most studies have emphasized the total acreage loss of wetlands, only recently has wetland function been considered equally important. As wetlands have been restored, several studies have documented recolonization patterns of invertebrates, birds, and plants on Iowa restored wetlands. Although many species recolonize restored wetlands within a few years, these studies have shown that restored wetlands are depauperate compared to natural wetlands (Wienhold and van der Valk 1989, Delphey and Dinsmore 1993, Hemesath and Dinsmore 1993, VanRees-Siewert 1993). Species richness and the abundance of some bird species (Delphey and Dinsmore 1993) and the species richness of invertebrates (VanRees-Siewert 1993) are lower in restored than in natural wetlands. In addition, wet meadow and low-prairie vegetation zones in restored wetlands have significantly fewer plant species than natural wetlands (Galatowitsch and van der Valk 1996).

Although bird, invertebrate, and plant species richness in restored wetland communities have been assessed, few workers have addressed other aspects of restored wetland function. These patchy and temporally unpredictable wetland habitats are often occupied by species that are generalists. In such habitats, a species density may be a poor measure of habitat quality (Van Horne 1983, Pulliam 1988, Pulliam and Danielson 1991). Areas with high

densities of a species may actually be "sink" habitats in which the species are not able to produce enough young to replace the population. Therefore, nesting success or other parameters might provide a better measure of habitat quality.

The goal of this study was to compare the nesting success of two marsh species, red-winged blackbird and yellow-headed blackbird, in restored and natural wetlands and to assess factors important in nest losses. The results will help planners, managers, and biologists evaluate the success of wetland restorations. Both of these species rapidly recolonize restored wetlands and are among the most abundant breeding species in those wetlands (Hemesath 1991, VanRees-Siewert 1993).

Red-winged blackbirds nest in marsh-edge habitat and are flexible in their nesting requirements (Miller 1968). Yellow-headed blackbirds are more specific in their nesting requirements, preferring large, open marshes where they build their nests in tall, robust emergents over water (Weller and Spatcher 1965). Yellow-headed blackbirds are also known to evict red-winged blackbirds from the center of marshes to outlying areas (Orians and Willson 1964, Miller 1968, Robertson 1972, Minock 1983). The breeding ecology is well-documented for both red-winged blackbirds (e.g., Orians 1961, Robertson 1972, Holm 1973, Voigts 1973) and for yellow-headed blackbirds (e.g., Willson 1966, Voigts 1973, Orians and Wittenberger 1991).

Generally, nests in marshes have greater nest success rates than those in the upland due to lower predation losses (Robertson 1972) and fewer species of egg predators (Picman and Schriml 1994). Several studies (e.g., Shipley 1979, Picman et al. 1993) have shown that predation is the most important mortality factor for marsh nesting birds. Factors influencing

these predation rates occur at spatial scales of the immediate nest-site, the entire wetland, and in relation to the surrounding landscape. Because interpreting habitat selection is scale-dependent, care must be taken to perform analyses at each of these levels to detect important factors influencing these species (Wiens and Rotenberry 1981, Orians and Wittenberger 1991). To date, I am unaware of any other study that considers all three levels in their analysis of nest success of any species.

The current dogma is that increased edge negatively affects various bird species by increasing depredation or parasitism rates of nests located near habitat edge (Paton 1994). Predators may increase their activity along habitat edges because of higher prey densities, using edges as traveling lanes, foraging opportunistically as they search for other prey, or by limited foraging into an adjoining yet less-preferred habitat (Andrén 1995). These ideas have been most intensively studied in forest habitats, and limited information is available for grassland and prairie ecosystems (Paton 1994, Andrén 1995). Yet, it appears that mammalian predators in prairie habitats prefer to travel along the edges of dense nesting cover (Pasitschnjak-Arts and Messier 1995). In less dense nesting cover, the size of the habitat patch is more influential in reducing nest losses to predation (Burger et al. 1994, Pasitschnjak-Arts and Messier 1995). One of the major mammalian predators, the raccoon (Procyon lotor), tends to follow the marsh edge when hunting for food (W. R. Clark, 1994, pers. commun.) and is the major predator when the water depth is less than 40 cm (Picman et al. 1993). Other potential major predators of blackbird nests in marshes include mink (Mustela vison), striped skunk (Mephitis mephitis), weasels (Mustela spp.), American crow

(Corvus brachyrhynchos), northern harrier (Circus cyaneus), garter snakes (Thamnophis sp.), and small mammals (Picman et al. 1993, Picman and Schriml 1994).

At the nest-site scale, the difference in predation rates may occur because predators have difficulty effectively searching the deep-marsh habitat (Robertson 1972, Picman et al. 1993, Picman and Schriml 1994). In marshes, Picman et al. (1993) showed that the diversity of nest predators decreased with increasing water depth with the marsh wren (Cistothorus palustris) as the only major predator in deep-marsh areas (i.e., water depth >40 cm). Nest predation rates also decreased with increasing water depth when marsh wrens were not present.

Very little has been done to directly analyze nest success predictors at the wetland scale. We do know that red-winged and yellow-headed blackbird densities decrease with decreasing percent emergent vegetation cover (VanRees-Siewert 1993, Linz et al. 1996). These blackbird species also react to vegetation patterns with greater red-winged blackbird densities in wetlands with emergent vegetation around the edges and lower in wetlands with very sparse emergent vegetation (VanRees-Siewert 1993). On the other hand, yellow-headed blackbird densities are greater in wetlands with emergent vegetation in the center of the wetland and in wetlands with sparse emergent vegetation (VanRees-Siewert 1993). Linz et al. (1996) also found that red-winged blackbird densities decreased with increasing water coverage. Weller and Spatcher (1965) found that nest densities of red-winged and yellow-headed blackbirds were greatest when there was a 50:50 ratio of emergent vegetation cover to water cover. Orians and Wittenberger (1991) found that female yellow-headed blackbirds selected nest sites with moderate vegetation density and extensive channeling in the

vegetation which coincides with Weller and Spatcher's 1965 findings. I proposed that the number of muskrat houses in a wetland would provide a measure of the amount of channeling by muskrats within a marsh.

Other ecological considerations at the wetland scale are the effect of avian competitors. Red-winged blackbirds are very aggressive toward nesting common grackles (Quiscalus quiscula) within the same marsh although they occupy separate territories (Wiens 1965). Meanley and Webb (1963) proposed that common grackles were preying on red-winged blackbird nests. Although Wiens (1965) saw no evidence of predation by common grackles, he proposed that breeding red-winged blackbirds may neglect their nest or young because of excessive aggression toward grackles. Snelling (1968) suggested that these two species are antagonistic because they are competing for space within the marsh. With any of these proposals, it is clear that red-winged blackbirds respond aggressively toward common grackles and see them as a threat. In relation to this, I hypothesized that red-winged blackbird nest success would be reduced in wetlands that also contained common grackles. With yellow-headed blackbirds, Picman and Isabelle (1995) have shown that marsh wrens were the most important predators of yellow-headed blackbird nests and that this predation was the most important source of mortality. Yellow-headed blackbirds and marsh wrens often nest in the same marsh but are spatially segregated. They also found that yellow-headed blackbirds were more likely to be successful the farther a nest was toward the center from the colony edge and the farther it was from a marsh wren nest.

Wetland scale factors of the wetland site may also play a role in predation by other species. Smaller wetlands are more likely to be completely searched and to have higher

predation rates (Burger et al. 1994, Pasitschnjak-Arts and Messier 1995). Presently, most

public wetland restorations in Iowa are grouped in complexes to best use the land and to

replicate the pattern of natural marshes in the area. In contrast, most private restorations

restore only 1 or 2 wetlands which makes them relatively isolated. A wetland within a

complex may be more difficult to search because of the increased complexity of vegetation

structure and density (see Duebbert and Lokemoen 1976, Ratti and Reese 1988, Burger et al.

1994). Bowman and Harris (1980) found that increasing spatial heterogeneity within a

habitat reduces the foraging efficiency of raccoons on ground nests. As stated above, we

know that restored wetlands have less diversity of vegetation than natural wetlands

(Galatowitsch and van der Valk 1996). In addition, abrupt edges of habitat can act as travel

lanes for raccoons (W. R. Clark, 1996, pers. commun.) and predation rates are often greater

along abrupt edges and in linear habitats (Haensly et al. 1987, Ratti and Reese 1988).

Restored wetlands have abrupt edges between their emergent vegetation zone and upland

grass cover that may serve as travel lanes for raccoons. Thus, I expected predation by

mammalian predators would be greater in restored than in natural wetlands.

On the landscape scale, many of the same arguments can be made. First, the ecology of

the predator community can have a great effect. Many predators in the Prairie Pothole region

are widespread generalists, and it appears that habitat fragmentation has not influenced their

populations except, in some cases, to increase population levels (Johnson et al. 1989,

Sargeant et al. 1993). For example, in forested areas of Sweden, those areas with increased

agricultural farmland had greater densities of crows that were habitat generalists (Andrén

1992). This is because these predators are not limited to specific patches since crop fields do

not present habitat barriers and do not fragment the population (Dobrowolski et al. 1993). In reality, intermediate-sized predators have large home ranges and readily cross barriers to forage in many patches even though they use other patches for resting (Fritzell 1978, Judson et al. 1994). This ability to move varies by species and their preferences in ways to move also vary. For example, raccoons use roads, fence rows, and single-row tree belts as travel lanes at night (Fritzell 1978). This tendency to use abrupt edges as traveling lanes was also noticed in a raccoon study in central Iowa (W. R. Clark, 1996, pers. commun.). There is some evidence that predation rates of ground nesting birds is greater in areas close to habitats frequented by mammals. For example, Burger et al. (1994) found increased predation rates in prairies that were closer to woody cover and predation rates were greater along abrupt edges and in linear habitats (Haensly et al. 1987, Ratti and Reese 1988). Fritzell (1978) found that raccoons use wetlands, building sites, and wooded areas extensively in the landscape and building site use decreased with increased use of wetlands. Yet prey species often are limited to one specific habitat patch. This is especially true for yellow-headed blackbirds that rely on large, deep marshes for nesting habitat. On the other hand, although red-winged blackbirds prefer marsh habitat for nesting (Albers 1978), it is a true generalist with floaters ranging widely to claim territories (Shutler and Weatherhead 1994).

In addition, numerical and functional behavioral responses to predator-prey interactions must be considered. In numerical responses, predator populations increase when there is an increase in prey populations (Holling 1959). This may be due to the immigration of predators into the area or to greater reproduction. These predators may concentrate their foraging in areas with high prey densities (e.g., Fleskes and Klaas 1991).

Functional responses are based on changes in the feeding rate with prey density. The rate of feeding can be reduced by having more hiding places for prey, fewer predators due to territoriality, and reduced number of breeding sites for predators. Alternative prey can also reduce the pressure on preferred prey when their densities are low. Having more wetlands with more water or a greater variety of habitats may reduce the foraging efficiency of predators (Bowman and Harris 1980, Johnson et al. 1989). Smaller areas can also be completely searched more easily and are more susceptible to predation (see Burger et al. 1994) although this has not been documented adequately for wetland/grassland/agriculture systems (Paton 1994). Fleskes and Klaas (1991) proposed that greater densities of red fox (Vulpes vulpes) in a national wildlife area in central Iowa was due to the greater availability of den sites. It is also known that as prey become more dense, predators switch to increasingly abundant prey types (Holling 1959). Wetland areas with water and more dense vegetation may have more available buffer prey which simultaneously attracts more predators and reduces predation pressure on specific species (Johnson et al. 1989).

With these scales in mind, I evaluated the habitat quality of natural and restored wetlands by investigating the nesting success of blackbirds in natural and restored wetlands. The objectives of this study were to (1) compare the daily survival rates and nest density of red-winged blackbird and yellow-headed blackbirds in natural wetlands in complexes, restored wetlands in complexes, and in isolated restored wetlands; and (2) compare the nest success patterns of red-winged blackbirds and yellow-headed blackbird nests in these three wetland types at the nest-site scale, the wetland habitat scale, and at the landscape scale.

Prior to this study, I predicted that daily survival rates and nest densities of blackbirds would be lower in isolated restored wetlands. In addition, I predicted at the nest-site scale that blackbird nests, in cattail or other robust emergent vegetation, over deep water, or far from shore would have greater nest success. On the wetland scale, I predicted that DSRs would be greater for red-winged blackbirds when grackles were absent and in natural wetlands that have gradual habitat edges and increased vegetation diversity. I predicted yellow-headed blackbirds would be more successful when marsh wrens were not present or nesting on the same wetland and where there were more muskrat houses present. I predicted that wetlands with greater emergent vegetation cover would have greater nest densities for both blackbird species. I also predicted that red-winged blackbird nest densities would be greater in wetlands with vegetation pattern 2, greater amounts of edge, and fewer yellow-headed blackbird nests and that there would be greater yellow-headed blackbird nest densities in wetlands with vegetation patterns 3 and 4 and greater total area. At the landscape scale, I hypothesized that areas with more wetland habitat nearby, a variety of habitats available, few linear traveling lanes, and little human presence would have the greatest nest success rates.

STUDY AREAS

Fifteen cattail-dominated prairie pothole wetlands in Clay, Dickinson, Emmet, and Palo Alto counties in northwestern Iowa were selected in 1994. Wetlands were categorized as follows: 5 natural wetlands in wetland complexes, 5 restored wetlands in wetland complexes, and 5 isolated restored wetlands. Two wetlands were substituted in 1995 for 2 wetlands with no nesting red-winged or yellow-headed blackbirds in 1994. All wetlands

were between 1 and 3 ha and, when selected, had about a 50:50 ratio of emergent vegetation to water (i.e., hemi-marsh conditions), the stage which usually supports the maximum number and diversity of birds (Weller and Spatcher 1965). Restored wetlands met 3 additional criteria: 3 to 6 years since restoration, basin completely drained using a tile system before restoration, and previously row cropped. All restored wetlands were surrounded by a matrix of planted brome grass (Bromus inermis) or switchgrass (Panicum virgatum). Natural wetlands retained some of their original vegetation which included several grasses along with the introduced bluegrass (Poa pratensis); various tree, shrub, and sedge species; and assorted herbs (see Galatowitsch and van der Valk 1996).

METHODS

Landscape Features

Surrounding landscape features of each wetland were determined during the 1995 field season. All wetlands within a 1-mile radius around each study wetland were drawn onto section maps using 1994 Natural Resource Conservation Service (NRCS) crop compliance slides. These were later computer digitized, and the area was measured. These wetland areas surrounding each wetland site were used to assign restored wetlands to isolated ($\leq$27 ha or <13 wetlands) or complex (>27 ha or >13 wetlands) categories.

Perimeter (km) and area (ha) of each wetland was measured using these same methods. Edge/area indices (Patton 1975) were also calculated from these to express shoreline irregularity. This index is the perimeter/$\{2 \ (area*\pi)^{1/2}\}$. As the shoreline deviates from a circle (edge/area index = 1.0), the index value increases.

Reproductive Success

Field work was done from 19 May to 7 July 1994 and 16 May to 14 July 1995. I searched wetlands every 5 (1995) to 8 (1994) days for red-winged and yellow-headed blackbird nests. All emergent vegetation from the edge of the emergent/open water zone to 3 m of upland was carefully searched in a systematic zig-zag pattern. Searches for new nests were done from 19 May to 27 June 1994 and 16 May to 24 June 1995. I marked nests with flagging tape 1 m from the nest, tied a numbered tag to the vegetation directly beneath the nest, and plotted the position of each nest on a map. Care was taken to conceal the tag. Each nest was revisited every 5 to 8 days until it failed or young fledged. The number of eggs or nestlings present were recorded on every visit. The condition of the nest, nest contents, and nest surroundings were noted to determine nest fate.

Nest failures were assigned to avian, small mammal, or mink; large mammal; marsh wren; muskrat (Ondatra zibethicus) activities; weather; desertion (including those due to brown-headed cowbird (Molothrus ater) parasitism); or unknown based on field observations, knowledge of potential nest predators, and previous studies (Rearden 1951, Picman 1977, Best 1978, Shipley 1979, Best and Stauffer 1980, Knight et al. 1985, Picman et al. 1988, Picman et al. 1993, Sargeant et al. 1993). The daily nest survival rates (DSR) for incubation and nestling periods were calculated using the Mayfield (1975) method. If the date that a nest failed was not known, failure was assumed to have occurred halfway between the last 2 visits. Red-winged blackbirds were assumed to have incubation and nestling periods of 11 days each (Allen 1914, Besser et al. 1987). Yellow-headed blackbirds were assumed to have an incubation period of 12 days and a nestling period of 11 days (Ammann 1938, Willson

1966). Both species were assumed to have full clutches of 4 eggs unless other evidence was available.

Since 13 of 15 wetlands were used in both 1994 and 1995, each year was analyzed separately using one-way analyses of variance for unbalanced sample sizes. The incubation and nestling DSRs of the 3 wetland categories for both species were compared. To increase sample size, DSRs were also compared for all restored wetlands and natural wetlands. Overall nest survival rates were calculated for each species using the DSR and the nesting intervals given above. For this and all other analyses, unless indicated otherwise, statistical significance was set at the 0.05 probability level.

Nest-Site Variables

For each nest, I measured the distance from shore (nearest 0.5 m), distance to nearest open water (nearest 0.5 m), nest rim height from the water surface (cm) and water depth below the nest (cm) when the nest was first located. I used principal components analysis on the correlation matrix to obtain uncorrelated variables for these 4 continuous variables. Only eigenvectors explaining more than 1 variable (i.e., eigenvalue >1.5) were chosen, since the proportion of variance explained did not meet the broken stick method of selection, to keep from overestimating the number of dimensions (Jackson 1993). This eigenvector was then substituted for the associated variables.

I also noted the principal nest-supporting vegetation species and the vegetation zone (see Stewart and Kantrud 1971) in which it was located. Vegetation zones were coded as emergent or other. For principal supporting vegetation species, only cattail was separated

into dead and live categories because of its prevalent use. Vegetation species which supported fewer than 10% of the nests for either blackbird species in either year were combined into an "other" vegetation category. Individual vegetation zones and vegetation species were coded as dummy variables (Zar 1984, pp. 346) for all analyses and were kept separate except in the above noted exceptions because of small sample sizes.

Using the individual nest as the observational unit, I used forward stepwise logistic regression analysis to test which nest-site variables were most useful in explaining the probability of nest success. Four models were fitted, 1 for each species and year. Dead cattail and the emergent zone were coded as the common situation, and its importance is then reflected in the intercept value of the model. Water depth below the nest and distance from shore (PC1), nest rim height from the water surface, distance to nearest open water, and categories for vegetation zones and vegetation species were entered into the analysis. Variables to be included in a final model were chosen based on the Wald Chi-square test with values of $P \leq 0.15$. The probability level was set high to insure all variables that may be important were included in the model-building process (Hosmer and Lemeshow 1989, pp. 86). I then used the likelihood ratio test, which compares the full model and a reduced model following a Chi-square distribution with 1 degree of freedom, to choose the best model of main effects. Changes in gamma, concordance, coefficients of independent variables, and standard errors of those coefficients were also examined between the reduced and final model (Hosmer and Lemeshow 1989). Higher values of gamma and concordance indicate a better-fitting model and, at the same time, changes in magnitude of the coefficients and/or the

standard errors of these coefficients can indicate problems with the model structure and

multicollinearity of the independent variables (Hosmer and Lemeshow 1989, pp. 131)

Vegetation Survey

The vegetation of each wetland basin was mapped from 3 to 10 July 1994 and 2 to 6

July 1995 using a modification of the relevé method (Mueller-Dombois and Ellenberg 1974,

Galatowitsch and van der Valk 1996). A list of plant species covering more than 10% of any

zone (i.e., dominant species) was developed for each site based on observations from site

visits. All plant species covering less than 10% of a zone were combined into their plant life-

form class. These included low trees and shrubs, weak emergents, robust emergents,

floating-leaved mats, and submergents and algae (Weller and Spatcher 1965, Kantrud et al.

1989). Robust emergents were defined as species used by blackbirds for nest supports in

1994. All other emergent species were classified as weak-stemmed. Cover of dominant

species and plant life-form classes were visually estimated for each of the following zones:

wet prairie, mudflat, sedge meadow, emergent zone, open water, and upland buffer zone

(Kantrud et al. 1989) and for the entire wetland. A 7 point cover scale (Mueller-Dombois

and Ellenberg 1974) was used: (r) solitary with insignificant cover, (+) few individuals with

insignificant cover, (1) 1-5%, (2) 6-25%, (3) 26-50%, (4) 51-75%, (5) >75%. Dispersion

classes for dominant species were also visually estimated as follows: large pure population

stands, small colonies, small patches, clumps, and solitary.

A detailed cover map was drawn for each basin, and the total percent emergent cover of

the entire basin was estimated for weak emergents, robust emergents, total emergents, and for

shrubs/trees. Voucher specimens are deposited in Ada Hayden Herbarium at Iowa State University (Ames, Iowa).

Wetlands were also classified by their emergent-vegetation-to-open-water cover pattern. Pattern 1 consists of open water covering >95% of the basin or a marginal band of vegetation <2 m in width. Pattern 2 has central areas of open water surrounded by a vegetation band >2 m in width around the periphery. Pattern 3 has central areas of dense vegetation surrounded by a peripheral band of open water (Stewart and Kantrud 1971).

Wetland Habitat Variables

Nest density (total nests/total wetland area (ha)) was calculated for red-winged blackbirds and for yellow-headed blackbirds in 1994 and 1995. I then compared nest density of natural wetlands, restored wetlands in complexes, and isolated restored wetlands for each year and species separately using the Kruskal-Wallis test, which is more sensitive for means with skewed distributions (Zar 1984). When I rejected the null hypothesis of no difference, a nonparametric Tukey-type multiple comparison test using rank sums from the Kruskal-Wallis test was used to find where significant differences between wetland category pairs occurred (Zar 1984, pp. 199).

Stepwise-multiple linear regression was used to compare wetland-scale independent variables that may affect daily survival rates (DSR) and nest densities of blackbirds. Pearson correlation coefficients and multicollinearity tests were used first to insure independence of the variables (see SAS Institute, Inc. 1988, Scheiner and Gurevitch 1993). Dummy variables were used for all categorical variables. A significance level of $P \leq 0.15$ was used to select

individual variables for the model, and a significance level of $\underline{P} \leq 0.05$ was used for selection of a final model. A higher level of significance was set to initially include variables in the model to reduce the chances of a Type II error, where variables that are important are not included. A reduced level of significance was set for the final model to reduce the chances of a Type I error, where models that are not important are included (Bendel and Afifi 1977).

When a significant model of factors related to DSRs or nest density was obtained, wetland type (i.e., natural, restored in complexes, isolated restored) was added as an independent variable to the significant variables list and a stepwise-multiple regression was run again. The same criteria were used as above. If a wetland type was added to the model variables, this denotes that there are values about the wetland type that are important to nests other than that explained by the original list of independent variables. If a wetland type replaced other significant variables, it was a better predictor of variance of the DSRs and nest densities than the original variables. Natural wetlands were coded as the baseline situation, and its influence is reflected in the value of the intercept.

DSR Models.--Tests for multicollinearity showed no significant problems with collinearity (values<30) so no corrective measures were needed (see Scheiner and Gurevitch 1993, pp. 189). I used total area of the wetland (ha), edge/area index, number of muskrat houses present, absence of grackles, and vegetation pattern 3 as independent variables and DSRs of incubation and nestling stages for red-winged and yellow-headed blackbirds as dependent variables in 1994. In 1995, I used total area of the wetland (ha), edge/area index, number of muskrat houses present, absence of marsh wrens, absence of nesting marsh wrens, and combined vegetation patterns 1 and 3 as independent variables and DSRs of incubation

and nestling stages for red-winged and yellow-headed blackbirds as dependent variables. Some vegetation patterns, marsh wren variables in 1994, and grackle variables in 1995 were not used or combined because of small sample sizes for these variables.

Nest Density Models.--Tests for multicollinearity showed problems with collinearity (values>30) so principal components analysis using a correlation matrix was used to obtain independent variables from the 4 continuous variables in each year and species. For red-winged blackbirds, percent cover of robust vegetation and trees/shrubs, percent cover of emergent vegetation and trees/shrubs, wetland perimeter (km), and natural log-transformed density of yellow-headed blackbird nests were entered into the analysis. For yellow-headed blackbirds, percent cover of robust vegetation, percent cover of emergent vegetation, wetland perimeter (km), and natural log-transformed density of red-winged blackbird nests were entered into the analysis. Eigenvectors explaining more variance than predicted by the broken stick model were selected (Jackson 1993) and substituted for the associated variables. Factor analysis using principal components as the initial factor method and varimax as the rotation method was used to simplify interpretation of eigenvectors although principal component values were used in the model (Manly 1994).

For red-winged blackbirds, I used percent cover of robust vegetation and trees/shrubs and emergent vegetation and trees/shrubs (PC1), wetland perimeter (km), natural log-transformed density of yellow-headed blackbird nests, absence of nesting marsh wrens, absence of grackles, and combined vegetation patterns 1 and 3 as independent variables and natural log-transformed density of red-winged blackbird nests in 1994 and 1995 as the dependent variables. I used percent cover of robust vegetation and emergent vegetation,

wetland perimeter (km), and natural log-transformed density of red-winged blackbird nests,

absence of nesting marsh wrens, absence of grackles, and combined vegetation patterns 1 and

3 as independent variables and natural log-transformed density of yellow-headed blackbird

nests as the dependent variable in 1994 and 1995. Vegetation pattern 2 was coded as the

baseline situation.

Landscape Variables

Five landscape variables were measured to estimate landscape heterogeneity: total area

(ha) of wetlands within 1 mile (wetland habitat area), straight line distance from the study

wetland edge to the nearest wetland edge (distance to wetland edge), straight line distance

from the study site wetland edge to the nearest habitat different from the surrounding wetland

matrix (distance to habitat edge)(e.g., road), number of continuous fences (segments limited

to 1 mile) within 1 mile of the study wetland (number of fences), and the number of roads

(segments limited to 1 mile) within 1 mile of the study wetland (number of roads). Patch

diversity was also calculated using Simpson's Diversity Index and the number of habitat

patches within 1 mile (McGarigal and Marks 1994). A habitat patch was defined as an area

of habitat surrounded on all sides by a different habitat or corridor. Habitat patch categories

were wetland/grass, buildings, cropland, grass, pasture, Conservation Reserve Program

(CRP), wooded, and lake. A 1 mile radius was used because it encompasses the largest

territory size of any predator expected within this study area.

Stepwise-multiple linear regression was used to compare the landscape-scale

independent variables that may affect nest success of red-winged and yellow-headed

blackbirds in 1994 and 1995. Pearson correlation coefficients and multicollinearity tests

were used to insure principal component analysis reduced collinearity problems in the

models. Principal component analysis was used to combine wetland habitat area, distance to

wetland edge, distance to habitat edge, number of fences, number of roads, and patch

diversity. Eigenvectors explaining more variance than predicted by the broken stick model

were selected (Jackson 1993). Factor analysis using principal components as the initial factor

method and varimax as the rotation method was used to simplify interpretation of the

eigenvectors although the original principal component values were used in the model. In the

multiple linear regression, I used the estimate of incubation DSRs for nest success in

wetlands which had no estimate of nestling DSRs for that species and year. Wetlands

without nest success estimates for the year and species in question were excluded from the

analysis. Significance levels of $P \leq 0.15$ were used to select individual variables, and a

significance level of $P \leq 0.05$ was used for the final model selection (Bendel and Afifi 1977).

Univariate regressions were run with wetland habitat area and patch diversity to

compare their relationships with nest success in each year and for each species. This was

done since the primary variables of interest were the effect of wetland habitat area and patch

diversity on nest success of red-winged blackbirds and yellow-headed blackbirds.

RESULTS

Reproductive Success

DSRs during incubation and the nestling period were the same in all three wetland

types for both species in 1994 and 1995 (Table 1). When DSRs on all restored wetlands were

compared with natural wetlands, only red-winged blackbirds in the incubation period were found to be lower in restored wetlands than in natural wetlands (Table 2).

The estimated overall nest success rates for red-winged blackbirds were 13.9% (SE = 3.9) in 1994 and 21.1% (SE = 3.2) in 1995. Overall yellow-headed blackbird nest success rates were 25.1% (SE = 5.7) in 1994 and 29.1% (SE = 9.3) in 1995.

Nest-Site Variables

Based upon the principal components analysis, I selected 1 principal component for each species in 1994 and 1995 for use in my logistic regression analysis (Table 3). I interpreted this PC in all cases to be a combination of distance from shore and water depth under the nest (i.e., physical position within the wetland). Red-winged blackbirds nested primarily in the emergent zone (1994, n = 87; 1995, n = 160) while a few nests were found in other zones (1994, n = 3; 1995, n = 21). All yellow-headed blackbirds nested in the emergent zone in 1994 (n = 207) and 1995 (n = 180). Red-winged blackbirds nested in several vegetation species including dead cattail (1994, n = 41; 1995, n = 80), live cattail (1994, n = 10; 1995, n = 10), Scirpus fluviatilis (1994, n = 11; 1995, n = 13), Phalaris arundinacea (1994, n = 14; 1995, n = 25), Carex atherodes (1995, n = 17), and other vegetation species (1994, n = 14; 1995, n = 36). Yellow-headed blackbirds nested in dead cattail (1994, n = 100; 1995, n = 140), live cattail (1994, n = 100; 1995, n = 36), and other vegetation species (1994, n = 7; 1995, n = 4).

In logistic regression models for red-winged blackbirds in 1994, water depth and distance from shore (PC1), live cattail, and S. fluviatilis were selected in the equation (χ^2 =

24.46, 3 df, $\underline{P}$ = 0.0001);(Table 4). A nest was more likely to survive if it was built in live

cattail, $\underline{S}$. fluviatilis, and in deep water far from shore. In 1995 for red-winged blackbirds, $\underline{S}$.

fluviatilis was removed from the analysis since all nests built in this species failed ($\underline{n}$ = 13).

In the resulting logistic regression model, height of the nest above water was the only

variable entered (χ^2 = 5.763, 1 df, $\underline{P}$ = 0.0164);(Table 4). In other words, a nest was more

likely to survive if it was built higher in the vegetation. For yellow-headed blackbirds in

1994, the fitted model predicting nest success included water depth and distance from shore

(PC1) and height of the nest above water (χ^2 = 20.813, 2 df, $\underline{P}$ = 0.0001);(Table 4). If a nest

was built in deep water far from shore and high in the vegetation, the more likely it would

survive until fledging. In 1995, only the variable nest height above water was significant in

explaining the probability of nest success (χ^2 = 9.186, 1 df, $\underline{P}$ = 0.0024);(Table 4). Nests

built lower in the vegetation were more likely to succeed.

Vegetation

Total emergent cover dropped from an average of 56% in 1994 to 42% in 1995 with

fewer wetlands having dense stands of vegetation (Table 5). Other vegetation measurements

were not considered further in this paper.

Wetland Habitat Variables

Red-winged blackbird nest densities were lower in restored wetlands in complexes than

in natural wetlands in both years (Table 6). In 1995, restored wetlands in complexes had

marginally lower nest densities for yellow-headed blackbirds than in natural wetlands. There

was a large, but insignificant, drop in the nest densities of yellow-headed blackbirds from 1994 to 1995 in isolated restored wetlands (Mann-Whitney test, U = 0.98, $\underline{P}$ = 0.33);(Zar 1984, pp. 139);(Table 6).

DSR Models.--The edge/area index was calculated but not included in the models because of its low variability (range 1.03 to 1.62). For red-winged blackbirds, stepwise-multiple regression showed that total wetland area (ha) was the best predictor of lower nestling period DSRs in 1995 ($\underline{F}$ = 10.33, 1 df, $\underline{P}$ = 0.01);(Table 7). For yellow-headed blackbirds, the number of muskrat houses was the best predictor of higher nestling period DSRs in 1994 ($\underline{F}$ = 3.50, 1 df, $\underline{P}$ = 0.10);(Table 7). All other periods showed no significant relationships with the independent variables.

When wetland types were added to these models, the red-winged blackbird model in 1995 remained unchanged with wetland area as the best predictor of nestling period DSR (Table 7). For yellow-headed blackbird nestlings in 1994, isolated restored wetlands were chosen as the best predictor of higher DSRs ($\underline{F}$ = 4.07, 1 df, $\underline{P}$ = 0.08);(Table 7). Pearson correlation coefficients showed no significant correlation between number of muskrat houses and isolated restored wetlands for yellow-headed blackbird nestlings in 1994 ($\underline{n}$ = 9, $\underline{r}$ = 0.38, $\underline{P}$ = 0.31).

Nest Density Models.--I identified 1 factor/principal component for each year and species that consistently combined robust vegetation and tree/shrub cover and total emergent vegetation and tree/shrub cover for red-winged blackbirds and robust vegetation cover and total emergent vegetation cover for yellow-headed blackbirds (Table 8). Stepwise-multiple regression showed that the presence of vegetation patterns 1 and 3 explained the most

variance in lower nest densities of red-winged blackbirds in 1994 ($F = 6.10$, 1 df, $P = 0.03$);(Table 7). In 1995 for red-winged blackbirds, greater length of the wetland perimeter and the absence of nesting marsh wrens were the best predictors of lower nest densities ($F = 6.83$, 2 df, $P = 0.01$);(Table 7). Stepwise regression models showed the absence of nesting marsh wrens was the best predictor of lower nest densities for yellow-headed blackbirds in 1994 ($F = 6.87$, 1 df, $P = 0.02$);(Table 7). In 1995, the absence of grackles was a reliable predictor of greater yellow-headed blackbird nest densities ($F = 3.67$, 1 df, $P = 0.08$);(Table 7).

When wetland type was added to these models for nest densities, 3 out of 4 models changed. Stepwise-multiple regression added presence of restored wetlands in complexes to presence of vegetation patterns 1 and 3 as significant predictors of lower nest densities of red-winged blackbirds ($F = 8.85$, 2 df, $P = 0.004$);(Table 7). In 1995 for nest densities of red-winged blackbirds, presence of restored wetlands in complexes and isolated restored wetlands were the best predictors of lower nest densities ($F = 11.35$, 2 df, $P = 0.002$);(Table 7). The multiple regression model for nest densities of yellow-headed blackbirds in 1994 remained unchanged with the absence of nesting marsh wrens as the best predictor of lower nest densities. For yellow-headed blackbird nest densities in 1995, the presence of isolated restored wetlands was chosen as the best predictor of lower nest densities ($F = 6.47$, 1 df, $P = 0.02$);(Table 7).

Landscape Variables

Two principal components/factors for each year and species were selected. The first

principal component/factor was interpreted as the amount of wetland area within a mile

(Table 9). This is because the amount of wetland area and distance to the nearest different

habitat edge increase while the number of fences and roads decrease (negative relationship)

which denotes more concentrated wetland area near the study wetland. Principal

component/factor 2 is an index of habitat heterogeneity (Table 9). This can be interpreted as

habitat heterogeneity because as the distance to the nearest wetland edge and number of roads

decrease, the index of habitat patch diversity increases so there are many different habitats

present with few connecting roads. The two principal components/factors were the same for

each species both years.

Stepwise-multiple regression for red-winged blackbirds in 1994 included greater habitat

heterogeneity (PC2) as the best predictor of greater nest success (F = 9.48, 1 df, P =

0.01);(Table 10). When wetland type was added for red-winged blackbirds in 1994, greater

habitat heterogeneity (PC2) and fewer restored wetlands in complexes were related to greater

nest success (F = 8.34, 2 df, P = 0.01);(Table 10). All other species and years showed no

significant relationships to the independent variables.

In univariate linear regressions, red-winged blackbird nest success rates in 1994

increased with greater patch diversity (F = 10.04, 1 df, P = 0.01) but were unrelated to

wetland habitat area (Table 10). In 1995, red-winged blackbirds nest success rates decreased

with greater amounts of wetland habitat area (F = 3.258, 1 df, P = 0.10) but were not related

to patch diversity (Table 10). Yellow-headed blackbirds nest success was greater in 1994

when patch diversity was greater ($\underline{F}$ = 3.59, 1 df, $\underline{P}$ = 0.09) but was not related to wetland

habitat area (Table 10). Nest success of yellow-headed blackbirds in 1995 was not related to

patch diversity or wetland habitat area (Table 10).

DISCUSSION

Reproductive Success

The DSRs for both species in both years were statistically the same on restored and

natural wetlands. There are slightly greater variances in DSRs for red-winged blackbirds and

the incubation stage of yellow-headed blackbirds in restored wetlands than natural wetlands.

I propose that this variance is an inherent part of the system because red-winged blackbird

nests on some restored wetlands failed early in the incubation or building stage with few

nests fledging young. Red-winged blackbirds nested along restored wetland edges as a result

of competition for nesting sites with yellow-headed blackbirds (Miller 1988) and were

probably more vulnerable to predation. This relationship is shown with the only difference in

DSRs between restored and natural wetlands showing up in the incubation stage for red-

winged blackbirds in 1994 (Table 2). Real differences may not have shown up statistically

because sample sizes are small, especially on restored wetlands. Natural wetlands had DSR

estimates for 5 and 5 sites (incubation, 1994 and 1995) and 5 and 5 sites (nestling, 1994 and

1995) for red-winged blackbirds. For yellow-headed blackbirds, the number of sites was 5

and 4 for incubation, and 4 and 4 for the nestling period. Restored wetlands had DSR

estimates for 6 and 9 sites (incubation, 1994 and 1995) and 2 and 6 sites (nestling period,

1994 and 1995) for red-winged blackbirds. For yellow-headed blackbirds, the number of

sites was 7 and 7 for incubation, and 5 and 5 for nestlings. Longer studies with increased effort are needed to adequately sample enough wetland sites to provide greater statistical power. With nesting success studies, much effort is used to sample many nests in few wetlands even though each wetland eventually has one estimate for statistical purposes.

The nest survival rates found in this study (13.9 - 29.1%) are comparable to other data found in the literature. Other studies in Iowa have cited apparent nest success values of 30% in marshes and 4% in uplands (Krapu 1978) while more recent studies using Mayfield methods estimate an overall nest success of 8% in grassed waterways (Bryan and Best 1994), 15% in Iowa CRP fields (Patterson and Best 1996), and 26% in Iowa roadsides (Camp and Best 1994). I expected yellow-headed blackbird nest success rates to approximate or exceed those of marsh-nesting red-winged blackbirds because yellow-heads typically select nest-sites over deeper water in the center of wetlands where nests tend to be more successful.

In 1994, habitat conditions were more favorable for yellow-headed blackbirds. Wetlands had denser stands of cattails available for nesting territories over the deep water areas they prefer (Weller and Spatcher 1965). In 1995, vegetation was reduced in density or completely gone in restored wetlands, conditions in which yellow-headed blackbirds do not nest because they are not able to form large nesting colonies which they prefer (Weller and Spatcher 1965). Therefore, red-winged blackbirds were able to nest in the remaining vegetation over deeper water and had greater nest success rates. Yellow-headed blackbirds still had a very good year in 1995 overall even without these additional wetland habitats. A closer look at related habitat variables may help further explain these differences.

Nest-Site Variables

Although some authors have shown that water depth under the nest is more important than distance from the marsh edge in reducing predation (e.g., Picman et al. 1993), in field studies these variables are generally linked. As expected, for both red-winged blackbirds and yellow-headed blackbirds in 1994, nesting in deeper water and farther from shore was advantageous to their nest success (Table 4). These variables were correlated with nesting in live cattails for red-winged blackbirds and with building nests higher above water for yellow-headed blackbirds. I did not expect cattail to show up as significant in predicting nest success for yellow-headed blackbirds since nearly all of their nests were in cattail. On the other hand, red-winged blackbirds nest in a great variety of vegetation substrates.

In 1995, nest height affected the 2 species in different ways. Red-winged blackbirds were more successful in higher nests because they were nesting in remnant cattail stands or other vegetation along the shore. This protected them from both terrestrial predators and provided protection from the wind. In contrast, yellow-headed blackbirds were more successful in nests built close to the water. With less vegetation density in the center of wetlands with deeper water, nests placed high in the vegetation had little protection from windstorms and were easily toppled.

Numerous studies of red-winged blackbird nest success and variables affecting it have shown that water depth under the nest and life-form of the vegetation the nest is built in are consistently associated with greater nest success (e.g., Francis 1971, Holm 1973, Krapu 1978). Other variables (e.g., nest height, vegetation species) change in their importance depending on water and vegetation conditions, locality, and weather patterns. In the prairie

pothole region, they also change between species and years. Further analysis using only

nests that were depredated would be more useful in analyzing factors that influence predation

rates, but may not be possible because of small sample sizes after other nests are removed

from the analysis.

Wetland Habitat Variables

DSR Models.--In terms of DSRs for 1994, red-winged blackbirds were not related to

any of the variables that we had predicted to be important. This may be because of the few

wetland sites that had survival rate estimates other than the 5 natural wetland sites (restored

wetlands incubation, n = 6; nestling, n = 2) which provides little variation in the independent

variables. Yellow-headed blackbirds had higher nestling success in 1994 when there were

more muskrat houses present. I interpreted this to be an indicator of moderate vegetation

density and extensive channeling by muskrats which simultaneously provided adequate nest

support from the wind yet provided safety from predators that can travel through the

vegetation (e.g., snakes and small mammals);(Orians and Wittenberger 1991). Yet isolated

restored wetlands proved to be the best predictor of higher nestling DSRs for yellow-headed

blackbirds in 1994 and was not correlated with the number of muskrat houses present. This

suggests that there are characteristics of isolated restored wetlands not taken into account by

other variables. In contradiction to my predictions, red-winged blackbirds had greater

nestling success in 1995 in smaller wetlands. In 1995, smaller wetlands did not have the

dense vegetation that yellow-headed blackbirds need for nesting territories; therefore, red-

winged blackbirds were able to select nest sites in deeper water without competition from

yellow-headed blackbirds. These, as shown by the nest-site models, are the better nest-sites and red-winged blackbirds were more successful.

Nest Density Models.--Marginal differences in nest densities were found between natural wetlands and restored wetlands in complexes. Although there were large differences in nest densities between wetland categories, large variances precluded being able to show those differences statistically. Increased sample sizes are needed to reduce the variation in the estimates and to increase statistical power.

In red-winged blackbird models for 1994 and 1995, nesting in restored wetlands in complexes was again related to lower nest densities. Red-winged blackbirds in marshes with little vegetation or central areas of vegetation surrounded by water (1994) or in isolated restored wetlands (1995) also had lower nest densities. I had predicted that red-winged blackbird nest densities would be greater in wetlands with vegetation pattern 2, but was surprised that restored wetlands were consistently better predictors of lower nest densities for the red-winged blackbirds than other variables included. I hypothesize that this is related to the decreased vegetation diversity and to the presence of abrupt habitat edges that places red-winged blackbird nests at risk from terrestrial predators.

Yellow-headed blackbirds tended to have greater nest densities where marsh wrens were nesting (1994). Although this was not predicted, both species nest in similar habitat although they do spatially segregate their nesting territories (Linz et al. 1996). In 1995, yellow-headed blackbirds had lower nest densities in isolated restored wetlands. Again, the inclusion of isolated restored wetlands was not expected but may be the result of reduced cattail cover in these wetlands which was not reflected in the estimates of robust vegetation

available since it includes other species as well. Yellow-headed blackbirds were shown to nest exclusively in cattails and to have the greatest nest densities when vegetation to water ratios are 50:50 (Weller and Spatcher 1965).

Although several wetland habitat variables that have previously been related to nest densities in these species were included in the initial modeling process (e.g., percent vegetation cover), restored wetland types consistently were the best predictor of lower nest densities. This suggests that there are characteristics inherent in these restored wetland types that are not explained by the other wetland habitat variables. I have suggested what these may be, but more studies are needed to describe differences between natural wetlands and restored wetlands in terms of physical characteristics that influence the communities of animals dependent on them for reproduction, migration, and wintering.

Landscape Variables

Higher red-winged blackbird nest success rates were most strongly affected by habitat heterogeneity (Table 10). This was not predicted, but is not surprising since the red-winged blackbird is a classic generalist species, doing well in a variety of edge habitats. Therefore, its nest success would be greater in habitats with more edge and many different habitats available in the landscape. Although it does better in marsh habitats, it is well known to fledge young in many different habitats including linear and abrupt edges that traditionally have higher predation rates.

On the other hand, yellow-headed blackbirds are more of a habitat specialist and mainly occupy emergent vegetation in deep-water marshes. They had greater nest success with

greater patch diversity, i.e., there was more balance of area with a variety of habitats including wetlands, although this relationship was not strong. I predicted yellow-headed blackbirds to have the greatest nest success in areas that are dominated by wetland/grass habitats where there are conditions for establishing larger colonies over deep water. Yellow-headed blackbirds have greater success in wetlands that have higher patch diversity because these are the areas with the greatest wetland concentrations, i.e., versus low patch diversity in northwestern Iowa consisting mainly of agricultural crops. They would also do better in areas where their potential predators, e.g., garter snakes, small mammals, and birds, were distributed more evenly across several habitat types with a variety of buffer prey from which to choose. Therefore, yellow-headed blackbirds do better in areas with greater patch diversity because their predators may be more numerous but are not as concentrated on them as prey within the wetland habitat.

MANAGEMENT AND RESEARCH IMPLICATIONS

Based on the findings of this study, two numerically dominant wetland species have comparable DSRs on restored and natural wetlands. If the results from these species are typical for other wetland species, then it appears the quality of restored wetlands is good and we should continue to support the restoration of more wetlands. These results are especially encouraging since they include species that nest on two important wetland habitats, wetland edge and over water.

But this study does agree with others in noting that there was a tendency for nest densities to be lower on restored wetlands when compared to natural wetlands for some

comparisons. For red-winged blackbirds, restored wetlands in complexes in particular have a stronger negative effect on nest density than other variables measured in this study. The effects on yellow-headed blackbird nest densities appear to be more variable depending upon the year and conditions. More research is needed to understand the variables inherent in restored wetlands that make them different from natural wetlands.

The restored wetlands studied here are also relatively young, being restored within the last 10 years. Research is still needed to track these wetlands as they age. More aggressive management may be needed to restore a more native and diverse vegetation community as suggested by Galatowitsch and van der Valk (1996).

The results of this study show the great year-to-year variability in habitat conditions on the prairie pothole region and its variable effects on different species. Habitat conditions appeared to be good for yellow-headed blackbirds in 1994 and 1995. Red-winged blackbirds were more variable with greater nest success in 1995 than 1994. This underscores the importance of maintaining a wide diversity of habitats to support the widest number of species possible in a given year. It also reinforces the idea that variables at different habitat scales influence species populations differently. In my study, the three habitat scales agreed and generally provided new information with each additional step. It was extremely helpful to see the differences that scale has on interpretation of habitat use for different species. In particular, it showed that habitat specialists and generalists respond very differently to habitat variables at all scales.

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Table 1. Daily survival rate (DSR) estimate means and variances for red-winged (RWBB) and yellow-headed (YHBB) blackbirds natural wetlands in complexes (nc), restored wetlands in complexes (rc), and isolated restored wetlands (ri) in northwestern Iowa, 1994 and 1995.

Species	Year	Stage	DSR[a]			DSR Variance			P > F[b]	n[c]
			nc	rc	ri	nc	rc	ri		
RWBB	1994	incubation	0.9008	0.8030	0.7944	0.0020	0.0319	0.0230	0.10	11
		nestling	0.9384	0.9615	0.9333	0.0030	0.0014	0.0041	0.92	7
	1995	incubation	0.9058	0.8945	0.8802	0.0006	0.0027	0.0041	0.61	14
		nestling	0.9302	0.9091	0.9742	0.0023	0.0060	0.0011	0.65	11
YHBB	1994	incubation	0.9263	0.8498	0.9143	0.0020	0.0049	0.0048	0.18	12
		nestling	0.9515	0.9511	0.9832	0.0011	0.0019	0.0001	0.25	9
	1995	incubation	0.9309	0.8848	0.7706	0.0005	0.0036	0.0248	0.47	11
		nestling	0.8787	0.7693	1.0	0.0026	0.0015	0.0	0.78	10

Table 1. Continued.

[a] daily survivorship rate calculated using the Mayfield method (Mayfield 1975)

[b] probability value from ANOVA analysis comparing the 3 wetland type means

[c] number of wetlands where a DSR could be calculated for that species and year and the number of wetlands in the ANOVA

analysis

Table 2. Daily survival rate (DSR) estimate means and variances for red-winged blackbirds (RWBB) and yellow-headed (YHBB) blackbirds in natural wetlands in complexes (nc) and restored wetlands (r) in northwestern Iowa, 1994 and 1995.

Species	Year	Stage	DSR[a]		DSR Variance		$\underline{P} > \underline{F}$ [b]	$\underline{n}$ [c]
			nc	r	nc	r		
RWBB	1994	incubation	0.9008	0.7987	0.0020	0.0274	0.03	11
		nestling	0.9384	0.9474	0.0030	0.0028	0.84	7
	1995	incubation	0.9058	0.8865	0.0006	0.0035	0.39	14
		nestling	0.9302	0.9417	0.0023	0.0036	0.83	11
YHBB	1994	incubation	0.9263	0.8774	0.0020	0.0030	0.21	12
		nestling	0.9515	0.9704	0.0011	0.0008	0.31	9
	1995	incubation	0.9309	0.8522	0.0005	0.0097	0.40	11
		nestling	0.8787	0.8077	0.0026	0.0012	0.74	10

Table 2. Continued.

[a] daily survivorship rate calculated using the Mayfield method (Mayfield 1975)

[b] probability value from ANOVA analysis comparing the 2 wetland type means

[c] number of wetlands where a DSR could be calculated for that species and year and the number of wetlands in the ANOVA

analysis

Table 3. Principal component (PC) loadings and eigenvalues for continuous nest-site variables for red-winged (RWBB) and yellow-headed (YHBB) blackbird nests in wetlands in northwestern Iowa, 1994 and 1995.

Species	Year	PC loadings of original variables				Eigenvalue	Variance explained (%)
		SHORE[a]	OPEN WATER[b]	NEST HEIGHT[c]	WATER DEPTH[d]		
RWBB	1994	0.63	-0.35	-0.22	0.65	1.94	0.49
	1995	0.59	-0.45	-0.32	0.59	2.11	0.53
YHBB	1994	0.63	-0.26	-0.35	0.64	1.89	0.47
	1995	0.64	-0.29	-0.28	0.66	1.59	0.40

[a] distance from shore (nearest 0.5 m)

[b] distance to nearest open water (nearest 0.5 m)

[c] nest rim height from the water surface (cm)

[d] water depth below the nest (cm)

Table 4. Logistic regression models of main effects of nest-site variables predicting the probability of success of red-winged (RWBB) and yellow-headed (YHBB) blackbird nests in northwestern Iowa wetlands, 1994 and 1995. Coefficients for each variable have been replaced by just their sign to simplify interpretation. The constant intercept is represented by C and denotes the base condition of nesting in dead cattail in the emergent zone. The Wald Chi-square p-value is given for each variable.

Species	Year	$\underline{n}$ [a]	Model	gamma [b]	concordance [c]
RWBB	1994	90	-C ($\underline{P}$ = 0.0001) +**SHORE/WATER DEPTH**[d] ($\underline{P}$ = 0.06) +**live cattail** ($\underline{P}$ = 0.004) +<u>**Scirpus fluviatilis**</u> ($\underline{P}$ = 0.07)	0.539	76.7%
	1995	181	-C ($\underline{P}$ = 0.0001) +**NEST HEIGHT**[e] ($\underline{P}$ = 0.02)	0.167	57.7%
YHBB	1994	207	-C ($\underline{P}$ = 0.0001) +**SHORE/WATER DEPTH** ($\underline{P}$ = 0.0001) +**NEST HEIGHT** ($\underline{P}$ = 0.0004)	0.340	66.8%
	1995	180	+C ($\underline{P}$ = 0.0968) -**NEST HEIGHT** ($\underline{P}$ = 0.005)	0.341	65.5%

Table 4. Continued.

[a] number of individual nests

[b] $(nc-nd)/(nc+nd)$ where nc is the no. of concordant pairs and nd is the number of discordant pairs (SAS Institute Inc., 1995)

[c] see SAS Institute Inc., 1995

[d] PC1 combining distance from shore and water depth beneath nest in a positive relationship

[e] height of nest rim above water (cm)

Table 5. Average percent vegetation cover and number of basins in each vegetation pattern (see Stewart and Kantrud 1971) for natural wetlands (nc), restored wetlands in complexes (rc), and isolated restored wetlands (ri) in northwestern Iowa, 1994 and 1995.

Year	Wetland type	n	Vegetation cover (%)				Vegetation pattern		
			weak emergents	robust emergents[a]	total emergents	shrubs/trees	1	2	3
1994	nc	5	24	46	65	7	0	5	0
	rc	5	22	40	49	2	0	4	1
	ri	5	17	42	53	2	1	2	2
1995	nc	5	22	43	54	1	0	5	0
	rc	5	21	29	39	4	1	4	0
	ri	5	23	32	34	5	1	3	1

[a] Robust emergents were defined as vegetation species used by blackbirds for nest supports in 1994. All other emergent species were classified as weak-stemmed.

Table 6. Mean nest density (nests/ha) and variances for red-winged blackbirds (RWBB) and yellow-headed blackbirds (YHBB) in natural wetlands (nc), restored wetlands in complexes (rc), and isolated restored wetlands (ri) in northwestern Iowa, 1994 and 1995.

Species	Year	$\underline{n}$[a]	Nest density (No./ha)			$\underline{P} > \chi^2$[b]	Significance[c]
			nc	rc	ri		
RWBB	1994	5	17.7 ± 405.97	1.3 ± 1.52	2.9 ± 9.63	0.04	A**
	1995	5	22.4 ± 215.34	2.6 ± 2.76	6.9 ± 29.55	0.008	A***
YHBB	1994	5	16.4 ± 518.24	14.1 ± 272.42	33.4 ± 1415.58	0.91	
	1995	5	18.6 ± 661.11	12.6 ± 122.76	1.5 ± 4.91	0.07	A*

[a] nest densities were determined for 5 wetlands in each wetland category

[b] significance value from the Kruskal-Wallis test for differences among the 3 wetland types

[c] significance value from Tukey-type multiple comparison test using Kruskal-Wallis rank sums. A = nc versus rc; B = nc versus ri; C = rc versus ri; if a letter does not appear, $\underline{P} > 0.20$. Significance levels: * = $\underline{P} < 0.20$, ** = $\underline{P} < 0.10$, *** = $\underline{P} < 0.05$.

Table 7. Stepwise-multiple regression models of main effects of wetland habitat scale variables and their relationships with the daily survivorship rates (DSR) and nest densities (No. nests/ha) of red-winged (RWBB) and yellow-headed (YHBB) blackbirds in northwestern Iowa wetlands, 1994 and 1995. Coefficients for each variable have been replaced by just their sign to simplify interpretation. *New model when restored wetlands in complexes (rc) and isolated restored wetland (ri) types were added to the previous model.

Dependent variable	Year	Model	R^2
RWBB nestling DSR	1995	-area ($\underline{P}$ = 0.01)	0.53
YHBB nestling DSR	1994	+number of muskrat houses ($\underline{P}$ = 0.10) +ri ($\underline{P}$ = 0.08)*	0.33 0.37
RWBB nest densities	1994	-vegetation pattern 1 & 3 ($\underline{P}$ = 0.03) -vegetation pattern 1 & 3 ($\underline{P}$ = 0.006) -rc ($\underline{P}$ = 0.01)*	0.32 0.60
	1995	-perimeter ($\underline{P}$ = 0.02) -absence of nesting marsh wrens ($\underline{P}$ = 0.004) -rc ($\underline{P}$ = 0.0005) -ri ($\underline{P}$ = 0.02)*	0.53 0.65
YHBB nest densities	1994	-absence of nesting marsh wrens ($\underline{P}$ = 0.02)	0.35
	1995	+grackles absent ($\underline{P}$ = 0.08) -ri ($\underline{P}$ = 0.02)*	0.22 0.33

Table 8. Rotated factor loadings and principal component (PC) eigenvalues of original factors for continuous wetland habitat variables for red-winged (RWBB) and yellow-headed (YHBB) blackbird nest densities in wetlands in northwestern Iowa, 1994 and 1995. Principal components was the original factor method and variance was maximized in rotation.

Species	Year	Rotated factor loadings of original variables							PC eigenvalue	Variance explained (%)
		YHBB	RWBB	ROBVEG[a]	RTSVEG[b]	EMGVEG[c]	ETSVEG[d]	PERIMETR[e]		
RWBB	1994	0.30	.	.	0.85	.	0.98	0.03	2.32	0.58
	1995	0.21	.	.	0.97	.	0.93	0.13	2.37	0.59
YHBB	1994	.	0.13	0.94	.	0.97	.	0.03	1.99	0.50
	1995	.	0.23	0.96	.	0.90	.	0.19	2.23	0.56

[a] percent cover of robust vegetation

[b] percent cover of robust vegetation and trees/shrubs

[c] percent cover of total emergent vegetation

[d] percent cover of total emergent vegetation and trees/shrubs

[e] length of perimeter (km) around the wetland

53

Table 9. Rotated factor (RF) loadings and original principal component (PC) eigenvalues for landscape-scale values within 1 mile of wetlands with nesting red-winged (RWBB) and yellow-headed blackbirds (YHBB) in northwestern Iowa, 1994 and 1995. Principal components was the initial factor method and variance was maximized in rotation.

RF	Landscape variables	RWBB		YHBB	
		1994	1995	1994	1995
1	Wetland habitat area	**-0.87**	**0.86**	**0.90**	**0.86**
	Distance to wetland edge	0.24	-0.00	-0.17	-0.35
	Distance to habitat edge	**-0.68**	**0.81**	**0.70**	**0.76**
	Patch diversity	0.00	0.13	0.03	-0.10
	Number of fences	**0.83**	**-0.78**	**-0.84**	**-0.74**
	Number of roads	**0.75**	**-0.60**	**-0.72**	**-0.70**
	PC eigenvalue	3.12	3.15	3.14	3.02
	Variance explained (%)	0.53	0.52	0.52	0.50
2	Wetland habitat area	0.35	-0.41	-0.29	0.33
	Distance to wetland edge	**-0.81**	**0.86**	**0.88**	**-0.69**
	Distance to habitat edge	0.21	-0.27	-0.21	-0.21
	Patch diversity	**0.91**	**-0.81**	**-0.86**	**0.86**
	Number of fences	0.27	-0.28	-0.24	-0.19
	Number of roads	**-0.58**	**0.68**	**0.59**	**-0.57**
	PC eigenvalue	1.41	1.41	1.45	1.20
	Variance explained (%)	0.24	0.23	0.24	0.20

Table 10. Stepwise-multiple regression and univariate linear regression models of main effects of landscape-scale variables and their relationships with nest success of red-winged (RWBB) and yellow-headed (YHBB) blackbirds in northwestern Iowa wetlands, 1994 and 1995. Coefficients for each variable have been replaced by their sign to simplify interpretation. *New model when restored wetlands in complexes (rc) and isolated restored wetland (ri) types were added to the previous stepwise-multiple regression model.

Species	Year	Model	R^2
Stepwise-Multiple Regression:			
RWBB	1994	+more Habitat heterogeneity (PC2)[a] ($\underline{P}$ = 0.01)	0.51
		+more Habitat heterogeneity (PC2)($\underline{P}$ = 0.004) -rc ($\underline{P}$ = 0.08)*	0.68
Univariate Linear Regression:			
RWBB	1994	+Patch diversity[b] ($\underline{P}$ = 0.01)	0.53
RWBB	1995	-Wetland habitat area[c] ($\underline{P}$ = 0.10)	0.21
YHBB	1994	+Patch diversity ($\underline{P}$ = 0.09)	0.26

Table 10. Continued.

[a] principal component combining several landscape variables interpreted as habitat heterogeneity

[b] number and evenness of habitat patch distribution within 1 mile radius of study site wetland using Simpson's Diversity Index

[c] total wetland area (ha) within 1 mile radius of the study site wetland

GENERAL CONCLUSIONS

Great amounts of effort and money have been spent by individuals, organizations, and governments to reverse the trend of wetland losses seen since the late 1700s. Although many studies have shown that many species of invertebrates, birds, and plants rapidly recolonize these restored habitats, they also point out that restored wetlands have striking deficiencies when compared with natural wetlands (Delphey and Dinsmore 1993, Hemesath and Dinsmore 1993, VanRees-Siewert 1993, Galatowitsch and van der Valk 1996).

This study has provided one more piece of evidence that restored wetlands are comparable to natural wetlands in some ways. I found that daily survival rates (DSR) of red-winged and yellow-headed blackbirds were the same for restored and natural wetlands and nest successes of both species were comparable to literature reports for marsh-nesting populations. Nest success differed between species and years with greater variation in red-winged blackbirds. Nest-site and wetland habitat-scale factors that influenced DSRs differed between species, years, and the two scales.

Nest densities between natural wetlands and restored wetlands in complexes were marginally different. For red-winged blackbirds, restored wetlands also negatively influenced nest densities at the habitat scale. Yellow-headed blackbirds were negatively influenced by the absence of nesting marsh wrens and isolated restored wetlands.

While red-winged blackbirds have greater nest success when the landscape is more diverse with greater amounts of edges, yellow-headed blackbirds have greater nest success

when the distribution of landscape patches is more equitably distributed between available habitat types (e.g., wetlands and crop).

The differences in response by a habitat generalist and a habitat specialist should lead us to contemplate where in the landscape a wetland is restored and to manage wetlands on a landscape level. Having a wide diversity of habitats available, natural and restored, is important to support a wide variety of species in a given year. This undoubtedly was the pattern that was present historically and is the one under which these species evolved.

Future Research Questions

This study has raised several questions and exposed gaps in the literature. More work is needed to describe and publish experimental work on descriptions of egg and nestling predation events for passerine birds. Several papers document their ideas of what to look for and how they classified predation events, but no one has done a thorough job as has been done for waterfowl (e.g., Rearden 1951, Sargeant et al. 1993). With this background information, assigning nests to failure categories would be more standardized and useful for comparisons.

In addition, more research is needed on how predators use fragmented habitats. As noted by Andrén (1995) and Paton (1994), most work on nest predation has been done in forested areas. From the few studies done in agricultural and prairie landscapes, predators use these habitats in very different ways and I expect that this is true of all habitats. More importantly, more work is needed on how predators move within and use fragmented habitats

in relation to nest success of birds. Very little research has been done by studying both simultaneously although many people have addressed the issue by studying predators or nest success separately.

Also, restored wetland vegetation was much more impacted by muskrats than in natural wetlands. An interesting research question would be to look at restored wetland vegetation and muskrat cycles and compare these with natural wetlands, much as Weller and Spatcher (1965) did to describe natural wetland cycles. This would provide one more piece of evidence that may help us manage and restore wetlands intelligently and responsibly.

APPENDIX A

LANDOWNER AND LOCATION OF WETLAND STUDY SITES

ID	Landowner/Title	County	Township/Range/Section
2	Spring Run NW	Dickinson	T99N R36W S24 SW1/4,NE1/4
5	Duhn	Palo Alto	T97N R34W S14 NE1/4,SW1/4
11	Nock	Palo Alto	T97N R32W S28 SW1/4,SW1/4
13	Center Lake	Dickinson	T99N R36W S7 NW1/4
15	Thu	Palo Alto	T97N R34W S8 NE1/4,NW1/4
16	Braby South	Palo Alto	T97N R34W S12 NE1/4,NW1/4
19	Henry	Emmet	T98N R34W S36 NW1/4,SW1/4
22	Clay Restored South	Clay	T97N R35W S26 SE1/4,NE1/4
24	Dewey's Pasture, C2	Clay	T97N R35W S25 NE1/4
25	Dewey's Pasture, A6	Clay	T97N R35W S25 NW1/4
27	Grover	Dickinson	T100N R37W S12 NW1/4,SE1/4
30	McBreen North	Dickinson	T100N R37W S13 N1/2,SW1/4
33	3-Corners Pond	Dickinson	T99N R37W S35 SW1/4,SW1/4
34	McBreen West	Dickinson	T100N R37W S13 SW1/4,SW1/4
35	Siemers South	Palo Alto	T97N R34W S3 SE1/4,SE1/4
36	Siemers North	Palo Alto	T97N R34W S3 N1/2,SE1/4
37	Braby North	Palo Alto	T97N R34W S1 SE1/4,NW1/4

APPENDIX B

TYPE, AREA, PERIMETER, AND EDGE/AREA INDEX OF WETLAND STUDY SITES

ID	Type	Isolation	Area (ha)	Perimeter (km)	Edge/area Index[a]
5	Restored 1987	Isolated	0.8	0.34	1.10
11	Restored 1989	Isolated	2.3	0.56	1.06
15	Restored 1988	Isolated	1.4	0.68	1.62
19	Restored 1988	Isolated	1.2	0.45	1.15
35	Restored 1988	Isolated	1.3	0.45	1.11
36	Restored 1988	Isolated	1.7	0.58	1.26
13	Restored 1990	Complex	0.8	0.32	1.01
16	Restored 1990	Complex	1.2	0.40	1.06
22	Restored 1990	Complex	1.1	0.47	1.28
30	Restored 1988	Complex	3.7	0.81	1.19
34	Restored 1988	Complex	3.3	0.66	1.03
37	Restored 1990	Complex	0.8	0.45	1.39
2	Natural	Complex	1.2	0.40	1.04
24	Natural	Complex	1.2	0.42	1.08
25	Natural	Complex	2.0	0.53	1.07
27	Natural	Complex	1.9	0.55	1.11
33	Natural	Complex	2.7	0.74	1.26

[a] Edge/area index = perimeter / $\{2(\text{area} * \pi)^{1/2}\}$ where perimeter is in km and area is in km^2.

APPENDIX C

WETLAND TYPE, NUMBER OF WETLANDS, AND TOTAL AREA OF WETLAND HABITAT WITHIN 1-MILE RADIUS OF WETLAND STUDY SITES

ID	Isolation[a]	Number of Wetlands	Wetland Habitat Area (ha)
5	isolated	4	9
11	isolated	1	27
15	isolated	10	4
19	isolated	13	14
35	isolated	2	2
36	isolated	4	3
13	complex	.	>107
16	complex	11	14
22	complex	48	455
30	complex	18	28
34	complex	9	21
37	complex	14	15
2	complex	36	97
24	complex	58	352
25	complex	51	342
27	complex	20	133
33	complex	16	35

[a] Wetland study sites with $\leq$ 14 ha or $\leq$ 13 wetlands were classified as isolated.

APPENDIX D

NESTING BIRD SPECIES FOUND ON THREE WETLAND CATEGORIES IN NORTHWESTERN IOWA, 1994[a]

Species	Wetland Category														
	nc[b]					rc[c]					ri[d]				
	2	24	25	27	33	13	16	22	30	34	11	15	19	35	36
red-winged blackbird	x	x	x	x	x		x	x	x	x	x	x		x	x
yellow-headed blackbird	x	x	x	x	x		x	x	x	x	x		x	x	
common yellowthroat	x	x	x	x	x		x	x	x	x		x		x	
American coot		x	x	x			x			x					
pied-billed grebe	x	x	x		x	x	x	x	x		x			x	
swamp sparrow												x			
marsh wren	x	x	x	x			x	x	x	x	x	x	x	x	
sedge wren								x				x			x
sora				x											
Virginia rail	x	x		x			x	x		x	x				
blue-winged teal		x	x	x		x	x	x	x		x	x	x	x	x
mallard				x		x	x		x	x		x	x	x	x
Canada goose	x	x	x			x	x	x	x			x		x	
common grackle		x	x			x									
brown-headed cowbird		x		x	x					x					

[a] Methods follow those of Schreiber (1994) except counts were done from May to July every 8 days and a 20-m radius census point was used.

[b] natural wetlands in complexes

[c] restored wetlands in complexes

[d] isolated restored wetlands

APPENDIX E

BIRD SPECIES PRESENT ON THREE WETLAND CATEGORIES IN NORTHWESTERN IOWA, 1994[a]

Species	Wetland Category														
	nc[b]					rc[c]					ri[d]				
	2	24	25	27	33	13	16	22	30	34	11	15	19	35	36
red-winged blackbird	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
yellow-headed blackbird	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
common yellowthroat	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
American coot		x	x	x			x			x		x			
pied-billed grebe	x	x	x	x	x		x	x	x	x	x		x	x	x
song sparrow			x		x			x				x		x	x
swamp sparrow	x	x	x	x	x		x		x	·		x		x	x
marsh wren	x	x	x	x	x		x	x	x	x	x	x	x	x	x
sedge wren		x		x	x			x				x			x
sora				x							x				
Virginia rail	x	x		x			x	x	x	x	x		x	x	
least bittern							x					x			
blue-winged teal	x	x	x	x	x	x	x	x	x		x	x	x	x	x
mallard	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Canada goose	x	x	x		x	x	x	x	x	x		x		x	
wood duck				x	x									x	x
killdeer						x	x	x	x		x	x	x	x	x
northern shoveler						x					x				
black tern	x		x								x				
barn swallow			x	x		x	x	x	x	x	x	x		x	x
American kestrel				x											

Continued.

Species	nc[b]					rc[c]					ri[d]				
	2	24	25	27	33	13	16	22	30	34	11	15	19	35	36
common grackle	x	x	x	x	x	x		x	x						
American robin				x											
ruddy duck							x		x						
redhead			x	x					x		x				
gadwall									x						
gray catbird				x											
American crow												x			
cliff swallow												x		x	
tree swallow													x		
bank swallow								x							
brown-headed cowbird		x		x		x				x					
American white pelican								x							

[a] Methods follow those of Schreiber (1994) except counts were done from May to July every 8 days and a 20-m radius census point was used.

[b] natural wetlands in complexes

[c] restored wetlands in complexes

[d] isolated restored wetlands

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