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Fluctuating Flows from Glen Canyon Dam and Their
Effect on Breeding Birds of the Colorado River

(U.S.) Glen Canyon Environmental Studies
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FLUCTUATING FLOWS FROM GLEN CANYON DAM
AND THEIR EFFECT
ON BREEDING BIRDS OF THE COLORADO RIVER

Terrestrial Biology
of the
Glen Canyon Environmental Studies

By

Bryan T. Brown and R. Roy Johnson
National Park Service

30 January, 1987

Abstract

Breeding birds were censused in Colorado River riparian habitat from 1984 to 1985 to determine the relative value of each major habitat zone to birds. Data were collected at ten paired study sites by means of the absolute count method. The new-high-water-zone (NHWZ) exhibited a significantly higher avian density compared to the old-high-water-zone (OHWZ). The avian diversity of both zones was similar. Avian density in several well-developed riparian areas exceeded 800 pairs/40 ha and therefore ranked among the highest avian densities reported for noncolonial breeding birds in North America.

Discriminant function analysis was used to indicate the habitat ordination of obligate riparian birds in the NHWZ. Habitat variables were measured in 0.04 ha circles centered at the nest sites of eleven species; ten variables were identified as having a substantial ability to differentiate between species. Obligate riparian birds in the NHWZ exhibited a high degree of differentiation in both the range and type of nesting habitat chosen. Bell's Vireo and Willow Flycatcher were extreme generalists, while American Coot and Blue Grosbeak were extreme specialists. American Coot, Willow Flycatcher, Common Yellowthroat, and Northern (Bullock's) Oriole were identified as management-sensitive species with respect to the effect of fluctuating flows on avian breeding habitat.

Bird nests were located from 1982 to 1985 to determine the rates of nest inundation at various dam-controlled flow levels. Data on nesting chronology and nest heights relative to both the ground and the surface of the water were measured at each nest. Fluctuating flows up to 31,000 cfs had little direct effect on breeding birds. Surplus water releases above 31,000 cfs inundated substantial numbers of Common Yellowthroat nests. Surplus water releases above 40,000 cfs inundated substantial numbers of Bell's Vireo and Yellow-breasted Chat nests; 60% of all vireo and 11% of all chat nests were inundated by releases of 62,000 cfs. The release of surplus water in June 1983 coincided with the peak of the breeding season for many species, causing a higher inundation rate of active nests. Nest inundation and habitat loss associated with the June 1983 event caused a 45% decline in Bell's Vireo density from 1982 to 1985. The extent and timing of surplus water releases can have serious consequences for some riparian breeding birds and should receive careful management attention.

Preface

Riparian birds of the Colorado River in Grand Canyon National Park have been greatly influenced by the construction and operation of Glen Canyon Dam. By preventing the annual floods which had formerly scoured portions of the riverbanks of virtually all woody vegetation, completion of the dam in 1963 and its subsequent operation allowed development of a new zone of riparian vegetation below the old-high-water-zone (OHWZ) (Carothers and Aitchison 1976, Turner and Karpiscak 1980). This new-high-water-zone (NHWZ) of the Colorado River corridor was the largest reported increase of riparian habitat in the Southwest during the last few decades, in contrast to drainages throughout the rest of the Southwest which have historically experienced a steady loss of riparian habitat with a related decline in wildlife values.

The emerging riparian vegetation of the NHWZ was quickly and vigorously colonized by breeding birds, some of which expanded their range upriver in response to the new habitat (Carothers and Johnson 1975, Carothers and Sharber 1976, Brown et al. 1983). The relatively stable water releases from the dam which allowed development of the NHWZ prevailed from 1963 until the early 1980s. During the early 1980s a series of progressively larger releases of surplus water from the dam began to occur which inundated or eroded away portions of the NHWZ, resulting in further changes to riverine bird populations within Grand Canyon.

Large releases of water from the dam which approximated pre-dam high-water conditions occurred in the spring and summer of 1980, 1983, 1984, and 1985. These large releases of water had several immediate effects on downstream riparian breeding birds and their habitat. The 20 preceeding years of relatively stable water conditions experienced by the NHWZ and its birdlife were replaced by a situation where flooding began to recur on an almost annual basis. Much of the NHWZ was temporarily inundated as a result, and many of those birds breeding in lower-lying areas experienced nest loss (Brown and Johnson 1983, 1985).

As the water from these high releases subsided, it was also evident that some portions of the NHWZ had been completely eroded away and lost. The physical structure of the remaining habitat that had been inundated was also changed. The potential for recurring high water releases in the future was great, given that the new operating criteria for the dam called for the maintenance of Lake Powell at or near maximum pool elevation, as well as for the range of fluctuating flows from the dam to increase slightly. This situation put forth several resource questions to management

regarding the future prospects for breeding birds in the NHWZ, given that the new operating criteria had the potential to induce further change in the system.

This study was designed to explore the interrelationships between the breeding birds of the Colorado River riparian systems in Glen Canyon National Recreation Area and Grand Canyon National Park and the operation of Glen Canyon Dam under current and projected future operating criteria. Fluctuating flows, meaning those daily changes in river level up to and including 31,000 cfs, were the primary aspect of dam operation addressed in this study. Flows in excess of 31,000 cfs, here referred to as surplus water releases, were the second aspect of dam operations to be addressed. The specific objectives of this study were:

1. Quantify the density and diversity of breeding birds in the OHWZ and NHWZ to determine the relative importance of each zone to the overall breeding bird community.

2. Ordinate the nesting habitat requirements of the obligate riparian bird community to determine if these resident breeding birds selected specific habitats within the NHWZ.

3. Document the effects of fluctuating water levels from the dam on riparian breeding birds, with special emphasis on obligate riparian species, and evaluate the effects of a package of possible future flow scenarios with respect to these findings.

Each of these three main objectives has been presented as a separate chapter in this report. The reason for this was that the objectives varied so widely in their methodology, scope, and meaning. However, the overall implications of the effect of the dam on downstream birds were brought together in Chapter Four in the form of a management summary with recommendations.

This project originally began in 1982 as research for a doctoral dissertation on the ecology of riparian breeding birds along the Colorado River in Grand Canyon. The unforeseen flood of June 1983 modified the focus of the research to include an examination of the effects of fluctuating water levels from Glen Canyon Dam on downstream breeding birds. This on-going research was absorbed into the Glen Canyon Environmental Studies Program in 1984, with funding provided by the Bureau of Reclamation (BOR). Additional slight modifications were made to the project at this time to answer the specific, applied management questions posed by the BOR and the National Park Service (NPS).

Acknowledgments

This project would not have been possible without the help of many people on many levels. David Wegner (Grand Canyon Study Manager), Martha Hahn-O'Neill (National Park Service), and John Thomas (National Park Service) provided invaluable direction and support as project directors and coordinators. Nancy Brian and Lauren Lucas of the Glen Canyon Environmental Studies Office also provided valuable support. Steven Carothers had substantial input to the overall project design; he also provided boats, equipment, and logistical support during the first several years of the project. Humphrey Summit Associates of Flagstaff deserves our special thanks for their logistical support from 1984 to 1985. Michael Trosset of the University of Arizona statistics department was instrumental in the development and analysis of the computer programs resulting in the habitat ordination model presented in Chapter Two. George Hill of the U.S. Geological Survey in Flagstaff provided the detailed flow printouts from the Phantom Ranch gauge for the four year study period.

Over thirty people volunteered their time as field assistants on the eleven river research trips undertaken during this study: to them we are most grateful. Field assistants who helped on two or more trips and who provided a significant amount of help were: Kathy Groschupf, Susan Jones, Kenneth Kingsley, Bill Leibfried, David Lynch, and Marie McGee.

This report was reviewed in its entirety by Nancy Brian, Steven Carothers, Reed Harris, Martha Hahn-O'Neill, Steve Hodapp, Lauren Lucas, Michael Pucherelli, and Lee Swenson. Chapter One was reviewed by Paul Krausman and Stephen Russell. Chapter Two was reviewed by William Hunter, Frances James, Paul Krausman, William Mannan, and Robert Ohmart.

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CHAPTER 1: AVIAN DENSITY AND DIVERSITY

Introduction

The pre-dam density and diversity of birds breeding in the riparian zones along the Colorado River within Grand Canyon is largely unknown. Various historic publications mention birds seen along the river, or list species hypothetically present, but no systematic study of the density and diversity of riparian breeding birds exists from that former time (Carothers and Sharber 1976, Brown et al. 1985). In contrast, the birdlife present along that upstream portion of river to be actually inundated by Glen Canyon Dam was relatively well-documented (Woodbury 1958, 1959).

The first detailed study of breeding birds along the river corridor within Grand Canyon was that of Carothers and Sharber (1976). They listed the relative and absolute densities of 38 species of breeding birds between Lees Ferry and Diamond Creek during the study period of 1974 to 1976. Their species list included those breeding birds of the riparian zones, with no differentiation between OHWZ and NHWZ, as well as species breeding in desertscrub immediately adjacent to the river. The avian densities identified by Carothers and Sharber provided historically important baseline figures for bird populations along the river during a period of rapid growth and proliferation in the NHWZ vegetation and its birdlife.

The purpose of this chapter was to identify the density and diversity of breeding birds in the NHWZ and OHWZ along the river. The specific objectives of this chapter were:

1. Quantify the number and species of birds breeding in the NHWZ and OHWZ in various river reaches.
2. Compare the density and diversity of breeding birds in the NHWZ and OHWZ to determine the relative value of each to the overall bird community.

Study Areas

Ten paired study sites in ten different river reaches were established between Glen Canyon Dam and Diamond Creek in the spring of 1984 (Table 1-1). The ten different river reaches selected for placement of the paired study sites represented the entire spectrum of riparian environments present between the dam and Diamond Creek, a distance of approximately 240 river-miles. The paired study sites (one

in the OHWZ, one in the NHWZ) were located in the largest and most well-developed stands of riparian vegetation present in each river reach as determined by personal observation and aerial photographs. The ten river reaches identified by the Bureau of Reclamation and National Park Service were used as a guide to site selection (River Miles refer to miles below Lees Ferry, River Mile 0): Glen Canyon Dam to Lees Ferry; River Miles 43-47; 70-73; 105-108; 121-124; 163-166; 168-171; 193-199; 206-209; and 220-223.

The area of each study site was calculated from aerial photographs (10/22-23/84 flight) of known scale on an electronic digital planimeter.

Methods

Breeding bird censuses were made using the absolute count method. With this method, the observer walked slowly through the small study site, stopped occasionally, and recorded each vocal or visual contact with a bird. The very small size and linear nature of the study sites, their habitat heterogeneity, and the limits of time and field work scheduling made use of this simple, absolute count method preferable to more sophisticated and time-consuming techniques such as the fixed or variable-strip census and the spot-map method (Ralph and Scott 1981).

The absolute count method called for several assumptions. The assumptions were: 1) no bird was counted more than once, 2) all male and female birds of each species were mated and nesting, with a resulting sex ratio of 1:1 (with certain exceptions, i.e. hummingbirds and cowbirds), and 3) all birds, or at least one member of a territorial pair, were detected within the small and narrow study sites.

An absolute count of each study site was made from between three to five times in the spring and early summer of 1984 and 1985. Actual census dates ranged from 10 April to 1 July 1984 and 20 April to 18 June 1985 because these times coincided with the peak of the breeding season. Censuses were conducted between 05:00 and 10:30 hours and 17:45 and 19:30 hours, even at times when weather was not favorable due to rain, high winds, or overcast skies. The latter was due to rivertrip scheduling demands: on an 18-day, oar-powered rivertrip with ten paired study sites to census, there were simply no extra days to make up for a postponed count.

The maximum number of pairs detected in any of the counts for each site was used as the final number of breeding pairs for that species. To a large extent, this compensated for the unavoidable necessity of conducting counts during the rare periods of unfavorable weather. An exception to this

Table 1-1. Location and description of OHWZ (-A) and NHWZ (-B) study sites along the Colorado River in Grand Canyon. River Miles are from Stevens (1983).

Site #	Location	River Mile*	Elev.(ft)	Area(ha)
01-A	Glen Canyon	7.4L**	3150	1.7
01-B	Lees Ferry	0.3R**-0.0R	3100	2.9
02-A	Saddle Canyon	46.9R-47.1R	2800	1.6
02-B	Saddle Canyon	46.4R-46.7R	2800	2.8
03-A	Cardenas Creek	70.8L-70.9L	2625	1.5
03-B	Cardenas Marsh	71.0L-71.1L	2625	1.7
04-A	Lower Bass Camp	108.6R	2200	0.1
04-B	Lower Bass Camp	108.6R	2200	0.1
05-A	Forster Canyon	122.8L	2075	0.6
05-B	Forster Canyon	122.7L-122.8L	2075	0.4
06-A	National Canyon	166.5L-167.0L	1750	2.2
06-B	National Canyon	166.1L-166.5L	1750	0.4
07-A	Stairway Canyon	170.7R-171.0R	1725	1.7
07-B	Stairway Canyon	171.0R-171.1R	1725	0.7
08-A	Parashant Canyon	198.0R-198.4R	1525	1.4
08-B	Parashant Canyon	198.0R-198.1R	1525	0.5
09-A	Granite Park	208.4L-208.8L	1450	5.6
09-B	Granite Park	208.7L-208.8L	1450	1.0
10-A	220-Mile Canyon	219.8R-220.1R	1375	0.9
10-B	Granite Spring Canyon	220.3L	1375	0.1

* R and L refer to river right and river left, respectively, as one faces downstream.

** These River Miles are upstream of River Mile 0 at Lees Ferry; all remaining River Miles are downstream of River Mile 0.

was the number of breeding pairs of House Finches, which were tallied only from the number of pairs present in the April census. House Finches along the river corridor nested almost entirely in March and April, making counts at that time more desirable in terms of count accuracy. In addition, larger numbers of House Finches were attracted to water in the increasingly drier months of May and June, which unnaturally inflated the perceived density of breeding pairs along the river.

Nest searches were conducted in the study sites after each census was completed to provide supplemental information. In some cases, these searches pointed out active nests of secretive species which had not been detected during the census. The discovery of an active or recently-vacated but identifiable nest in a situation such as this was treated as one pair of birds in the final data analysis.

A single bird of either sex as well as two birds of opposite sex together were counted as a pair. With this method there was a small danger of counting a male and female of the same pair as two different pairs, but it nevertheless provided a more accurate estimate of the true density.

For certain species with sex ratios that did not conform to the 1:1 assumption, this method could have resulted in error. Both Costa's and Black-chinned Hummingbirds exhibited a breeding system in which the females may outnumber the males, while the sex ratios of Brown-headed Cowbirds may vary from predominantly male to predominantly female throughout the breeding season for a variety of reasons (Mayfield 1981). Nest searches, as supplemental indicators of breeding bird density, provided much information on the true breeding density of hummingbirds. However, as cowbirds did not build and defend their own nests but instead laid their sometimes numerous eggs in the nests of other species, nest search information did not do as much to help determine actual cowbird breeding densities.

For cowbirds, the number of females observed was used to represent the number of pairs present (Stamp 1978), unless only males or juveniles were present. In this case, the presence of males or the presence of juveniles recently fledged without the presence of adults was arbitrarily chosen to represent one pair. All of these techniques may have resulted in an underestimation of true cowbird population densities.

For hummingbirds, the number of single birds of either sex was used to represent the number of pairs present, unless there were more active nests discovered than birds observed. In this case, only the number of nests present was used to indicate the number of pairs present (Stamp 1978). Nevertheless, the result probably was an underestimation of true hummingbird density.

The territory or extent of activity of a breeding pair of birds was in some cases found to be only partly within the study sites examined. An example of this was the pair of Black-headed Grosbeaks at OHWZ site O1-A in Glen Canyon. Here, both the male and the female ranged widely over both the OHWZ and NHWZ, although the actual nest was located well within the NHWZ. The final density count for OHWZ site O1-A included Black-headed Grosbeak, but only for a value of 0.5 pair. If it was determined by observation that approximately half of a territory of a pair of breeding birds was included within a study site, a value of 0.5 pair was assigned to that species for the final site count. Partial or occasional use of a study site by a pair was arbitrarily assigned a value of 0.25 pair. This value assignment for partial use was important at small sites at which no active nest were known to occur, such as Lower Bass Camp and Forster Canyon. In these instances, the assignment of a partial pair or pairs for occasional use by breeding birds may have resulted in an overestimation of the true population density at small study sites (≤ 0.4 ha).

Only birds that were breeding or potentially breeding in riparian vegetation along the river corridor were included in the tables detailing avian densities. Data on migrant and visitant species were gathered, but not analyzed in this report. Several common species of the river corridor which were only visitants to riparian vegetation from their breeding habitats in adjacent cliff or desert scrub areas were likewise excluded from the final tables. These include Turkey Vulture, American Kestrel, White-throated Swift, Black and Say's Phoebe, Violet-green Swallow, Common Raven, Canyon and Rock Wren, and Black-throated and Rufous-crowned Sparrow.

Transients occurring far in advance of the known breeding season, as determined for the river corridor in this study, were also omitted from the final counts. An example of this would be Yellow Warblers in April. Yellow Warblers do not begin to breed along the river until early May, and many individuals seen in mid-April are migrants on their way to breeding grounds further north. Only coots, doves, hummingbirds, and passerines which nested in riparian vegetation in the study area were included in the census results.

Several species of birds occurred in the study sites which were not known to breed, but were nevertheless present on a continual basis throughout the study periods. These were termed "potentially-breeding species", those that may or may not have nested on the study sites during the census period but were included in the final count because they are known or thought to breed at nearby areas in the Canyon. Males of these species exhibiting territorial behavior theoretically represented a breeding pair. These potentially breeding

species included Western Screech-Owl, Marsh Wren, Northern Mockingbird, Crissal Thrasher, Summer Tanager, and Lazuli Bunting. Although five of these six species were known to breed up sidestreams to the Colorado River or on the rims, there were no confirmed nests of these birds along the river. In addition, none of the males of these species seen along the river was known to be paired with a female. In spite of this evidence, the possibility remained that nests and females of these species were overlooked, and the males seen were assumed to represent breeding pairs in the final density counts.

Bird species diversity for each site was calculated from the formula

$$H' = -\sum \text{ of } P_i \log P_i$$

where P_i was the proportion of a given bird species present (Shannon and Weaver 1963, Pielou 1966). Evenness was calculated from the formula

$$J' = H' / \log S$$

where S was the number of species (Pielou 1966).

Cover, or percent cover, was the proportion of an area covered by the vertical projection of plant crowns to the ground surface (Schemnitz 1980). Percent cover was of greater ecological significance than plant density, while providing more precise information about actual vegetative structure (Daubenmire 1968). The following measurements on vegetative structure were taken to control for variables that potentially could have influenced avian density and diversity (Willson 1974). For this study, only cover provided by living woody plants greater than 0.5 m in height was considered. Percent canopy cover was measured in April of 1984 along 60 m of unbiased line-intercept vegetation transects in each study site after the methods of Canfield (1941). The total distance of transect length covered by living vegetation of each species was added together (so that the total could theoretically exceed 100%) and divided by 60 to generate a percent canopy cover value for each site.

Maximum canopy height was measured to the nearest 0.5 m at 15 unbiased points along each 60 m length of transect. Mean canopy height values for each site were obtained from these measurements.

Results

Avian Density. The number of pairs of breeding birds present by site and year are summarized in Table 1-2. Absolute density by species for each site by year is indicated in Appendix I.

The mean density of breeding birds in NHWZ sites was higher than that of OHWZ sites for both 1984 and 1985. When NHWZ sites were statistically compared to OHWZ sites (both years combined), the density of birds in the NHWZ was significantly greater than OHWZ bird densities (ANOVA; $F = 7.96$; $df = 1, 27$; $p = .008$). When compared on a site-by-site basis, the density of birds in the NHWZ was also significantly greater than that of the OHWZ in both 1984 (two-sided Wilcoxon signed rank test, $p=.032$) and 1985 (two-sided Wilcoxon signed rank test, $p=.024$).

Avian Diversity Index. Diversity indices (H') and evenness (J') for breeding birds by site and year are presented in Table 1-3. There was no significant difference between the diversity indices of OHWZ and NHWZ sites in 1984 (two-sided Wilcoxon signed rank test, $p=.55$) or 1985 (two-sided Wilcoxon signed rank test, $p=1.0$).

The absolute number of species per site by year in the OHWZ and NHWZ are summarized in Appendix I. These basic measures of diversity were also statistically tested for differences between zones. There was no significant difference in 1984 (two-sided Wilcoxon signed rank test, $p=.67$) or 1985 (two-sided Wilcoxon signed rank test, $p=.81$) between the number of species in the OHWZ and NHWZ when compared on a site-by-site basis.

Vegetative Influences on Avian Density and Diversity. Percent vegetative cover by species for OHWZ and NHWZ sites are presented in Tables 1-4 and 1-5. Honey mesquite (*Prosopis glandulosa*) and, to a lesser extent, catclaw acacia (*Acacia greggii*) were the dominant woody plants present in OHWZ sites below Lees Ferry. Above Lees Ferry, at Glen Canyon site 01-A, OHWZ plant composition was markedly different. There, dominant woody plants were scrub oak (*Quercus turbinella*) and single-leaf ash (*Fraxinus anomala*). This difference between sites upriver and downriver of Lees Ferry was due to the limited range of mesquite (only as far upstream as River Mile 40) and the change in climate with the increase in elevation above River Mile 40 and Lees Ferry. Salt cedar (*Tamarix chinensis*) was the dominant and ever-present woody plant of all NHWZ sites.

Total percent vegetative cover and canopy height for all sites are summarized in Table 1-6. NHWZ sites exhibited a slightly higher mean vegetative cover than OHWZ sites. However, this difference was not statistically significant when compared on a site-by-site basis (two-sided Wilcoxon

Table 1-2. Breeding bird density in OHWZ and NHWZ sites along the Colorado River in Grand Canyon, 1984-1985. Site numbers correspond to those used in Table 1-1.

Site Number	Location	Density (pairs/40 ha)			
		1984		1985	
		OHWZ	NHWZ	OHWZ	NHWZ
01	Glen Canyon- Lees Ferry	318	441	200	552
02	Saddle Canyon	538	486	300	571
03	Cardenas Canyon	747	941	613	824
04	Bass Camp	200	500	300	100
05	Forster Canyon	200	400	200	400
06	National Canyon	182	600	73	300
07	Stairway Canyon	565	857	529	1085
08	Parashant Wash	986	1200	943	1200
09	Granite Park	357	480	229	220
10	220-Mile Canyon- Granite Springs Canyon	400	200	400	400
Average Density (mean)		449	611	379	565

Table 1-3. Diversity indices (H') and evenness (J') for breeding birds in OHWZ (-A) and NHWZ (-B) study sites along the Colorado River in Grand Canyon, 1984 to 1985. Site numbers correspond to those used in Table 1-1.

Study Site	1984		1985	
	Diversity	$H'/\text{Evenness } J'$	Diversity	$H'/\text{Evenness } J'$
01-A	.9017	.9449	.8141	.9015
01-B	1.0620	.9265	.9517	.8808
02-A	.9611	.8906	.7904	.9353
02-B	1.1085	.9425	1.0237	.9190
03-A	1.0143	.9105	.5908	.5908
03-B	1.1761	.9198	1.0902	.9054
04-A	.3010	.9999	.4771	1.0000
04-B	.3010	.9183	0	0
05-A	.4771	1.0000	.4771	1.0000
05-B	.4771	.9464	.6021	1.0000
06-A	.5300	.8805	.4515	.9464
06-B	.5396	.8962	.3768	.7896
07-A	.9940	.9940	.8141	.8531
07-B	.8800	.9744	.9894	.9500
08-A	.9294	.8612	1.0605	.8619
08-B	.6065	.6065	1.0757	.9657
09-A	1.0029	.8750	1.0628	.9273
09-B	.7378	.8730	.5829	.9681
10-A	.8874	.9826	.7283	.9359
10-B	0	0	0	0

Table 1-4. Percent vegetative cover by species for OHWZ avian study sites along the Colorado River in Grand Canyon. Site numbers correspond to sites described in Table 1-1; plant names are after Lehr (1978).

Species	Percent Vegetative Cover									
	01	02	03	OHWZ 04	Site 05	Number 06	07	08	09	10
<i>Acacia greggii</i>			1	5	18	45	19	1	9	9
<i>Atriplex canescens</i>	7	7			2		4			
<i>Baccharis</i> <i>sarathroides/</i> <i>sergiloides</i>						3		3		
<i>Chrysothamnus</i> spp.	2									
<i>Celtis reticulata</i>	7							14		
<i>Condalia globosa</i>							9			
<i>Encelia farinosa</i>				5						4
<i>Ephedra viridis</i>				10						
<i>Fraxinus anomala</i>	14									
<i>Gutierrezia sarothrae</i>				1		1				
<i>Haplopappus</i> spp.				8	1		7			2
<i>Hymenoclea</i> spp.					7				1	
<i>Larrea tridentata</i>									12	16
<i>Lycium</i> spp.						7				
<i>Oenothera albicaulis</i>					1					
<i>Opuntia</i> spp.				2						
<i>Phoradendron</i> <i>californicum</i>							1			
<i>Porophyllum gracile</i>						1				
<i>Prosopis glandulosa</i>		73	56			2	37	70	50	27
<i>Quercus turbinella</i>	22									
<i>Sphaeralcea</i> spp.					2		1			
<i>Stanleya</i> spp.							1			
<i>Suaeda torreyana</i>			14							
<i>Tessaria sericea</i>						1		1		
<i>Tamarix chinensis</i>					10					
<i>Yucca angustissima</i>					9					
TOTAL COVER (%)	52	80	71	31	50	60	79	89	72	58

Table 1-5. Percent vegetative cover by species for NHWZ avian study sites along the Colorado River in Grand Canyon. Site numbers correspond to sites described in Table 1-1; plant names are after Lehr(1978).

Species	<u>Percent Vegetative Cover</u>									
	01	02	<u>NHWZ</u>		<u>Site Numbers</u>				09	10
			03	04	05	06	07	08		
Baccharis emoryi/salicifolia		11%			5	8				
Baccharis sarathroides/sergiloides						7	6	6	4	
Phragmites australis							17			
Prosopis glandulosa							6	5		
Salix exigua		6			5					
Salix gooddingii	3		34							
Tamarix chinensis	63	71	60	50	30	23	50	54	37	18
Tessaria sericea	4						15	19	28	17
TOTAL COVER (%)	70	88	94	50	40	38	94	84	69	35

Table 1-6. Percent vegetative cover and canopy height for OHWZ and NHWZ study sites along the Colorado River in Grand Canyon. Site numbers correspond to sites described in Table 1-1.

Site Number	% Vegetative Cover		Canopy Height (m)			
	OHWZ	NHWZ	OHWZ		NHWZ	
			Mean	Range	Mean	Range
01	52%	70	1.0	0-4.5	3.8	0-7.0
02	80	88	1.6	0-5.5	3.7	0-7.0
03	71	94	1.5	0-5.5	4.7	0-12.0
04	31	50	0.3	0-1.0	0.9	0-4.0
05	50	40	0.7	0-2.5	0.8	0-2.0
06	60	38	1.8	0-4.0	0.9	0-4.0
07	78	94	1.5	0-3.5	2.3	0-5.5
08	89	84	3.0	0-5.5	3.0	0-6.0
09	72	69	1.9	0-4.5	1.4	0-4.5
10	58	35	1.5	0-4.0	2.1	0-3.0
Overall Mean or Range	64	66	1.5	0-5.5	2.4	0-12.0

signed rank test, $p > 0.1$). The mean and range of canopy heights was also greater in NHWZ sites, but this difference was not statistically significant (two-sided Wilcoxon signed rank test, $p = .08$). However, a p value of .08 could have been interpreted as being marginally significant.

Discussion

Avian Density and Diversity. There were significantly more birds in the NHWZ than the OHWZ, a difference which remained constant through two years' time. Although the number of species present at any given NHWZ site may have been more or less than the number of species present at a corresponding OHWZ site for the same year, there was no overall difference between the number of species in either zone. Therefore, the number of species alone did not account for the greater number of birds present in the NHWZ.

The density of breeding birds at most OHWZ and NHWZ sites was comparable to similar habitats in the Southwest. Mean avian densities of from 379 to 449 pairs/40 ha observed in the OHWZ were similar to the 476 pairs/40 ha observed in mesquite-dominated riparian habitat along the San Pedro River in southern Arizona (Gavin and SOWLS 1975). Approximately half of the NHWZ sites exhibited densities that were similar to or less than other salt cedar-dominated riparian areas in Arizona. The 388 pairs/40 ha observed by Szaro and Jakle (1982) along a tributary of the Gila River compared well or slightly exceeded the range of 100 to 486 pairs/40 ha seen at five of the ten NHWZ sites. However, the mean avian density of the NHWZ was higher than that reported for other salt cedar habitats in Arizona. This was due to several NHWZ sites which consistently exhibited extremely high avian densities.

OHWZ sites at Cardenas Marsh and Parashant Wash as well as NHWZ sites at Cardenas, Stairway Canyon, and Parashant Wash exhibited very high avian densities which were among the highest ever reported for non-colonial breeding birds in North America. Carothers et al. (1974) reported breeding bird densities in cottonwood (Populus fremontii) forests along the Verde River of central Arizona of 847 pairs/40 ha. Avian densities of these structurally-diverse cottonwood forests were the highest breeding bird densities that have yet been reported in the literature. The range of 747 to 1200 pairs/40 ha observed in this study was comparable to or exceeded those of Carothers et al. (1974).

However substantial the avian densities observed in this study may have been, they should be examined carefully in the light of bias they may contain. The study areas along the river corridor were relatively small, ranging in size

from 5.6 ha to 0.1 ha (Table 1-1). Two factors came into play when study areas were of this size.

The first was a very high edge to habitat ratio, which tended to increase the density and diversity of birds (Odum 1959). This edge effect was also a factor in the work of Carothers et al. (1974), in which such high avian densities were reported, as their study areas ranged from 3.0 to 4.9 ha. Not only did a high degree of edge tend to increase the density and diversity of birds, but the relatively small areas of productive riparian habitat harbored breeding birds which used not only the riparian areas, but also used to a lesser extent the distinctly different but adjacent non-riparian areas.

Many riparian breeding birds ranged varying distances outside of the riparian zone, areas not included when calculating the size of the riparian study sites. An example of this was provided by Black-chinned Hummingbirds. They nested strictly in the riparian zone along the river corridor, to the extent that they would be all but absent as breeders were it not for the presence of riparian habitat. Hummingbirds foraged some distance away from their nests and out into the arid desert scrub. When the number of pairs in each study site was converted to the standard density comparison of pairs/40 ha, the concentration of nests and territory centers in the small riparian areas resulted in high comparative densities. Avian densities of a homogenous riparian area measuring a full 40 ha would almost always be less than those of a very small riparian area due to edge differences, even if the two sites were similar in vegetative species and structural composition.

The second factor was sample error. Simply, any slight miscalculation of absolute avian density in a very small study site could have been magnified many times in converting the absolute density (number of pairs actually counted at the site) to the comparative density (number of pairs per 40 ha). A miscalculation of only one pair per site, which would cause acceptable error in a 40 ha study area, could have increased or decreased the comparative density by 80 pair at a 0.5 ha study site such as the NHWZ site at Parashant Wash (08-B). There, the absolute number of birds had to be multiplied by a factor of 80 in order to make the density comparable with the standard method of reporting avian densities.

A good test of error of this sort was provided by the number of active nests found in the Cardenas Marsh study site in 1985. Census data from the Cardenas NHWZ site indicated an absolute density of 35 pairs of breeding birds in the 1.7 ha area, for a comparative density of 824 pairs/40 ha. An intensive nest search through approximately one-half of the study area after each census period revealed a total of 18 active nests, for a comparative density of 410 nests/40 ha.

The discovery of actual nests in only half of the study area therefore accounted for 51% of the observed avian density. This rate of accountability placed high confidence in avian densities resulting from census data alone.

Avian diversity in both OHWZ and NHWZ sites were generally lower than diversities reported from similar areas in Arizona. The small study sites in the river corridor supported a maximum of 15 to 17 species (Appendix I), while other Arizona riparian areas of larger size reported 13 to 26 species (Carothers et al. 1974, Gavin and SOWLS 1975, Szaro and Jakle 1982). This was due largely to the equilibrium theory of island biogeography, which states that the number of species in an isolated habitat island will increase with increasing island size (MacArthur and Wilson 1963). The relatively small diversity exhibited in riparian habitats in the study area was due to their relatively small size. Willson and Carothers (1979) substantiated this by illustrating that species richness in breeding birds increased with increasing habitat island size along the Colorado River in Grand Canyon.

Vegetative Influences on Avian Density and Diversity. The relatively slight differences between vegetative structure and percent cover in the OHWZ and NHWZ did not fully explain the significantly greater density of birds in the NHWZ. Vegetation structure and total percent cover have been positively correlated with bird species diversity (Willson 1974). The findings of no significant difference between the OHWZ and NHWZ for both avian diversity and vegetation structure went hand in hand. However, the greater range in vegetation heights in the NHWZ (up to 12 m) apparently explained the preference of certain high-canopy nesting birds in the NHWZ, birds which were largely absent from the OHWZ. These include Willow Flycatcher, Yellow Warbler, Hooded Oriole, and Northern (or, Bullock's) Oriole. However, the vegetation structure variables examined did not fully explain the higher avian densities observed in NHWZ habitats. Further work on other aspects of vegetative structure, such as foliage volume or foliage height diversity, or on availability of food resources would be needed to fully account for differences in avian density.

Conclusions And Management Considerations

The NHWZ which has developed along the river corridor since the completion of Glen Canyon Dam was host to a significantly greater number of birds than the relict OHWZ. The avian diversity of both zones was similar. Vegetation structure and percent cover alone did not account for the higher density of birds in the NHWZ, though vegetation height differences may have explained the preference of some high canopy nesters for the NHWZ.

The densities of birds in that zone were among the highest ever reported for non-colonial birds in North America, and as such deserve special attention from management. The NHWZ was, in effect, a naturalized habitat which could be considered partial mitigation for those bird populations lost when Lake Powell inundated riparian habitat in Glen Canyon. With these considerations in mind, future management actions accelerating the rate of riparian substrate erosion and the associated loss of avian breeding habitat in the NHWZ have the potential for substantially reducing overall avian densities along the river corridor.

Any management action which would accelerate the rate of riparian substrate erosion and avian habitat loss would also, in effect, serve to reduce the number of species present in the NHWZ. Any reduction in size of habitat "islands" presently existing in the NHWZ would, as predicted by the theory of island biogeography and studies in the river corridor relating to species richness, result in fewer species of birds. Conversely, management actions acting to increase sediment deposition, riparian substrate development, and the resulting habitat island enlargement would tend to increase the number of species.

Since the NHWZ supported such a significantly higher density of birds, relative to both the OHWZ in particular and Southwest riparian habitat in general, management may eventually require information as to the factors causing this difference. The most obvious and likely question to be asked would be one concerning the availability of food resources: is the NHWZ highly productive itself, or are insects emerging from the river to provide additional food to the NHWZ? If the latter possibility is the case, then the extent, timing and duration of fluctuating flows or surplus flows from the dam may indirectly have a major influence on avian densities in the river corridor through insect production.

CHAPTER 2: HABITAT ORDINATION OF OBLIGATE RIPARIAN BREEDING BIRDS

Introduction

Most birds are dependent upon specific structural vegetation types in which to breed (James 1971). This basic physical configuration of the ecological niche, the niche-gestalt of James (1971), has been established as a workable model of species differentiation in a number of avian habitat studies during the last two decades (see Rice et al. 1983 for literature summary). The purpose of this chapter was to show that habitat ordination, and therefore habitat selection, existed among obligate riparian breeding birds in the NHWZ of the river corridor. Habitat ordination suggests useful possibilities for long-term avian habitat management via water releases from Glen Canyon Dam.

Habitat ordination was defined as an arrangement of transformed vegetation-structure variables that has been ordered to produce a visual synthesis of species habitat relationships along a complex environmental gradient (Whitmore 1977). The graphic differentiation achieved in the model indicated which variables were important in habitat selection, as well as determining the range of habitat use. Habitat ordination was typically determined by using multivariate statistical techniques to analyze vegetative data gathered in 0.04 ha circles centered either at nest sites (Connor and Adkisson 1977, MacKenzie and Sealy 1981, MacKenzie et al. 1982) or at male perch sites (James 1971; Whitmore 1975, 1977; Smith 1977) within the territory of a pair of breeding birds.

Obligate riparian birds were those which were completely dependent on riparian habitat for breeding in the Southwest (Johnson et al. 1977). The eleven species of obligate riparian breeding birds which occurred in the study area are listed in Table 2-1. Many of these species occurred in mesic nonriparian situations in other parts of North America, and were dependent upon riparian habitats only in the Southwest where water was a limiting factor. One of the eleven, Bell's Vireo, occasionally nested in dense, nonriparian vegetation of the Southwest lowlands. However, in the Grand Canyon region, the dense lowland vegetation required for its breeding occurred only in riparian areas. The category of obligate riparian birds considered here also included species normally associated with lacustrine and marsh habitats (American Coot and Common Yellowthroat) or agricultural and urban areas (Great-tailed Grackle) in the Southwest.

Obligate riparian breeding birds were chosen for this study due to their narrow range of habitat requirements. Birds

Table 2-1. Species of obligate riparian birds along the Colorado River in Grand Canyon, species codes, sample size of nests by zone, and abundance and distribution.

Species	Species		Total Sample (N)	No. Nests		% in NHWZ
	Code	Status*		OHWZ	NHWZ	
American Coot	AC	R,r	3	0	3	100
Willow Flycatcher	WF	R,r	8	0	8	100
Bell's Vireo	BV	C,w	47	9	38	81
Yellow Warbler	YW	C,w	20	1	19	95
Common Yellowthroat	CY	C,w	15	0	15	100
Yellow-breasted Chat	YbC	C,w	21	2	19	90
Blue Grosbeak	BG	U,w	4	1	3	75
Indigo Bunting	IB	R,w	2	1	1	50
Great-tailed Grackle	GtG	U,w?	1	0	1	100
Hooded Oriole	HO	U,r	7	0	7	100
Northern (Bullock's) Oriole	BO	C,r	11	0	11	100
Total			139	14	125	\bar{X} = 90

* Abundance codes: C = abundant to common, U = fairly common to uncommon, R = rare. Distribution codes: w = widespread where riparian vegetation is present, r = geographically restricted. ? = uncertain or in a state of change.

Table 2-2. Vegetative parameters of each circular plot that were included in the analysis.

Parameter	Abbreviation
Length of edge	Ledge
Foliage volume at 1-2 m	Vol2
Foliage volume at 2-3 m	Vol3
Foliage volume at over 3 m	Vol4
Maximum canopy height	Mcanht
No. of trees in plot	Alltre
No. of salt cedar shrubs	Tach
No. of <u>Baccharis</u> shrubs	Basa
No. of <u>willow</u> shrubs	Saex
No. of arrowweed shrubs	Tese

limited to riparian areas were more sensitive to the effects of water management practices of upstream water control structures which manipulated their nesting habitat. Tributaries to the Colorado River in Grand Canyon also supported populations of the birds in question. However, the river corridor hosted the great majority (50-90%, depending on the species) of the overall populations of these birds in the entire Grand Canyon region (Brown and Johnson 1985). This was because 50-90% of the available habitat for any given species of obligate riparian breeding bird was in the river corridor. For this reason, any habitat changes along the river resulting from the operations of Glen Canyon Dam have the potential for disproportionately affecting the regional well-being of these sensitive species.

Study Area

Nests of obligate riparian birds were located at a number of sites in the river corridor between Glen Canyon Dam and Diamond Creek. The river corridor was defined as the aquatic, marsh, and riparian habitats up to and including the OHWZ vegetation. Sites from which the majority of data were obtained included: Lees Ferry, Saddle Canyon, Cardenas Marsh, Stairway Canyon, Lava Falls, Whitmore Wash, Parashant Wash, and Granite Park.

Methods

Sampling Procedures. Nest-site and perch-site vegetative structure may differ significantly for some species, primarily birds of open areas (Collins 1981). Therefore, nest sites were chosen as points around which to measure habitat variables, as opposed to male perch sites. Nest-site measurements were used because, in finding nests, additional information was obtained on nest location and basic breeding biology. The narrow and highly patchy nature of riparian habitat in the study area was also a factor in favor of using nest-site measurements in order to illustrate the actual differentiation between species.

Nests of obligate riparian birds were located by systematic ground searches of both riparian zones by up to six skilled observers from April through July, 1982 to 1985. Observers moved in close formation through representative samples of each habitat zone to locate nests. Time spent searching each riparian habitat zone was in direct proportion to the extent of each habitat at individual study sites. For example, the OHWZ:NHWZ ratio of nest searching time was 25:75 at sites whose vegetation was one-fourth mesquite in the OHWZ and three-fourths tamarisk in the NHWZ.

Habitat and vegetative variables were measured within 0.04 ha circular plots centered at nest sites (James and Shugart 1970, James 1971). The ten variables that were analyzed in this study are indicated in Table 2-2.

Maximum canopy height, or the height of the tallest vegetation within each circular plot, was measured to the nearest 1 m. The total number of trees of all sizes within each plot was counted: trees were classified as all woody vegetation with a diameter-breast-high (dbh) of greater than 7.5 cm. The length of edge was measured in each circular plot: edge was defined as the border between two structurally distinct vegetation types (Schemnitz 1980) or the perimeter between a patch of vegetation and an open area (Martinka 1972) such as a sandy beach, cobble bar, river or open desertscrub.

The number of shrubs of the four most abundant and widespread species in the study area was recorded in two perpendicular armlength transects at dbh across the center of each circular plot. The shrubs considered were salt cedar (tamarisk), coyote willow (Salix exigua), arrowweed (Tessaria sericea), and the seepwillow and waterweed complex (Baccharis sarathroides and sergiloides). These two species of Baccharis were treated as one species due to their ecological, structural, and taxonomic similarity (Turner and Karpiscak 1980). Shrubs were defined as woody vegetation at least 1.5 m in height with a dbh of less than 7.5 cm.

An index to percent foliage volume was calculated by using frequency counts of foliage in each of four foliage layers (0-1 m, 1-2 m, 2-3 m, greater than 3 m) at 20 non-biased points within each circular plot (Mauer and Whitmore 1981). At each point, the presence or absence of foliage (living or dead plant material) in each of the layers was recorded. This resulted in a frequency representing the probability of encountering foliage in any layer within a given distance around nests.

Both active nests and those that were recently vacated but identifiable were used in the analysis. Without the presence of adults or eggs that exist at an active nest, positive identification could be made only on the recently vacated nests of Bell's Vireo, Common Yellowthroat, Hooded and Northern (Bullock's) orioles. Identification of these nests was possible because of their characteristic construction and placement.

Statistical Techniques. Classical discriminant analysis (CDA), a multivariate statistical technique, was used to classify species based on habitat variables measured at nest sites. CDA is the most common classification technique currently used. Fisher (1936) first proposed it for the case of two groups; generalization to several groups is at

least as old as Rao (1952). CDA was first applied to avian habitat ordination by James (1971).

CDA was best suited to multivariate normal data. For this reason, standard transformations were performed on the raw data to comply with the normality assumption. Count data (e.g. number of trees) were converted to their square roots, while the arcsine of the square root was used on all proportional data (e.g. percent foliage volume). All distance data (e.g. length of edge) were transformed to their logarithms. The final classification analyses were performed on the transformed data.

The final habitat ordination analysis considered only the NHWZ. Besides differing radically from the OHWZ, the majority of obligate riparian birds in the river corridor nested exclusively or primarily in the NHWZ (Table 2-1). Only 10% of the nests of obligate riparian birds were located in the OHWZ. These OHWZ nests were largely those of Bell's Vireo, the only common obligate riparian species to make widespread use of that habitat type. To gain further insight into the habitat differences between the two zones (as indicated by nest site selection), a separate CDA was performed in which nest sites were classified as OHWZ or NHWZ.

Habitat ordination was based on the five common species of obligate riparian birds in the river corridor (Bell's Vireo, Yellow Warbler, Common Yellowthroat, Yellow-breasted Chat, and Northern (Bullock's) Oriole). The model was subsequently applied to the six rarer species, but sample sizes were insufficient to permit their inclusion in its derivation.

The ten habitat variables chosen for the final analysis (Table 2-2) were selected by preliminary analysis directed at finding the most useful set of variables. Rejected variables had a poor ability to differentiate between species. These rejected variables included: the total number of shrubs, foliage volume from 0 to 1 m, width of the riparian zone, and the number of various species of rarer shrubs.

CDA constructed a new set of habitat variables from the original ones. These new variables, called discriminant functions or discriminant coordinates, were linear combinations of the original variables. The first discriminant function was chosen from all possible coordinates to maximize the F-ratio of the between-groups variation to the within-groups variation. The second discriminant function was chosen from all coordinates perpendicular to the first to maximize the same F-ratio; the third discriminant function was chosen from all coordinates perpendicular to the first two (Gnanadesikan 1977).

The ten original habitat variables contained a considerable amount of redundant information. Variables such as number of trees, maximum canopy height, and foliage volume above 3 m were highly correlated and their information content overlapped. For this reason, it was never necessary to consider more than the first three discriminant functions and therefore a substantial reduction in dimensionality was achieved. CDA actually constructed the lower dimensional space that was best for classification purposes. The discriminant functions were computed using Statistical Package for the Social Sciences (SPSS) software (Nie et al. 1975). Nest sites were classified by computing their distances (in appropriate standard deviations) from the five species means and choosing the closest.

Several lines of analysis were pursued after the discriminant space (habitat space) was constructed. First, the species means were computed and compared. This allowed an inspection of the average habitat preferences of each species. Differences between species were easily interpreted by considering the standardized coefficients of the original variables on the relevant discriminant function.

Information about average habitat did not identify habitat generalists or specialists. Therefore, the dispersion characteristics of each species had to be considered. Species covariance matrices were computed in order to compare habitat generality in terms of (1) species standard deviation in the first discriminant function and (2) species concentration ellipsoids (points within one standard deviation of the species mean) in the first two discriminant functions.

Finally, a measure of the statistical distance between species was derived in three dimensions in order to indicate the extent to which pairs of species differed with respect to their habitat preferences. The statistic used was analogous to the univariate t-statistic, and reflected the importance of differences in species means relative to the ranges of the species in question. This statistic was the square root of the test statistic proposed by James (1954) for use in a two sample problem with multivariate normal distributions having unequal covariance matrices (Seber 1984).

Results And Discussion

Zone Differences. CDA correctly classified the habitat zone (OHWZ or NHWZ) of 94% of the nest sites, with 100% of the variance being explained by the first discriminant function. The variables most important in differentiation were: number of honey mesquite, number of salt cedar, and the amount of foliage volume above 3 m. This extraordinarily high degree of separation justified restricting the habitat ordination analysis to the NHWZ.

Analysis of Discriminant Space. A CDA of the five most abundant species using all ten habitat variables correctly classified 64% of all nests (Table 2-3). All Common Yellowthroat nests were correctly classified and nearly perfect classification was achieved for Bullock's Oriole. Bell's Vireo nests were correctly classified in more than half the cases. However, Yellow Warbler nests were incorrectly classified in more than half of all cases, and even poorer classification was obtained for Yellow-breasted Chats. CDA was unable to differentiate well between warblers and chats due to an overlap in their habitat use.

Three discriminant functions were sufficient to explain 96% of the variation between species (Table 2-4). This was a higher percentage than that achieved by most previous habitat ordination models (James 1971, Connor and Adkison 1977, Raphael 1981). The data for each variable incorporated into the different functions is summarized in Appendix II.

The first discriminant function loaded primarily on the number of Baccharis shrubs, maximum canopy height, the number of salt cedar shrubs, and length of edge (Table 2-4). The first function was therefore primarily associated with three interrelated factors: (1) the relative density of the two most common and widespread shrubs (decreasing values indicate increasing shrub density), (2) overall vegetative height (increasing values indicate taller vegetation), and (3) habitat patchiness (increasing values indicate more patchy habitats). Length of edge was a rough, but effective index to habitat patchiness. The need for such an index was suggested by James (1978) although Martinka (1972) had previously found length of edge to be a significant factor in the habitat preferences of Blue Grouse. The first function alone accounted for 53% of the variance.

The second function loaded primarily on the three foliage volume variables (1-2 m, 2-3 m, and greater than 3 m) and the number of trees present (Table 2-4). This function accounted for 31% of the variation.

The third function loaded primarily on foliage volume above 3 m, the number of trees present, and maximum canopy height (Table 2-4). It accounted for 12% of the variance.

Table 2-3. Classification for the five primary species upon which the analysis was based. Species codes as in Table 2-1.

Actual Species	Number of Cases (N)	BV	Predicted Species			CY
			YbC	YW	BO	
Bell's Vireo	38	25	7	1	1	4
Yellow-breasted Chat	19	3	6	6	2	2
Yellow Warbler	19	1	3	9	3	3
Northern (Bullock's) Oriole	11	0	0	1	10	0
Common Yellowthroat	15	0	0	0	0	15

Overall percent of cases correctly classified - 63.7%

Table 2-4. Standardized canonical discriminant function coefficients.

Variable	Function 1	Function 2	Function 3
Percent of total variance accounted for	53.4	31.0	12.2
Cummulative percent of variance accounted for	53.4	84.4	96.6
Standardized coefficients			
Ledge	.387	-.147	.327
Vol2	-.072	-.991	.351
Vol3	.380	1.265	.161
Vol4	-.184	-.454	-.978
Mcanht	.419	-.061	.403
Alltre	.293	.543	.912
Tach	-.394	-.058	.254
Basa	-.587	.248	.259
Saex	.259	.142	-.017
Tese	-.230	.040	-.041

Average Habitat Preferences. The average location of each species in the habitat space was indicated by plotting the species mean vectors (Table 2-5) in three-dimensional habitat space (Fig. 2-1). Such an illustration was necessary to fully capture the complexity of the ordination; however, projections onto each pair of discriminant functions gave two-dimensional illustrations (Fig. 2-2) that were more accurate and comprehensible. The latter permitted a critical analysis of habitat relationships between species.

The first discriminant function served to separate the species into three rough classes. The first class (smallest scores on the first function) preferred lower, denser vegetation dominated by salt cedar and Baccharis shrubs. This class included Bell's Vireo, Common Yellowthroat, and Yellow-breasted Chat. The second class (largest scores on first function) preferred a combination of vegetation that was either taller, patchier (more open), or exhibited fewer salt cedar and Baccharis shrubs. This class included the grackle, coot, and Northern (Bullock's) Oriole. The third class was composed of species whose habitat preferences were between those of the other two.

Differences with respect to the second discriminant function were useful in separating marsh-nesting species from those that preferred more trees or more foliage volume above 3 m. Common Yellowthroat, coot, and grackle preferred marshy habitats with dense foliage up to approximately 2 m.

The third discriminant function did not separate any major class of species. Instead, the third function refined the discrimination based on complex interactions between the original habitat variables. This function loaded strongly on the total number of trees and foliage volume above 3 m, but in opposite directions. For example, further differentiation was achieved for Hooded and Northern (Bullock's) Oriole, Willow Flycatcher, and Yellow Warbler by using this function. The four species were only slightly dissimilar in their preference for taller vegetation. However, the third function indicated that it was the structure of the taller vegetation that separates the species. The flycatcher and warbler preferred tall vegetation with more foliage volume above 3 m and fewer trees, while orioles preferred tall vegetation with less foliage volume above 3 m and more trees.

Breadth of Habitat Use: Generalists vs. Specialists. All information about species dispersion is contained in the group covariance matrices which are presented in Appendix II-1. However, a simpler, rough index to the range of habitat use for each species was obtained by comparison of the species standard deviation with respect to the first discriminant function (Table 2-6). A more sophisticated

Table 2-5. Species mean vectors for each of the three discriminant functions.

Species	Function 1	Function 2	Function 3
American Coot	1.10	-2.82	0.03
Willow Flycatcher	0.99	0.03	-0.64
Bell's Vireo	-1.06	0.24	0.03
Yellow Warbler	0.99	0.38	-0.79
Common Yellowthroat	0.07	-1.74	-0.05
Yellow-breasted Chat	0.11	0.39	0.27
Blue Grosbeak	0.62	0.72	-0.10
Indigo Bunting	0.43	0.37	0.10
Great-tailed Grackle	1.53	-0.51	-0.90
Hooded Oriole	0.85	1.45	0.62
Northern (Bullock's) Oriole	1.68	0.21	0.85

Table 2-6. Generalist and specialist species of obligate riparian birds within the NHWZ as indicated by values of standard deviation in the first discriminant function of each species. Only those birds with sample sizes larger than one are indicated.

Standard deviation of discriminant function 1	Species	Range of habitat use
1.22	Bell's Vireo	 Generalist Specialist
1.15	Willow Flycatcher	
.98	Yellow Warbler	
.97	Yellow-breasted Chat	
.97	Hooded Oriole	
.62	Common Yellowthroat	
.44	Bullock's Oriole	
.19	Blue Grosbeak	
.17	American Coot	

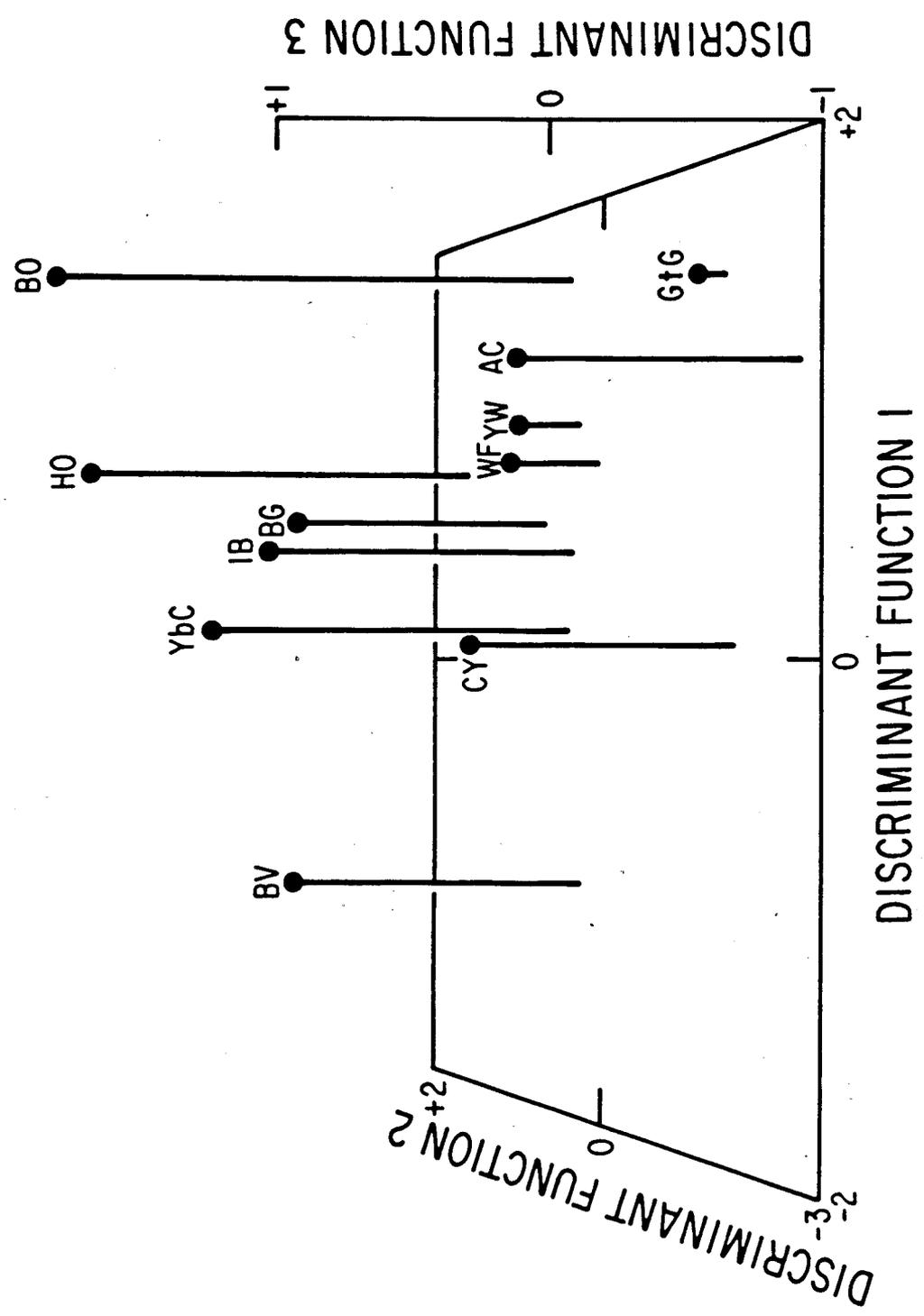


Figure 2-1. Location of each species in three-dimensional habitat space, as indicated by species mean vectors. Species codes as in Table 2-1.

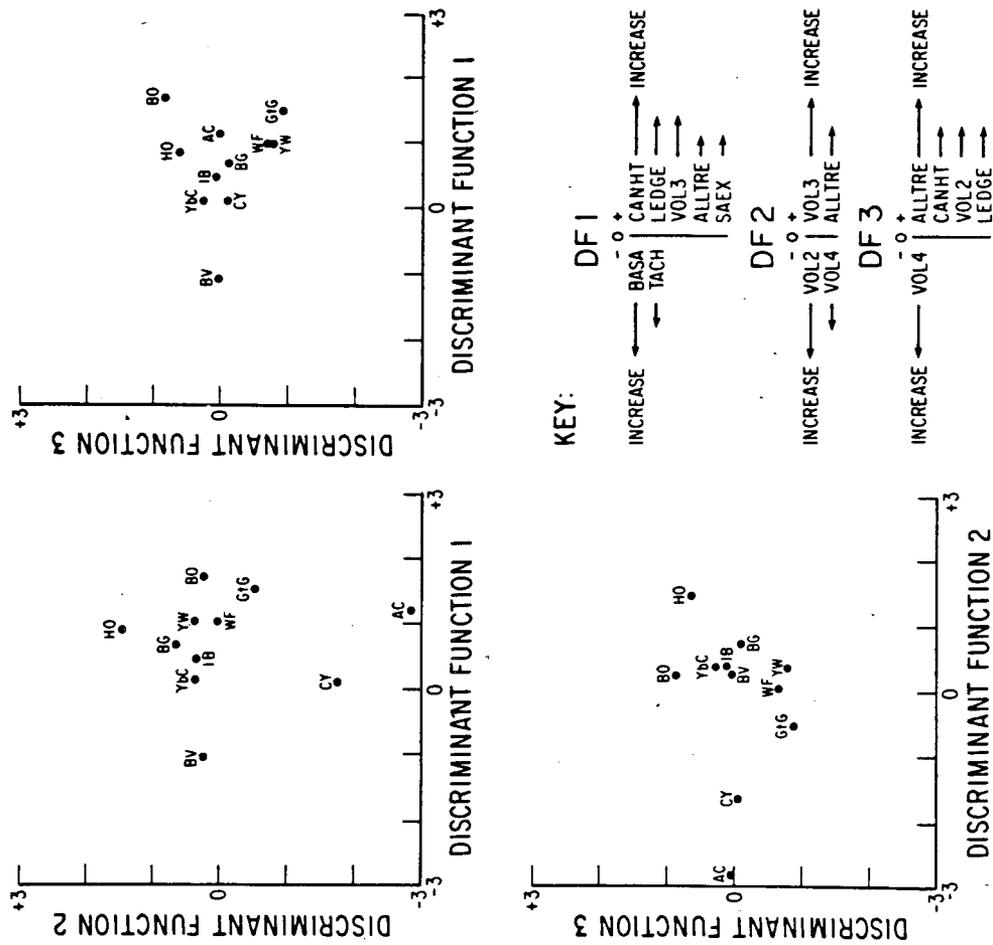


Figure 2-2. Location of each species in two-dimensional habitat space, as indicated by species mean vectors. Species codes as in Table 2-1; vegetative parameter codes as in Table 2-2.

description was the group concentration ellipsoid with respect to the first two discriminant functions (Fig. 2-3).

Table 2-6 suggested that the species with the largest range of habitat use (generalist) was Bell's Vireo; this was consistent with Figure 2-3. Table 2-6 also suggested that American Coot exhibited the smallest range of habitat use (specialist), although Figure 2-3 revealed that the coot has a slightly wider range of habitat use than Blue Grosbeak. Overall, Bell's Vireo and Willow Flycatcher were the most extreme generalists within the river corridor, while the Yellow Warbler, Yellow-breasted Chat and Hooded Oriole were moderate generalists. Common Yellowthroat and Northern (Bullock's) Oriole were moderate specialists. The most extreme specialization was shown by the grosbeak and coot.

If riparian vegetation studies demonstrate that fluctuating flows are altering the vegetative character of the NHWZ, then special attention should be focused on the long-term effect of this alteration on specialists. Moreover, information on the range of habitat use can be combined with information presented elsewhere in this study to gain further management insights. For example, three of the four habitat specialists (yellowthroat, coot, Bullock's Oriole) nested very close to the water's edge (Chapter 3). Their habitat specialization, combined with their proximity to water, identified them as being much more susceptible to habitat alterations caused by fluctuating flows or surplus water releases.

Ecological Similarity. The locations of the species mean vectors roughly illustrated the degree of ecological similarity between species. Figures 2-1 and 2-2 did not, however, take into account the wide differences in range of habitat use that have just been discussed. Simultaneous plotting of the species concentration ellipsoids (Fig. 2-4) helped to illustrate the effective overlaps in habitat use. This information was quantified by computation of the statistical distances between the species means (Table 2-7). Small distances represented ecological similarity between species pairs; large distances indicated ecological dissimilarity.

American Coot was the only species whose ellipsoid did not overlap with any other species. The Common Yellowthroat ellipsoid only overlapped that of Willow Flycatcher. The flycatcher's ellipsoid was the largest, totally encompassing those of Yellow Warbler, Blue Grosbeak, and Northern (Bullock's) Oriole, and partially encompassing those of the vireo, chat, and Hooded Oriole.

These inferences were strengthened by analysis of the statistical distances. American Coot and Bell's Vireo were the most dissimilar species, indicating that management actions affecting one would not necessarily affect the

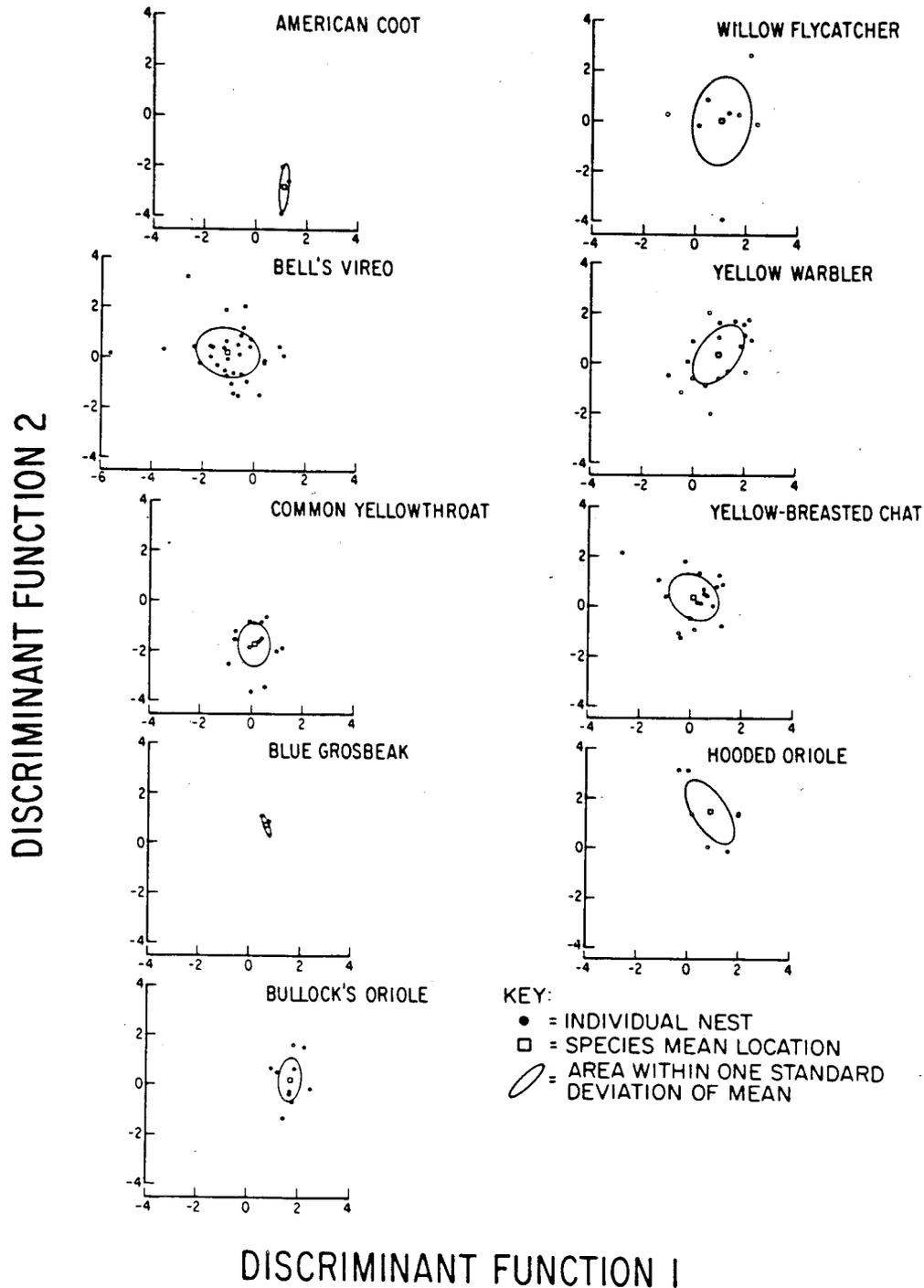


Figure 2-3. Plots in two-dimensional habitat space of (1) individual nest sites, (2) mean vector, and (3) concentration ellipsoid for each of the nine species with a sample size of at least three nests.

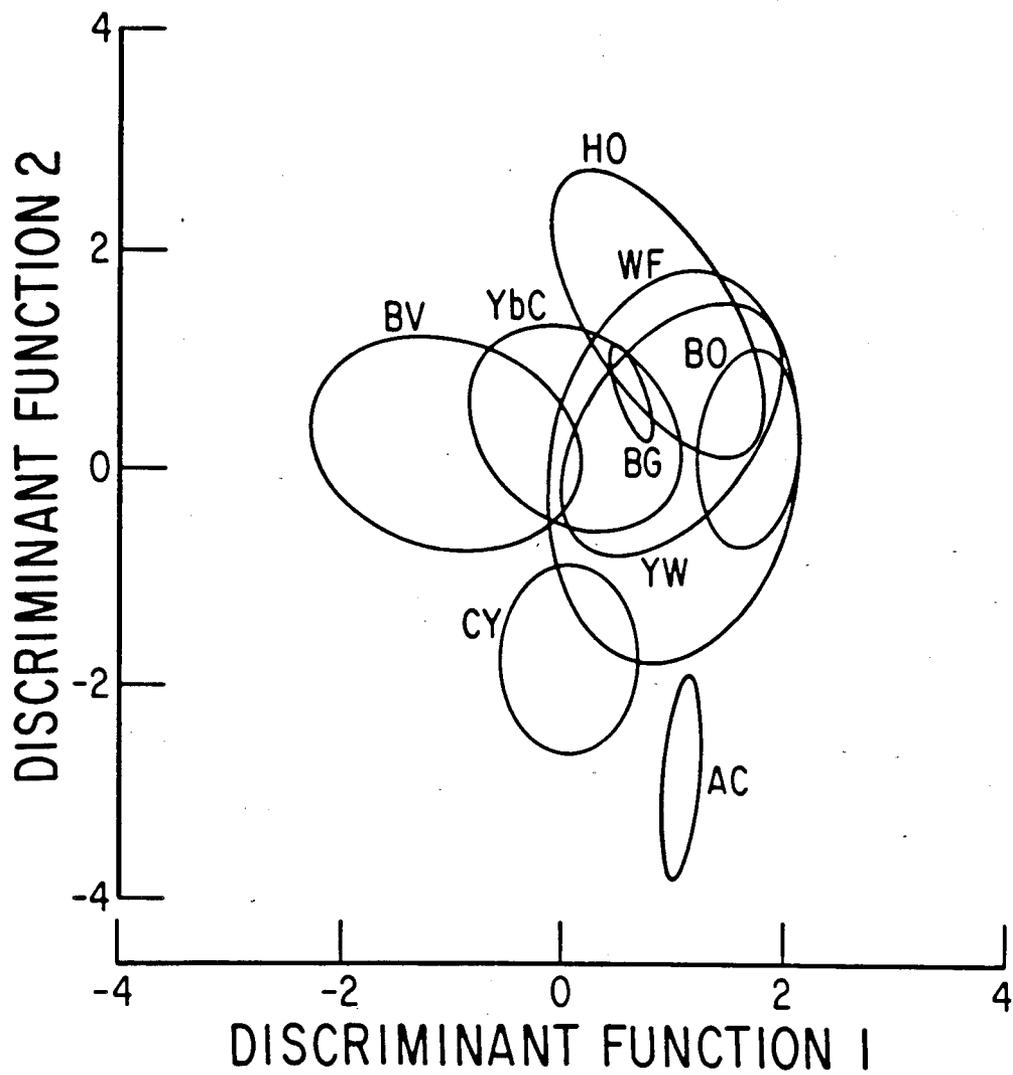


Figure 2-4. Simultaneous plot of species concentration ellipsoids in two-dimensional habitat space. Species codes as in Table 2-1.

Table 2-7. Statistical distances between species means, based on all three functions. Only those species with a sample size of greater than or equal to three nests are included. Species codes as in Table 2-1.

Species	Relative statistical distances*							
	WF	BV	YW	CY	YbC	BG	HO	BO
AC	3.6	15.2	6.5	6.8	9.1	6.9	8.3	7.5
WF		5.5	0.6	4.2	2.9	1.4	2.3	2.8
BV			7.1	8.1	4.2	10.1	9.2	11.7
YW				6.3	3.7	1.8	5.9	6.2
CY					7.3	10.8	11.8	10.5
YbC						3.2	5.1	6.6
BG							2.4	8.1
HO								3.4

* As indicated by the square root of the James test statistic.

other. Willow Flycatcher and Yellow Warbler exhibited the greatest ecological similarity, a similarity reinforced by the observation that active nests of the two species were occasionally found less than 4 m apart. From a management point of view, the flycatcher and warbler could be treated as one species. However, the danger of creating groups of similar species has been pointed out by James (1971), who noted that the choice of variables may influence the results to such an extent that caution is advised in the interpretation of group relationships. In general, the coot was the most different from all other species. Bell's Vireo was the next most different from other species. Willow Flycatcher and Yellow Warbler were the two species consistently closest to all other species.

Another approach to ecological similarity was to consider the proximity of each species to the average nesting habitat exploited by all species. Thus, species ellipsoids which were farthest from the center of the habitat space represented the most unusual habitats. From a management perspective, the species with the most unusual or restricted habitat were those which may require special attention. American Coot and Bullock's Oriole were farthest from the central habitat space. Both were restricted to the NHWZ and nested close to water; therefore they would be influenced the most by fluctuating flows or surplus water releases.

Possible Sources of Error. Because some sample sizes were small, caution should be exercised in making inferences about any of the six rarer species. The size of their concentration ellipsoids was reassuring (note how tightly clustered are the nest sites of American Coot and Blue Grosbeak, each with a sample size of only three) and suggested that these data were surprisingly reliable. However, only a small amount of additional data could have a radical effect. Moreover, since the habitat space was constructed without reference to these species, variables may have been omitted that were critical to them. For example, Willow Flycatcher, here identified as a generalist, may have specialized with respect to a variable not included in the CDA.

The NHWZ was also in an early successional stage (< 20 years old) of development. For this reason, habitat relationships within the bird community can be expected to change with the passage of time and continued plant succession. Therefore, the model created here has an estimated useful lifespan of approximately 15-25 years.

Conclusions And Management Considerations

Obligate riparian birds in the NHWZ of the river corridor exhibited a high degree of habitat differentiation in their

choice of nest sites. The species mean habitat location illustrated their average habitat preferences. A habitat model created for these eleven species of birds indicated the presence of both habitat generalists and habitat specialists. Bell's Vireo and Willow Flycatcher were the most extreme generalists, while American Coot and Blue Grosbeak represented the most extreme specialists. The difference between species was shown by a comparison of the statistical distances between species mean vectors. Bell's Vireo and American Coot were the most widely separated species; Willow Flycatcher and Yellow Warbler were the most closely associated. The flycatcher and the warbler were also consistently located closest to all other species.

Management of obligate riparian birds in the river corridor has been effectively achieved by managing their breeding habitat in the NHWZ. Habitat management in this zone is, and has previously been, a function of controlled, fluctuating flows from Glen Canyon Dam. The habitat model presented in this chapter can be used alone to predict the effects of management actions on the birds involved. The model is a much more powerful tool, however, when used in combination with other information presented in this study.

Above all, management should strive to maintain the current diversity of habitat types present in the NHWZ. The model indicated that a wide range of vegetation structure was essential to the group of eleven species under consideration. If future management actions alter conditions in the NHWZ, and if these alterations could be adequately measured, then the effects on any given species could be predicted.

Habitat specialists were the species most in need of attention from management with regard to the potential effects of fluctuating flows on their breeding habitat. Those habitat specialists that were (1) restricted to the NHWZ, (2) of rare or localized occurrence, and (3) nested closest to the water's edge or in marshy areas deserve the most careful attention. This management-sensitive group would include American Coot, Common Yellowthroat, and Northern (Bullock's) Oriole. The coot, however, was only known to breed irregularly (in years when river flow was unusually stable (coots may have only nested in 1985), and therefore should not receive the priority of the other two. Willow Flycatcher should also be included in the management-sensitive group. Even though the flycatcher appeared to be a habitat generalist in the localized areas in which it occurred, it was rare and met all the other criteria of a management-sensitive species outlined above.

Those species intermediate in habitat use between generalists and specialists, and especially those which nested to some extent in the OHWZ, will do well as long as typical NHWZ habitats are maintained. Typical NHWZ habitats

were diverse and represented a relatively early successional stage of riparian shrubs and trees in a narrow, complex mosaic with open areas. Continued successional development may favor older, taller, more dense vegetation types in this zone, a situation which might not be favorable to specialists such as Blue Grosbeak. A scenario of this sort could require some management action to maintain earlier successional stages to provide young, low shrubs and open areas favored by some obligate riparian birds. Occasional flooding or other disturbances to portions of the NHWZ could be beneficial to this end by mimicking the natural processes that control succession, provided that riparian substrate erosion and subsequent habitat loss associated with surplus water releases were not excessive. Habitat loss through riparian substrate erosion should be a major concern with respect to the nesting habitat required by obligate riparian birds.

CHAPTER 3: EFFECT OF FLUCTUATING WATER LEVELS AND SURPLUS
WATER RELEASES ON RIPARIAN BREEDING BIRDS

Introduction

Prior to the construction of Glen Canyon Dam in 1963, annual floods on the Colorado River through Grand Canyon averaged 86,000 cubic feet per second (cfs) (Turner and Karpiscak 1980). Floods of up to 300,000 cfs through the Canyon were estimated to have occurred within historic times. Glen Canyon Dam prevented the annual floods which had previously scoured away virtually all vegetation below the pre-dam high water mark, and in doing so created a dense new zone of riparian habitat in the pre-dam flood zone (Turner and Karpiscak 1980). This NHWZ vegetation was colonized by riparian birds within the next decade.

Annual maximum water releases from the dam during the period from 1966 to 1979 were approximately 31,000 cfs (Fig. 3-1). The vegetative colonization of the NHWZ was limited by these maximum water releases in much the same way as the pre-dam floods maintained the OHWZ vegetation above the pre-dam high water mark: after 1966, any emergent vegetation below the approximately 30,000 cfs level was scoured away. As the NHWZ vegetation spread downslope to the new edge of the river, riparian breeding birds colonizing the new habitat likewise began nesting in this developing vegetation at the river's edge.

This relatively stable situation prevailed until 1980, when a series of high water releases from the dam began to occur. The filling of Lake Powell behind Glen Canyon Dam for the first time in 1979, combined with unusually heavy snowpack in the Colorado River drainage in the winters of 1979-80, 1982-83, 1983-84, and 1984-85 resulted in surplus water releases from the dam much higher than the previously-recorded post-dam maximum. In June 1980, a record release of 49,889 cfs occurred, while in June 1983 an even greater flow of 93,200 cfs was released from the dam (Fig. 3-2). High water in May and June of 1984 and 1985 sent the river up over the 40,000 cfs level. Without exception, these surplus water releases all coincided exactly with the peak of the breeding season for many riparian birds nesting along the river corridor in Grand Canyon.

These spring high water releases caused the river to overflow its newly-stabilized banks, inundate the NHWZ riparian habitat to varying depths depending upon local geomorphology and channel configuration, and to scour away a portion of NHWZ habitats in lower-lying areas. The purpose of this chapter was to document the effects of surplus water releases and fluctuating flows on those riparian birds

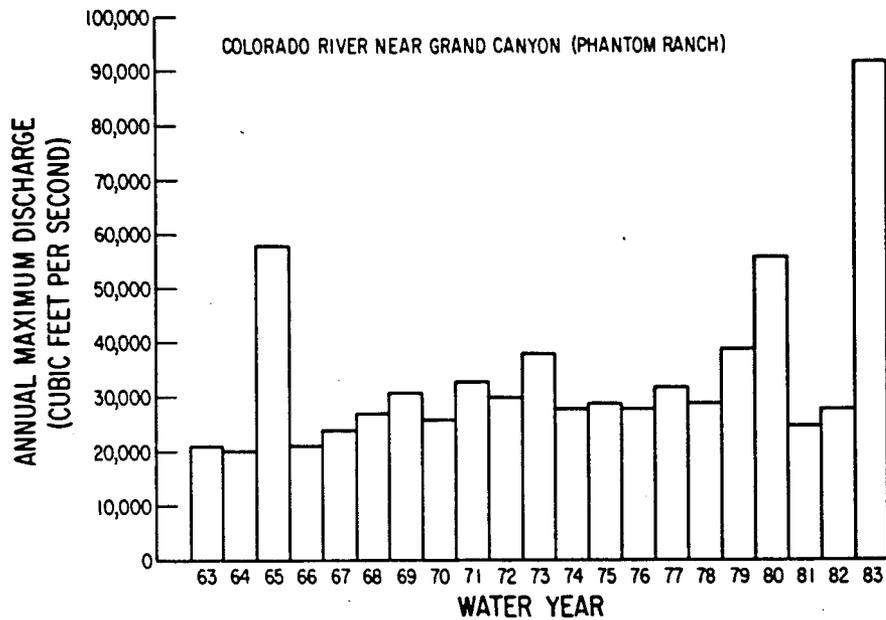


Figure 3-1. Annual maximum discharge of the Colorado River in Grand Canyon, 1963-1983.

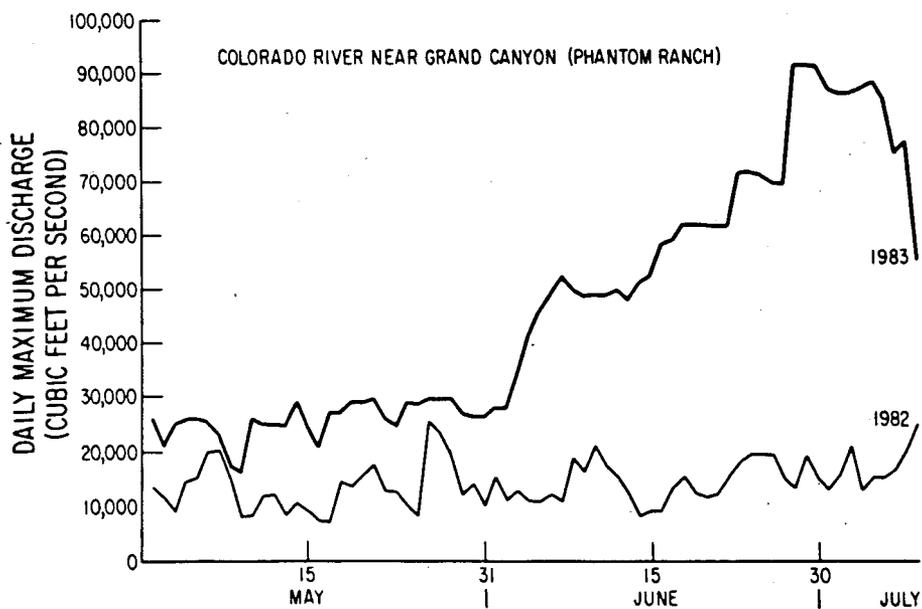


Figure 3-2. Daily maximum discharge of the Colorado River in Grand Canyon during the spring of 1982 (a normal year) and 1983 (a year of exceptionally high water).

breeding along the river corridor, with special emphasis on the commonly-occurring obligate riparian species. Surplus water releases were those spring and summer releases in excess of maximum powerplant discharge of 31,000 cfs; fluctuating flows were those daily releases at or below maximum powerplant discharge.

The specific objectives fulfilling the purpose of this chapter included:

1. Document the extent of nest inundation experienced by selected riparian breeding birds under varying flow levels, using the high water of June 1983 as a primary example.
2. Document any changes in avian densities under pre- and post-1983 conditions.
3. Indicate the long-term effects of fluctuating water levels on riparian breeding birds.

Study Area

The area encompassed in this chapter includes the Colorado River corridor from Glen Canyon Dam to Diamond Creek. This stretch of the river was subdivided into four major reaches identified by the Bureau of Reclamation and National Park Service. These subdivisions allowed a clearer description of where the majority of nest inundation was occurring among the common species of obligate riparian birds. These four major reaches were: Glen Canyon Dam to Lees Ferry, Lees Ferry to Little Colorado River, Little Colorado River to National Canyon, and National Canyon to Diamond Creek.

Data on nest inundation was gathered at a number of sites throughout the four major river reaches, but primarily at Cardenas Marsh, Fern Glen Canyon, Lava Falls, Whitmore Wash, and Granite Park. Additional sites at which inundation data was gathered are listed in Appendix III.

Methods

Study Design. Field work was conducted from 1982 to 1985 during the peak avian breeding months of April, May, and June. Nests were located largely by coordinated, systematic searches involving up to six investigators (methodology of nest searching described in greater detail in previous chapter). Data recorded on nests included specific location, nest height above ground, presence and age of eggs or young, distance from nest to water, and depth of water below or at nest. Nests were mapped and then marked nearby with surveyor's flagging to facilitate relocation. Call

counts of selected species were made using the methods of Bull (1981) to obtain an index to population densities of those species in the river corridor. Call count data was collected by recording the number of singing males of selected species heard during an oar-powered rivertrip between Lees Ferry and Diamond Creek. This provided a comparative index to the densities of certain birds from year to year.

During the high water of June 1983, a rivertrip was made from June 7 to 24 to determine if or to what extent the known nests of riparian birds were being inundated. The known nests were those that had been originally located and mapped in 1982 or in April and May of 1983. Nests or nest sites were relocated in June 1983 and the water depth at or below the nest recorded to the nearest 0.15 m. Where deep water made it difficult to reach the exact nest site, several depths were taken and their average was recorded. In situations where the riparian vegetation in which the nest was located had been entirely eroded away and removed, water depths were taken as near to the original nest site as possible.

Amounts of water released from the dam and river discharge volumes were obtained from unpublished sources of the U.S. Geological Survey (USGS) in Flagstaff, Arizona, and the Bureau of Reclamation in Page, Arizona. River discharge values are from the USGS gauging station named "Colorado River near Grand Canyon" at Phantom Ranch, 104 miles (167 km) downstream from Glen Canyon Dam. River discharge volumes are referred to in this chapter as river level, flow rate, or water level. The volume of water actually coming through the dam is referred to as a release.

Glen Canyon Dam had previously operated as a peaking power facility, resulting in daily water fluctuations of up to 3 m. The water released from the dam during June 1983, however, was essentially a constant base flow with few fluctuations. Daily river level fluctuations throughout early and mid-June 1983 were normally less than 0.3 m/day. However, several large, rapid rises from the 62,000 cfs release up to the peak release of 93,200 cfs and then back down again occurred in late June (Fig. 3-2). The end result of the relatively constant releases was that the amount of water coming from the dam usually equalled the river flow at Phantom Ranch except for the 12 to 24 hour lag time when a large, rapid rise or fall occurred. For this reason, releases and river flows indicated in connection with the June 1983 high water in this chapter were generally equivalent.

In some cases it was necessary to calculate back to the river level in cfs at which a specific nest was initially inundated, based on available data. In these cases, the depth to which a nest was inundated on a certain date by a

specific water level was known. From this it was possible to make a ratio of the height of the nest to the depth to which the nest was inundated vs. known gauge readings. The known water levels were taken, in all cases, from the USGS gauging station at Phantom Ranch.

An example of this procedure is seen in the case of Bell's Vireo active nest #15 at Parashant Wash, which was the vireo nest found to be inundated to the greatest extent by releases in the 62,000 cfs range in June of 1983 (Appendix III-1). Here, it was possible to calculate the approximate range of water levels which caused its initial inundation. This nest was found to be 1.24 m below the surface of the river on June 21, while the gauge height at Phantom Ranch on the previous day (June 20) ranged from 6.94 to 6.91 m for river flows between 62,410 and 61,840 cfs (USGS unpublished data). This water level reached Bell's Vireo nest #15 on June 21, when it was measured. Assuming that the depth of water was measured at the peak flow for that day, and that a gauge height to river flow relationship was equivalent at both Phantom Ranch and Parashant Wash, the nest appears to have been initially inundated by flows corresponding to gauge heights of 5.70 m, or 41,170 cfs (USGS unpublished data). However, the gauge heights at Phantom Ranch were certainly not the direct equivalent of those at Parashant Wash (the river was somewhat wider at Parashant, probably causing it to rise slower there than at the Phantom Ranch gauge). Barring these inconsistencies, it appeared that this nest was inundated at river levels in the 41,000 cfs range, plus or minus approximately 2,500 cfs. This method was used to calculate the apparent level of initial nest inundation in the case of Bell's Vireo, Common Yellowthroat, and Yellow-breasted Chat.

The percent of nests inundated at the highest release level of 93,200 cfs in late June 1983 was similarly calculated. The 30,000 cfs increase in river flow above the 62,000 cfs level at which most nests were observed caused at least a 0.5 m rise in downstream water levels, as estimated from USGS gauging station data. This conservative estimate was viewed as a generalization when considering the differences in channel morphology present along the river. The observed rise in water level, as observed on the gauge height at Phantom Ranch, was 0.9 m for the increase from 62,000 to 93,200 cfs (USGS unpublished data). Therefore, any nest that was less than approximately 0.5 m above the surface of the river at the 62,000 cfs release was considered to have been inundated by the 93,200 cfs level (see Appendix III for details).

The duration and timing of the breeding season for all birds known to nest in the river corridor was calculated from data gathered on active nests from 1982 to 1985. The number of days a nest appeared to have been under construction, number of eggs present, number and age of young, or behavior of

adults were recorded for each nest during one to three visits per nest per season. This information was used to reconstruct the length of known nesting attempts for each species. The peak of the breeding season (more than 50% of nests active) for each species was determined by plotting the period of activity for each nest of that species on a calendar.

The period during which a nest was considered active was that time from initial nest construction to the day when all young had fledged from the nest. Pettingill (1970) defines the various phases of nesting activity. Nest-building time included not only the number of days required to build a nest, but also the number of days between nest completion and the initiation of egg-laying. Species conspicuously exhibiting this lag time between nest completion and egg-laying included Bell's Vireo and Common Yellowthroat. The number of days required for egg-laying generally equalled the total number of eggs in a full clutch, as a single egg was usually laid each day at dawn. The incubation period was the number of days that passed between the onset of incubation (in most species just before the last egg is laid) and the hatching of the last egg. The period between the hatching of the first egg and the day the last young fledged was the nestling phase of the breeding cycle. Precocial young, such as those of the American Coot, could leave the nest under their own power after only one day or less. In this case, the nestling phase was considered to be only one day, even though the young may have returned to the nest at night for brooding.

The average duration for nest-building, egg-laying, incubation, and nestling time that was used to reconstruct the length of the breeding season for each species is presented in Table 3-1. The average time for each of these major nesting phases varied within a species, depending on geographic location, local climatic conditions, and seasonal variation in food resources. Data from Arizona or the Southwest were used wherever possible to eliminate geographic variation. When nesting chronology data were unavailable for certain species, data from another similar species in the same genus was substituted.

Nests found under construction were assigned an age in days based on published descriptions of nest-building (Table 3-1). These ages were accurate to approximately plus or minus two days. Nests containing less than the average clutch size were assumed to be in the egg-laying phase until the appropriate number of days had passed which would theoretically enable the laying of a full clutch. This time period was considered accurate to approximately plus or minus two days. Nests in which a full clutch was observed were assumed to be at the mid-point of the incubation phase. Nests that were too high in the trees to observe, but containing young being fed by adults, were assumed to be at

the mid-point of the nestling phase. These two latter assumptions were accurate to approximately plus or minus six days. The age of young observed was calculated to plus or minus two days, based on published descriptions of nestling development (Table 3-1).

These assumptions, and the fact that each nest was observed only a limited number of times and not systematically throughout the breeding season, may have resulted in errors in the reconstruction of the length of individual nesting events. The duration of the breeding season for each species as a whole was subject to error as a result. For birds with a relatively short nesting duration, such as Yellow and Lucy's warbler, these assumptions may have influenced the calculation of each nesting attempt by as much as plus or minus two to six days (largest error if nest was discovered in incubation phase). This would have, in turn, incorrectly influenced the initiation and termination of the overall breeding season for that species by as much as plus or minus six days. This potential error in the calculations was somewhat compensated for by the cumulative use of four years' data in calculating the duration of breeding seasons for the entire riparian bird community.

Two categories of Bell's Vireo nests were analyzed for this study: active and old nests. Active nests were those that were built during the season in which they were discovered and contained eggs or young. Old nests were those that had been built in previous years and were sufficiently intact to obtain data on nest location and height above ground. Both categories of nests were treated together in this chapter.

Site Selection. The portion of this study dealing with nest inundation was designed so that those nests which were located and ultimately analyzed were representative samples of the nesting sites of that population as a whole. To ensure this representative sample, nests of riparian birds were located in over 20 different sample sites along the river corridor from Lees Ferry to Diamond Creek. These sites varied in size from small island habitats of less than one hectare to approximately eight hectares. They represented a wide variety of riparian habitat types in both zones (OHWZ, NHWZ) of riparian vegetation relative to the surface of the river. The NHWZ habitats comprised approximately three-fourths of the total extent of habitat available to birds of the river corridor; accordingly, three-fourths of the sample sites were located primarily in the NHWZ and the same proportion of time was expended in sampling the NHWZ. This systematic method resulted in a sample of nest sites for each species which was representative of the birds' overall nest placement preferences.

Table 3-1. Nesting chronology of riparian birds known to breed along the Colorado River corridor in Grand Canyon.

Species	Nest-build	Egg-lay	Incubate	Nestling	Literature Source
American Coot	4	9	24	1	Gullion 1954, Fredrickson 1970
Mourning Dove	3	2	14	15	Bent 1932, Sanderson 1977
Black-chinned Hummingbird	4	1	16	22	Bent 1964a, Demaree 1970
Willow Flycatcher	6	4	12	14	Bent 1963a
Black Phoebe	13*	4	16	17	Bent 1963a
Say's Phoebe	13*	4	13	14	Bent 1963a
Ash-throated Flycatcher	3	4	15	14	Bent 1963a
Bewick's Wren	10	6	14	14	Miller 1941, Bent 1964b
Blue-gray Gnatcatcher	14	4	14	12	Bent 1964c, Root 1969
Phainopepla	4	3	15	19	Rand and Rand 1943, Bent 1965a
Bell's Vireo	6	4	14	11	Pitelka and Koestner 1942, Barlow 1962
Yellow Warbler	4	4	11	10	Schranz 1943, Bent 1963b
Lucy's Warbler**	8	4	12	11	Bent 1963b
Common Yellowthroat	10	4	12	10	Stewart 1953, Bent 1963b
Yellow-breasted Chat	5	4	15	11	Petrides 1938, Bent 1963b
Black-headed Grosbeak	8	4	13	12	Bent 1968, Ritchison 1983
Blue Grosbeak	4	4	12	12	Bent 1968, Genung 1976
Indigo Bunting	5	4	13	10	Trautman 1940, Bent 1968
Brown-headed Cowbird	0	1	11	10	Bent 1965b, Scott 1979
Hooded Oriole	4	4	13	14	Bent 1965b
Bullock's Oriole	8	5	14	14	Bent 1965b
House Finch	13	4	13	15	Evendon 1957, Bent 1968
Lesser Goldfinch	11	4	12	12	Linsdale 1957, Bent 1968

* Black and Say's Phoebe nest-building time unavailable, so that of Eastern Phoebe substituted (Bent 1963a).

** Nest-building, incubation, and nestling time of Lucy's Warbler unavailable, so that of another warbler in the same genus, Nashville Warbler, was substituted.

Results

Nest Inundation: Obligate Riparian Birds. Those species of birds which nest both closest to the ground and closest to the water's edge (i.e. in low-lying areas) were the species most susceptible to nest loss through inundation due to rising water. Figures 3-3 and 3-4 illustrated that Bell's Vireo, Common Yellowthroat, and Yellow-breasted Chat were the three species of obligate riparian birds which nested both low to the ground and close to the water. The American Coot also nested close to the ground and near (or over) water, but it was a rare and irregular breeder in the river corridor. The occurrence of American Coots was an anomaly and did not warrant the attention reserved for common and widespread summer residents.

Common Yellowthroats, Bell's Vireos, and Yellow-breasted Chats were the only species of obligate riparian birds whose nests were known to have been inundated by rising water in June of 1983. The percentage of vireo and chat nests known or calculated to have been inundated by various release levels at that time are indicated in Figures 3-5 and 3-6. The apparently high percentage of Common Yellowthroat nests that were inundated in June 1983 (Table 3-2) was not just a result of the inadequate sample size for that species (N=1, or less than 5% of the known population). The inundation of Common Yellowthroat nests began to occur at much lower release levels than either vireo or chat nests. The only known Yellowthroat nest in the spring of 1983 was extrapolated to have been inundated by releases of approximately 36,000. Based on later work and a larger sample size, the height of this nest relative to the river surface was found to be near the mean for the species, strongly indicating that the majority (approximately 90%) of Yellowthroat nests were inundated by the river's initial rise to the 40,000 cfs range. This would identify Common Yellowthroat as the species most susceptible to significant nest loss through inundation as a result of a river rise of the sort that occurred in June 1983.

The two most abundant obligate riparian birds, vireos and chats, were also the two species experiencing sizeable nest loss during the June 1983 high water for which an adequate sample size existed to analyze nest loss in each of the four major river reaches (Table 3-3). The majority of the breeding populations of these species were located in reach number four (National Canyon to Diamond Creek). Here, Bell's Vireo experienced substantial nest loss at 62,000 cfs and both species experienced substantial nest loss at 93,000 cfs. River reaches one through three (Glen Canyon Dam to National Canyon) hosted only a small proportion of the overall nesting populations of these two species. Nest inundation in vireos and chats may have varied from none to 100% in these first three reaches, but the meaning of these

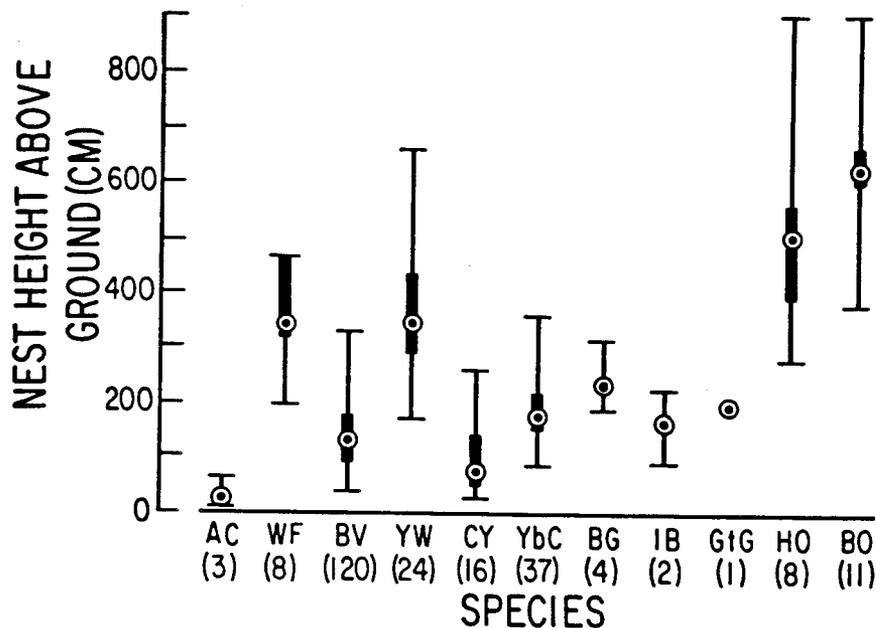


Figure 3-3. Nest height above ground for obligate riparian birds. Median, 50% interquartile range, and overall range are indicated. Species codes as in Table 2-1. Numbers in parentheses indicate sample size of nests.

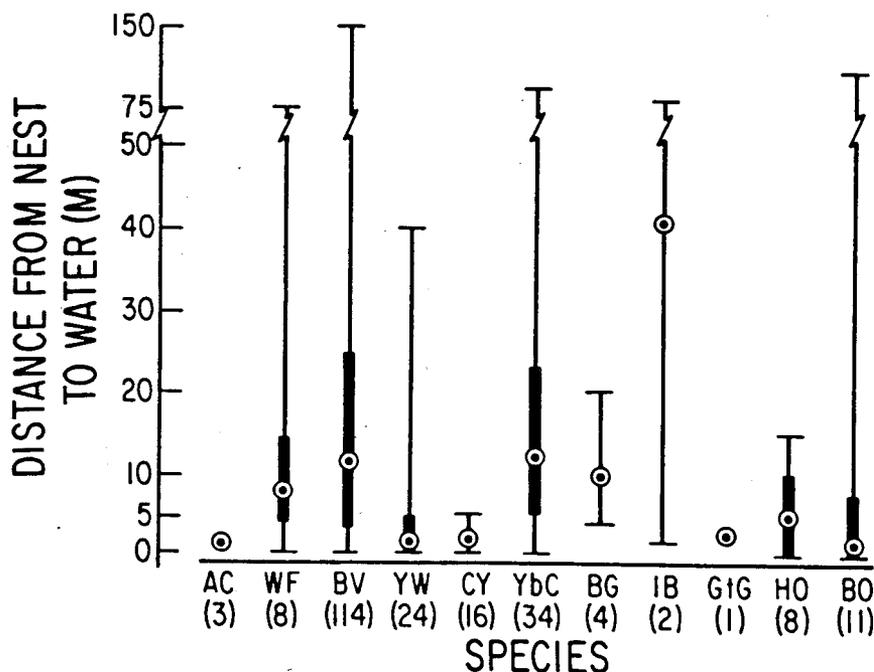


Figure 3-4. Distance from nest to water for obligate riparian birds. Median, 50% interquartile range, and overall range are indicated. Species codes as in Table 2-1. Numbers in parentheses indicate sample size of nests.

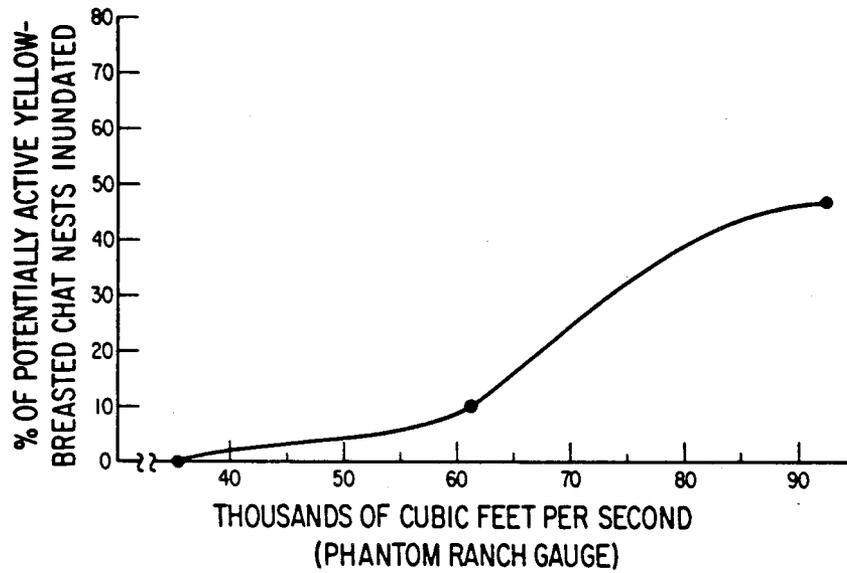


Figure 3-5. Percent of Yellow-breasted Chat nests inundated at various release levels, June 1983.

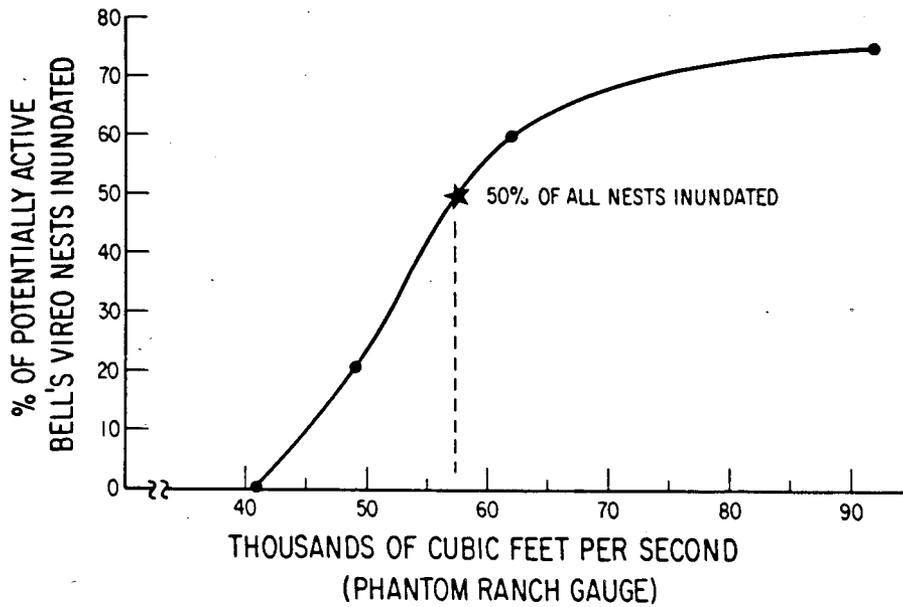


Figure 3-6. Percent of Bell's Vireo nests inundated at various release levels, June 1983.

Table 3-2. Extent of nest inundation among obligate riparian breeding birds along the Colorado River at releases of 62,000 cfs during the high water of June 1983.

Species	# Nests Inundated	% Nests Inundated	Sample Size (N)
Willow Flycatcher	0	0	2
Bell's Vireo	45	60	75
Yellow Warbler	0	0	2
Common Yellowthroat	1	100	1
Yellow-breasted Chat	2	11	19
Hooded Oriole	0	0	2
Northern Oriole	0	0	1
Indigo Bunting	0	0	1
Blue Grosbeak*	-	-	-

* No nests of this species were under observation at this time.

Table 3-3. Bell's Vireo and Yellow-breasted Chat nest inundation by major river reaches* during the June 1983 high water releases.

	Bell's Vireo				Yellow-breasted Chat			
	-River Reach-				-River Reach-			
	1	2	3	4	1	2	3	4
Initial inundation occurs at (cfs x 1000)	-	45	50	41	-	36	-	60
Nests inundated at 62,000 cfs (#)	0	1	0	44	0	1	0	1
Nests inundated at 62,000 cfs (%)	0	100	0	63	0	25	0	7
Nests inundated at 93,000 cfs (#)	0	1	1	53	0	1	0	8
Nests inundated at 93,000 cfs (%)	0	100	100	76	0	25	0	57
Sample Size (N)	0	1	4	70	0	4	1	14

* Major river reaches as defined by the National Park Service and the Bureau of Reclamation. 1=Glen Canyon Dam to Lees Ferry; 2=Lees Ferry to Little Colorado River; 3=Little Colorado River to National Canyon; 4=National Canyon to Diamond Creek.

figures was obscured by the unavoidably small sample sizes involved.

Another obligate riparian bird which apparently nested on a rare and irregular basis in the river corridor was the Marsh Wren. No active Marsh Wren nests were found in the study area, but a recently-constructed dummy nest, or false nest constructed by the male in his territory and not intended to contain eggs, was found at Lees Ferry on April 9, 1984. This nest was located at a height of 0.6 m directly over the water surface at river flows of 27,000 cfs. Dummy nests were built to mimic active nests that will soon be or were already built nearby, both in habitat type chosen and nest placement. The river rose to 44,000 cfs on May 5 (Lees Ferry gauge height reading of 0.6 m above that of April 9), inundating both the dummy nest and theoretically the active nest that would have been or already had been built nearby.

Nest Inundation: Other Riparian Birds. Other riparian birds experienced nest inundation during the June 1983 high water event, but little hard data were available to substantiate the extent of this. Nest heights above ground for facultative or preferential riparian birds are listed in Table 3-4. Mean nest heights for these species may be used as a general guide to species that probably experienced nest loss in June 1983 and would be susceptible to nest loss through inundation in the future. Mean nest heights below 200 cm for a species should be interpreted to mean that nest inundation occurred in that species during the June 1983 high water event.

Black-chinned Hummingbird was one of the two species of facultative or preferential birds known to have experienced nest loss through inundation in June 1983, although only a relatively small percentage of nests appeared to have been involved. Total nest loss at 62,000 cfs was not known, but was estimated at less than 20% of the total hummingbird population. A small portion of Black-chinned Hummingbird nests were known to have been inundated by releases of as low as 23,000 cfs when these releases have been preceded by several weeks of lower releases early in the breeding season.

Other facultative and preferential riparian breeding birds were known to have experienced nest inundation at various release levels, both during and after June 1983. An active Violet-green Swallow nest was found on June 2, 1985, only 0.3 m directly above the water in a Redwall limestone cavity at River Mile 28 (L. Stevens, pers. comm.). River flows on that day were a constant 45,000 cfs; if the water had risen to 55,000 cfs (Lees Ferry gauge height increase of 0.3 m over that of June 2), this nest would certainly have been inundated. An active Say's Phoebe nest was observed at the mouth of Three Springs Canyon on May 7, 1985, on a rock ledge only 1.0 m directly over the river surface at flows of

Table 3-4. Nest heights above ground for selected species of facultative and preferential riparian breeding birds along the Colorado River in Grand Canyon.

Species	Nest Height (cm)		Sample Size (N)
	mean	range	
Mourning Dove	259	121-450	21
Black-chinned Hummingbird	172	76-360	86
Ash-throated Flycatcher	162	155-168	2
Bewick's Wren	195	-	1
Blue-gray Gnatcatcher	404	67-610	32
Lucy's Warbler	178	108-218	4
Black-headed Grosbeak	323	220-425	2
House Finch	290	185-400	6
Lesser Goldfinch	231	133-335	8

Table 3-5. Densities of selected species of obligate riparian birds along the Colorado River from Lees Ferry to Diamond Creek, 1976 to 1985.

Species	Number of Singing Males Heard				
	1976	1982	1983	1984	1985
Willow Flycatcher*	1+	2	4	4	8
Bell's Vireo**	67++	135	78+++	92	75
Yellow Warbler***	17+	32	39	33	61
Common Yellowthroat***	8+	-	-	21	21
Yellow-breasted Chat*	18+	46	53	65	62

* Census data from June of each year.

** Census data from April of each year.

*** Census data from May or early June of each year.

+ From Carothers and Sharber (1976). Average absolute density for April, May, and June, 1974 to 1976.

++ From S.W. Carother's field journal, April 1976 (Brown et al. 1983)

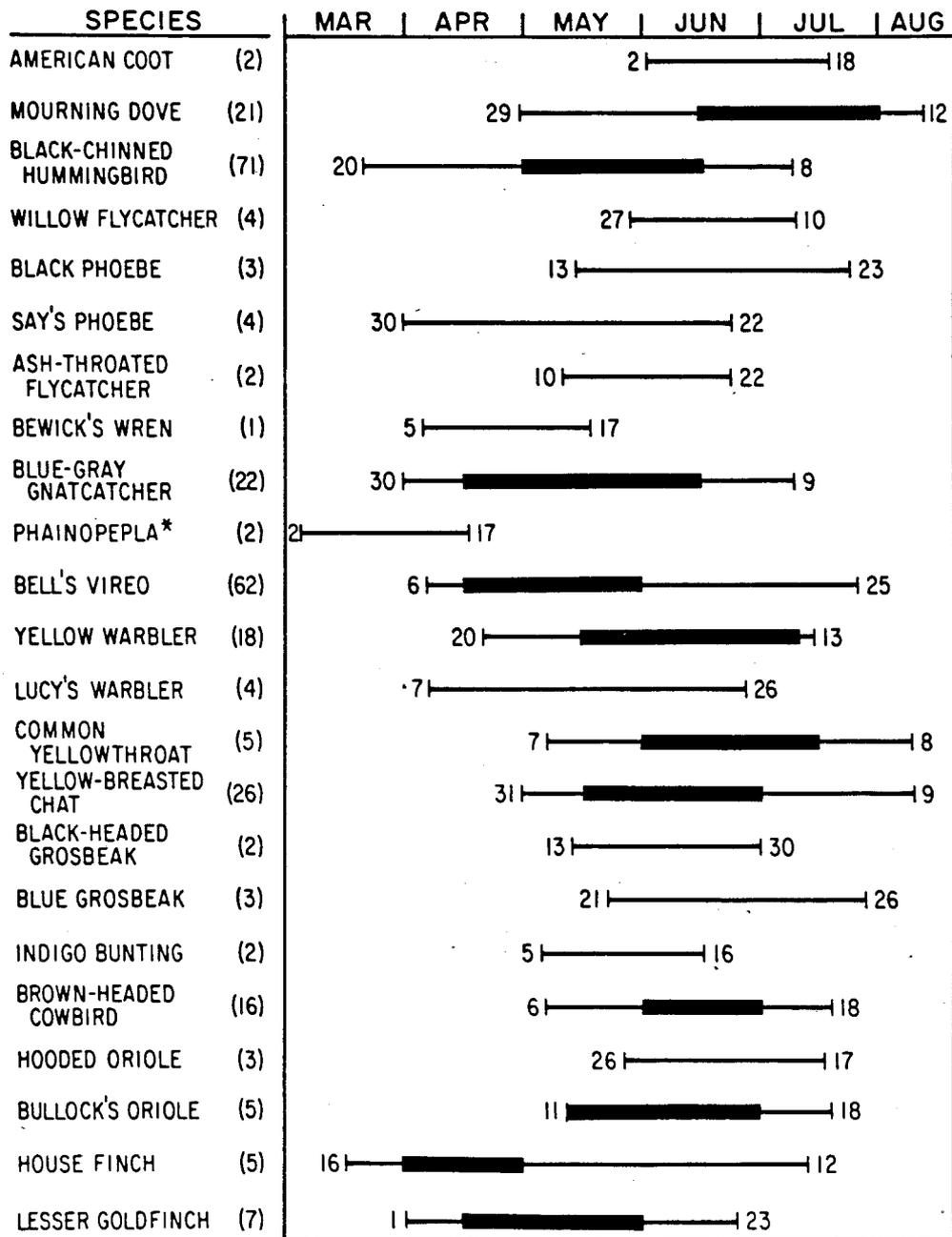
+++ This census is inaccurate due to interference from bad weather, high winds, and the noise of high water.

26,000 cfs. The nest was observed to be 0.3 m beneath the water surface on June 17, at river flows of 45,000 cfs. An active Black Phoebe nest was found at the mouth of Olo Canyon on June 18, 1983, only 0.1 m directly above the river at flows of 62,000 cfs. The subsequent rise to 93,000 cfs on June 28 would have inundated this nest to a depth of 0.5 m or more.

Nesting Chronology. The breeding season for the community of riparian birds which nested in OHWZ or NHWZ vegetation along the river was between the extremes of March and early August. Black-chinned Hummingbird, Phainopepla, and House Finch were among the first to breed in March, while Mourning Doves were the last to finish breeding in early August (Fig. 3-7). Obligate riparian birds nested between April (Bell's Vireo was first) and late July to August (Common Yellowthroat and Yellow-breasted Chat were last). As Common Yellowthroat, Bell's Vireo, and Yellow-breasted Chat were identified as those species which experienced the greatest nest loss due to high water in June 1983, an examination of their nesting chronology revealed how the timing of large releases might affect future nesting seasons.

Yellowthroat nesting in the river corridor occurred from early May to early August, with the peak of nesting in June. The number of active vireo nests peaked in May, with the number of eggs reaching a peak in early May and the number of young reaching a maximum in late May. The peak number of active chat nests and the largest number of both chat eggs and young present reached a maximum in early June.

Density Changes in Obligate Riparian Birds. The relative densities through time of selected species of obligate riparian birds, as obtained through call-counts of singing males, are given in Table 3-5. These five species of birds all showed a general trend of increasing numbers from 1976 through 1982, with Yellow-breasted Chat being the only species which sustained its density increase through 1984. Bell's Vireo was the only one of these species which showed a marked decline in numbers between 1982 and 1985, for a 45% drop in numbers during that period. There was an extraordinary increase of Yellow Warblers from 1984 to 1985.



* FROM CAROTHERS AND AITCHISON (1976).

————— TOTAL BREEDING SEASON ■ PEAK BREEDING (50% OR MORE OF NESTS ACTIVE)

Figure 3-7. Length and peak of the breeding season for riparian birds in the river corridor, as determined from data gathered from 1982 to 1985. Numbers in parentheses indicate sample size of nests.

Discussion

Nest Inundation. Nest inundation was a function of the growth and development of suitable riparian vegetation relative to the surface of the river. The vegetation of the NHWZ vigorously colonized the pre-dam flood zone from 1966 to 1979, its downslope colonization held in check only by the 31,000 cfs post-dam high water line.

This was the situation when the June 1980 release of 50,000 cfs occurred. That high water event inundated a large percentage of Common Yellowthroat nests and a small percentage of vireo and chat nests. However, this release was not large enough, nor was it of sufficient duration to scour away much shoreline vegetation in the NHWZ. Then came the 93,000 cfs release of late June 1983 which not only inundated a significant percentage of yellowthroat, vireo, and chat nests, but which also scoured away much NHWZ vegetation below the 40,000 cfs level. The habitat that was lost was particularly important to yellowthroats, as it represented the low-lying marshy areas where they formerly occurred in the highest densities.

Water levels remained above 20,000 cfs from June 1983 through the summer of 1984, reaching over 40,000 cfs in May and June of the latter year. However, the 1984 high water inundated few nests due to the fact that there was little habitat remaining below the 40,000 cfs level in which birds could have nested. Also contributing to this was the timing of the initial rise of the river to the 40,000 cfs level, which occurred before the main nesting season began.

The point illustrated here is that the zone of riverside vegetation in which birds nested in the period 1984 to 1985 was different from what it was prior to the high water event of 1983. This cycle of downslope growth followed by upslope scouring in a high water year could become a recurring feature of the system, and the rate of nest inundation in the 30,000 to 45,000 cfs range would vary annually as a result. The timing of high water releases also had a great bearing on nest inundation, but more will be said about this in the next section. However, the following portion of this discussion was based upon the situation as it was immediately prior to and during the June 1983 event, a situation which will doubtless reappear if maximum annual flows return to the 31,000 to 33,000 cfs range for several years.

The three most vulnerable riparian birds (yellowthroat, vireo, chat) first begin to experience nest inundation in the 36,000 to 41,000 cfs range (Figs. 3-5, 3-6). However, these lower flows quickly resulted in significant (i.e., greater than 50%) yellowthroat nest inundation. By 40,000 cfs, most yellowthroat nests were lost, while only a small

fraction of vireo and chat nests were destroyed. The largest number of vireo nests were inundated per 1,000 cfs river rise in the approximately 49,000 to 62,000 cfs range (Fig. 3-6), while the largest number of chat nests were inundated per 1,000 cfs rise above the 62,000 cfs level (Fig. 3-5).

Those populations of yellowthroats, vireos, and chats in the river corridor represented the bulk of the total populations of these species within Grand Canyon National Park. This disproportionate occurrence was due to the fact that the bulk of the total habitat available to these birds was in the river corridor. A minimum of 135 pairs of vireos occurred in the river corridor in 1982 (Table 3-5), while other low-elevation riparian habitats within the region were estimated to have supported less than half that number. At least 65 pairs of chats were known from the river corridor in 1984 (Table 3-5), while less than half that number were estimated to exist in low-elevation riparian areas away from the river. An accurate census for yellowthroats in the river corridor was not available just prior to the June 1983 event, but based on nesting habitat available, yellowthroats in the river corridor probably outnumbered those elsewhere in the region.

These estimates suggested that the river corridor hosted the vast majority of nesting yellowthroats, vireos, and chats which existed in the region. Any river corridor event which affected these species had a disproportionately large bearing on their overall, regional well-being. This chapter addressed primarily those obligate riparian species which were restricted to low-elevation riparian habitats for exactly this reason. Preferential or facultative riparian birds nesting along the river may have experienced some nest loss due to inundation, but these species also used other habitat types for nesting. Nest inundation of up to approximately 20% of the total breeding populations of Black-chinned Hummingbird, Violet-green Swallow, Black Phoebe, and Say's Phoebe were estimated to have occurred both during and after the June 1983 surplus water event, but this loss was not significant. For those species, the river corridor did not hold the same importance as it did for the obligate riparian birds.

Yellowthroats, vireos, and chats all had the capability to renest if their initial nesting attempt was inundated by high water. More will be said about this in the next section on nesting chronology, but a difference in the renesting ability of these three species in response to inundation should be noted. Vireos and chats established territories (from which only other vireos and chats were excluded) throughout the NHWZ. Vireos used the OHWZ to a large extent as well. Yellowthroats, on the other hand, largely nested and established territories along the water's edge (Fig. 3-4). When the water rose in June 1983, the

vireos and chats whose nests were destroyed attempted to renest if they could move to higher areas or if their original territory was not too badly disturbed by the rising water. However, any attempt by vireos and chats to establish new territories resulted in conflicts with previously-established vireo and chat territories. For this reason, it was likely that very few vireo and chat renesting attempts were successful, and none were observed to occur during the study period. Yellowthroats were more successful in their renesting attempts because there were no previously-established, up-slope yellowthroat territories to contend with. While the rate of yellowthroat nest inundation was very high, their ability to renest successfully on higher ground may have buffered some of the negative impacts of initial nest inundation.

Yellowthroats and vireos could inadvertently experience significant nest inundation if the Little Colorado River or Paria River went into flood during the breeding season. Normal breeding season releases from the dam (33,000 cfs or less) in combination with floods that could occur on these tributaries (which have exceeded 20,000 cfs within the last decade) have the potential for creating river conditions that could destroy many yellowthroat and vireo nests. The chance occurrence of a situation such as this is a very real possibility that should be foreseen and considered by management. Flash floods are natural occurrences. However, when tributary flooding augments the unnatural flow from the dam it creates a resource management problem. Releases from the dam could be lowered temporarily during the brief period when larger tributaries were in flood. Data from upstream gauging stations on the larger tributaries, which is easily available, could be used to anticipate flash floods.

Nest inundation was the most direct impact to several riparian breeding birds, but other indirect impacts were casually observed during this study. Water flowing through a habitat pushed over shrubs, inundating nests in these shrubs that would otherwise have remained above the actual water levels. Inundation of riparian vegetation also eliminated the lower foraging levels upon which some species rely. Bell's Vireo foraged for insects largely below 3.0 m above ground (Goldwasser 1981); much of this foraging stratum along the river corridor was inundated during late June of 1983. Water flowing beneath nests that were not yet inundated may have reduced the survival rate of fledgling birds. As many fledglings fall, rather than fly, from the nest in their initial bid for independence, any water below the nest would have resulted in drowned young. This negative aspect may have been partly offset by the water below the nest acting to reduce predator access to nests, as has been shown for nesting blackbirds (Brown and Goertz 1978).

Inundation of habitat by swiftly-moving water may also have altered habitat structure on a short-term basis. As Bell's Vireo constructed its nests largely below 1.2 m in height (Fig. 3-3), potential vireo nesting sites may be disturbed or eliminated for several years following habitat inundation. Foliage volume and shrub stem density may have been reduced in habitats disturbed by inundation, features important to several species (see Chapter Two). However, these vegetative features can be expected to recover in time.

Nesting Chronology. The initial rise to the 62,000 cfs range in June 1983 (Fig. 3-2) coincided exactly with the peak of Common Yellowthroat and Yellow-breasted Chat nesting (Table 3-6, Fig. 3-7). Comparison of Figure 3-2 with Figure 3-7 revealed how the high water coincided with nesting activity of all riparian birds nesting along the river. Bell's Vireo nesting had just passed its peak at the time the high water of June 1983 arrived. At levels of 62,000 cfs, 11% of the chat nests were inundated (Fig. 3-5), with virtually 100% of those active at the time (Table 3-6). Although 60% of Bell's Vireo nests were inundated under these conditions (Fig. 3-5), only 46% of those nests that were destroyed were active (Table 3-6). By multiplying percent inundated by percent active ($.60 \times .46$), it can be seen that only 28% of the vireo nests active at the time were inundated by releases of 62,000 cfs, while 24% ($.75 \times .32$) of the active vireo nests would have been inundated by the peak release of 93,000 cfs in late June if it had come as a single event. The nest inundation charts (Fig. 3-5, 3-6) can be used in conjunction with the nesting chronology information (Table 3-6, Fig. 3-7) to calculate the effective nest loss (i.e. loss of active nests only) due to inundation for various release levels and times during the breeding season.

The timing of the high water event of June 1983 was at the worst possible time for yellowthroats and chats, but was past the most sensitive time for nesting vireos. If the initial rise to the 62,000 cfs level had occurred only 2-4 weeks earlier, a much higher percentage of active vireo nests would have been destroyed, but many yellowthroats and chats would have had time to adjust their nesting sites to higher locations.

Most passerines along the river normally built a new nest and laid a second clutch of eggs shortly after the young have fledged from the season's first nest. For vireos, this resulted in a series of active nests in late April and May, with a second series of nests in June and July. Renesting also occurred when nests or eggs were destroyed, but only when this allowed construction of a new nest and the raising of another brood within the normal breeding period. Late July and early August was the end of this period for vireos, yellowthroats, and chats.

Table 3-6. Percent of nests which are active at any given time throughout the breeding season for Bell's Vireo, Common Yellowthroat, and Yellow-breasted Chat. Figures below are averages determined through chronology analysis of nests from along the Colorado River in Grand Canyon, 1982 to 1985 (sample size in parenthesis).

Species	Percent of nests active by 2-week periods									
	April		May		June		July		Aug	
	a*	b**	a	b	a	b	a	b	a	b
Bell's Vireo (62)	23	56	71	74	46	32	10	5	0	
Common Yellowthroat (6)	0	0	33	50	83	67	67	17	17	
Yellow-breasted Chat (27)	0	4	37	78	96	70	26	15	4	

* a = first through the fifteenth of each month

** b = sixteenth through the end of each month

Table 3-7. Riparian birds restricted largely or exclusively to NHWZ habitats, as indicated by census findings or nest-search results (from Chapters 1 and 2).

Species	Riparian Habitat Dependence*
American Coot	Obligate
Black-chinned Hummingbird	Preferential
Willow Flycatcher	Obligate
Yellow Warbler	Obligate
Common Yellowthroat	Obligate
Yellow-breasted Chat	Obligate
Great-tailed Grackle	Obligate
Hooded Oriole	Obligate
Bullock's Oriole	Obligate

* from Johnson et al. 1977.

If water levels had peaked in early June 1983 and then receded to less than 30,000 cfs, birds whose first clutch was inundated could have renested. However, most nesting attempts were precluded by the persistence of high water until early August, with the exception of yellowthroats.

Density Changes in Obligate Riparian Birds. Bell's Vireo was the only obligate riparian bird for which there were data showing a marked decline in numbers (45% drop) after the June 1983 high water (Table 3-5). However, the relationship between this decrease in numbers and the high water event was not entirely clear. Simple cause-and-effect may have been responsible for the decline, but the drop in density may have been partly due to other factors. Population densities of riparian birds in the Southwest are known to fluctuate widely due to annual variations in precipitation, weather, and resulting food resources. Avian densities in the Verde Valley of Arizona have been shown to decrease by 50% over a period of 2 years due to variations of this sort (Carothers and Johnson 1973). In the case of Bell's Vireo along the river corridor, though, the significance of the 20 to 40% reduction in NHWZ habitats (M. Pucherelli, personal communication) and the simultaneous loss of 28% or more of all active nests which accompanied the June 1983 high water event was hard to overlook. For these reasons, the vireo population decrease from 1982 to 1985 was seen largely as a result of the June 1983 high water event. Longer-term population monitoring which showed population increases accompanying any NHWZ habitat recovery would be necessary to firmly establish this relationship.

Common Yellowthroats declined somewhat in numbers due to the great loss of their preferred marshy habitats and the high rate of nest loss experienced during the June 1983 high water event. However, there was little data to firmly document this. Yellowthroat census data were not available for the entire river corridor just prior to the flood, but comparative density figures for selected sites did exist. The small marshy area just downstream from the mouth of Buckfarm Canyon supported a pair of yellowthroats in the spring of 1983; the entire marshy area was eroded away by the June 1983 high water and there were no yellowthroats present in 1984. The large marshy area at River Mile 51.1L was host to five pairs of yellowthroats in the spring of 1983; the entire marshy area had disappeared and there were no yellowthroats present by 1984. Another large marshy area at River Mile 55.3R supported several pair of yellowthroats in the spring of 1983. The same area was greatly reduced in extent by the high water, resulting in a complete absence of yellowthroats in 1984. A single pair of yellowthroats inhabited Cardenas Marsh during the spring of 1983 as well as 1984, even though marshy habitat declined greatly in extent at the site after the high water.

These figures indicated that yellowthroat populations declined sharply, at least in a small number of areas representing prime habitat. The approximately 85% decrease in density documented by this small sample size cannot be extrapolated to the entire river corridor, but would apply largely to those marshy areas of preferred habitat which existed in lower Marble Canyon prior to the high water. The final conclusion regarding the yellowthroat population decline was that the population decreased somewhat in numbers due to the high water release, with a simultaneous loss of large amounts of preferred habitat. The extent of loss of marshy habitats in the river corridor due to the 1983 flood was not known, but was substantial.

The extraordinary increase of Yellow Warblers from 1984 to 1985 was difficult to explain. The increase may have been related to population surges from outside of the river corridor, or the increase may have been related to the opening up of new habitat areas in the riparian zone by the riverside erosion of June 1983. This high water event eroded away most of the low and dense vegetation immediately beside the river, exposing the tall and thin salt cedar growing in what were formerly the interiors of riparian habitat patches. These patches of recently-exposed, tall and thin salt cedar which lined much of the new riverside in the spring of 1985 were observed to contain larger numbers of Yellow warbler nests than were present in any other habitat type in previous years. This observation suggested that by opening up new habitat exposures, the flooding and erosion were beneficial to Yellow Warblers on a short term basis. However, continued erosion could remove this habitat type that presently appears to be beneficial to the warblers. Caution is advised in the interpretation of this population increase, with further work and continued population monitoring being needed to scientifically explain it.

Erosion Scenarios. Nest inundation is an important short-term consideration for management, but riparian substrate erosion and subsequent habitat loss is the most serious long-term threat to riparian breeding birds in the river corridor. The riparian bird community can tolerate short-term perturbations, even on a recurring basis, as long as suitable breeding habitat remains. However, if future management actions concerning water released from the dam were demonstrated to initiate or accelerate substrate erosion in the NHWZ, the effect on riparian birds would be clear. First, riparian vegetation in the NHWZ would be lost. And secondly, as the overall extent of NHWZ vegetation began to decline and the patches in which it occurs became smaller, the overall density and diversity of breeding birds in the NHWZ would decrease.

Studies in progress by the U.S. Geological Survey are quantifying rates of sediment transport in the river system,

but no information is available at present. If trends of sediment accumulation or erosion that would result from future management actions could be identified, then accurate predictions could be made regarding the future of riparian breeding birds.

Portions of Chapter 1 have previously addressed the positive aspects of either overall sediment deposition or no erosion in the river corridor: avian density and diversity would increase. Diversity would increase along the regression line created by Willson and Carothers (1979), while density would increase arithmatically according to the mean density figures for the NHWZ outlined in Chapter 1.

The purpose of this section was to discuss how long-term habitat erosion would affect avian density and diversity in the river corridor. Three scenarios have been selected in which to frame the discussion:

1. Possible future loss of 10% of NHWZ vegetation through riparian substrate erosion caused by any combination of surplus or fluctuating flows.

2. Possible future loss of 50% of NHWZ vegetation through riparian substrate erosion caused by any combination of flows.

3. Worst case scenario: possible future loss of 100% of NHWZ vegetation through riparian substrate erosion by any combination of flows.

Table 3-7 indicated those riparian birds which were primarily or exclusively dependent on the NHWZ. This table and the findings of Chapters 1, 2, and 3 of this report will be used as a basis for analysis of the above three scenarios.

Loss of 10% of NHWZ Vegetation. Habitat loss of slightly greater than this magnitude was essentially what resulted from the June 1983 surplus water release from Glen Canyon Dam. Overall avian density and diversity may have decreased slightly, but was not well documented. Two species, Bell's Vireo and Common Yellowthroat, were known to have declined in numbers following this habitat loss. However, their decline was partially related to the effects of nest inundation and the sole effect of habitat loss was unclear. This loss of riverside vegetation may have proved beneficial to Yellow warblers, but this was also unclear. Future losses of this sort would not necessarily be of benefit to warblers if the habitat components presently exposed at the river's edge were reduced in extent. No species of breeding birds were known to have been eliminated from the overall riparian bird community due to the erosion caused by the June 1983 event.

In summary, the long-term loss of approximately 10% of the presently-existing NHWZ habitats would not have a substantial negative effect on the breeding bird community, as indicated by a qualitative evaluation of the effects of the June 1983 high water event. Those species that were sensitive to habitat loss at the water's edge, such as Bell's Vireo and Common Yellowthroat, would decline somewhat in numbers. Species restricted primarily or exclusively to the NHWZ may experience a slight decline in numbers, but any decline would be within the normal range of annual population fluctuations as seen in Southwest riparian habitats in general. However, these effects would probably only hold true for a one-time loss of 10% of the NHWZ: continued losses in sequence would have a much more substantial negative effect on breeding birds.

Loss of 50% of NHWZ vegetation. Habitat losses of this magnitude would have a significant negative effect on bird populations presently found along the river corridor. There would be a substantial reduction in overall NHWZ avian density. Species identified in Table 3-7 would be most susceptible to density decreases. Species occurring largely or exclusively in the NHWZ would decline the most, up to 50% or more, while species that were widespread in both zones could experience substantial density decreases as well. Overall diversity in the NHWZ would decline somewhat, on the regression line of Willson and Carothers (1979). This would result in lower avian diversity in the entire river corridor as well, as any species eliminated from the NHWZ would probably be ones that were restricted to it.

Worst case scenario: possible 100% loss of NHWZ habitats. A habitat loss of this magnitude would completely change the character of the breeding bird community in the river corridor. Avian density and diversity would revert to that existing under pre-dam conditions, when the NHWZ was essentially absent. Those species of birds pointed out in Table 3-7 would decline radically in numbers, or even be completely eliminated from the system. There would be some adjustment, however, as Yellow Warbler, Yellow-breasted Chat, and Hooded Oriole would move into the OHWZ in small numbers. Their overall densities would decline by 80% or more, even with limited adjustment. Small patches of NHWZ vegetation would persist even in this scenario, and those species of NHWZ birds exclusively dependent on salt cedar, willows, and marshy habitat would persist in small habitat pockets at the larger eddies and in other protected situations. Bell's Vireo and Blue Grosbeak would be the only species of obligate riparian birds continuing to exist in numbers in this scenario, due to their ability to make widespread use of the OHWZ. Overall, the number and diversity of obligate riparian birds would decline sharply.

Evaluation Of Flow Scenarios

The Bureau of Reclamation and National Park Service identified seven flow scenarios for evaluation with respect to their effects on breeding birds of the river corridor. These seven flow scenarios were:

1. Monthly base loaded power plant releases.
2. Status quo releases with maximized power.
3. Restricted maximum and minimum flows.
4. Base loaded recreation season.
5. Maximized fishery releases.
6. How to route water downstream if water had to be bypassed (in the case of high water years and above-normal runoff resulting in surplus water releases from the dam).
7. How to parcel the water out during low water years (in the case of a drought year).

These seven flow scenarios were to be evaluated with respect to their direct and indirect effects on breeding birds along the river. Direct effects primarily included nest inundation, which did not become a significant factor until flows reached or exceeded 35,000 cfs. Indirect effects included both short-term and long-term habitat erosion, as habitat loss would eventually cause a decline in overall avian density and diversity. Indirect effects also included changes in habitat structure and the manipulation of avian food resources via those insects which emerged from the river into the riparian zones in abundance.

1. Monthly base loaded releases. This is the optimal scenario with respect to its effect on breeding birds. Nest inundation would not occur, as maximum flows would not exceed 15,000 cfs. Unless this scenario were to be shown to accelerate riparian substrate erosion, NHWZ vegetation would continue to colonize downslope to the 15,000 cfs mark, creating additional breeding habitat with a probable associated increase in avian density. Stable flows with respect to the available habitat would create ideal conditions under which certain formerly irregular marsh nesters might become regular breeding birds throughout the river corridor, increasing the overall diversity of the avian community. These species include some species of ducks as well as American Coot. The effect of this scenario on river-based insect productivity is unknown.

2. Status quo releases. This scenario would effectively return breeding bird populations along the river to the

point at which they were in 1982 (prior to the high water of 1983 to 1985), unless releases of this sort were shown to result in riparian substrate erosion causing substantial habitat loss in the future. Nest inundation would not occur to any appreciable amount, as maximum flows would not exceed 31,000 cfs. The effect of this scenario on river-based insect productivity is unknown.

3. Restricted maximum and minimum releases. This is the second best scenario with respect to breeding birds. Nest inundation would not occur, as maximum flows would not exceed 25,000 cfs. If flows remained below this level, NHWZ vegetation would colonize downslope to the 25,000 cfs line, increasing the amount of habitat available to birds. As with the other scenarios, the rate of riparian substrate erosion and subsequent habitat loss caused under this release schedule is unknown, but would be a major long-term factor influencing its effect on breeding birds. The effect of this scenario on river-based insect productivity is unknown.

4. Base loaded recreation season. This would have essentially the same effect as scenario number two, that is, maintaining the status quo by returning breeding bird populations to the point at which they were in 1982, unless these releases were shown to cause substantial riparian substrate erosion and subsequent habitat loss. Nest inundation would not occur, as flows would not exceed 25,000 cfs during the breeding season. The effect of this scenario on river-based insect productivity is unknown.

5. Maximized fishery releases. This would have essentially the same effect as scenarios number two and four. The status quo would be maintained by returning breeding bird populations to the point at which they were in 1982, unless these releases were shown to cause substantial riparian substrate erosion and subsequent habitat loss. Nest inundation would not occur, as flows would not exceed 31,500 cfs during the breeding season. The effect of this scenario on river-based insect productivity is unknown.

6. How to route surplus water downstream. The findings of this study are well-suited to evaluate the different options present in a scenario of this sort. Historically, surplus water has been released from the dam during June and July (1980, 1983, 1984, 1985). This was the time when peak inflow from the upper Colorado River drainage typically reaches Lake Powell, but it was also the peak of the breeding season for downstream birds most susceptible to nest inundation through surplus water releases. With respect to breeding birds, the best way to route surplus water downstream is to release it during the fall, winter, and early spring (before late April) in a manner that would minimize riparian substrate erosion. The release of surplus water above 31,000 cfs should be avoided during the period

of May 1 through July 15 to avoid inundating active nests. Lake Powell should be maintained at a level just below its maximum pool elevation in order to achieve the storage space necessary to absorb unexpectedly high spring runoff, precluding the need to release surplus water at the time when it arrives (i.e., May through July).

In the event that surplus water must be released during the peak of the breeding season, several management options exist which would minimize the negative effects of downstream nest inundation. First, if precipitation, snowpack, and runoff forecasting systems can predict a surplus water release in advance, then the releases from the dam should be increased as early as possible so that birds can adjust to the higher water as they arrive on the breeding grounds. Nest inundation occurs when water levels rise during the breeding season. If the water is at high levels at or before the onset of breeding, then birds will naturally adjust to breed above the higher levels. Second, if managers are in doubt as to how high to initially increase releases from the dam when a surplus of water is imminent, management should initially raise surplus release levels more than enough to deal with a large inflow to the reservoir during the breeding season. A sustained release of 55,000 cfs for a time beginning at or before the onset of breeding in early April (which would inundate no nests) is far better than an inadequate surplus release of 40,000 cfs through the initial portion (April and May) of the breeding season which later rises to 60,000 cfs in June. If an optimistically small surplus release of 40,000 cfs in April had to be suddenly increased to 60,000 cfs in early June to bypass the peak runoff during the height of the breeding season, the result would be a large number of needlessly inundated nests.

Surplus water should be routed downstream in a manner which would minimize riparian substrate erosion and associated habitat loss.

7. How to parcel water out during low water years. Amounts of water released in this scenario would have little or no effect on breeding birds, unless the release schedules were shown to cause accelerated riparian substrate erosion or to reduce river-based insect productivity. Since maximum water levels in a scenario of this sort would no doubt be kept below 31,500 cfs, nest inundation would not occur. However, if maximum releases were kept to a minimum during a drought lasting several years, there would be a substantial downslope colonization of NHWZ vegetation. This temporary habitat increase would be a short-term benefit to breeding birds. As drought conditions ended, the associated return of normal maximum releases would largely scour away this new vegetation. The only recommendation regarding release schedules during drought years would be to restrict maximum flows to 25,000 cfs or less and to release this water in a

manner that would minimize riparian substrate erosion. This would serve to stabilize marshy riverside habitats by allowing the growth and development of vegetation in those areas. Vegetational development of this sort in the NHWZ would prove beneficial in both the short-term and long-term to marsh-nesting birds, primarily Common Yellowthroat but possibly also American Coot.

Conclusions And Management Considerations

Fluctuating flows up to 31,000 cfs had little or no direct effect on riparian breeding birds. The release of surplus water in excess of 31,000 cfs during the breeding season had strong, direct impact on nesting birds in the form of nest inundation. Releases which rise quickly to 40,000 during the breeding season will inundate a significant number of Common Yellowthroat nests (assuming yellowthroat habitat was available), although few other species experience nest loss at this level. Releases above 40,000 cfs during the breeding season have the potential to inundate a significant portion of Bell's Vireo and Yellow-breasted Chat nests. Population declines in Common Yellowthroat and Bell's Vireo may also result from a combination of habitat loss and nest inundation.

The extent and timing of surplus water releases should receive careful management attention. Breeding activity peaks from May to mid-July in the three species of obligate riparian birds most susceptible to nest inundation. Surplus water releases above 31,000 cfs should be avoided during this time, with surplus water released prior to or after the breeding season if possible. If surplus releases above 31,000 cfs during the breeding season cannot be avoided, water levels should be raised as soon as possible and either remain constant or decrease through the breeding season. This would allow nesting birds to adjust their nest-site preferences to the new water level. Information presented in this chapter will allow an accurate prediction of the effects of various future surplus water releases at any given time in the breeding season.

Seven different flow scenarios were evaluated with respect to their direct and indirect effects on breeding birds. Scenarios one and three, calling for monthly base loaded releases or restricted maximum and minimum flows respectively, would be the best for breeding birds. However, any release schedule with maximum flows below 31,000 cfs and which minimized riparian substrate erosion would be acceptable from the standpoint of maintaining the status quo for riparian breeding birds. An important aspect of river fluctuations, that of the effect of fluctuating water levels on river-based insect productivity which becomes available to birds as food, could not be properly

evaluated due to a lack of information. The availability of aquatic insects which emerge from the river and move into the riparian zones as a food resource to riparian birds could greatly affect avian density, productivity, and territoriality. Another aspect of fluctuating flows concerned with riparian substrate erosion rates associated with various releases could not be evaluated for similar reasons.

The most serious long-term concern for the future of the breeding bird community in the river corridor is that of riparian substrate erosion and subsequent habitat loss. If alluvial river terraces exhibiting riparian vegetation remain stable or increase in extent, then the overall density and diversity of birds along the river will remain the same or will increase somewhat. However, if fluctuating flows or surplus flows initiate or accelerate riparian substrate erosion, then bird populations can be expected to decline as a result. A long-term loss of 10% of the NHWZ would not result in a substantial reduction in avian density and diversity along the river corridor. On the other hand, a long-term loss of NHWZ vegetation in excess of that would begin to cause a substantial decrease in overall avian density and diversity.

Management should consider the possibility of floods on the Little Colorado River and the effect this might have on riparian birds susceptible to nest inundation. Floods in excess of 10,000 cfs down the Little Colorado River during the peak of the breeding season could create conditions that would inundate many nests along downstream portions of the main Colorado River if Glen Canyon Dam were simultaneously releasing up to 31,000 cfs. If a situation of this sort did arise, releases from the dam should be immediately and temporarily reduced to minimize downstream nest inundation.

CHAPTER 4: CONCLUSIONS

The range and timing of fluctuating flows and surplus water releases from Glen Canyon Dam have had substantial effects on breeding birds of the Colorado River. These effects have been both beneficial and detrimental. Development of the NHWZ has been beneficial by increasing the density and overall diversity of birds. The NHWZ has been of particular benefit to obligate riparian birds which have colonized it within the last twenty years. However, fluctuating flows above 31,000 cfs during the breeding season were detrimental during the surplus water releases of June 1983 by (1) causing substantial nest inundation in some species, and (2) causing population declines. Future management action should be directed toward a balance between these effects.

The NHWZ was found to exhibit a significantly greater density of birds than the OHWZ. The avian diversity of both zones was similar. Avian density in some well-developed riparian areas in the river corridor was extremely high, and ranked among the highest densities ever reported for noncolonial breeding birds in North America. The breeding birds which have recently colonized the NHWZ were, in effect, partial mitigation for those bird populations which were lost when Glen Canyon was inundated and should be recognized as such.

The eleven species of obligate riparian birds that nested in the NHWZ exhibited a high degree of habitat differentiation in their choice of nest sites. The average habitat preferences of each species indicated the presence of both habitat generalists and habitat specialists. Bell's Vireo and Willow Flycatcher were the most extreme generalists, while American Coot and Blue Grosbeak represented the most extreme specialists. Bell's Vireo and American Coot were the most widely separated species; Willow Flycatcher and Yellow Warbler were most closely associated.

Fluctuating flows up to 31,000 cfs had little direct effect on breeding birds. However, surplus water releases above this level inundated the nests of several obligate riparian species. Flows up to 40,000 cfs inundated a substantial portion of Common Yellowthroat nests. Flows in excess of 40,000 cfs inundated substantial numbers of Bell's Vireo and Yellow-breasted Chat nests; flows of 62,000 cfs inundated 60% of all vireo nests and 11% of all chat nests. Bell's Vireo density declined 45% from 1982 to 1985, largely as a result of nest inundation and habitat loss associated with the June 1983 surplus water release.

The extent and timing of surplus water releases above 31,000 cfs should receive careful management attention. Breeding

activity peaked from May to July in the river corridor, which indicated that surplus releases should be avoided at this time. If surplus releases above 31,000 cfs during the breeding season cannot be avoided, water levels should be raised to higher levels as soon as possible and either remain constant or decrease. Information was presented which can predict the effects of future surplus releases on those species most susceptible to nest inundation.

The three species of obligate riparian birds (yellowthroat, vireo, chat) which experienced the most severe nest inundation during the June 1983 surplus water release formed a distinct management class with respect to their breeding habitat requirements. The fact that they experienced the most substantial nest inundation during the June 1983 flood indicated that their preferred habitat (low, dense areas with more salt cedar and Baccharis shrubs) occurred closer to the water. Their habitat represented an earlier successional stage of riparian vegetation which was more susceptible to manipulation by management. These successional stages of vegetation were largely maintained by the range and extent of fluctuating flows prior to 1983. These three species of common and widespread obligate riparian birds will probably experience the most substantial population fluctuations in the future in response to management actions which directly or indirectly affect their preferred habitat.

Management attention should also be focused on those habitat specialists that were (1) restricted to the NHWZ, (2) of rare or localized occurrence, or (3) nested closest to the water's edge or in marshy habitats. This management-sensitive group included American Coot, Willow Flycatcher, Common Yellowthroat, and Northern (Bullock's) Oriole. Any future habitat loss would be especially detrimental to these four management-sensitive species.

Future flow scenarios that would be most beneficial to breeding birds included those scenarios with the smallest maximum releases, provided those scenarios did not accelerate riparian substrate erosion. Scenarios one and three, as identified by the Bureau of Reclamation, are the two that would be best for birdlife. Scenario one called for monthly base loaded releases, while scenario three called for restricted maximum and minimum releases.

The most serious long-term management consideration with respect to breeding birds is riparian substrate erosion and subsequent habitat loss. If, for example, fluctuating flows were demonstrated to be causing substantial riparian substrate erosion, then the overall density and diversity of riparian breeding birds would decline as a result. Likewise, fluctuating flows that were shown to stabilize or increase river terraces exhibiting riparian vegetation would be of long-term benefit to birds. Periodic surplus water

releases could be a useful management tool in the maintenance of earlier successional stages of vegetation, provided that riparian substrate erosion associated with flooding were not excessive.

The future of riparian breeding birds in the river corridor is closely tied to the operation of Glen Canyon Dam. Changes will no doubt continue to occur in the bird community regardless of the manner in which the dam is operated, but management has the power to predict, direct, and even enhance this process of change. Management should recognize the importance of basic habitat requirements in the maintenance of healthy riparian bird populations. The rate and extent of riparian substrate erosion have the long-term ability to substantially influence the amount and quality of riparian habitat available to the bird community.

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Appendix I-1. Actual numbers of pairs of breeding or potentially breeding birds in OHWZ study sites along the Colorado River in Grand Canyon, 1984.

Species	OHWZ Study Sites									
	01	02	03	04	05	06	07	08	09	10
Mourning Dove		1	1		1				4	2
Black-chinned Hummingbird	2	6	4			2	4	3	11	1
Costa's Hummingbird	1		1	.25					4	
Ash-throated Flycatcher	1	1	1		1		1	2	1	1
Bewick's Wren	2	2	2					3	1	
Blue-gray Gnatcatcher		3	3			2	4	4	6	1
Phainopepla									2	
Bell's Vireo							3.5	7	7	1
Lucy's Warbler		3	6	.25	1	5	6	8	7	1
Yellow Warbler			1				0.5	0.5		
Yellow-breasted Chat	1	0.5					1	2	1	
Summer Tanager		1	1				1			
Black-headed Grosbeak	0.5									
Blue Grosbeak	1		1				1		1	
Lazuli Bunting		1								
Indigo Bunting		1								
Brown-headed Cowbird	3	1	1					2	1	
Hooded Oriole								1		
House Finch	2	1	4			1	2	2	3	1
Lesser Goldfinch			2						1	1
Total Density/Site (pairs)	13.5	21.5	28	.5	3	10	24	34.5	50	9
Number of Species/ Site	9	12	13	2	3	4	10	11	14	8

Appendix I-2. Actual numbers of pairs of breeding or potentially breeding birds in NHWZ study sites along the Colorado River in Grand Canyon, 1984.

Species	NHWZ Study Sites									
	01	02	03	04	05	06	07	08	09	10
Mourning Dove	1	1								
Black-chinned Hummingbird	1	3	5		1	1	2	1	1	
Costa's Hummingbird				.25						
Willow Flycatcher		2	1							
Ash-throated Flycatcher		2	1							
Bewick's Wren	4	3	3					1		
Marsh Wren	1									
Blue-gray Gnatcatcher	3	4	3		1	3	2	2	1	
Bell's Vireo			2				2	2	2	
Lucy's Warbler	3	6	5		2	1	3	2	1	0.5
Yellow Warbler	2	2	3			1	2	3		
Common Yellowthroat	1	1	1	1			2	1	1	
Yellow-breasted Chat	5	3	2				1	1		
Summer Tanager		1	1							
Indigo Bunting		1								
Great-tailed Grackle	1								1	
Brown-headed Cowbird	4	2	4				1		5	
Hooded Oriole			1					1		
Northern Oriole	1									
House Finch	4	2	7							
Lesser Goldfinch	1	1	1					1		
Total Density/Site (pairs)	32	34	40	1.25	4	6	15	15	12	0.5
Number of Species/ Site	14	15	15	2	3	4	8	10	7	1

Appendix I-3. Actual numbers of pairs of breeding or potentially breeding birds in NHWZ study sites along the Colorado River in Grand Canyon, 1985.

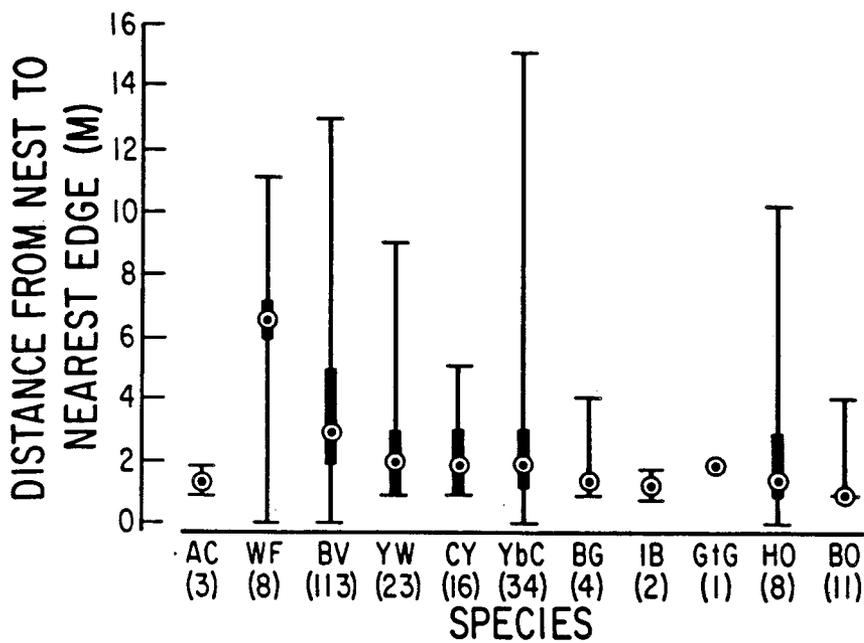
Species	NHWZ Study Sites									
	01	02	03	04	05	06	07	08	09	10
American Coot	1									
Screech Owl			1							
Mourning Dove	3	2	1		1		1			.5
Black-chinned Hummingbird		8	7	.25	1	2	2	2	2	
Willow Flycatcher		2	1							
Ash-throated Flycatcher	1	2	1							
Bewick's Wren	5	3	3					1		
Blue-gray Gnatcatcher	2	5	3			.5	1	1		
Bell's Vireo							2	2		.5
Lucy's Warbler	6	6	5		1	.5	3	1		
Yellow Warbler		2	2		1		3	2		
Common Yellowthroat	2	1	1				1	1	1	
Yellow-breasted Chat	4	4	1				3	1		
Summer Tanager							1	.5		
Blue Grosbeak		1						.5		
Lazuli Bunting		1					1			
Great-tailed Grackle	2		1					1	1	
Brown-headed Cowbird	2	3	2							
Hooded Oriole			1							
Northern Oriole	1									
House Finch	10		4					1		
Lesser Goldfinch			1				1	1	1.5	
House Sparrow	1									
Total Density/Site (pairs)	40	40	35	.25	4	3	19	15	5.5	1
Number of Species/Site	13	13	16	1	4	3	11	13	4	2

Appendix I-4. Actual numbers of pairs of breeding or potentially breeding birds in OHWZ study sites along the Colorado River in Grand Canyon, 1985.

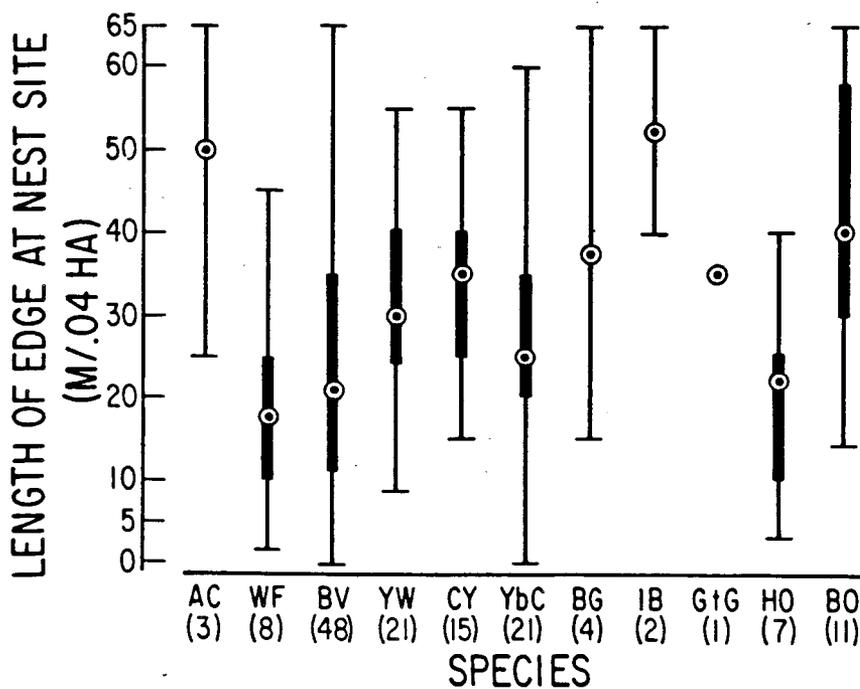
Species	OHWZ Study Sites									
	01	02	03	04	05	06	07	08	09	10
Mourning Dove	1	1	2	.25				3	3	1
Black-chinned Hummingbird	1	1	3		1	1	2	2	3	3
Ash-throated Flycatcher	1	1	1			1	1	1	1	
Bewick's Wren		2	2					2	1	
Blue-gray Gnatcatcher	1	3	4	.25	1		5	1	4	1
Phainopepla									1	
Mockingbird									2	1
Crissal Thrasher								1		
Bell's Vireo			1				5	5	6	1
Lucy's Warbler		3	5	.25	1	2	4	4	4	2
Yellow Warbler							1	1		
Yellow-breasted Chat	.5						3	3	2	
Summer Tanager								.5		
Black-headed Grosbeak	.5									
Blue Grosbeak	.5							.5	1	
Lazuli Bunting		1						1		
Brown-headed Cowbird	3		1					1	2	
Hooded Oriole							.5	1		
House Finch		2						4	1	
Lesser Goldfinch		2					1	2	1	
Total Density/Site (pairs)	8.5	12	23	.75	3	4	22.5	33	32	9
Number of Species/Site	8	7	10	3	3	3	9	17	14	6

Appendix II-1. Species covariance matrices for the three discriminant functions. Only species with sample sizes larger than one have been included.

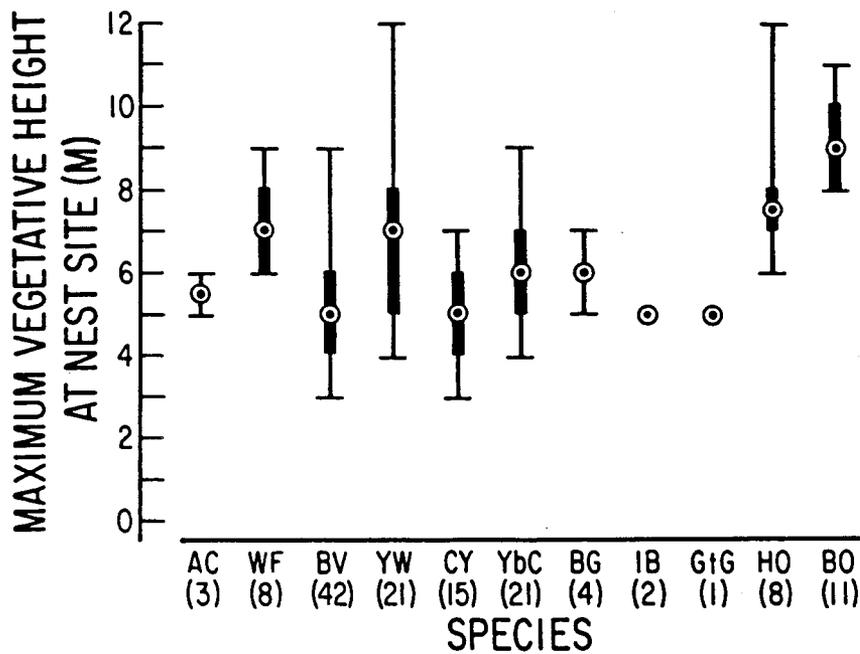
Species	Function 1	Function 2	Function 3
American Coot			
Function 1	.0289		
Function 2	.0611	.8856	
Function 3	.0252	-.4662	.3784
Willow Flycatcher			
Function 1	1.3162		
Function 2	.2562	3.2298	
Function 3	.6018	1.0906	2.1778
Bell's Vireo			
Function 1	1.4935		
Function 2	-.1755	.9866	
Function 3	.3986	.4957	.9613
Yellow Warbler			
Function 1	.9681		
Function 2	.5723	1.3809	
Function 3	-.5812	-.7582	1.4850
Common Yellowthroat			
Function 1	.3843		
Function 2	-.0167	.7754	
Function 3	-.0948	-.1149	.3849
Yellow-breasted Chat			
Function 1	.9465		
Function 2	-.2261	.9244	
Function 3	-.1109	-.1967	1.1455
Blue Grosbeak			
Function 1	.0369		
Function 2	-.0666	.1880	
Function 3	-.1615	.5474	1.6731
Hooded Oriole			
Function 1	.9503		
Function 2	-.7795	1.6804	
Function 3	-.6761	-.3098	.6400
Northern (Bullock's) Oriole			
Function 1	.1899		
Function 2	.0496	.8144	
Function 3	-.0962	.0453	.8694



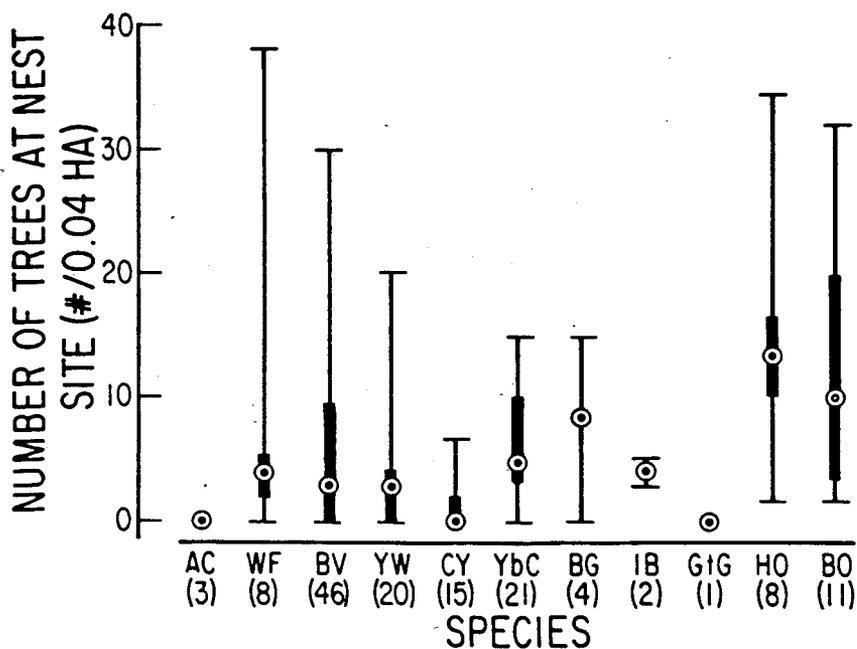
Appendix II-2. Overall range, interquartile range, and median distance from nest to nearest edge for riparian birds in both the OHWZ and NHWZ. Species codes as in Table 2-1. Numbers in parentheses indicate sample sizes.



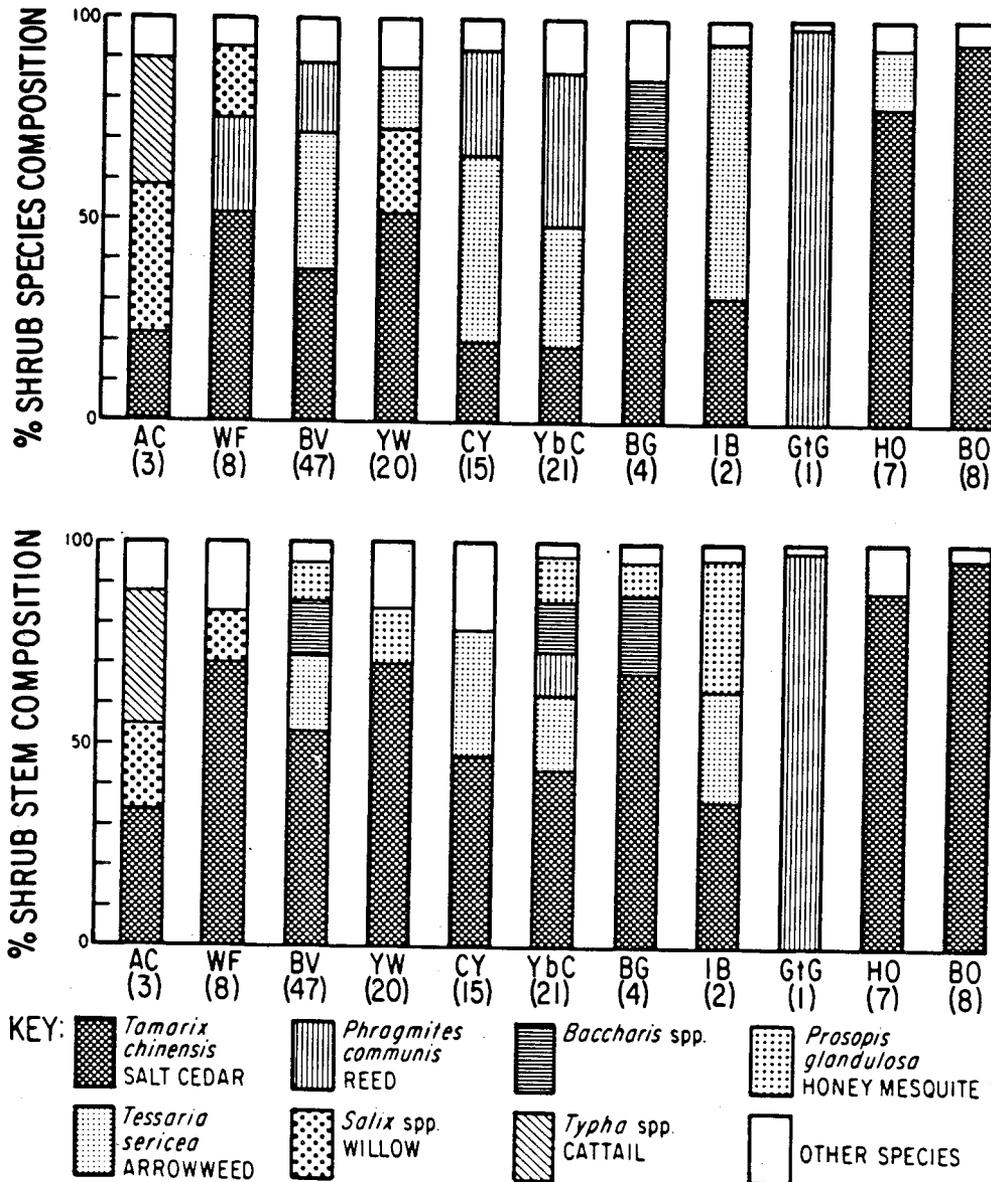
Appendix II-3. Overall range, interquartile range, and median of length of edge in 0.04 ha circles centered at nests of obligate riparian birds in both the OHWZ and NHWZ. Species codes as in Table 2-1. Numbers in parentheses indicate sample sizes.



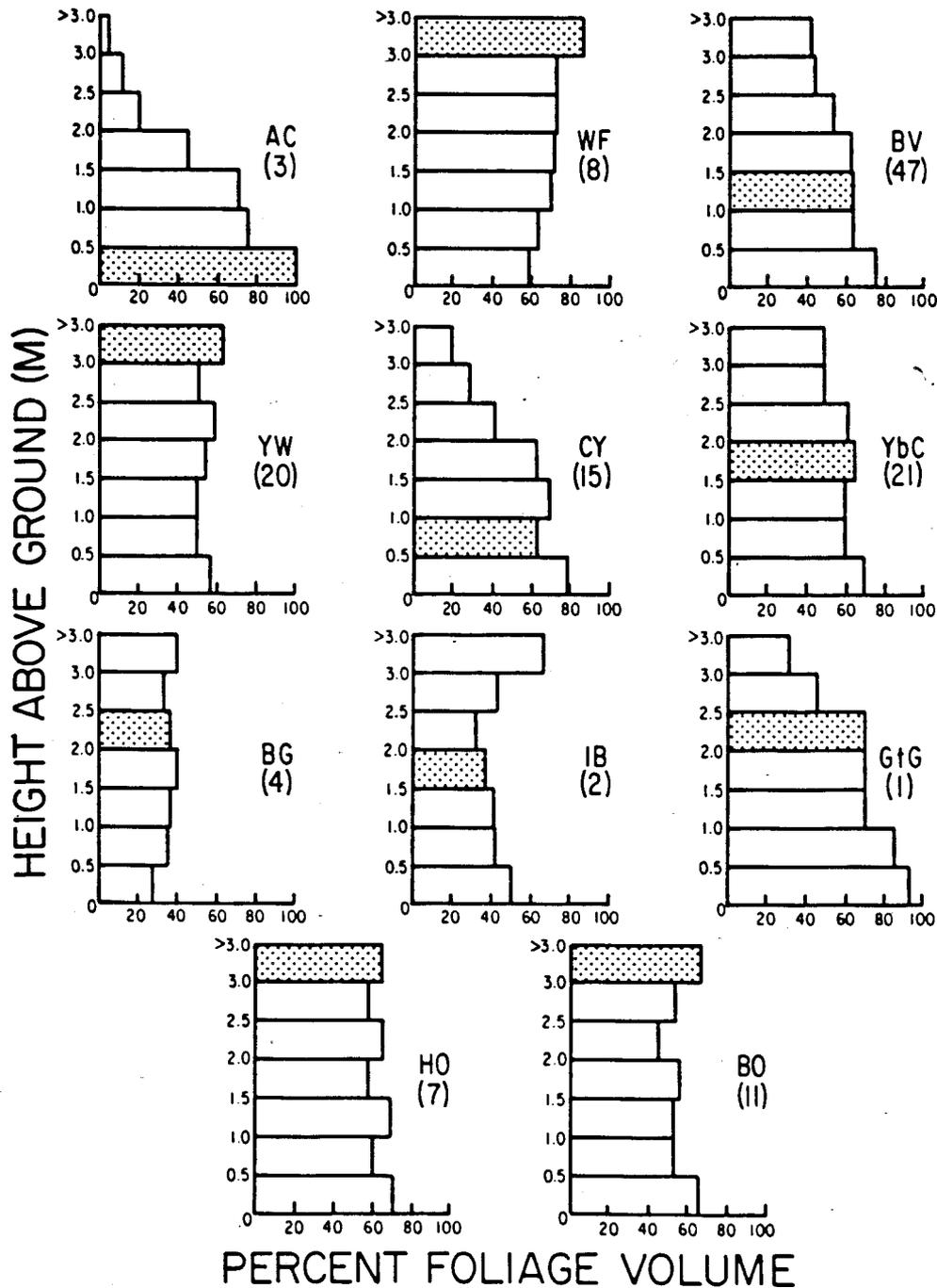
Appendix II-4. Overall range, interquartile range, and median of maximum vegetative height present in 0.04 ha circles at nests of obligate riparian birds in both the OHWZ and NHWZ. Species codes as in Table 2-1. Numbers in parentheses indicate sample sizes.



Appendix II-5. Number of trees present in 0.04 ha circles at nests of obligate riparian birds in both zones. Overall range, interquartile range, and median are indicated. Species codes as in Table 2-1. Numbers in parentheses indicate sample sizes.



Appendix II-6. Percent shrub species and shrub stem composition in two perpendicular armlength transects (north-south, east-west) through the center of 0.04 ha circles centered at nests of obligate riparian birds in both zones. Species codes as in Table 2-1. Numbers in parentheses indicate sample sizes.



Appendix II-7. Median percent foliage volume by level in 0.04 ha circles centered at nests of obligate riparian birds in both zones. Shaded bar indicates the level in which the median nest height for each species occurs. Species codes as in Table 2-1. Numbers in parentheses are sample sizes.

Appendix III-1. Bell's Vireo nest locations, nest heights, and extent of inundation during the June 1983 high water along the Colorado River in Grand Canyon.

Nest No.*	Nest Location	Nest Ht. Above Gnd. (cm)	Water Depth at Nest in June (cm)	Date Checked	Extent of Inundation (cm)
a 1	208.7L	96	150	6/23/83	54
a 2	208.7L	68	90	6/23/83	22
a 4	208.5L	74	30	6/23/83	none**
a 5	208.7R	125	30	6/23/83	none
a 6	213.3L	103	150	6/23/83	47
a 7	71.1L	182	180	6/12/83	none**
a 8	71.0L	163	?	6/12/83	?
a 9	167.8L	143	150	6/19/83	7
a10	167.9R	114	180	6/19/83	66
a11	178.9R	100	150	6/20/83	50
a12	178.7R	167	120	6/20/83	none**
a13	187.6R	108	120	6/20/83	12
a14	187.5R	171	150	6/20/83	none**
a15	198.5R	116	240	6/21/83	124
a16	204.0R	115	165	6/22/83	50
a17	211.2L	98	150	6/23/83	52
a18	211.2L	121	150	6/23/83	29
a19	225.6L	111	120	6/24/83	9
a20	42.9L	97	120	6/ 9/83	23
a21	204.4R	105	150	6/22/83	45
a22	211.2L	295	150	6/23/83	none
a23	178.8R	68	150	6/20/83	82
a24	178.9R	121	150	6/20/83	29
a25	179.0R	77	150	6/20/83	73
a26	198.2R	175	240	6/21/83	65
a27	208.8L	51	90	6/23/83	39
a28	208.6L	96	30	6/23/83	none
a29	208.7L	81	0	6/23/83	none
a30	217.15L	185	150	6/23/83	none**
a31	169.2R	79	105	6/19/83	26
a32	170.0L	83	120	6/19/83	37
a33	170.6R	121	165	6/19/83	44
a34	207.4L	175	0	6/22/83	none
a35	174.2R	111	0	6/19/83	none
a36	174.2R	151	0	6/19/83	none
a37	187.5R	91	60	6/20/83	none**
a38	187.5R	91	0	6/20/83	none
a39	187.9R	67	0	6/20/83	none
o 1	208.7L	74	90	6/23/83	16
o 2	208.6L	103	150	6/23/83	47
o 3	167.9R	70	180	6/19/83	110
o 4	167.9R	104	150	6/19/83	46
o 5	178.8R	65	120	6/20/83	55
o 6	178.7R	143	150	6/20/83	7

Appendix III-1. Continued.

Nest No.	Nest Location	Nest Ht. Above Gnd. (cm)	Water Depth at Nest in June (cm)	Date Checked	Extent of Inundation (cm)
o 7	187.6R	89	105	6/20/83	16
o 8	187.7R	125	120	6/20/83	none
o 9	187.7R	118	120	6/20/83	2
o10	198.4R	166	150	6/21/83	none**
o11	198.4R	95	150	6/21/83	55
o12	204.0R	51	?	6/22/83	?
o13	211.2L	142	150	6/23/83	8
o14	211.2L	88	?	6/23/83	?
o16	191.9L	82	150	6/21/83	68
o17	191.9L	99	150	6/21/83	51
o18	191.9L	87	135	6/21/83	48
o19	167.9R	167	180	6/19/83	13
o20	171.3L	73	?	6/19/83	?
o21	204.4R	105	150	6/22/83	45
o22	204.4R	135	150	6/22/83	15
o23	208.8L	76	?	6/22/83	?
o24	208.8L	124	120	6/23/83	none**
o25	208.8L	79	?	6/23/83	?
o26	208.6L	118	?	6/23/83	?
o27	217.15L	165	180	6/23/83	15
o28	217.2L	110	180	6/23/83	70
o29	217.2L	118	180	6/23/83	62
o30	169.2R	129	75	6/19/83	none**
o31	169.2R	90	105	6/19/83	15
o32	169.2R	112	105	6/19/83	none**
o33	169.2R	166	105	6/19/83	none
o34	169.3R	101	150	6/19/83	49
o35	207.4L	140	150	6/22/83	10
o36	217.1L	106	180	6/23/83	74
o37	70.9L	136	0	6/12/83	none
o38	70.9L	81	0	6/12/83	none

 * a = active nests, o = old nests.

**These nests were not inundated by water levels observed between June 7 and 24. Water levels recorded during this time at the Phantom Ranch gauging station correspond to river flows between 48,000 and 63,000 cfs. However, these nests were calculated to have been inundated by the peak high water of June 29 (92,000 cfs), assuming the river rose a conservative 0.5 m above water levels present between June 7 and 24.

Appendix III-2. Yellow-breasted Chat nest locations, nest heights, and extent of inundation during the June 1983 high water along the Colorado River in Grand Canyon.

Nest No.	Nest Location	Nest Ht. Above Gnd. (cm)	Water Depth at Nest in June (cm)	Date Checked	Extent of Inundation (cm)
1	187.6R	186	180	6/20/83	none*
2	198.4R	230	180	6/21/83	none*
3	51.0L	85	180	6/ 9/83	95
4	204.4R	200	180	6/22/83	none*
5	170.6L	240	135	6/19/83	none
6	187.8R	180	60	6/20/83	none
7	191.8L	202	150	6/21/83	none*
8	198.2R	170	180	6/21/83	10
9	207.6L	171	60	6/22/83	none
10	217.1L	210	180	6/23/83	none*
11	47.1R	128	0	6/10/83	none
12	55.1R	171	0	6/11/83	none
13	55.1R	152	0	6/11/83	none
14	70.9L	151	0	6/12/83	none
15	174.2R	110	0	6/19/83	none
16	187.9R	104	40	6/21/83	none*
17	187.9R	275	0	6/21/83	none
18	204.3R	202	0	6/22/83	none
19	204.3R	140	100	6/22/83	none*

* These nests were not inundated by water levels observed between June 7 and 24. Water levels recorded during this time at the Phantom Ranch gauging station correspond to river flows between 48,000 and 63,000 cfs. However, these nests were calculated to have been inundated by the peak high water of June 29 (92,000 cfs), assuming the river rose a conservative 0.5m above water levels present during the period of observation.

Appendix IV. Common and scientific names of birds mentioned in the text. Names conform to those used by the American Ornithologists' Union (1983).

Common Name	Scientific Name
Turkey Vulture	<i>Cathartes aura</i>
American Kestrel	<i>Falco sparverius</i>
American Coot	<i>Fulica americana</i>
Mourning Dove	<i>Zenaida macroura</i>
Western Screech-Owl	<i>Otus kennicottii</i>
White-throated Swift	<i>Aeronautes saxatalis</i>
Black-chinned Hummingbird	<i>Archilochus alexandri</i>
Costa's Hummingbird	<i>Calypte costae</i>
Willow Flycatcher	<i>Empidonax traillii</i>
Black Phoebe	<i>Sayornis nigricans</i>
Eastern Phoebe	<i>Sayornis phoebe</i>
Say's Phoebe	<i>Sayornis saya</i>
Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>
Violet-green Swallow	<i>Tachycineta thalassina</i>
Common Raven	<i>Corvus corax</i>
Rock Wren	<i>Salpinctes obsoletus</i>
Canyon Wren	<i>Catherpes mexicanus</i>
Bewick's Wren	<i>Thryomanes bewickii</i>
Marsh Wren	<i>Cistothorus palustris</i>
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>
Northern Mockingbird	<i>Mimus polyglottos</i>
Crissal Thrasher	<i>Toxostoma dorsale</i>
Phainopepla	<i>Phainopepla nitens</i>
Bell's Vireo	<i>Vireo bellii</i>
Nashville Warbler	<i>Vermivora ruficapilla</i>
Lucy's Warbler	<i>Vermivora luciae</i>
Yellow Warbler	<i>Dendroica petechia</i>
Common Yellowthroat	<i>Geothlypis trichas</i>
Yellow-breasted Chat	<i>Icteria virens</i>
Summer Tanager	<i>Piranga rubra</i>
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>
Blue Grosbeak	<i>Guiraca caerulea</i>
Lazuli Bunting	<i>Passerina amoena</i>
Indigo Bunting	<i>Passerina cyanea</i>
Rufous-crowned Sparrow	<i>Aimophila ruficeps</i>
Black-throated Sparrow	<i>Amphispiza bilineata</i>
Great-tailed Grackle	<i>Quiscalus mexicanus</i>
Brown-headed Cowbird	<i>Molothrus ater</i>
Hooded Oriole	<i>Icterus cucullatus</i>
Northern (Bullock's) Oriole	<i>Icterus galbula bullockii</i>
House Finch	<i>Carpodacus mexicanus</i>
Lesser Goldfinch	<i>Carduelis psaltria</i>
House Sparrow	<i>Passer domesticus</i>