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AVIAN COMMUNITIES IN BAYHEADS, WILLOWHEADS, AND SAWGRASS MARSHES OF THE CENTRAL EVERGLADES

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ABSTRACT.—We compared avian community composition, species richness, and total bird abundance among three vegetation types (bayheads, willowheads and marshes), and between a reduced-hydroperiod and relatively unimpacted landscape in the central Everglades during July–August, 1996. Our results showed that the collective Everglades bird community contained a substantial number of forest birds as well as marsh species. Red-winged Blackbirds (*Agelaius phoeniceus*), Common Yellowthroats (*Geothlypis trichas*), and White-eyed Vireos (*Vireo griseus*) accounted for 65% of total individual birds during the period of study. Wading birds accounted for a relatively small proportion of the total avian community. White-eyed Vireo was the most abundant bird species in bayheads and was closely associated with that habitat. Red-winged Blackbird and Common Yellowthroat were the most abundant species in both willowheads and marsh vegetation. We found no significant difference in bird abundance among vegetation types ($P > 0.05$) nor between landscapes ($P > 0.05$). We also found no difference in species richness between landscapes ($P > 0.05$). A significant ($P = 0.02$) interaction between vegetation and landscape indicated that species richness differed among vegetation types in the unimpacted landscape, but not in the reduced-hydroperiod landscape. In the unimpacted landscape we detected significantly more species in bayheads than the other two vegetation types (both tests, $P \leq 0.004$). An ordination revealed that in the unimpacted landscape, bird communities were more specific to vegetation types than in the reduced-hydroperiod landscape. Our study demonstrates that two characteristics of a relatively unimpacted landscape in the central Everglades are higher avian species richness and a more distinct avian community in bayheads than in willowheads or marshes. The Everglades restoration process will promote the conservation of avian diversity by restoring the landscape matrix of both marsh and bayhead vegetation. *Received 8 May 1997, accepted 3 Oct. 1997.*

The Everglades has been described as a vast lake covered with tall sawgrass (*Cladium jamaicense*) and studded with thousands of tree islands (Smith 1848 *in* Gunderson and Loftus 1993). The vertical structure of tree islands provides nesting and foraging opportunities for many avian species that could not otherwise exist in this marsh dominated ecosystem. Thus, the mosaic of naturally fragmented forest patches imbedded in expansive herbaceous marshes produces a landscape that supports both forest and marsh birds. The recent focus on the Everglades restoration effort (e.g., Cohn 1994, Ogden 1994, Culotta 1995) provides several examples of how birds are used to reflect the condition of an ecosystem. Despite the usefulness of birds as environmental indicators, habitat-specific associations of avian species inhabiting the Everglades are largely unknown. Only limited quantitative data exist on bird use of marshes (Kushlan and Kushlan 1977) and to the best of our knowledge, only qualitative data exist for tree islands (Robertson 1955, Robertson and Kushlan 1984, Richter and Meyers 1993).

In the Everglades, the term tree island has been used interchangeably to represent bayheads, cypressheads, willowheads, and hardwood hammocks. Bayheads are dominated by red bay (*Persea borbonia*), sweet bay (*Magnolia virginiana*), dahoon holly (*Ilex cassine*), and wax myrtle (*Myrica cerifera*) (Robertson 1955, Olmstead and Loope 1984, Gunderson 1994). Willowheads usually occur as monotypic stands of willow (*Salix caroliniana*; Loveless 1959, Gunderson and Loftus 1993) that are associated with soil disturbance (Gunderson 1994). Historical records of Everglades vegetation suggest that bayheads in the central Everglades have declined in number since the Central and Southern Florida Drainage Project was initiated in the 1910s (Davis et al. 1989), whereas willowheads have become much more widespread (Craighead 1971). The construction of impoundments to create the Water Conservation Areas (WCAs) has intensified these changes. Marshes with shorter hydroperiods (defined as the length of time an area is inundated with water) were created in northern portions of the reservoirs, as were

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marshes with longer hydroperiods and deeper water in southern regions of the reservoirs (Zaffke 1983). Tree island vegetation changed under both extremes with bayheads converting to willow and Brazilian pepper (*Schinus terebinthifolius*) in reduced hydroperiod areas and converting to willow, cattail (*Typha* spp.) and melaleuca (*Melaleuca quinquenervia*) in extended hydroperiod areas (Davis et al. 1989, Davis et al. 1994).

Creation of the impoundments also changed the landscape matrix of tree islands and marshes. In the reduced hydroperiod marshes of WCA-3A (i.e., the area north of I-75; Fig. 1), shrubs invaded the most severely drained portions and the aerial extent of cattail increased. Severe peat fires burned off muck edges of tree islands, thereby lowering the elevation and producing a vegetation shift away from the dense sawgrass fringe often associated with tree island edges (Zaffke 1983, Gunderson and Snyder 1994). Collectively, these changes produced a landscape of sawgrass marshes with scattered shrubs, cattail patches and smaller tree islands. The smaller tree islands have sharply defined edges that lack the extensive sawgrass fringe associated with tree islands in longer-hydroperiod marshes further south in WCA-3A.

The relationship between vegetation structure and bird density and diversity has been well-documented but was not always consistent among regions or studies (MacArthur and MacArthur 1961, Karr and Roth 1971, James and Wamer 1982, Mills et al. 1991, Willson and Comet 1996). Inconsistencies usually resulted from a specific measure of bird diversity or abundance not correlating as strongly with a particular measure of vegetation diversity or volume in one study as in another. Nevertheless, the generalization emerges that vertical vegetation structure and volume are often correlated with increased bird abundance and, or, diversity. Thus, we hypothesized that the greatest bird abundance and diversity would be in bayheads, willowheads, and marshes, respectively because of their vegetation structure. Vegetation changes that have occurred in the Everglades, such as increases in the number of monotypic willowheads and losses of bayheads, therefore, may have greatly altered the avian community.

Landscape patterns of vegetation in addition to the structure of individual tree islands, can also affect bird species diversity and density (Virkkala 1991, Steele 1992, Pearson 1993). The configuration of vegetation patches in the landscape affects the movements of organisms among patches, which has consequences for finding mates, avoiding predation, and finding adequate food resources. Thus, it is possible that bird communities associated with similar vegetation types may differ between landscapes with different patch configurations. The two contrasting landscapes in our study, likely caused by historic differences in water management, provided an opportunity to test these potential effects on the Everglades' bird community.

The ongoing Everglades restoration process has the potential to once again alter the mosaic of vegetation communities in the Everglades through a reduction in nutrient loads entering the WCAs and the establishment of more natural hydropatterns (South Florida Water Management District 1995). Hydropattern restoration will likely result in longer hydroperiods in northwestern WCA-3A and shorter hydroperiods in southeastern WCA-3A. Habitat associations of avian species will provide resource managers with critical information to predict the effects of landscape changes on the Everglades' bird community. We define community as a group of individuals of several species that co-occur in time and space (Wiens 1989a).

In this study, we compared bird communities among three vegetation types (bayheads, willowheads, and marshes), in both a reduced-hydroperiod and relatively unimpacted landscape in the central Everglades. Although the entire Everglades ecosystem has been affected by human activities to some degree, we use the term "unimpacted landscape" because the west-central portion of WCA-3A (Fig. 1) still has vegetative and hydrologic characteristics similar to those in historic accounts (Davis et al. 1994). We term the reduced-hydroperiod area in WCA-3A north of I-75 as "impacted." We addressed the management questions: (1) do bird communities differ among vegetation types, and (2) are bird communities within vegetation types similar in landscapes with different management histories?

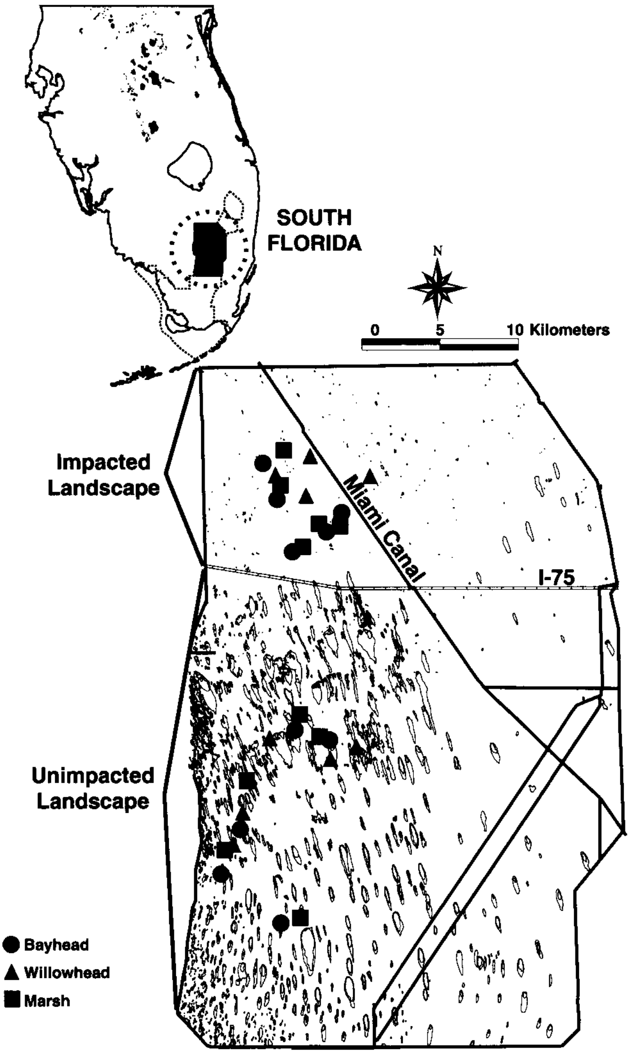

FIG. 1. Sampling sites in Water Conservation Area 3A in the central Everglades.

METHODS

Study area.—All study sites were located in WCA-3A (Fig. 1) within the central Everglades. We selected 14 sites (5 bayheads, 4 willowheads, and 5 marsh) in the impacted landscape and 15 sites (5 bayheads, 5 willowheads, and 5 marsh) south of I-75 in the unimpacted landscape. We assumed bayheads would be limited in number in the impacted landscape so we chose those sites first with the criteria that they contained more than 50% woody species other than willow, were qualitatively as similar as possible in composition and size, and were separated by at least 1 km. A distance of 1 km is greater than the territory size of most passerines and reduced the chance of counting the same individuals at more than one site. For the Ciconiiformes, this assumption probably does not hold true because of their tendency for long-range flights (Kushlan 1976). However, we surveyed adjacent sites in sequence and surveyed all sites within the same landscape in the same day to reduce the chances of individuals moving among sites. Willowheads were selected on the criteria of being the closest tree island of predominantly (>75%) willow, at least 1 km from other sites, and being as similar in size as possible based on availability. Only four willowheads met those criteria in the impacted landscape. Excluding one large bayhead, tree islands were small, averaging 5 ha. Island size did not differ significantly between landscapes ($P > 0.05$) nor among vegetation types ($P > 0.05$). The criteria for marsh sites were that they were at least 1 km from other sites and, for logistic reasons, close to the line of travel among tree islands.

Data collection.—Each site was surveyed by the same observer once per week for 4 weeks in July–August 1996 (17 Jul, 23 Jul, 30 Jul, 5 Aug). Surveys began within 30 minutes before or after sunrise and were usually completed by late morning. To reduce any variation in detection caused by time of day, we reversed the sequence in which sites were surveyed within landscapes each week. Because of the prolonged nesting season for many birds in south Florida (March–August), the intensity of singing by territorial males, and thus their detection probability, varied throughout the summer. Also, juveniles were present for much of the year. Therefore, we considered our surveys to be measures of relative abundance rather than absolute density of nesting pairs.

Surveys were conducted using a modified variable circular-plot method (Reynolds et al. 1980). Because of accessibility constraints, and to reduce disturbance to birds, plots at tree islands were centered on tree island edges. This protocol produced two semicircular subplots that consisted of either tree island or marsh vegetation. We believe that centering plots on island edges did not bias our counts toward "edge-species" because islands were too small to provide a true forest interior at the scale of individual bird territories. We recorded birds separately for each subplot and included during the analysis only those birds in the tree islands. To standardize our plot size and shape for marsh sites, we randomly selected the orientation of two semicircular subplots at each marsh site. Subplots remained fixed throughout the study. For the analysis of marsh sites, we included counts from only one randomly selected subplot.

We arrived at each site by airboat and preceded each survey with a two-minute waiting period to allow birds to adjust to initial disturbance. We then surveyed birds for the subsequent six minutes. We developed our methodology for this unique environment based on a pilot study which indicated that two minutes was sufficient to allow birds to recover from initial disturbance. Our pilot study also showed that six-minute surveys identified the majority of species at each plot and counts of up to 25 minutes produced little overall gain in species richness (e.g., Gates 1995).

During surveys, each bird seen or heard was identified to species when possible, and its distance from the survey point was estimated as <50 m, 50–100 m, and >100 m. We also recorded the subplot in which it occurred. Our pilot study indicated that the probability of detecting birds as a function of distance from observer decreased substantially beyond 100 m. Therefore during the analysis we excluded birds detected at more than 100 m. We also excluded birds that flew over the site without landing and may not have been associated with vegetation at our sampling sites.

In five instances we detected unidentified small passerines in the vegetation. These birds were classified as unknowns and were included in the analysis of total bird abundance but not of species richness patterns or multivariate analyses. During the final sampling period of our study we recorded the presence of Tree Swallows (*Tachycineta bicolor*). We believe these birds were migrants because of their initial appearance late in the season and because Tree Swallows are not known to nest in south Florida (Stevenson and Anderson 1994). To avoid confounding patterns of resident birds, we reported the presence of Tree Swallows in Table 1 but did not include them in any statistical analyses.

Univariate analyses.—We used a three-factor repeated measures design analyzed as a split-plot ANOVA with landscape and vegetation type as the crossed factors and sampling period as a repeated measure factor (Cody and Smith 1991). Dependent variables were species richness (i.e., the number of species/site/survey) and total bird abundance (i.e., the total individuals/site/survey). Statistical comparisons were made using PROC GLM in SAS (SAS Institute Inc. 1988) for a UNIX operating system. Differences in least-square means were considered significant at $P \leq 0.05$. Least significant difference tests were conducted on the least-square means when a model term was deemed significant as per our a priori critical level. We specified "site nested within landscape × vegetation" as the error term for least significant difference tests of landscape, vegetation, and landscape × vegetation.

Multivariate analyses.—To identify individual species patterns related to landscape and vegetation types without conducting an undesirably large number of univariate tests, we conducted a canonical variate analysis (CVA), also called canonical discriminant analysis, using PROC DISCRIM in SAS (SAS Institute Inc. 1988) for a UNIX operating system. This technique is an exploratory ordination procedure that reduces the dimensionality of the data by deriving linear combinations of the original variables (e.g., bird abundances) called canonical variates (CAN) (Williams 1983). Canonical variates are uncorrelated and constructed to maximize differences among groups defined by a single nominal variable. The effectiveness of a CAN in differentiating among groups can be evaluated with the canonical correlation coefficient, a measure of association between a canonical variate and the groups. This coefficient ranges from zero to one with large values indicating a strong relationship and zero indicating no relationship (Klecka 1980).

Canonical variate analysis differs from related ordination procedures, such as principal components analysis, in that principal components analysis maximizes total variance along the first ordination axis whereas CVA maximizes the ratio of the between-group sum of squares and the within-group sum of squares (ter Braak 1995). Thus, by examining the total structure coefficient, which is the pairwise correlation between a CAN and an original variable, it is possible to identify which of the original variables contribute most to differences among groups. In our study, the groups were vegetation types and the original variables were species abundance values at each site during each survey.

Because our initial univariate analyses indicated that the relationship between the avian community and

TABLE 1. Abundance and species richness of birds in bayheads, willowheads, and marshes in the central Everglades, July–August 1996.[a]

	Unimpacted landscape						Impacted landscape						All sites	
	Bayhead ($n = 5$)		Willowhead ($n = 5$)		Marsh ($n = 5$)		Bayhead ($n = 5$)		Willowhead ($n = 4$)		Marsh ($n = 5$)		($n = 29$)	
Species	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Anhinga											0.05	0.11	0.01	0.05
Great Egret											0.05	0.11	0.01	0.05
Green Heron	0.05	0.11							0.13	0.14			0.03	0.08
Turkey Vulture	0.25	0.35	0.05	0.11	0.10	0.22	0.05	0.11	0.19	0.24	0.15	0.34	0.13	0.24
Osprey			0.05	0.11					0.06	0.13			0.02	0.06
Snail Kite					0.05	0.11							0.01	0.05
Red-shouldered Hawk	0.15	0.34											0.03	0.14
Common Moorhen			0.05	0.11	0.65	0.80	0.05	0.11	0.25	0.35	0.55	0.69	0.26	0.50
Yellow-billed Cuckoo							0.05	0.11	0.06	0.13			0.02	0.06
Great Horned Owl					0.05	0.11							0.01	0.05
Red-bellied Woodpecker	0.45	0.51	0.05	0.11			0.15	0.14	0.06	0.13			0.12	0.26
Eastern Kingbird	0.15	0.22					0.75	1.16					0.16	0.53
Tree Swallow					0.05	0.11					0.20	0.33	0.04	0.15
Carolina Wren	0.05	0.11											0.01	0.05
Blue-gray Gnatcatcher			0.05	0.11			0.10	0.22					0.03	0.10
Loggerhead Shrike							0.25	0.43			0.05	0.11	0.05	0.19
White-eyed Vireo	1.70	0.69	0.20	0.27			1.10	0.78	0.88	0.97			0.64	0.83
Common Yellowthroat	0.50	0.35	0.95	0.94	0.80	0.60	0.35	0.22	0.56	0.13	0.65	0.34	0.64	0.51
Northern Cardinal	0.70	0.51	0.20	0.21			0.10	0.14	0.25	0.29			0.21	0.34
Red-winged Blackbird	0.55	0.21	1.40	0.63	1.10	0.68	0.95	0.69	2.31	1.09	2.65	1.13	1.47	1.04
Boat-tailed Grackle	0.85	0.58	0.30	0.33			0.40	0.38	0.13	0.14	0.30	0.11	0.34	0.40
Unknown[b]	0.20	0.21	0.05	0.11			0.05	0.11					0.05	0.12
All species	5.60	1.88	3.35	0.72	2.80	1.12	4.35	1.72	4.88	1.64	4.65	1.59	4.25	1.66
Species richness	3.35	0.95	1.95	0.45	1.60	0.45	2.35	0.84	2.81	0.88	2.10	0.45	2.34	0.86

[a] Values represent the average number of individuals or species detected at a site during a 6-min survey.

[b] Unidentified small passerines.

vegetation types differed between landscapes, we conducted separate CVAs for each landscape. We excluded from the analyses four species for each landscape that were detected during only one survey and thus had no variance. Species excluded from the analysis in the unimpacted landscape were Anhinga (*Anhinga anhinga*), Great Egret (*Casmerodius albus*), Loggerhead Shrike (*Lanius ludovicianus*), and Yellow-billed Cuckoo (*Coccyzus americanus*). Species excluded from the analyses in the impacted landscape were Carolina Wren (*Thryothorus ludovicianus*), Great Horned Owl (*Bubo virginianus*), Red-shouldered Hawk (*Buteo lineatus*), and Snail Kite (*Rostrhamus sociabilis*).

RESULTS

Community composition.—With all sites pooled, the three most abundant species were Red-winged Blackbird (*Agelaius phoeniceus*), Common Yellowthroat (*Geothlypis trichas*), and White-eyed Vireo (*Vireo griseus*). Collectively they accounted for 65% of all individuals.

In the unimpacted landscape, the most abundant species in bayheads were White-eyed Vireo, Boat-tailed Grackle (*Quiscalus major*), Northern Cardinal (*Cardinalis cardinalis*), Red-winged Blackbird, Common Yellowthroat, and Red-bellied Woodpecker (*Melanerpes carolinus*), respectively (Table 1). Willowhead communities were dominated by Red-winged Blackbird and Common Yellowthroat, respectively. Marsh communities were dominated by Red-winged Blackbird, Common Yellowthroat and Common Moorhen (*Gallinula chloropus*), respectively.

The CVA of bird communities in the unimpacted landscape indicated that the discriminatory power of CAN1 (r^2 = 0.76) was considerably higher than that of CAN2 (r^2 = 0.28). A plot of the canonical variate scores for each site (Fig. 2a) indicated that CAN1 mainly differentiated a bayhead community from those in willowheads and marshes, whereas CAN2 distinguished between bird communities in marshes and willowheads. Structure coefficients indicated that White-eyed Vireo, Red-bellied Woodpecker, and Northern Cardinal were more abundant in bayheads and these species best distinguished the bayhead community from those in the other vegetation types (Table 2). The Common Moorhen was more abundant in marshes and best distinguished that community from one in willowheads.

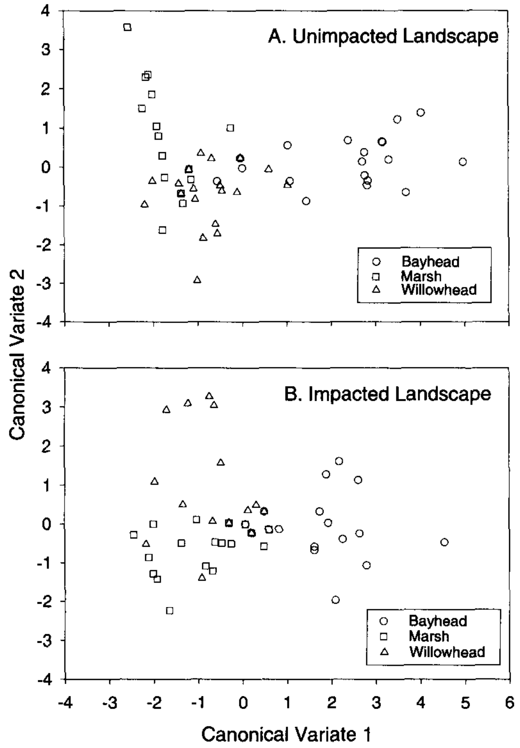

FIG. 2. Canonical variate scores based on avian abundance for sites in bayheads, willowheads, and marshes, in the (A) unimpacted landscape and (B) impacted landscape in the central Everglades, July–August 1996.

In the impacted landscape, bayhead communities were dominated by White-eyed Vireo, Red-winged Blackbird, Eastern Kingbird (*Tyrannus tyrannus*), and Boat-tailed Grackle, respectively (Table 1). Willowheads were dominated by Red-winged Blackbird, White-eyed Vireo, and Common Yellowthroat, respectively. The most abundant species in marshes were Red-winged Blackbird, Common Yellowthroat, and Common Moorhen, respectively.

The CVA in the impacted landscape indicated that the bayhead bird community was more similar to those of other vegetation types than it was in the unimpacted landscape. This finding was apparent from the lower canonical correlation coefficient of CAN1 in the impacted landscape (r^2 = 0.58) than in the unimpacted landscape and the similar canonical correlation coefficient of CAN2 in the impacted (r^2 = 0.30) and unimpacted landscape.

TABLE 2. Total structure coefficients for canonical variate analysis of birds in bayheads, willowheads, and marshes in the central Everglades, July–August 1996.[a]

Species	Unimpacted landscape		Impacted landscape	
	Canonical variate 1	Canonical variate 2	Canonical variate 1	Canonical variate 2
Anhinga[b]	—	—	−0.149	−0.260
Great Egret[b]	—	—	−0.149	−0.260
Green Heron	0.206	0.072	−0.158	0.514
Turkey Vulture	0.189	0.151	−0.143	0.072
Osprey	−0.066	−0.333	−0.111	0.360
Snail Kite[c]	−0.141	0.261	—	—
Red-shouldered Hawk[c]	0.279	0.097	—	—
Common Moorhen	−0.394	0.636	−0.394	−0.309
Yellow-billed Cuckoo[b]	—	—	0.090	0.237
Great Horned Owl[c]	−0.141	0.261	—	—
Red-bellied Woodpecker	0.553	0.097	0.309	0.141
Eastern Kingbird	0.364	0.126	0.565	−0.068
Carolina Wren[c]	0.206	0.072	—	—
Blue-gray Gnatcatcher	−0.066	−0.333	0.237	−0.028
Loggerhead Shrike[b]	—	—	0.305	−0.118
White-eyed Vireo	0.851	0.140	0.445	0.535
Common Yellowthroat	−0.188	−0.187	−0.204	−0.054
Northern Cardinal	0.525	−0.065	0.012	0.505
Red-winged Blackbird	−0.236	−0.247	−0.510	−0.067
Boat-tailed Grackle	0.454	−0.113	0.176	−0.239

[a] Total structure coefficient is the pairwise correlation between a canonical variate and a single variable.

[b] Rare species not included in the analysis of the unimpacted landscape.

[c] Rare species not included in the analysis of the impacted landscape.

A plot of the site scores (Fig. 2b) indicated that CAN1 mostly differentiated a bayhead community from those in the other vegetation types and CAN2 primarily distinguished between willowhead and marsh communities. Structure coefficients indicated that Eastern Kingbird, Red-winged Blackbird, and White-eyed Vireo distinguished the bayhead community from those in the other vegetation types (Table 2). Eastern Kingbird and White-eyed Vireo were more abundant in bayheads whereas Red-winged Blackbird was less abundant in bayheads than other vegetation types. White-eyed Vireo, Green Heron (*Butorides virescens*), and Northern Cardinal were more abundant in willowheads and best distinguished that community from one in marshes.

Species richness.—We detected 21 bird species at our sites over the course of the study (Table 1). Several additional species were seen during surveys or on travel between sites, but they did not meet our stated criteria for inclusion in the analysis. There was no significant difference ($P > 0.05$) in the number of species per survey between landscapes (Table 3). There was a significant difference ($P = 0.008$) in species richness among vegetation types but a significant interaction ($P = 0.02$) between landscape and vegetation type indicated that the differences among vegetation types were not consistent for both landscapes. Least significant difference tests revealed that in the unimpacted landscape, species richness was higher in bayheads compared to willowheads ($P = 0.004$) and marshes ($P < 0.001$). Whereas in the impacted landscape, there was no difference in species richness between any two vegetation types (all tests, $P > 0.05$). There was also no difference in species richness between marshes and willowheads in the unimpacted landscape ($P > 0.05$).

Total bird abundance.—Total abundance did not differ between landscapes ($P > 0.05$) nor among vegetation types ($P > 0.05$; Table 3). Bird abundance differed significantly across sampling periods ($P = 0.03$) and the interaction of sampling period × vegetation type × landscape ($P = 0.05$). However, because sampling period was included in our design to reduce unwanted variability rather than to provide inferences across time, we did not

TABLE 3. Split-plot ANOVA for bird abundance and species richness of birds in bayheads, willowheads, and marshes in the central Everglades, July–August 1996.

		Bird abundance model		Species richness model	
Source of variation	df	Mean square	*P*	Mean square	*P*
Landscape	1	12.3	0.25	0.28	0.70
Vegetation	2	19.3	0.13	11.6	0.008
Landscape × vegetation	2	27.0	0.06	9.23	0.02
Site (landscape × vegetation) (*Error A*)	23				
Sampling period	3	20.5	0.03	2.58	0.26
Landscape × sampling period	3	2.3	0.77	1.24	0.58
Vegetation × sampling period	6	7.4	0.33	1.78	0.48
Landscape × vegetation × sampling period	6	13.6	0.05	1.37	0.64
Site × sampling period (landscape × vegetation) (*Error B*)	69				

address differences in means. No other terms in the model were significant (all tests, $P > 0.05$).

DISCUSSION

Community composition.—Habitat specificity is a characteristic that makes a species useful for predicting future response to changes in landscape composition (i.e., a good indicator species; Weller 1995). However, this same trait is likely to make a species more vulnerable to changes in its respective habitat. The CVA allowed us to identify species most likely to be affected by changes in a particular vegetation type. For example, Common Yellowthroats and White-eyed Vireos were equally abundant when all sites were pooled (Table 1). However, the yellowthroat occurred in all vegetation types and was not indicative of any single habitat whereas the White-eyed Vireo was more abundant in bayheads and willowheads and largely defined the CANs associated with these two vegetation types.

Instances where species demonstrated habitat specificity based on the CVA, were usually consistent with our understanding of their general habitat requirements. For example, Red-bellied Woodpecker, Northern Cardinal, and White-eyed Vireo characterized bayheads or willowheads, and all these species are known to inhabit forests or brushy areas. The Osprey (*Pandion haliaetus*) was found exclusively in willowheads, which provided perch substrate and also frequently contained alligator holes that support the large fish Osprey prey upon. The Blue-gray Gnatcatcher's (*Polioptila caerulea*) association with willowheads in the impacted landscape was unusual. Although this species occurs in the Everglades during the breeding season (Stevenson and Anderson 1994) it is generally associated with larger trees than those found on willowheads. Thus, it is possible that the bird's association with willowheads in the impacted landscape reflected individuals foraging during migration.

Wading birds occurred in low abundances relative to other species and several species of wading birds that occur in the Everglades were absent from both our counts and those of earlier studies. Although this pattern may seem surprising given that the Everglades is often associated with large numbers of wading birds, few quantitative comparisons between wading birds and other avian species have been conducted. Also, the distribution of wading birds in the Everglades is closely linked to the distribution and depth of surface water (Bancroft et al. 1994, Hoffman et al. 1994). These factors often produce a very clumped distribution of birds with large portions of the marsh containing no birds at all and some portions of the marsh containing very high densities of birds. Finally, although the low numbers of wading birds we detected during the wet season reflects a real characteristic of the ecosystem, our 1.6-ha sampling plots are probably smaller than plots designed optimally to determine densities of only wading birds.

Historic community composition.—No quantitative bird community studies were conducted in the Everglades before drainage of the system began, thus we cannot get a complete assessment of how the avian community has changed if indeed it has. In the southern Everglades, qualitative data (Robertson 1955) were collected in marshes and bayheads at the time the eastern perimeter levee of the Everglades was being constructed and before any of the WCAs were built (Light and Dineen 1994), and quantitative data (Kushlan and Kushlan 1977) were collected shortly after the WCAs were built. Comparison of species richness data from these earlier studies in Everglades National Park with data from the unimpacted landscape in this study provides some insight as to whether species richness has changed since the WCAs were built. However, because all these studies were conducted in slightly different areas, they may reflect some degree of spatial as well as temporal variability. Robertson (1955) reported 15 species, Kushlan and Kushlan (1977) reported 16 species, and we observed 16 species (excluding Tree Swallows) in the unimpacted landscape, indicating similar numbers of nesting species in the central and southern Everglades over a 40-year period. Most likely, none of the studies above recorded the presence of every species in the community because of the difficulty in accessing the Everglades interior and because of the large number of rare species present. Indeed, some differences in species composition among studies can be attributed to the presence of rare species showing up in one study but not in another. Two notable exceptions are Common Moorhen and White-eyed Vireo. Neither species was reported in the earliest studies in the southern Everglades (Robertson 1955, Kushlan and Kushlan 1977), but in our study, Common Moorhen was one of the most abundant marsh-species and White-eyed Vireo was one of the most abundant species in tree islands. Because these birds exhibited strong habitat associations, they contributed greatly to our ability to distinguish bird communities among vegetation types in the ordination.

We do not believe that the absence of Common Moorhen and Common Yellowthroat in earlier studies indicates that these species were absent from the Everglades during those times because both species were recorded in the southern Everglades during the 1960s (North American Breeding Bird Survey, unpubl. data). Two possible explanations for the marked differences in abundance of these two species between our study and earlier ones is that: (1) these two species have increased in abundance over time or (2) there are strong spatial differences with the two species being more abundant in the central Everglades than in the southern portions.

To further explore these hypotheses, we examined an independent data set consisting of one North American Breeding Bird Survey route conducted for 14 years from 1974–1994 in the east-central Everglades, and one route conducted for three years from 1983–1986 in the southern Everglades. These were the only routes that occurred completely within the Everglades. Spatial comparisons between routes revealed that for the Common Moorhen, the number of birds/survey was considerably higher at the northern route ($\bar{x} = 65$, range 21–99, $n = 14$) than at the southern route ($\bar{x} = 1$, range 0–2, $n = 3$). Whereas, the opposite was true for the White-eyed Vireo (northern route: $\bar{x} = 14$, range 0–34, $n = 14$; southern route: $\bar{x} = 62$, range 55–70, $n = 3$). To identify possible temporal changes in bird abundance we examined data from the northern route only and conducted a Spearman rank correlation test between the number of birds/survey and the year of survey. There was no significant trend in the abundance of the Common Moorhen over time ($r = -0.23$, $P > 0.05$, $n = 14$) but there was a significant increase in the White-eyed Vireo ($r = 0.85$, $P < 0.001$, $n = 14$). Collectively, patterns from the North American Breeding Bird Survey corroborate the differences in the abundance of Common Moorhen and White-eyed Vireo between our study and earlier ones in the southern Everglades. This independent data set suggests that the abundance patterns of the Common Moorhen reflect spatial differences between the northern and southern Everglades whereas the abundance patterns of the White-eyed Vireo may reflect increases over time.

Species richness.—Differences in species richness among vegetation types suggests that species richness was determined in large part at the habitat level (e.g., Mills et al. 1991, Craig and Beal 1992, Willson and Comet 1996). In the unimpacted landscape, we detected more species in bayheads, willowheads, and marshes, respectively, which was consistent with our initial prediction based on vegetation structure. However, the significant interaction between landscape and vegetation type indicated that landscape characteristics also played a role in structuring the avian community. Strong differences in species richness among vegetation types were not evident in the impacted landscape. Our ordination identified a similar pattern with regard to species abundances. In the unimpacted landscape, we were better able to distinguish distinct avian communities among vegetation types than in the impacted landscape, where bird communities were more similar to one another.

The influence of landscape should be most important in open systems with small patches such that animals have to move among patches to find adequate resources (Wiens 1989b, Pearson 1993). Under these circumstances, the quality of one patch is less important than the average of all patches from which resources are obtained. This is likely the case for many bird species in the Everglades, particularly those with large home ranges such as wading birds and raptors. However, we also observed smaller birds such as Red-winged Blackbirds and Common Yellowthroats flying between tree islands or among vegetation patches within marshes. As compared to the unimpacted landscape, the impacted landscape has more cattail and shrub patches and a larger percentage of small tree islands. Thus, the small scale (several ha) diversity of patches within the marsh may have actually increased through past management practices, benefiting those species that are not adapted to obtaining resources from widely separated patches. Regardless of which species benefited from past management of the impacted landscape, the result is a collective avian community that differs from the one inhabiting the unimpacted region.

Our study demonstrates that in the central Everglades, two characteristics of a relatively unimpacted landscape are higher species richness in bayheads and a more distinct avian community in that vegetation type than in either willowheads or marshes. Although these characteristics are now absent in the impacted landscape, it is possible that restoration efforts aimed at restoring the historic vegetation communities at the landscape scale (South Florida Water Management District 1995) will restore avian community structure as well. Monitoring both structural characteristics of the avian community as well as population levels of key species will provide information on the success of the ecosystem restoration process.

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LITERATURE CITED

BANCROFT, G. T., A. M. STRONG, R. J. SAWICKI, W. HOFFMAN, AND S. D. JEWELL. 1994. Relationships among wading bird foraging patterns, colony locations, and hydrology in the Everglades. Pp. 615–658 *in* Everglades: the ecosystem and its restoration (S. M. Davis and J. C. Ogden, Eds.). St. Lucie Press, Delray Beach, Florida.

CODY, R. P. AND J. K. SMITH. 1991. Applied statistics and the SAS programming language. Prentice-Hall Inc., Englewood Cliffs, New Jersey.

COHN, J. P. 1994. Restoring the Everglades. Bioscience 44:579–583.

CRAIG, R. J. AND K. G. BEAL. 1992. The influence of habitat variables on marsh bird communities of the Connecticut River Estuary. Wilson Bull. 104: 295–311.

CRAIGHEAD, F. C., SR. 1971. The trees of South Florida, vol. I: the natural environments and their succession. Univ. of Miami Press, Coral Gables, Florida.

CULOTTA, E. 1995. Bringing back the Everglades. Science 268:1688–1690.

DAVIS, S. M., L. H. GUNDERSON, W. A. PARK, AND J. RICHARDSON. 1989. Vegetation coverage and heterogeneity in a changing Everglades landscape. Unpubl. abstract, Everglades Symposium, Key Largo, Florida.

DAVIS, S. M., L. H. GUNDERSON, W. A. PARK, J. R. RICHARDSON, AND J. E. MATTSON. 1994. Landscape dimension, composition, and function in a changing Everglades ecosystem. Pp. 419–444 *in* Everglades: the ecosystem and its restoration (S. M. Davis and J. C. Ogden, Eds.). St. Lucie Press, Delray Beach, Florida.

GATES, J. E. 1995. Point count modifications and breeding bird abundances in Central Appalachian forests. Pp. 135–144 *in* Monitoring bird populations by point counts (C. J. Ralph, J. R. Sauer, and S. Droege, Eds.). USDA Forest Service, Gen. Tech. Rep. PSW-GTR-149. Albany, California.

GUNDERSON, L. H. 1994. Vegetation of the Everglades: determinants of community composition.

Pp. 323–340 *in* Everglades: the ecosystem and its restoration (S. M. Davis and J. C. Ogden, eds.). St. Lucie Press, Delray Beach, Florida.

GUNDERSON, L. H. AND W. F. LOFTUS. 1993. The Everglades. Pp. 199–256 *in* Biodiversity of the southeastern United States (W. H. Martin, S. G. Boyce, and A. C. Echternacht, eds.). John Wiley & Sons, New York.

GUNDERSON, L. H. AND J. R. SNYDER. 1994. Fire patterns in the southern Everglades. Pp. 291–306 *in* Everglades: the ecosystem and its restoration (S. M. Davis and J. C. Ogden, eds.). St. Lucie Press, Delray Beach, Florida.

HOFFMAN, W., G. T. BANCROFT, AND R. J. SAWICKI. 1994. Foraging habitat of wading birds in the Water Conservation Areas of the Everglades. Pp. 585–614 *in* Everglades: the ecosystem and its restoration (S. M. Davis and J. C. Ogden, eds.). St. Lucie Press, Delray Beach, Florida.

JAMES, F. C. AND N. O. WAMER. 1982. Relationships between temperate forest bird communities and vegetation structure. Ecology 63:159–171.

KARR, J. R. AND R. R. ROTH. 1971. Vegetation structure and avian diversity in several New World areas. Am. Nat. 105:423–435.

KLECKA, W. R. 1980. Discriminant analysis. Sage Publications, Inc., Beverly Hills, California.

KUSHLAN, J. A. 1976. Wading bird predation in a seasonally-fluctuating pond. Auk 93:464–476.

KUSHLAN, J. A. AND M. S. KUSHLAN. 1977. Breeding Bird Census. Am. Birds 31:83.

LIGHT, S. S. AND J. W. DINEEN. 1994. Water control in the Everglades: a historical perspective. Pp. 47–84 *in* Everglades: the ecosystem and its restoration (S. M. Davis and J. C. Ogden, eds.). St. Lucie Press, Delray Beach, Florida.

LOVELESS, C. M. 1959. A study of the vegetation in the Florida Everglades. Ecology 40:1–9.

MACARTHUR, R. H. AND J. W. MACARTHUR. 1961. On bird species diversity. Ecology 42:594–598.

MILLS, G. S., J. B. DUNNING JR., AND J. M. BATES. 1991. The relationship between breeding bird density and vegetation volume. Wilson Bull. 103: 468–479.

OGDEN, J. C. 1994. A comparison of wading bird nesting colony dynamics (1931–1946 and 1974–1989) as in indication of ecosystem conditions in the southern Everglades. Pp. 533–570 *in* Everglades: the ecosystem and its restoration (S. M. Davis and J. C. Ogden, eds.). St. Lucie Press, Delray Beach, Florida.

OLMSTEAD, I. C. AND L. L. LOOPE. 1984. Plant communities of Everglades National Park. Pp. 167–184 *in* Environment of south Florida: present and past II (P. J. Gleason, ed.). Miami Geological Society, Coral Gables, Florida.

PEARSON, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecol. 8:3–18.

REYNOLDS, R. T., J. M. SCOTT, AND R. A. NUSSBAUM. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309–313.

RICHTER, W. AND E. MYERS. 1993. The birds of a short-hydroperiod, *Muhlenbergia*-dominated wetland prairie in southern Florida. Fla. Field Nat. 21: 1–10.

ROBERTSON, W. B. 1955. An analysis of the breeding bird population of tropical Florida in relation to the vegetation. Ph.D. diss, Univ. of Illinois, Urbana.

ROBERTSON, W. B. AND J. A. KUSHLAN. 1984. The southern Florida avifauna. Pp. 219–257 *in* Environment of south Florida: present and past II (P. J. Gleason, ed.). Miami Geological Soc., Coral Gables, Florida.

SAS INSTITUTE INC. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute Inc., Cary, North Carolina.

SOUTH FLORIDA WATER MANAGEMENT DISTRICT. 1995. South Florida ecosystem restoration plan. South Florida Water Management District, West Palm Beach.

STEELE, B. J. 1992. Habitat selection by breeding Black-throated Blue Warblers at two spatial scales. Ornis Scand. 23:33–42.

STEVENSON, H. M. AND B. H. ANDERSON. 1994. The birdlife of Florida. Univ. Press of Florida, Gainesville.

TER BRAAK, C. J. F. 1995. Ordination. Pp. 91–173 *in* Data analysis in community and landscape ecology (R. H. G. Jongman, C. J. F. ter Braak, and O. F. R. van Tongeren, eds.). Cambridge Univ. Press, Cambridge, UK.

VIRKKALA, R. 1991. Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: a multiscale approach. Oikos 62:59–66.

WELLER, M. W. 1995. Use of two waterbird guilds as evaluation tools for the Kissimmee River restoration. Restoration Ecol. 3:211–224.

WIENS, J. A. 1989a. The ecology of bird communities, vol. 1: foundations and patterns. Cambridge Univ. Press, Cambridge, UK.

WIENS, J. A. 1989b. Spatial scaling in ecology. Functional Ecol. 3:385–397.

WILLIAMS, B. K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64: 1283–1291.

WILLSON, M. F. AND T. A. COMET. 1996. Bird communities of northern forests: ecological correlates of diversity and abundance in the understory. Condor 98:350–362.

ZAFFKE, M. 1983. Plant communities of Water Conservation Area 3A; base-line documentation prior to the operation of S-339 and S-340. South Florida Water Management District Technical Memorandum, West Palm Beach.