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AVIAN COMMUNITY RESPONSES TO HYDRILLA INVASION

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ABSTRACT.—Changes in a bird community associated with increased coverage of the exotic submergent hydrilla (*Hydrilla verticillata*) were studied on a Texas reservoir. Hydrilla was the only major plant exhibiting a significant increase in areal coverage from 1986 to 1987. Bird species richness and total bird numbers in 1987 correspond to increased hydrilla coverage, as well as substantial increases in populations of birds shown to be closely associated with hydrilla, e.g., American Coots (*Fulica americana*), Pied-billed Grebes (*Podilymbus podiceps*), and several duck species. Observations of sample plots demonstrated a correlation between hydrilla coverage and bird use, especially for American Coots. Experimental removal of hydrilla from plots resulted in a decrease of bird use of plots lacking hydrilla. The addition of the submergent layer of hydrilla was beneficial to the bird community, presumably due to increased horizontal vegetative diversity and foraging opportunities. *Received 12 April 1989, accepted 6 Nov. 1989.*

Vegetation influences bird community structure, i.e., bird numbers and diversity. Most studies of such relationships have considered terrestrial systems, concentrating either on the role of vertical (MacArthur and MacArthur 1961, MacArthur et al. 1962, Karr and Roth 1971, Willson 1974, and many others) or horizontal structure (Wiens 1974, Roth 1976, Rotenberry and Wiens 1980, Rice et al. 1984). The relationship between wetland bird communities and habitat diversity has been addressed for nesting birds and emergent vegetation (Weller and Spatcher 1965, Weller 1979, Weller and Voigts 1983, Burger 1985). The present paper focuses on the dynamics of the wetland bird community during the early stages of the invasion of the submergent hydrilla (*Hydrilla verticillata*) in a Texas reservoir. Using both experimental and observational methods, the role of hydrilla as an influencing factor on bird numbers and species richness was addressed.

Hydrilla, an exotic submerged macrophyte, was first reported in the United States from Florida in 1960 (Blackburn and Weldon 1969) and has spread to at least 12 other states (Johnson and Montalbano 1987). Once established, hydrilla often dominates water bodies and causes significant changes in vegetation structure (Haller and Sutton 1975). This dramatic habitat change also influences other components of lake systems. Aquatic macroinvertebrate abundance and richness generally increase with the addition of submergents (Krull 1970), as is the case with hydrilla

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(Moxley and Langford 1982, Watkins et al. 1983). Forage fish production also increases with the initial hydrilla invasion (Moxley and Langford 1982). These system changes would be expected to influence abundance of birds utilizing fish and invertebrate resources.

The relationship between birds and hydrilla has been described in a number of Florida studies. Hydrilla was an important food for American Coots (*Fulica americana*) (Montalbano et al. 1979, Hardin et al. 1984), Common Moorhens (*Gallinula chloropus*) (Mulholland and Percival 1982, O'Meara et al. 1982), and several duck species (Montalbano et al. 1978, 1979; Hardin et al. 1984). Hydrilla also has been shown to be a highly utilized habitat component by Florida waterfowl. Reductions in waterfowl abundance were observed following hydrilla removal by grass carp (*Ctenopharyngodon idella*) (Gasaway and Drda 1977). Hydrilla was highly used by waterfowl on Lake Okeechobee and supported a greater diversity of duck species than other plant communities (Johnson and Montalbano 1984). This study serves to further describe bird-hydrilla relationships in a reservoir outside of Florida, and for a wide range of birds, providing the first assessment of associated community change.

STUDY AREA AND METHODS

Lake Fairfield is located 18 km east of Fairfield in Freestone County, Texas. Dam construction was completed in 1969, and the lake reached mean pool level of 94.5 m above sea level in 1971. Hydrilla was first observed in Lake Fairfield in 1984 (Durocher 1986, K. Strawn, pers. comm.), and this study was initiated in 1986. Mean water depth is 6.5 m and annual water fluctuation less than 1 m. The main body of the lake encompasses 1053 ha with an adjacent 60-ha cooling pond and 3.3 km of canals. Recreational use includes fishing, boating, and water skiing, but no hunting is permitted on the lake or in adjacent areas. Upland vegetation surrounding the lake is typical of the post oak savannah region of Texas (Gould 1962).

Vegetation sampling.—Vegetation of the lake was surveyed every three months from summer 1986 through fall 1987. Seasons were defined by equinoxes and solstices, and vegetation surveys were conducted at mid-season. Twenty-three 50 × 50 m plots were located throughout the lake and marked with survey flagging and buoys. Three plots were randomly located in open water areas where variance was zero due to lack of any vegetation. The remaining 20 plots were randomly placed adjacent to shore, encompassing the band where all aquatic vegetation was located. Plots on shore were sampled using line transects. Three randomly located, 50-m lines perpendicular to shore were established within each shoreline plot. Beginning at the shoreward edge above the high water mark, plant species present directly above or below a point at each 0.5 m along each line were recorded. Results from the 20 plots adjacent to shore were extrapolated to represent the vegetated portion (227.4 ha) of the lake which was within 50 m of shore, and open water plot results represented the 825.6 ha of the lake which was more than 50 m from shore. Friedman's two-way analysis of variance (ANOVA) (Conover 1980:299–308) was used to detect changes in abundance of a single plant species or habitat type over the six seasons of vegetation sampling. In this case, and in all other instances in which Friedman's test is used, the F approximation was used rather than the Chi-squared approximation due to increased test efficiency (Conover

1980:300). A Fisher's Least Significant Difference (LSD) multiple comparisons procedure (Ott 1984:365–370) was used to separate seasons differing in abundance.

Abundance of all habitat types over all seasons combined was compared using Friedman's two-way ANOVA. Fisher's LSD was used to determine where differences in habitat abundance lay.

Bird surveys. —The avifauna of Lake Fairfield was surveyed by boat to determine species richness and population sizes. Surveys were conducted semimonthly during fall, winter, and spring, weekly during summer 1986, and monthly during summer 1987. Forty-eight total surveys were completed; 28 in 1986 and 20 in 1987. Surveys were conducted soon after sunrise and on weekdays, when possible, to avoid weekend boat disturbance. Duration of surveys ranged from three to six hours and direction around the lake was alternated.

Bird species richness was compared across habitats for each season using a one-way ANOVA followed by Fisher's LSD post-test to determine interhabitat differences. This assessment was designed to determine the relative value of each habitat throughout the seasons and was conducted both for all birds and for ducks.

Bird survey data were used to compare community structure parameters across seasons using a one-way ANOVA with a Fisher's LSD post-test. This procedure allowed for the detection of changes in community structure parameters through the seasons and across years for individual species, groups of species, and for the bird community as a whole. Species diversity indices were not used as measures of community structure due to questionable use and interpretation (Hurlbert 1971, James and Rathbun 1981).

Bird observation plots. —Plot observations were conducted to assess the relationship between vegetation and bird use. Plots were the same as those used for vegetation analyses and were observed on each of seven dates throughout winter and fall 1987. Plots were observed from a boat for a period of 10 min, during which time bird species and number of individuals present were noted. Using data collected from plot observations, coefficients of linear correlations (Neter et al. 1985:96–99) were calculated to determine if there was a significant correlation between bird use and the amount of hydrilla across plots.

Experimental plots. —Four hydrilla-free plots were created in August 1986 within hydrilla beds to further assess the importance of hydrilla to certain bird species and assemblages. Hydrilla-free plots were created with the herbicide Aquathol K (Pennwalt Corp., 3 Parkway, Philadelphia, PA 19102), and the openings were maintained by manual removal as necessary through fall 1986 and winter 1987. The cleared plots were 50 × 50 m and each was located near one of the bird observation plots which showed an abundance of hydrilla. The experimental plots and adjacent hydrilla plots were observed on seven dates in fall 1986, six dates in winter 1987, and five dates in spring 1987 in the same manner as described for the plot observations.

Experimental plots lacking hydrilla and corresponding hydrilla plots were compared using the Wilcoxon signed-rank paired comparison (Conover 1980:280–288) to determine if there was a difference in bird use between the two treatments. This was done for the entire bird community and selected groups and species of birds.

RESULTS

Vegetation of Lake Fairfield was grouped into nine habitat types: hydrilla, emergents, emergent-hydrilla interface, submergents other than hydrilla, floating-leaf plants, nonpersistent emergents, terrestrial vegetation, unvegetated shoreline/shallow water, and open water. Coverage of each habitat type by season is presented in Table 1. Significant differences

TABLE 1

SEASONAL HABITAT COVERAGE IN HECTARES AT LAKE FAIRFIELD, TEXAS (1986–1987)

Habitat	1986 Summer	1986 Fall	1986 Winter	1987 Spring	1987 Summer	1987 Fall
Open water	954.6 (90.66)[a]	944.9 (89.73)	993.4 (94.34)	983.6 (93.41)	929.7 (88.29)	911.9 (86.60)
Hydrilla	29.2 (2.77)	41.1 (3.90)	19.9 (1.89)	10.4 (0.99)	44.1 (4.19)	53.2 (5.05)
Emergent	22.6 (2.15)	24.9 (2.36)	25.5 (2.42)	26.6 (2.53)	24.7 (2.35)	23.3 (2.21)
Floating leaf	21.1 (2.00)	17.2 (1.63)	0.0 (0.00)	15.6 (1.48)	25.1 (2.38)	14.8 (1.41)
Unveg. shore shallow water	8.6 (0.82)	15.4 (1.46)	10.6 (1.01)	10.7 (1.02)	10.0 (0.95)	25.0 (2.37)
Other submergents	9.0 (0.85)	5.5 (0.52)	0.3 (0.03)	2.0 (0.19)	10.1 (0.96)	10.8 (1.03)
Terrestrial vegetation	0.5 (0.05)	0.1 (0.01)	1.9 (0.18)	1.8 (0.17)	5.3 (0.50)	6.6 (0.63)
Emergent-hydrilla	5.9 (0.56)	2.9 (0.28)	1.3 (0.12)	1.1 (0.10)	3.8 (0.36)	4.6 (0.44)
Nonpersist. emergent	1.5 (0.14)	0.9 (0.09)	0.0 (0.00)	1.2 (0.11)	0.1 (0.01)	2.6 (0.25)

[a] Percent coverage is in parentheses.

(F = 24.59, $P < 0.001$) in coverage were found across habitats. Open water was more abundant than all other habitat types. Hydrilla and emergent habitat types were more abundant than the remaining habitat types. Floating-leaf, unvegetated shoreline/shallow water, and other submergent habitat types were more abundant than terrestrial vegetation, emergent-hydrilla interface, and nonpersistent emergent habitats.

Hydrilla was the only common habitat type to increase significantly ($P < 0.05$) across years. An increase in areal coverage of hydrilla of 51% was observed from summer 1986 to summer 1987 and an increase of 33% was noted across corresponding falls. The other submergent habitat type, which consisted primarily of spiny naiad (*Najas marina*), also increased across years. However, its influence on the bird community was minimal because it was uncommon and received very little bird use. Nonpersistent emergent and terrestrial vegetation habitats exhibited increases across years; however, these uncommon habitats also received little bird use. Open water coverage decreased across years, corresponding to invading hydrilla.

Avian species richness was compared across the six major habitats to determine the relative value of each habitat (Table 2). Unvegetated shoreline/shallow water habitat averaged the most species per survey with open water being second, although the two did not differ statistically. Hydrilla ranked fourth and had more species than floating-leaf and emergent-hydrilla interface habitats. Hydrilla was ranked first in species richness for fall 1987 and second, although not significantly less rich than the top-ranked open water habitat, for fall 1986 and winter 1987.

Comparisons of species richness across habitats also were calculated for ducks only (Table 3). In summer 1986, only Wood Ducks (*Aix sponsa*), found almost exclusively in American lotus, were present. Hydrilla supported the greatest duck species richness in the falls of both years and winter 1987, the seasons of greatest duck abundance. Johnson and Montalbano (1984) found similar results in Florida, where hydrilla attracted a greater diversity of waterfowl species than several other habitats.

Plot observations indicated a significant ($P < 0.001$) correlation between bird numbers and the amount of hydrilla in plots for winter and fall 1987 and also for these seasons combined ($R^2 = 0.541$). American Coots constituted most of the bird use of the plots in these seasons and the strength of the correlation between number of individuals and hydrilla amount for coots is similar ($R^2 = 0.520$). Coots were the only species observed in the plots in sufficient abundance to independently support analysis.

Experimental plots also served to elucidate the relationship between birds and hydrilla. The coverage of hydrilla in the plots of both treatments was similar in summer 1986 before herbicide application and manual removal of hydrilla from experimental plots (Fig. 1). However, in the following fall and winter, hydrilla coverage in experimental plots was significantly less than that in hydrilla plots. By spring 1987, the plots of both treatments again had similar hydrilla coverage. Fall 1986 and winter 1987 seasons provided the best comparisons of differential bird use between treatments because they had the greatest difference in hydrilla amounts and, also, were the seasons with greatest bird abundance.

Total bird use was substantially lower in plots without hydrilla for fall 1986 ($P = 0.0062$) and winter 1987 ($P = 0.0007$) (Fig. 2); however, total bird use was similar between treatments for spring 1987, the season for which hydrilla amounts also were similar (Fig. 1). American Coots constituted a large portion of the total bird use for both treatments, reflecting the relative abundance of this species, and were much more numerous in hydrilla plots. The difference in coot numbers between treatments was significant in fall 1986 ($P = 0.0062$) and in winter 1987 ($P = 0.0002$). Pied-billed Grebes (*Podilymbus podiceps*) also demonstrated a significant

TABLE 2

MEAN BIRD SPECIES RICHNESS ACROSS SEASONS AND MAJOR HABITATS ON LAKE FAIRFIELD, TEXAS (1986–1987). WITHIN SEASONS, HABITATS SHARING A LETTER DID NOT DIFFER ($P > 0.05$)

Season	Habitat					
	HYD	EMG	E/H	FLT	USS	OPN
Summer 1986	2.182 (E)	5.636 (AB)	2.364 (DE)	4.455 (BC)	7.000 (A)	3.727 (CD)
Fall 1986	6.833 (AB)	3.167 (C)	3.000 (C)	2.500 (C)	5.667 (B)	7.667 (A)
Winter 1987	7.200 (AB)	6.200 (B)	2.400 (C)	1.400 (C)	6.400 (B)	9.800 (A)
Spring 1987	3.333 (CD)	8.500 (AB)	1.833 (D)	1.500 (D)	11.000 (A)	5.833 (BC)
Summer 1987[b]	5.000	4.333	2.000	3.000	3.000	3.667
Fall 1987	13.167 (A)	5.000 (BC)	2.167 (C)	3.000 (C)	7.500 (B)	11.333 (A)
Overall	5.116 (C)	5.860 (BC)	2.000 (D)	2.767 (D)	7.349 (A)	6.698 (AB)

[a] Habitat abbreviations: HYD = hydrilla; EMG = emergent; E/H = emergent-hydrilla interface; FLT = floating leaf; USS = unvegetated shoreline/shallow water; OPN = open water.
[b] Habitats were not different ($P = 0.1018$).

TABLE 3

MEAN WATERFOWL SPECIES RICHNESS ACROSS SEASONS AND MAJOR HABITATS AT LAKE FAIRFIELD, TEXAS (1986–1987). WITHIN SEASONS, HABITATS SHARING A LETTER DID NOT DIFFER ($P > 0.05$)

Season	Habitat[a]					
	HYD	EMG	E/H	FLT	USS	OPN
Summer 1986	0.091 (B)	0.000 (B)	0.000 (B)	0.636 (A)	0.000 (B)	0.00 (B)
Fall 1986	2.167 (A)	0.000 (B)	0.167 (B)	0.333 (B)	0.167 (B)	0.833 (B)
Winter 1987	2.400 (A)	0.800 (B)	0.000 (B)	0.600 (B)	0.200 (B)	1.200 (AB)
Fall 1987	5.833 (A)	0.333 (B)	0.167 (B)	1.333 (B)	0.167 (B)	1.167 (B)
Overall	1.500 (A)	0.386 (BC)	0.045 (C)	0.500 (BC)	0.318 (BC)	0.545 (B)

[a] Habitat abbreviations are the same as those in Table 2.

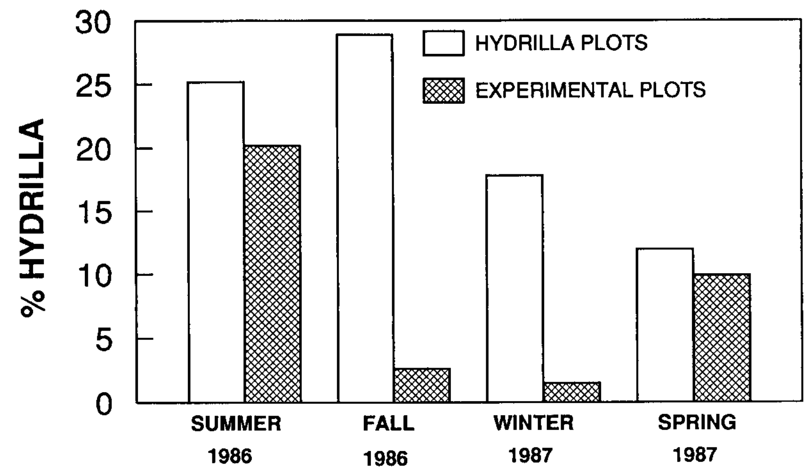

FIG. 1. Percent hydrilla coverage in hydrilla and experimental plots, Lake Fairfield, Texas, 1986–1987. Herbicide was applied to experimental plots between summer and fall 1986.

(P = 0.0312) preference for hydrilla plots in fall 1986 but not in the following winter (P = 0.5332).

Changes in bird community structure reflected typical seasonal differences in taxa and bird numbers and yearly differences due to habitat changes. Species richness differed ($F = 5.75$, $P < 0.001$) across seasons

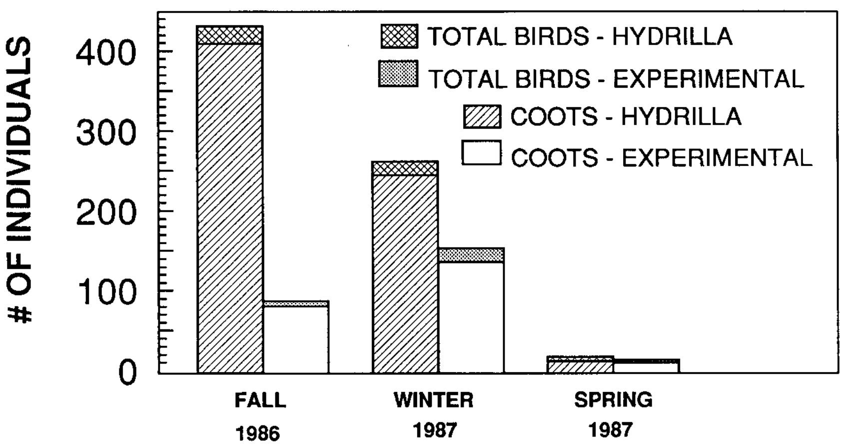

FIG. 2. Total bird numbers and American Coot proportions in hydrilla and experimental plots, Lake Fairfield, Texas, 1986–1987.

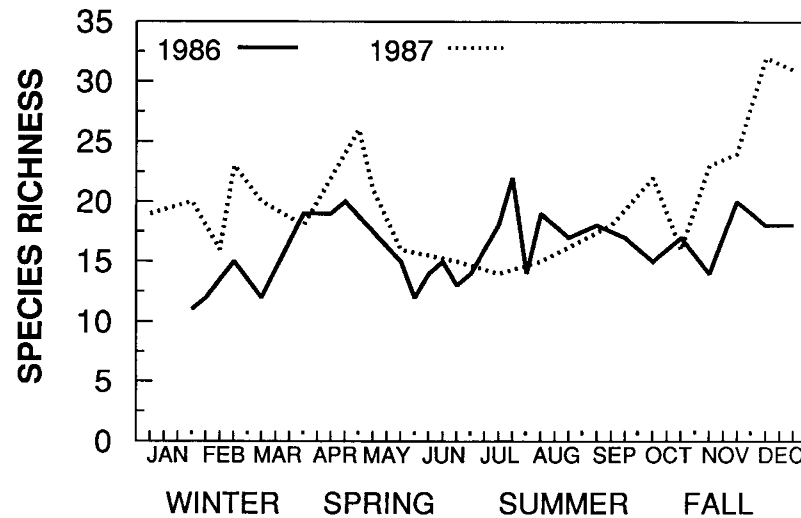

FIG. 3. Bird species richness on Lake Fairfield, Texas, 1986–1987.

and years and was generally higher in 1987 (Fig. 3). Species richness was highest in fall 1987, when the mean number of species per survey was 24.7. This was significantly greater than species richness for all other seasons. Winter 1987 had greater species richness than the corresponding season in 1986. No differences in species richness were detected between years for spring or summer seasons. Much of the increase in species richness in winter and fall 1987 was attributable to increases in duck species richness. In fall 1986, seven species of ducks were observed on the study site, compared to 16 in fall 1987. In winter 1986 and 1987, three and 10 waterfowl species were observed, respectively.

Total bird numbers per survey (Fig. 4) differed across seasons ($F = 9.94$, $P < 0.001$) and was greatest for fall 1987. Fall 1986 and winter 1987 ranked second and third, respectively, and were not different from one another. Winter 1987 did not have more individuals than winter 1986. Spring and summer seasons of both years had fewest individuals and did not differ. Much of the increase in numbers between 1986 and 1987 was attributable to American Coots and ducks.

Results of species and family comparisons across seasons illustrated that most taxa did not vary in abundance between years but exhibited typical seasonal fluctuation due to migration chronology and seasonal changes in habitat use. Several species, however, did show changes in abundance between years. Pied-billed Grebe abundance was higher ($P <$

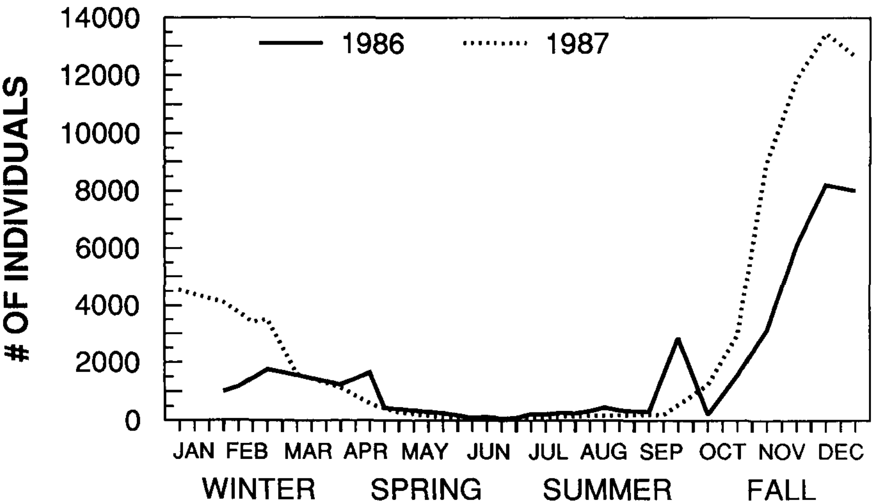

FIG. 4. Total number of individual birds on Lake Fairfield, Texas, 1986–1987.

0.05) in 1987 for winter and fall. American White Pelican (*Pelecanus erythrorhynchos*) abundance in winter was greater ($P < 0.05$) in 1987 than 1986. White Pelicans often were found in hydrilla, although not nearly as much as in open water, making conclusive statements tenuous regarding the effects of increasing hydrilla on the abundance of this species.

Overall duck abundance differed across years. Mean duck abundance in fall 1987 was more than five times that of fall 1986. Species exhibiting significant ($P < 0.05$) increases included Buffleheads (*Bucephala albeola*), Canvasbacks (*Aythya valisineria*), Green-winged Teal (*Anas crecca*), Gadwalls (*A. strepera*), and Ring-necked Ducks (*Aythya collaris*). Mallards (*Anas platyrhynchos*) increased from an average of 6.5 birds per survey in fall 1986 to 164 in fall 1987. Winter 1987 had greater waterfowl abundance than winter 1986. Seven duck species showed increased abundance from winter 1986 to winter 1987. This difference was significant ($P <$ 0.05) for Green-winged Teal and Ring-necked Ducks.

Mean American Coot abundance increased by more than four times between winter 1986 and 1987 and two times between falls. Also, coot density in hydrilla increased from 94.8 to 135.4 coots per ha from fall 1986 to fall 1987.

DISCUSSION

Increased hydrilla was the only major habitat change on Lake Fairfield from 1986 to 1987 and may have been the primary factor influencing changes in bird community structure across years. Increases in bird numbers on Lake Fairfield were not a result of local or regional increases. Duck, American Coot, and Pied-billed Grebe numbers, which increased on Lake Fairfield from 1986 to 1987, did not increase on a sample of 108 ponds located within 10 km of the lake (L. A. Reynolds, unpubl. data). Moreover, Christmas Bird Count data (Drennan 1987, 1988) from east-central Texas demonstrate that population increases on Lake Fairfield were not a reflection of region-wide trends.

Birds that showed population increases across years, differential responses to experimental plot treatments, and positive correlations to hydrilla coverage within plots were largely species that have been shown to use hydrilla, including American Coots, Pied-billed Grebes (Esler 1988), and ducks (Johnson and Montalbano 1984, Esler 1988). The increases in species richness demonstrated across years was due largely to ducks.

Many bird populations were unaffected by increased hydrilla coverage. Birds which primarily used any of the other major habitat types did not exhibit population changes. The coverage and quality of other habitats were largely unaffected by hydrilla because hydrilla mainly invaded open water areas. If hydrilla coverage were to increase to the point of dominating most of the open water habitat, birds selecting open water such as Eared Grebes (*Podiceps nigricollis*), cormorants, gulls, terns, and some duck species could be inhibited.

The influence of hydrilla on the bird community was seasonal, due both to the annual chronologies of bird use of the lake and hydrilla growth. Its impact was most important in fall and winter when overall bird abundance was greatest and birds closely associated with hydrilla were present. In spring, both bird and hydrilla abundance were low. In summer, wading birds and birds that utilized open water, such as swallows, gulls, and terns, were prevalent; habitat use data indicated that hydrilla was largely unused by these birds (Esler 1988).

The vegetative structure of Lake Fairfield exhibited horizontal heterogeneity based on concentric rings of habitat types reflecting water depth, which is typical of many wetland basins (Weller and Spatcher 1965). Horizontal heterogeneity has been shown to affect bird community structure in terrestrial systems (Wiens 1974, Roth 1976, Rotenberry and Wiens 1980, Rice et al. 1984, and others), and patchiness and vegetative diversity likewise affect wetland bird communities (Weller 1979, Weller and Voigts

1983). Rice et al. (1984) suggest that the effect of increasing horizontal heterogeneity on bird communities is related to birds' reacting to the addition of patches of suitable habitat rather than to the increase in diversity, per se. The birds of Lake Fairfield likely were reacting to both the increase of vegetative structure in a water body dominated by open water and to the addition of hydrilla specifically. The addition of the layer of hydrilla led to increased foraging opportunities for birds utilizing fish and macroinvertebrates associated with submergents, i.e., Pied-billed Grebes and Northern Shovelers (*Anas clypeata*). However, herbivorous birds may have been reacting to hydrilla, specifically, because of its food value (Montalbano et al. 1978, 1979; Hardin et al. 1984).

Wetlands are dynamic systems, typically experiencing annual fluctuation. Many marsh birds are well adapted to habitat change and quickly respond to variation in resource availability (Weller and Spatcher 1965). Habitat change, in the form of increased hydrilla from 1986 to 1987, resulted in an immediate response by wetland birds in the form of increased species richness and number of individuals. Little evidence for neophobia regarding an exotic species was exhibited, as has been suggested for forest birds (Greenberg 1983).

This study addressed the community changes associated with the invasion of exotics rather than competition between native species and exotics. Posey (1988) stressed that the effect of exotics on natural systems may be indirect and related to habitat change rather than direct competition between natives and exotics. This appeared to be the case on Lake Fairfield, where hydrilla was invading only little-used open water areas, and benefited the bird community through increased vegetative diversity and foraging opportunity. The benefits of hydrilla for wetland birds should be examined when hydrilla management questions arise with both natural and artificial water bodies (Johnson and Montalbano 1987).

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