

RIPARIAN BIRD COMMUNITY ECOLOGY IN THE GRAND CANYON

Final Report

Cooperative Agreement: 8031-8-0002

Project Name: GRAND CANYON AVIAN COMMUNITY MONITORING

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Short Title of Work: RIPARIAN BIRD COMMUNITY FINAL REPORT

Funded By: Glen Canyon Environmental Studies, Bureau of Reclamation

Supported By: The Bureau of Reclamation
Glen Canyon Environmental Studies Program
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Submitted To: Resource Management
Grand Canyon National Park
Grand Canyon, AZ

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This report may be cited as follows: Sogge, M.K., D. Felley and M. Wotawa. 1998. Riparian Bird Community Ecology in the Grand Canyon -final report. U. S. Geological Survey, Colorado Plateau Field Station report.

Note: Material from Chapter 4 of this report was previously released as a separate project report, and when used should be referenced to: Yard, H.K. 1996. Quantitative diet analysis of selected breeding birds along the Colorado River in Grand Canyon National Park. U.S.G.S. Colorado Plateau Field Station/Northern Arizona University Report. 41 pp.

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Executive Summary

Riparian habitat and avian communities along the Colorado River in Grand Canyon have changed significantly since completion of Glen Canyon Dam. Although some of the most dramatic changes to the riparian avifauna along the river corridor may have already occurred, future operation of Glen Canyon Dam may continue to have significant effects far into the future. In 1991, the Bureau of Reclamation modified the operation of Glen Canyon Dam by adopting an interim flow operations program that included a reduced operation regime (reduced fluctuation levels and flow rates) with specific changes in maximum flows and daily flow fluctuations. Interim flows were initiated in the hopes of reducing negative impacts to the biological, cultural, and physical resources of the Grand Canyon. In 1992, the U.S. Geological Survey Colorado Plateau Field Station (at that time a unit of the National Park Service) was asked to carry out an avian monitoring project for the Bureau of Reclamation's interim flow monitoring program, in order to examine the potential of both direct and indirect impacts.

This project was designed to emphasize the following objectives:

1. determine the direct impacts of Glen Canyon Dam interim flow operations on the nests and nesting of riparian birds along the Colorado River Corridor.
2. investigate possible long-term effects of Glen Canyon Dam flows by documenting patterns of avian use of riparian habitats, particularly with regard to bird species composition and habitat patch size/vegetative composition.
3. determine breeding and residence status, and seasonal and yearly migratory movements of bird species using the Colorado River riparian corridor.
4. develop and test methodologies suitable for the long-term monitoring of avian population levels and distribution within the river corridor.
5. document patterns of insect abundance in riparian habitats and in the diets of common insectivorous birds, in order to better understand how terrestrial birds use the aquatic and terrestrial food resources.

This is the final report associated with this avian community monitoring project. This report is organized by chapters that separately particular study objectives. Each chapter is self-contained. Following are summaries of the major findings associated with each major project component.

Chapter 2: *Determining direct impacts of interim flow operations on the nests and nesting of riparian birds.*

We observed no direct destruction of nests through inundation over the course of this study. Compared with historic dam operations, the interim flow guidelines under effect during our study restricted both the daily and seasonal flow rates and fluctuations. This greatly reduced the amount of vegetation and shoreline in the hydrologically active zone (HAZ), which in turn greatly reduced the potential of birds nesting in this zone.

The potential for nest inundation under interim flows was limited to only a few species that nest very low in the vegetation and close to the river. Most of the species breeding at our study sites did not place their nests even close to the HAZ. Only the Common Yellowthroat nested in such areas, and only one of the five yellowthroat nests was actually placed low enough to be inundated at 20,000 cfs. Another species with the potential for inundation impacts is the Black Phoebe, which builds its nest on vertical rock surfaces, often only a meter or two above water. For all other species, interim flow levels were never high enough to reach the nest itself. In fact, most nests were placed well away from the HAZ and water never reached the base of the vegetation in which the birds nested.

Most of the species that we documented nesting along the river corridor have been noted by other researchers. Black-chinned Hummingbird, Bell's Vireo and Lucy's Warbler continue to be the most abundant breeders, and accounted for 50% of all nests found. We did record several important nest records. The Cliff Swallows that we observed nest building during 1993 and 1995 (at RM 3 and RM 2, respectively) are the first documented for the Canyon since 1975. The Verdin nest at RM 204 is the first breeding records above the head of Lake Mead, where the bird's status was uncertain. The Bushtit nest at Lees Ferry is also rare.

Chapter 3: *Banding Studies:*

Netting and banding provided valuable data including verification of breeding status, timing and patterns of breeding and migration, and information on bird movements. Netting also gave an index of bird abundance, and we captured all of the most common breeding and wintering species. We also captured a number of inconspicuous and less vocal species that would otherwise have been overlooked or less frequently detected. Many of these captures added significantly to what was previously known about that species in the canyon. However, some less common species were detected during surveys but were not netted. Locally breeding birds are more effectively surveyed by point counts or other survey methods, which gather more data points over a shorter period of time. In general, we recommend netting and banding studies only where specific, objective-driven research needs can best be met through banding.

During the winter, almost all of the species that breed in the canyon are gone. Recapture data demonstrate that some of the Bewick's Wrens that breed along the river are year round residents, while some appear to leave their breeding patch and/or the canyon entirely. All other breeding species migrate out of the canyon before the winter.

Brood patch and cloacal protuberance patterns provided excellent data on the timing of breeding and migration activity in the canyon. Small numbers of birds (all males) begin showing signs of breeding in March. Breeding activity picks up rapidly in April, peaks in May and June, then declines rather steeply in July. Almost no breeding activity was detected in August. Migrants account for a large percentage of the Yellow Warblers and Common Yellowthroats detected along the river corridor. This was most pronounced for the warbler, for which 80% of the captured individuals showed no sign of breeding.

Chapter 4: *Avian Diet Study*:

Note: This chapter was previously released as a separate project report, and when used should be referenced to: Yard, H.K. 1996. Quantitative diet analysis of selected breeding birds along the Colorado River in Grand Canyon National Park. U.S.G.S. Colorado Plateau Field Station/Northern Arizona University Report. 41 pp.

Diets of the six species of insectivorous birds examined were significantly different, each species of bird showing a preference for a particular order of arthropod. The significant difference in prey order proportions in the diets of the six species of birds suggests that resource partitioning may help shape the bird community co-existing in the riparian vegetation along the Colorado River.

Identification of arthropod prey remains revealed that birds primarily consumed arthropods of terrestrial origin, comprising approximately 90% of their diet. Insects from aquatic origins comprised only about 8% of the total diet. In arthropod sampling, five times as many terrestrial-origin arthropods were found in the riparian habitat as opposed to those arthropods with aquatic origin. The riparian vegetation along the Colorado River supports an abundance of terrestrial-origin arthropods providing a rich food resource for riparian birds. Although, the river is clearly important in that it supports the riparian vegetation which in turn supports arthropod food resources, its role as a direct source of arthropod prey for these species of birds is minor.

Arthropods collected at the two sites (Paria and Saddle Canyon) sampled above the Little Colorado River (LCR) contained a higher percent of those from aquatic origins (46.5%) than the samples taken at sites below the LCR (Parashant and Spring Canyon with 13.4%). However, there was no significant difference in the proportion of aquatic insects in the diets of the six species of birds at the upper sites than in the diets of the birds at the lower sites. This suggests that consumption of aquatic insects was relative constant regardless of the observable abundance of aquatic origin invertebrates.

Chapter 5: *Survey Techniques Comparison:*

We compared several different survey techniques, including floating surveys, walking surveys, and point counts. Floating surveys provided the least labor-intensive index of the composition of the riparian breeding bird community. They provide a fairly accurate estimate of *relative* abundance, though for some species results are seriously biased. Population estimates from floating survey tended to be closer to estimates from walking surveys for especially loud species and those more closely associated with NHWZ habitats. Populations of quiet or more upland-associated species were more seriously underestimated by floating surveys. Clearly, floating surveys provide different results depending on the species habitat choice, singing frequency, and loudness. Further, accuracy of the floating survey varies between sites, depending on physical characteristics.

As one would expect, walking surveys detected significantly more species than did floating counts. Similar numbers of species were observed during walking surveys and unbounded point counts. However, the number of species in common for the walking and point count surveys was low. This lack of agreement was probably due to observations of rare species. Excluding rare species, the reliability of the unbounded point counts and walking surveys to detect a species were similar overall, and higher than the reliability of 50m point counts. Also, certain species-specific differences were evident. Common species with small territories were equally well detected by all three methods, while loud species with larger territories were poorly detected by 50m point counts only. Relatively quiet and rare species were equally poorly detected by all methods. Thus, survey methodology must be tailored to reflect the life history of the species to be monitored.

Linear regression analyses of abundance data summed for the ten most common species showed that abundance estimates from walking and point count surveys were highly correlated and strikingly similar. Both point count methods were near one-to-one with the walking surveys, with 50m point counts undercounting and unbounded point counts over-counting relative to walking surveys.

Except when only a few birds were present at a site, observers recorded different things. This was true whether observer pairs were both highly experienced or one observer was less experienced. Because of the relatively simple communities of the Grand Canyon's riparian habitat, observer variability may not be an important factor in survey accuracy overall. However at large sites, with a rich and abundant bird community, observer variability was among the most important sources of variability. At such sites observer variability must be carefully controlled. Though mean difference in number of species detected was generally small, the overall range of differences was sometimes large (up to five species). The total number of birds observed was more variable than number of species observed. Potential ways to minimize observer variability are to standardize methodologies and survey areas, maintain the same observers between years, and through training programs for observers.

Chapter 6: *Avian Survey Summary:*

Approximately 75 - 90 percent of the birds detected during walking surveys or point counts were heard, rather than seen. This emphasizes the importance of using only highly skilled and trained survey personnel who can accurately identify species based on songs and calls. This is critical during the breeding season, when song rates are high and dense vegetation inhibits seeing the bird that is vocalizing. Our data on detections suggest that walking counts may be preferable to point counts when conducting winter surveys.

Comparisons of annual and seasonal survey results showed that the details of survey timing, technique, efforts, and locations greatly affect estimates of species richness (the number of species) and abundance (the number of individuals detected), as well as patterns of relative abundance (the percent of detections attributable to each species). Variables such as species presence/absence and rank abundance of common species appear to be less influenced by inconsistencies in surveys protocols, though potentially of lower management value.

The riparian and upland habitats along the river corridor are used by a large number of bird species. Although abundance was highest during the breeding season (partly due to a large number of migrating birds), species richness was high and similar during both the breeding and non-breeding seasons. During the breeding season, Lucy's Warbler, Bell's Vireo, Bewick's Wren were the most common and widely distributed species between Lees Ferry and Diamond Creek. They, as well as two other species (Blue-gray Gnatcatcher and House Finch) accounted for over half of the birds detected. There does not appear to have been a major shift in the numeric dominance and ecological importance the most common breeding-season species over the last decade.

During the non-breeding season, the most common species (Ruby-crowned Kinglet) accounted for almost 20 percent of detections. The remainder of species present during this season were found in low abundance, such that the 15 most common species failed to provide even 50% of the detections. Only a few of the common breeding species were also common during the non-breeding season, illustrating a major change in bird community composition and ecology during these two times.

The use of "decision rules" to determine which species bred in a given patch and to estimate the number of breeding pairs resulted in different species composition and abundance values than if we had simply taken the highest number of birds detected during breeding season surveys. The latter approach almost certainly overestimates the abundance and density of breeding birds in each patch. Such overestimations are probably considerable for species that both breed in, and migrate through, the canyon.

Survey timing is another factor important in minimizing variation in the breeding bird counts. Breeding community surveys are best conducted during the months of April, May and June (although the large influx of migrants in May needs to be taken into account). Surveys before April are too early to detect many locally breeding birds. By July, most local nesting activity has ended and recently fledged and hatching year individuals can

inflate species counts, resulting in an overestimate of breeding pairs (young birds can not always be differentiated from adults during surveys). Although they have limited utility for breeding data, censuses conducted before April and after June may be useful in studying migrant and wintering bird communities.

Chapter 7: *Avian Community and Habitat Relationships:*

We focused our efforts on determining the relationship between the breeding bird community and patch/landscape level habitat variables relative to vegetation structure, composition and size. Bird species abundance, species richness, and community diversity (Shannon Diversity Index; SDI) per patch did not differ between 1994 and 1995. There was a strong positive correlation among the three response variables (bird species richness, breeding abundance, and SDI) and 14 of the 17 covariates (habitat measurements). Eleven covariates were considered good predictors. Covariates associated with large vegetation structures and with tamarisk (eg. tree area and volume, new-high-water zone area, and tamarisk area and volume) were the best predictors for each of the three bird community response. Additionally, total area and vegetated area had good potential as predictors for abundance of breeding pairs. Thus, the overall pattern is that as patch size increased, the number of breeding bird species and individuals increased, as did SDI.

Our best predictive models worked better for bird abundance than for species richness or diversity. For all bird community variables, the lowest average values were found in patches located between RM 96 and RM 131. The highest bird abundance, richness and diversity values were generally found in the lower river, where patches are largest and most contiguous, and often bordered by extensive OHWZ and upland vegetation.

The area and volume of tree habitat (defined as woody vegetation 2 m or higher) was a much better predictor of bird community response variables than were shrub (woody vegetation >2 m high) and herb (nonwoody vegetation, usually ground cover). This suggests that larger woody vegetation plays a more important role in structuring the riparian bird community than do shrub or herbaceous vegetation. Of the major dominant plant species, only mesquite and tamarisk vegetation types functioned as good predictors of bird community parameters. Areas of willow, arrowweed, baccharis, and grass vegetation types contributed less predictive value.

Several of our models accounted for approximately two-thirds of the variation in bird communities along the canyon. We feel this is a remarkably strong model response given that we addressed primarily vegetation-related habitat components, and did not measure a number of other difficult to assess but potentially influencing factors that also function to shape the breeding bird community. The remaining bird community variation not accounted for in our models is likely influenced by a number of regional and local factors such as environment (e.g., temperature) and geomorphology, adjacent upland habitat, species' range expansions and limits, cowbird nest parasitism, quality and quantity of migratory stopover areas and wintering habitat, and species-specific life history traits.

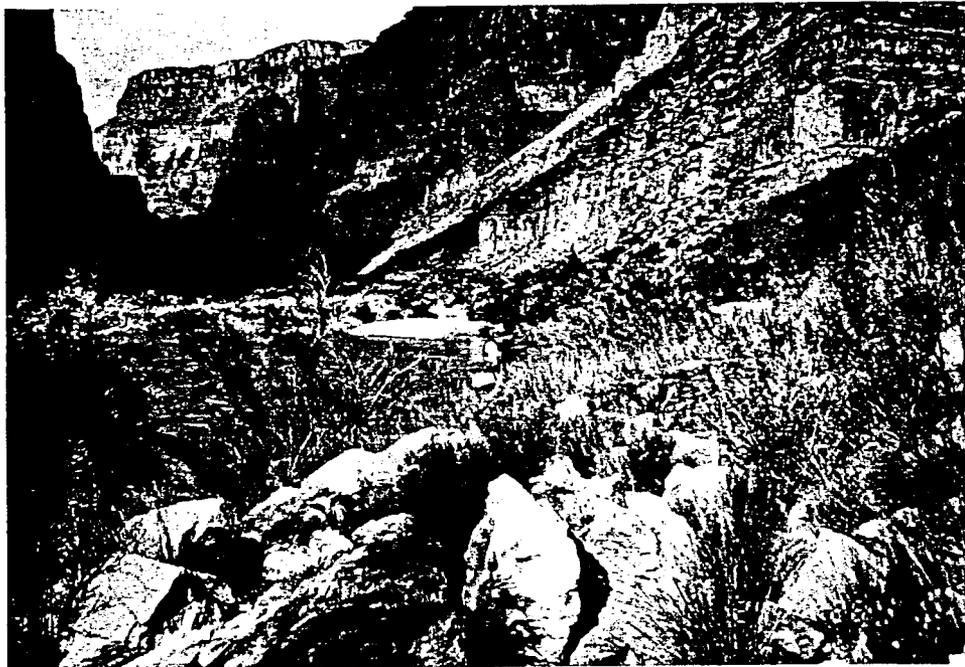
Chapter 8: *Annotated Species List:*

This is a list of all records of birds seen and captured along the river corridor over the course of this study, with detailed notes on prevalence, distribution, seasonality and breeding status. It includes clarification of the breeding and seasonal status of many species, adds new records for previously rarely-detected species, as well as documenting unusual and new breeding records.

ACKNOWLEDGMENTS

We would like to thank the staff of Grand Canyon National Park and Glen Canyon National Recreation Area for their support of this project. We also thank the Bureau of Reclamation Glen Canyon Environmental Studies (GCES) program for funding, and for their substantial technical and logistical support. Patricia Hodgetts and Helen Yard conducted hundreds of surveys and operated mist-nests for hundreds of hours, often under difficult circumstances. Their efforts were invaluable to this project. Support from Jim Petterson and John Ray (Grand Canyon National Park Division of Resources Management) and Christine Karas (Bureau of Reclamation, Salt Lake City) has been crucial to this project. The staff of O.A.R.S. and the GCES program have provided excellent logistical field support. Marlene Bennett and Don Henry (US Fish and Wildlife Service, Phoenix) helped develop and implement the vegetation measurement techniques used in these analyses. Paul Deshler provided critical GIS technical support and assistance, and Dan Spotsky (Grand Canyon National Park) provided insight on spatial data issues. We are grateful for volunteer field assistance from John Grahame, Aurora Hindman, Bill Howe, Matt Johnson, Bill Maynard, Albert Miranda, and Lia Spiegel. Linda Sogge and Charles Drost reviewed earlier drafts of this report and made many useful revisions.

Chapter 1: General Introduction



GRAND CANYON AVIAN COMMUNITY MONITORING: 1993 - 1995

GENERAL INTRODUCTION

Avian communities along the Colorado River in Grand Canyon¹ have changed significantly since completion of Glen Canyon Dam. Once warm, sediment-laden and free-flowing, the Colorado River was transformed into a cold, clear, flow-regulated river. The extent of daily flow rate fluctuations increased, and as a result river level elevation changed as much as 2-3 meters daily in some areas. Also, reduced sediment load influenced beach formation and erosion, and scouring of the lower riparian zone. Because of these and other changes, riparian habitat characteristics were dramatically altered, with an overall increase in the amount of riparian vegetation (Turner and Karpiscak 1980). These habitat changes have caused changes in the canyon bird community as well (Brown et al. 1987, Carothers and Brown 1991).

Although some of the most dramatic changes to the riparian avifauna along the river corridor may have already occurred, future operation of Glen Canyon Dam may continue to have significant effects far into the future. The fluctuating flows released from the dam could have both direct and indirect impacts on the bird community. Direct (short-term) impacts could occur if birds or their nests are drowned, or if the nest substrate is destroyed. Indirect (long-term) impacts could arise primarily from flow-induced changes in riparian habitat (e.g., distribution, amount, patch size, composition, and structure) or avian food resources.

In 1991, the Bureau of Reclamation modified the operation of Glen Canyon Dam by adopting an interim flow operations program that included a reduced operation regime (reduced fluctuation levels and flow rates) with specific changes in maximum flows and daily flow fluctuations (USDI 1993). Interim flows were initiated in the hopes of reducing negative impacts to the biological, cultural, and physical resources of the Grand Canyon. An interim flow monitoring program was also initiated in 1991, with the intent to determine if the interim flow regime was actually reducing these impacts.

In 1992, the U.S. Geological Survey Colorado Plateau Research Station (at that time a unit of the National Park Service) was asked to carry out an avian monitoring project for the Bureau of Reclamation's interim flow monitoring program, in order to examine the potential of both direct and indirect impacts. Such data would provide resource managers and decision makers with the information needed to make resource and operation decisions.

¹Note that the Grand Canyon, as used in this report, includes the Colorado River corridor from Glen Canyon Dam downstream to Diamond Creek. Thus, the area we call the Grand Canyon includes portions of Glen Canyon National Recreation Area, Hualapai Tribe lands, Navajo Nation lands, and Grand Canyon National Park.

This project was designed to emphasize the following objectives:

1. determine the direct impacts of Glen Canyon Dam interim flow operations on the nests and nesting of riparian birds along the Colorado River Corridor.
2. investigate possible long-term effects of Glen Canyon Dam flows by documenting patterns of avian use of riparian habitats, particularly with regard to bird species composition and habitat patch size/vegetative composition.

We also felt that it was important to develop and test methodologies that would allow resource managers to monitor the status of the bird communities along the river, in order to detect and react to changes in species composition or population levels. Furthermore, in order to better interpret and understand changes in the avian community, it would be necessary to understand the resident status, migratory patterns, and habitat use of the birds using the riparian corridor. Therefore, our project also included efforts directed at the following objectives:

3. determine the residence status and movements of bird species using the Colorado River riparian corridor (e.g., do individuals stay within the canyon, and do they move between habitat patches).
4. develop and test methodologies suitable for the long-term monitoring of avian population levels and distribution within the river corridor.
5. document patterns of insect abundance in riparian habitats and in the diets of common insectivorous birds, in order to better understand how terrestrial birds use the aquatic and terrestrial food resources.

Past research, some of it associated with GCES Phase I, documented the overall composition and general distribution of bird communities (Carothers and Sharber 1976, Brown 1988, Brown et al. 1987) or particular species (Pettersen and Sogge 1996) within the Grand Canyon, or looked at the direct (flooding) impacts of previous flow regimes (Brown and Johnson 1987). However, our avian monitoring project is the first designed specifically to meet all of the objectives listed above.

This is the final report associated with this avian community monitoring project. The two previous project reports summarized the nature and status of project efforts in 1993-94 (Sogge et al. 1994) and 1995 (Sogge et al. 1995). All information and data from those earlier reports are incorporated into this final report.

In order to effectively present the results and interpretation of research directed toward so many objectives, this report is organized by chapters that address each of the study objectives. Each chapter is self-contained, and includes introduction, methods, results, discussion and literature cited.

Following is a summary of the report structure and chapter contents:

Chapter 1: *General Introduction*

Chapter 2: *Determining direct impacts of interim flow operations on the nests and nesting of riparian birds.* This chapter deals with loss of nests from flooding within the hydrologically active zone. It also presents information on the number, species, and placement characteristics of bird nests found during this study.

Chapter 3: *Banding Studies:* Here we report the results of our banding program, including overall capture results, including seasonal and annual species abundance and diversity patterns, timing of breeding and migration, and important information on breeding status of selected species.

Chapter 4: *Avian Diet Study:* This chapter is comprised of the final report for the avian diet component, which was released prior to this overall project final report. Because it was an important component of the overall project, we have included it herein. It documents the composition of invertebrates in riparian habitats and the diet of six passerine bird species breeding along the river corridor. Data in this chapter should be attributed to the original diet study report: *Yard, H.K. 1996. Quantitative diet analysis of selected breeding birds along the Colorado River in Grand Canyon National Park. U.S.G.S. Colorado Plateau Field Station/Northern Arizona University Report. 41 pp.*

Chapter 5: *Survey Techniques Comparison:* This section includes a detailed comparison of different avian survey techniques, including total counts, point counts, walking surveys, and floating surveys. Degrees and sources of variation are discussed for each survey technique.

Chapter 6: *Avian Survey Summary:* In this chapter, we summarize the results of our avian surveys, including types of detections, habitat in which species were detected, listing of all species detected, and patterns in annual and seasonal abundance, species richness, and diversity.

Chapter 7: *Avian Community and Habitat Relationships:* Here we investigate how patterns of breeding bird abundance, species richness, diversity are related to vegetation structure and composition at study sites along the river corridor.

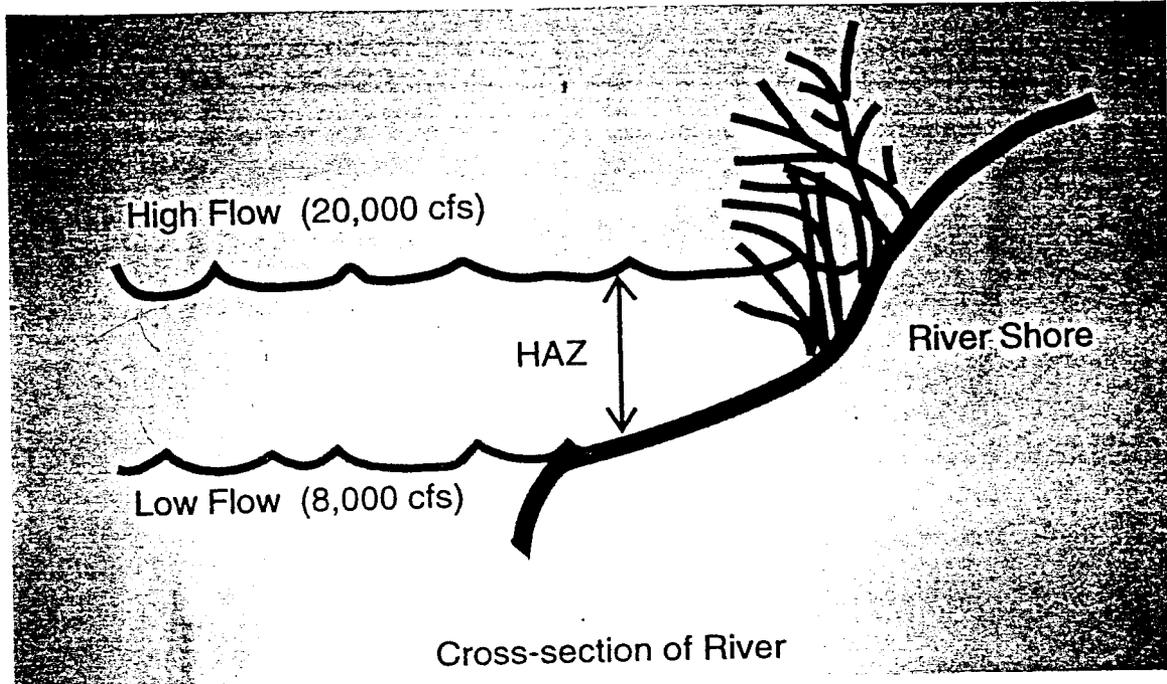
Chapter 8: *Annotated Species List:* This is a list of all records of birds seen and captured along the river corridor over the course of this study, with detailed notes on prevalence, distribution, seasonality and breeding status.

Each chapter is "self-contained" and includes introduction, methods, results, discussion and literature cited sections. Many chapters include detailed appendices specific to that chapter. Following Chapter 7 we provide a set of general appendices with information relating to several different chapters. At the end of the report we have provided aerial photographs of each site, as an aid to relocating the exact study sites we used.

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Chapter 2: Determining Direct Impacts



DETERMINING DIRECT IMPACTS OF INTERIM FLOW OPERATIONS ON THE NESTS AND NESTING OF RIPARIAN BIRDS

INTRODUCTION

Since the completion of Glen Canyon Dam in 1963, the manipulation of river flows has allowed the development of new riparian habitat for breeding birds along the Colorado River in the Grand Canyon. This new high water zone (NHWZ) vegetation is dominated by salt cedar (*Tamarix chinensis*), seepwillow (*Baccharis salicifolia*), sandbar willow (*Salix exigua*), common reed (*Phragmites communis*), and cattail (*Typha* spp.). The NHWZ is very different from the old high water zone (OHWZ) vegetation dominated by catclaw (*Acacia greggii*), honey mesquite (*Prosopis glandulosa*), and netleaf hackberry (*Celtis reticulata*; Turner and Karpiscak 1980). Brown and Johnson (1987) found that fluctuating flows directly affected birds breeding in this new environment by flooding active nests. Their study was conducted during a period of high daily fluctuations (sometimes over 2 m daily change in river level), and enormous seasonal fluctuations (e.g. high flows of 93,000 cubic feet/second [cfs] in June, 1983). They found that flows as high as 31,000 cfs (maximum power plant output from Glen Canyon Dam) flooded few nests, while flows over 40,000 cfs began having significant impacts on some riparian breeding species.

Under the Bureau of Reclamation's interim flow regime in operation from 1991 through 1995, peak flows could not exceed approximately 20,000 cfs and daily fluctuations were limited to between 5,000 and 8,000 cfs (USDI Bureau of Reclamation 1993). Given Brown and Johnson's (1987) findings that few nests were flooded until flows reached 40,000 cfs, flooding of active nests under the interim flows might be expected to be negligible. However, changes in riparian vegetation associated with interim flows have concentrated new vegetative growth in a narrower band near the river's edge (Stevens and Ayers 1994). Also, the relationship between daily and seasonal variations in river stage under interim flows may influence nest inundation more than the maximum daily or seasonal stage alone. These factors may have effects that were not seen in earlier studies on the riparian breeding birds.

In order to determine if interim flows were flooding nests of riparian birds, we conducted searches for bird nests along the river corridor from 1993 through 1995. We concentrated on NHWZ habitats in the hydrologically active zone (HAZ), the area potentially inundated by flows between the low water mark and the high 20,000 cfs flows. We monitored all nests to see if nest inundation occurred. In this way we were able to determine how many of the nests that we found were below river stage at 20,000 cfs (i.e., how many nests were potentially in danger of inundation).

METHODS

We conducted nest searches at five direct-impact study sites (Figure 1; river mile designations follow Stevens 1983): Lees Ferry (RM 0.0 R, above and below the boat ramp), Triple Alcoves above Saddle Canyon (RM 46.7 R), Stairway Canyon (RM 171.0 R; 1993 only), above Parashant Wash (RM 198.0 R), and Spring Canyon (204.5 R; 1994 and 1995). We concentrated our nest

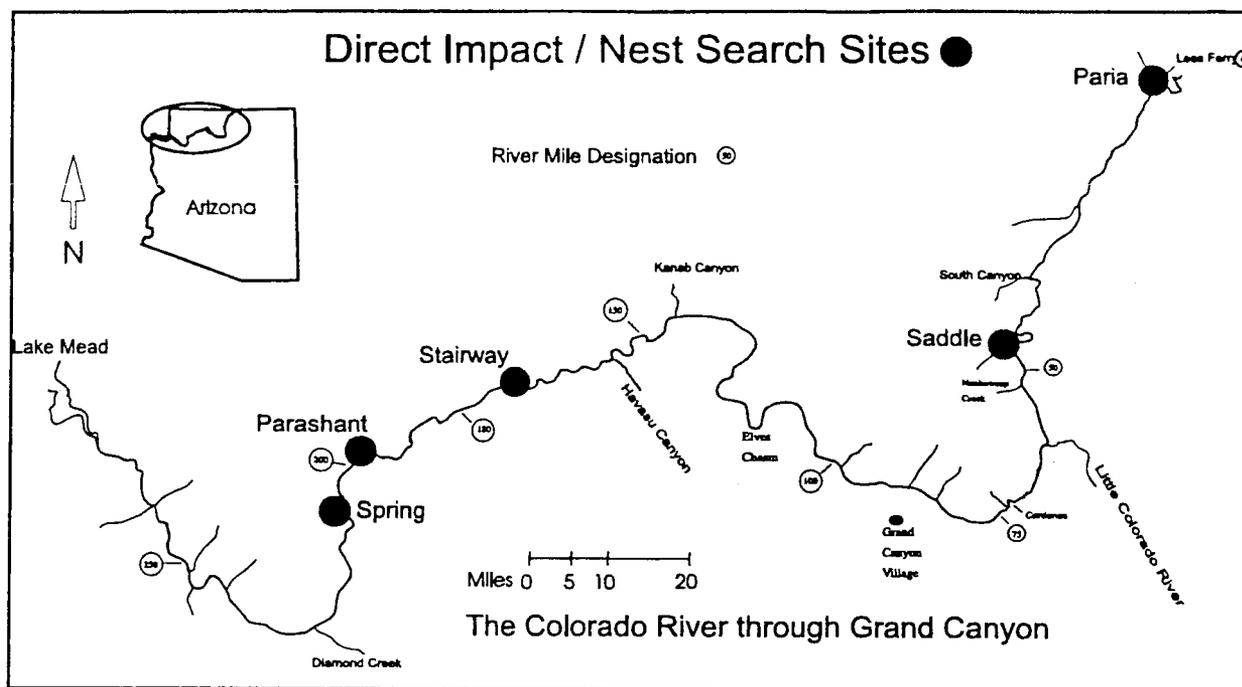


Figure 1. Location of direct impact / nest search study sites along the Colorado River in the Grand Canyon, 1993 - 1995.

search efforts in the projected HAZ at each site, and looked for nests from May through July, 1993; March through July, 1994; and March through June 1995.

Brown and Johnson (1987) used up to six observers to search for nests by conducting walking "sweeps" through NHWZ and OHWZ habitats. We felt that such a technique had high potential to damage the vegetation and any associated nests within the HAZ. Therefore, our nest searches were conducted following the protocol of Martin and Guepel (1993), where observations of bird behavior, especially during nest construction and brood-rearing, were used to locate active nests. We also monitored all nests found during other field activities, but outside the HAZ. Data collected at the nest site included date found, river mile, species, stage of nest development, number of eggs or young, description and sketch of the nest site, habitat type (NHWZ, OHWZ, upland), nest substrate (i.e. what nest was built on), height above ground, distance to water, distance above water, and water depth below nest (when applicable). Nests were revisited on following trips to determine nest fate and number of eggs or young when nest was revisited.

Because no hydrological model existed at the time to accurately define the relationship between flows from Glen Canyon Dam and river stage (elevation) at each of our study sites, we intended to determine the relationships between nest placement, river stage, and water releases by following the methods of Brown and Johnson (1987). We measured peak daily river stage with a staff gage vertically referenced to a permanent point at each direct impact study site. River stage relative to this point could then be related to river flow by back-dating to the corresponding peak flows at the Lees Ferry gaging station, or the nearest upstream gage if tributaries were flooding. However, one of our 1995 river trips corresponded with a constant flow of approximately 20,000 cfs, allowing direct determination of the upper limit of the HAZ at each site.

RESULTS

We located and positively identified a total of 98 nests, representing 21 different species of birds (scientific names of all species are given in Appendix 1), in the NHWZ and OHWZ habitats along the river corridor from 1993 to 1995 (Table 1). Fifty-eight of these nests were located at the five direct impact study sites, with the remainder found at other locations along the river corridor (Table 2). Forty-five nests belonged to species classified by Brown and Johnson (1987) as "obligate riparian birds" - those species which nest only in NHWZ vegetation (Bell's Vireo, Bewick's Wren, Blue Grosbeak, Common Yellowthroat, Great-tailed Grackle, Lesser Goldfinch, Mallard, Yellow-breasted Chat, and Yellow Warbler). Overall, only one¹ of these 98 nests (a Common Yellowthroat in 1994) was located within the HAZ at any of the major study sites, and this nest did not fail due to inundation (Sogge et al. 1994, Sogge et al. 1995). Nests were found from March through July, with most from April through June (Table 3).

Table 1. Bird species and number of nests found in riparian habitat along the Colorado River in Grand Canyon National Park, 1993-95. Species marked with asterisk are considered riparian obligates per Brown and Johnson (1987). Scientific names for all species are given in Appendix 1.

Species nesting	Number	Species nesting	Number
Mallard*	1	Blue-gray Gnatcatcher	13
Mourning Dove	4	Bell's Vireo*	22
Black-chinned Hummingbird	13	Lucy's Warbler	6
Black Phoebe	8	Yellow Warbler*	5
Say's Phoebe	2	Common Yellowthroat*	5
Ash-throated Flycatcher	1	Yellow-breasted Chat*	3
Cliff Swallow	2	Blue Grosbeak*	3
Common Raven	1	Great-tailed Grackle*	1
Verdin	2	Hooded Oriole	1
Bushtit	1	Lesser Goldfinch*	1
Bewick's Wren*	3	Total	98

¹Sogge et al. (1994) reported a preliminary estimate of three nests within the HAZ. However, more accurate delineation in 1995 of the upper level of the HAZ showed that two of these three nests were actually above the 20,000 cfs level.

Table 2. Results of nest searches in the hydrologically active zone (HAZ) at direct impact study (DIS) sites and at other locations along the Colorado River corridor from 1993-1995.

Site	Search hours in HAZ			# nests found in HAZ			# nests found out of HAZ			total # nests that were "riparian obligates"		
	1993	1994	1995	1993	1994	1995	1993	1994	1995	1993	1994	1995
Lee's Ferry and Paria	7	15	30	0	0	0	2	3	2	1	2	0
Saddle	10	32	38	0	0	0	0	5	10	0	3	4
Stairway	12	8	na	0	0	na	7	2	1	5	2	0
Parashant	9	28	34	0	0	0	3	8	5	2	4	4
Spring	na	18	36	na	1	0	na	6	3	na	5	1
Total at DIS sites	38	101	138	0	1	0	12	24	21	8	16	9
Total from other locations	na	na	na	0	0	0	3	19	18	0	8	4
Grand Total	277 hrs			1			97			45		

Nesting Habitats

Sixty-three of the 98 nests were located in NHWZ habitats, while 21 nests were placed in the OHWZ. The remaining 14 nests were found on rocks or cliffs along or within the river channel (Black Phoebe and Cliff Swallow), on cliffs away from the channel (Common Raven), in uplands (Say's Phoebe and Lucy's Warbler), or unspecified zones (2 nests). Eleven species nested only in the NHWZ, two species only in the OHWZ, and five species nested in both (Table 3).

Table 3. Nesting habitats and nest placement characteristics for birds in riparian habitat along the Colorado River in Grand Canyon National Park, 1993-95. Species marked with asterisk are considered riparian obligates per Brown and Johnson (1987). Values given are the number \pm one SD (where applicable), and range (in parentheses).

Species nesting	Number of Nests in			Nest Substrates	Height Above Ground (m)	Horizontal Distance From Water (m)	Month(s) Nest Found
	NHWZ	OHWZ	Other				
Mallard*	1			ground	0	1	Jun
Mourning Dove	4			tamarisk	2.3 \pm 0.5 (2 - 3)	9 \pm 8.5 (3 - 15)	May - Jul
Black-chinned Hummingbird	8	4	1	tamarisk (5) hackberry (3) baccharis (2) other (3)	2.3 \pm 0.9 (1.2 - 3.7)	9.8 \pm 7 (2 - 20)	Mar - Jul
Black Phoebe	2		6	rock/cliff	2.1 \pm 0.6* (1.5 - 2.5)	3.4 \pm 5.3* (0 - 12)	Apr - Jun
Say's Phoebe			2	rock/cliff	(2.5 - 4)	(0 - 300+)	Mar
Ash-throated Flycatcher		1		hackberry	5	15	May
Cliff Swallow			2	rock/cliff	(12 - 15)	0	Jun
Common Raven			1	rock/cliff	100	100+	Mar
Verdin		2		greythorn	2.3	50+	Jun
Bushtit	1			tamarisk	3.5	200+	May
Bewick's Wren*	1	1	1	mesquite (1) tamarisk (1) willow (1)	1.1 \pm 0.4 (0.7 - 1.5)	7 (n=1)	Apr - May
Blue-gray Gnatcatcher	7	6		tamarisk (7) acacia (3) mesquite (3)	3 \pm 0.7 (2 - 4)	30.9 \pm 26.5 (7 - 100)	May - Jun
Bell's Vireo*	18	4		tamarisk (13) mesquite (5) other (4)	1.5 \pm 0.7 (0.6 - 4)	7.6 \pm 6.0 (2 - 20)	Mar - Jul
Lucy's Warbler	2	3	1	tamarisk (2) mesquite (2) other (2)	5.2 \pm 8.3 (0.6 - 20)	87.5 \pm 88 (25 - 150)	Apr - May
Yellow Warbler*	5			tamarisk	3.5 \pm 1.1 (2.3 - 5.2)	2 (n=1)	May - Jun
Common Yellowthroat*	5			baccharis (2) typha (1) phragmites (1) other (2)	0.8 \pm 0.2 (0.5 - 1)	7.7 \pm 6.4 (3 - 15)	May - Jul
Yellow-breasted Chat*	3			tamarisk (2) baccharis (1)	1.4 \pm 0.3 (1.2 - 1.6)	5 (n=1)	May - Jul
Blue Grosbeak*	3			tamarisk	2.5 \pm 0.4 (2.2 - 3.0)	10 (n=1)	May - Jul
Great-tailed Grackle*	1			tamarisk	6.3	9	Jul
Hooded Oriole	1			tamarisk	4	2	Jun
Lesser Goldfinch*	1			baccharis	1.9	12	May

* = 6 of 8 BLPH nests were on rocks/cliff over water, and therefore 0 m from water. For these nests, height above ground is actually height above water (which could vary depending on river stage) when found.

Nest Placement Characteristics

Tamarisk was the most common nesting substrate, followed in decreasing order by rock/cliff, mesquite, and hackberry, acacia, and other substrates (Table 3). Mourning Dove, Bushtit, Bell's Vireo, Yellow Warbler, Yellow-breasted Chat, Blue Grosbeak, Great-tailed Grackle and Hooded Oriole nests were found only or predominantly in tamarisk. No species showed a strong preference for nesting in mesquite. Only Common Yellowthroat nested directly in marsh/wetland vegetation such as *typha* and *phragmites*.

DISCUSSION

Direct impact through inundation

In order for fluctuating flows to have an impact on nesting birds, areas within the HAZ must be exposed above waterline long enough to attract a nesting bird and allow it to build its nest. If the upper flow limit occurred regularly at least once every 3 - 4 days, it is unlikely that a bird could finish nest construction within the zone (most species require at least this long to complete nest building; Terres 1980). If inundation of the HAZ occurred more irregularly or less frequently, most species would have time to complete a nest (possibly including laying eggs and hatching young), which would then be flooded or destroyed as river flows increased. Thus, episodic or irregular inundation of the HAZ has a greater potential for flooding impacts than does regular, frequent inundation.

Flooded nests could be impacted in several ways. High flows could directly destroy a nest through mechanical action, tearing it apart, washing it from its substrate, or burying it under sand, soil, or plant material. The eggs of non-aquatic birds are sensitive to submersion in water, which interferes with gas exchange and metabolism, and can prevent creation of the egg's air cell which provides oxygen for hatching chicks (Romanoff and Romanoff 1949). Effects of submersion range from delayed hatching (up to several days delay after as little as 30 seconds of submersion; M. Kern, Wooster College, pers. comm.) to death of the developing embryo (Sotherland et al. 1984). Young chicks are also susceptible to death due to chilling (from even temporary wetting) and drowning (Terres 1980).

If nest loss occurs early in the nesting cycle, birds may make subsequent nest attempts with at least some chance of success. However, if birds repeatedly build nests in the HAZ, each attempt could be lost and the birds would experience zero productivity for the season. Similarly, if the flooding and loss of a nest occurs late in the nesting cycle, environmental conditions may preclude additional nest attempts and therefore productivity for that year.

We observed no direct destruction of nests through inundation over the course of this study. Compared with historic dam operations, the interim flow guidelines under effect during our study restricted both the daily and seasonal flow rates and fluctuations. The interim flow regime in

operation from 1991 through 1995 dictated that peak flows could not exceed approximately 20,000 cfs and daily fluctuations were limited to between 5,000 and 8,000 cfs (USDI Bureau of Reclamation 1993). This greatly reduced the amount of vegetation and shoreline in the HAZ, which in turn greatly reduces the potential of birds nesting in this zone.

The potential for nest inundation under interim flows is limited to only a few species that nest very low in the vegetation and close to the river. Most of the species breeding at our study sites did not place their nests even close to the HAZ (Table 3). Only the Common Yellowthroat nested in such areas, and only one of the five yellowthroat nests was actually placed low enough to be inundated at 20,000 cfs. Another species with the potential for inundation impacts is the Black Phoebe, which builds its nest on vertical rock surfaces, often only a meter or two above water. For all other species, interim flow levels were never high enough to reach the nest itself. In fact, most nests were placed well away from the HAZ (Table 3) and water never reached the base of the vegetation in which the birds nested.

The lack of significant direct impacts to nesting birds from the interim flows is not surprising given Brown and Johnson's (1985, 1987) results that few nests were inundated by flows up to 31,000 cfs (well above the interim flow guidelines). They demonstrated that it required flows of 40,000 cfs or more to have significant impacts on most riparian breeding species. Apparently, the recent concentration of new vegetative growth in a narrower band near the river's edge changes (associated with interim flows; Stevens and Ayers 1994) has not significantly increased the probability of nest loss under low flow regimes.

Nesting species

Most of the species that we documented nesting along the river corridor have been noted by other researchers (Brown and Johnson 1987, Brown et al. 1987). Black-chinned Hummingbird, Bell's Vireo and Lucy's Warbler continue to be the most abundant breeders, and accounted for 50% of all nests found.

We did record several important nest records. The Cliff Swallows that we observed nest building during 1993 and 1995 (at RM 3 and RM 2, respectively) are the first documented for the Canyon since 1975 (Brown et al. 1987). The Verdin nests at RM 204 is the first breeding records above the head of Lake Mead, where the bird's status was uncertain (Brown et al. 1987). The Bushtit nest at Lees Ferry is also rare, in that Brown et al. (1987) consider the species a common winter visitor.

Refer also to Annotated Species List Chapter for additional information on new or interesting nesting records.

Nest site characteristics

Although tamarisk has been shown to be unacceptable or suboptimal habitat for many nesting birds in some areas of the southwest, particularly the lower Colorado River below Lake Mojave (Rosenberg et al. 1991), it continues to be an important nesting substrate along the Colorado

River in the Grand Canyon. The structure, density, habitat associates, associated invertebrate communities and physical environment (temperature, humidity) of tamarisk-dominated habitats in the Grand Canyon are apparently favorable and allow a variety of bird species to successfully nest and raise young. Brown and Johnson (1987), Brown et al. (1987) and Brown and Trosset (1989) found tamarisk to be an important nesting substrate when much of the NHWZ was newer (< 20 years old) and in a relatively early successional stage (although tamarisk has occurred in portions of the OHWZ since at least the 1930s). Our data demonstrate that tamarisk continues this important function even as the many of the stands have reached a more climax/decadent structure.

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Appendix 1. List of common and scientific names of all bird species for which nests were found in riparian habitats in the Grand Canyon, 1993-95.

Common Name	Scientific Name
Mallard	<i>Anas platyrhynchos</i>
Mourning Dove	<i>Zenaida macroura</i>
Black-chinned Hummingbird	<i>Archilochus alexandri</i>
Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>
Black Phoebe	<i>Sayornis nigricans</i>
Say's Phoebe	<i>Sayornis saya</i>
Cliff Swallow	<i>Hirundo pyrrhonota</i>
Common Raven	<i>Corvus corax</i>
Verdin	<i>Auriparus flaviceps</i>
Bushtit	<i>Psaltriparus minimus</i>
Bewick's Wren	<i>Thryomanes bewickii</i>
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>
Bell's Vireo	<i>Vireo bellii</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>
Blue Grosbeak	<i>Guiraca caerulea</i>
Great-tailed Grackle	<i>Quiscalus mexicanus</i>
Hooded Oriole	<i>Icterus cucullatus</i>
Summer Tanager	<i>Piranga rubra</i>
Lesser Goldfinch	<i>Carduelis psaltria</i>

Chapter 3: Banding Studies



MIST-NETTING AND BANDING STUDIES

INTRODUCTION

Value and Uses of Banding Studies

The placing of metal bands on the legs of birds for scientific purposes began at least 150 years ago in Europe (McClure 1984). Mist-nets were introduced to North American biologists in 1947 (Keyes and Grue 1982). Since that time, literally tens of millions of birds have been mist-netted and banded, providing data that has contributed greatly to our knowledge of bird ecology. Banding efforts can supplement avian monitoring studies by augmenting general survey data and by providing information that could not be gathered without handling and marking of individual birds. Following are brief descriptions of how banding studies and associated data may be used.

As a Census Technique

Mist nets have recently been used to monitor bird populations (Karr 1981), usually through an index such as the number of birds captured per net hour (defined as one net standing open for one hour). However, for most species and in most situations, netting provides fewer data points per unit time, and therefore is more costly in terms of energy and funds than are techniques such as bird censuses (Bibby et al. 1992, Ralph et al. 1993). In addition, mist-netting is biased toward capture of birds in dense habitats (where the mist-nets are not conspicuous to the birds) and within 2 to 3 m of the ground (typical net height). This bias, while not suitable as a stand-alone monitoring technique, actually augments more general censuses by increasing the odds of capturing and detecting birds in dense habitats where visual detection is difficult. Mist-netting also does not require aural or visual detection of birds (other than once they are caught), which means that quiet or inconspicuous species may be detected (via capture) more frequently than in general surveys.

Mist-netting allows detection of physiological traits such as brood patches or cloacal protuberances (Ralph et al. 1993) that are present when a bird is in breeding condition. In cases where a particular species both breeds at, and migrates through, a given area netting provides an index of the proportion of breeders versus migrants. This can greatly improve estimates of local breeding abundance. Further, in-hand examination of difficult to identify species (such as migrating *Empidonax* flycatchers) allows for positive identification, even for groups or species of birds that are often poorly surveyed.

However, it must be kept in mind that netting and banding efforts require extensively trained individuals with specialized skills, in order to minimize the danger of injury or death to captured birds. Furthermore, bird banding in the United States is highly regulated and allowed only through permits from the U.S. Geological Survey National Bird Banding Laboratory.

Documenting Local Residence Status

Riparian habitats along the Colorado River in Grand Canyon National Park provide breeding habitat, migratory stopover sites, and wintering areas for birds throughout the year (Brown et al. 1987). Habitat affiliations and patterns of resource use may differ between resident, migrant and wintering individuals. To better understand habitat use in this context, it is useful to distinguish between these three groups. By capturing and individually marking birds, and following up with recapture and/or resighting programs, it is possible to determine if individuals and species of birds found along the river corridor are year-round residents, spring/summer breeders, or simply migrants.

Determining Breeding Status and Success

The primary focus of many avian monitoring programs (including this one) is on the breeding avifauna, rather than on migrants or wintering species. However, in many cases it is difficult to determine breeding status of some species (especially for those with cryptic nesting habits). Furthermore, in systems such as the Colorado River in the Grand Canyon where both breeders and migrants of a given species may be present, general survey techniques alone often cannot differentiate between the two.

Netting and banding efforts can verify breeding status of individuals and species based on in-hand examination of physiological traits. For example, birds develop visible brood patches (if female) or cloacal protuberances (if male) during their nesting cycle, but not during migration. Thus, if a captured bird has a brood patch or cloacal protuberance, it can confidently be considered a local breeder. Lack of a brood patch or cloacal protuberance during any single month is not absolute proof an individual is not a local breeder, but capture of a high ratio of birds showing no physiological evidence of breeding suggests that there are many migrants in that system during that time. The ratio and pattern of cloacal protuberance and brood patches also provides information on the timing of breeding in local birds. The capture of a recently fledged bird (usually evident by plumage or other physical characteristics) also verifies local breeding for that species, even in cases where no nest has been found.

Determining Site Fidelity and Movements

Site fidelity (the degree to which migratory birds return to specific locations year-to-year) and philopatry (the tendency for birds to return to the place where they hatched) both relate to management of Glen Canyon Dam and its effects on the riparian habitat of the river corridor. Weins and Rotenberry (1985) found that breeding site fidelity and philopatry remained high for several years after vegetation removal. If breeding birds in the Canyon display strong site fidelity, then changes in breeding bird densities may lag behind changes in riparian habitat. Also, a higher degree of site fidelity means that breeding bird populations may be less flexible at responding to rapid changes in the riparian habitat of the river corridor. Marking, recapture and resighting of color banded birds is the only way to document patterns of site fidelity, philopatry, and local movement between patches.

Voucher Specimens

When conducting an avian inventory, monitoring, or research project, it is crucial that species are correctly identified. Whenever possible, verification and archival proof of that identification increases the confidence assigned to the data, particularly for similar-appearing species, unusual occurrences, and when the data may be used as the basis for later historical comparisons. In the past, this was often done through the collection of voucher specimens. Such specimens were obtained by killing and preparing ("stuffing") study skins, which were then deposited in natural history collections. Such specimens have great scientific value, and have repeatedly formed the basis for important taxonomic studies and historic comparisons (e.g., Phillips et al. 1964, Unitt 1987). The primary drawback to collection of voucher specimens is that entails killing the subjects. This may be acceptable in some areas and for some abundant species, but for uncommon species and in many national parks such practices are now often discouraged and considered incompatible with protection and conservation.

Fortunately, netting and banding studies make it possible to "collect" voucher specimens in the form of close-up photographs of the species captured. In most cases, one or more photographs can be taken that are sufficient to show the field characteristics essential for positive species identification. Furthermore, morphological measurements taken during banding operations can help differentiate between morphologically similar species.

As part of the overall Grand Canyon avian monitoring project, we mist-netted and color-banded birds at riparian sites in the Canyon each year from 1993 through 1995 to determine species presence and relative abundance, residency status and migration patterns, site fidelity, and movement patterns along the Colorado River within the Grand Canyon. By noting the color of bands and the identification of recaptured and resighted birds on successive trips, it was possible to infer if individuals stayed in a patch in successive months, and if they moved among vegetation patches. Preliminary results of these efforts have been reported in Sogge et al. (1994) and Sogge et al. (1995). This chapter includes and expands upon the information presented in these earlier progress reports.

METHODS

We used mist nests (per McClure 1984, Ralph et al. 1993) to capture birds at each of the five direct impact study sites (Fig. 1). Each bird was fitted with a numbered Fish and Wildlife Service aluminum leg band and a site-specific color band. Each bird was banded and its wing chord length, tail length, tarsus length, culmen length, and weight were measured. The age and sex of each bird was recorded, and all birds were examined for external parasites. If a bird was recaptured, its band number, color band, date, time, and breeding condition were recorded. Birds recaptured more than once per visit at the same site were only counted once in the totals for returned and recaptured birds.

We mist-netted for three days at each of four study sites per trip. We recorded the number and location of each net, as well as the number of hours each net was open. This provided a standard index of capture rate per unit effort. Nets were set up the previous evening and opened after the morning avian monitoring survey was completed. Nets remained open for a minimum of four hours per morning and longer if we were still catching birds. In 1994, if a particular net location proved unproductive, the net was moved to a new location the following day in order to increase capture rates. In 1995, 11 nets were placed in fixed locations at each site during each trip.

All banding sites were in large vegetation patches. Whenever possible, nets were placed in all available habitats: tamarisk, willow, arrowweed, mesquite and acacia. Of the banding sites, only Paria is without any OHWZ vegetation.

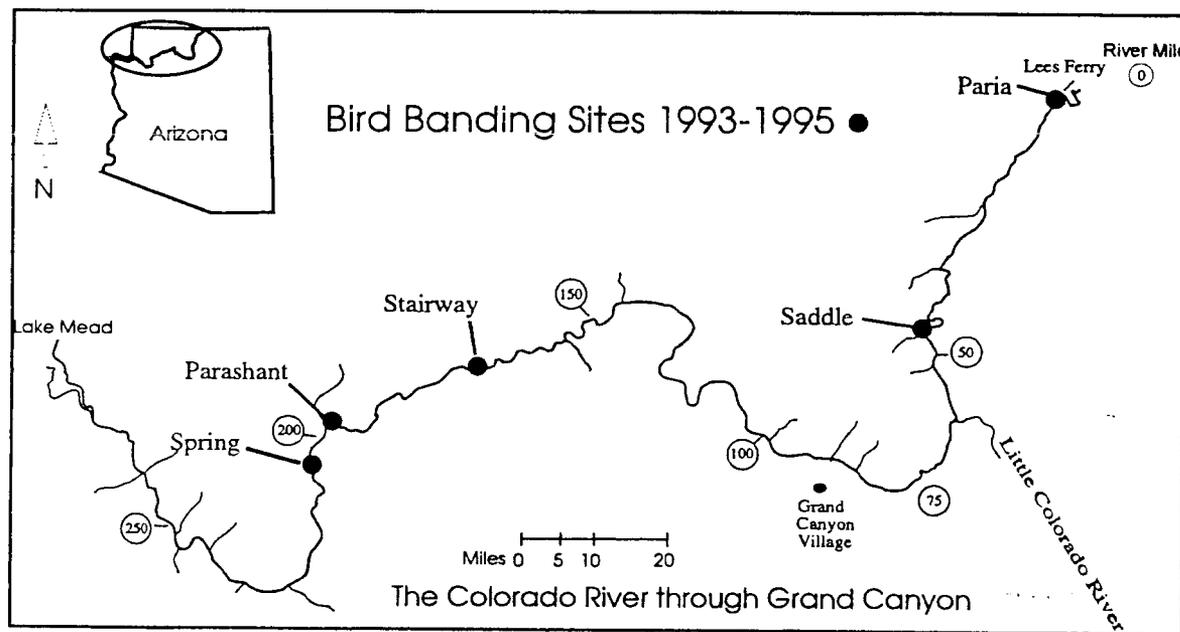


Figure 1. Location of bird banding sites along the Colorado River in the Grand Canyon, 1993 - 1995.

In 1994, all 8 - 10 nets at Paria were located in tamarisk or a mixture of tamarisk and willow. Seven to nine nets at Saddle were placed in the NHWZ and two nets were in a mixture of mesquite and tamarisk. At Stairway three to four nets were located in a mix of OHWZ and NHWZ, and five to six were in tamarisk. Due to a low number of birds at Stairway and the need to increase capture rates, we switched the banding station from Stairway to Spring Canyon in May 1994. We placed seven nets at Parashant in a mix of OHWZ and NHWZ, one in OHWZ vegetation and three in the NHWZ. At Spring Canyon, three nets were set up in a mix of OHWZ and NHWZ vegetation, two in OHWZ, and two in riparian vegetation crossing a tributary stream. Except during migration, the majority of the birds caught here were in the stream nets. Whenever possible in 1995, nets were placed in all available habitats: tamarisk, willow, arrowweed, mesquite and acacia (Table 1).

Table 1. Vegetative zone of mist-net placement at each 1995 banding site. Data for 1993 and 1994 not included because the number of nets and habitats in which they were placed were not constant for each banding session.

Zone	Paria	Saddle	Parashant	Spring	Total
Old High Water Zone			2	5	7
New High Water Zone	11	8	1	2	22
Mixture of OHWZ and NHWZ		3	8	4	15
TOTAL	11	11	11	11	

RESULTS

Banding Efforts and Success

During approximately 4,000 net-hours in 1993 and 1994, we caught 959 birds, including 178 hummingbirds (which in both years were immediately released without banding or measurements), recaptured birds, and escapees (Table 2). During over 2,500 net-hours in 1995, we caught 680 birds, including 220 recaptured birds, hummingbirds, and escapees (Table 3). Capture success was relatively similar between years (Appendix 9), ranging from 21-27 birds per 100 net hours (mean = 25.5). The number of birds banded each year was directly related to netting effort.

Overall, we banded over 1,400 individuals, with the 10 most frequently caught species being Lucy's Warbler (n=315, 22% of total birds), Bell's Vireo (n=120), Yellow Warbler (n=118), Bewick's Wren (n=89), Ruby-crowned Kinglet (n=66), Yellow-breasted Chat (n=62), White-crowned Sparrow (n=61), Bushtit (n=57), Dark-eyed Junco (n=55) and Ash-throated Flycatcher (n=51) (Appendices 3 and 9).

Some species were mist-netted much more frequently than they were seen during surveys. For example, 22 MacGillivray's Warblers were netted as opposed to only 5 counted on surveys. Similarly, 45 Wilson's Warblers were netted, as compared to only 8 detected on surveys.

Table 2. Net hours and capture information for mist-netting birds along the Colorado River in Grand Canyon National Park from May 1993 through July 1994.

Site	Mist net hours	# of species caught	# of birds banded	# of recaptures, hummingbirds, and escapees from nets	Birds per 100 net hours
Paria	930	28	135	27	17
Saddle	1122	25	208	41	22
Stairway *	615	12	50	9	10
Parashant	1278	35	265	63	26
Spring	210	22	123	38	77
Total	4,155	59	781	178	23

* Replaced with Spring Canyon in May, 1994.

Table 3. Net hours and capture information for mist-netting birds along the Colorado River in the Grand Canyon from March through June 1995.

Site	Mist net hours	# of species caught	# of birds banded	# of recaptures, hummingbirds, and escapees from nets	Birds per 100 net hours
Paria *	940	31	142	68	22
Saddle	475	16	31	38	16
Parashant	662	27	121	57	27
Spring	591	29	166	57	38
Total	2,667	49	460	220	25

* includes data from banding efforts in January and February at the Paria site.

Species Banded

We banded a total of 69 species from 1993 through 1995 (Appendix 9). The number of species banded each year was correlated with the the degree of banding effort, being lowest in 1993 (27 species, 1356 net-hours), intermediate in 1995 (49 species, 2667 net-hours), and highest in 1994 (61 species, 3500 net hours).

The most abundant breeding species were Lucy's Warbler and Bell's Vireo (Figures 2 and 3), and the most frequently caught non-breeding species were Ruby-crowned Kinglet, Bushtit and Dark-eyed Junco (Appendix 3). Sixteen species were represented by only one capture (Appendices 1, 2, and 5).

Netting provided data that clarified the local status and/or added to an otherwise limited number of sightings for over a dozen species. Mist-netting also resulted in detection of species that would have otherwise been missed. The following species (some rarely recorded in the canyon) were netted, but never seen during our other avian surveys: Hammond's Flycatcher ($n = 1$, only three previous confirmed records in the canyon); Dusky Flycatcher ($n = 10$, only two previous records); Gray Flycatcher ($n = 6$, only one previous record from river corridor); Gray Vireo ($n = 1$); Solitary Vireo ($n = 4$); Warbling Vireo ($n = 6$); Nashville Warbler ($n = 1$, only two other records along the river corridor); Virginia Warbler ($n = 1$, only a few previous sightings along the river); Black-throated Blue Warbler ($n = 1$, only one other canyon record); Blackpoll Warbler ($n = 1$, a new record for the canyon); and Golden-crowned Sparrow ($n = 1$, one of only a few records canyon records).

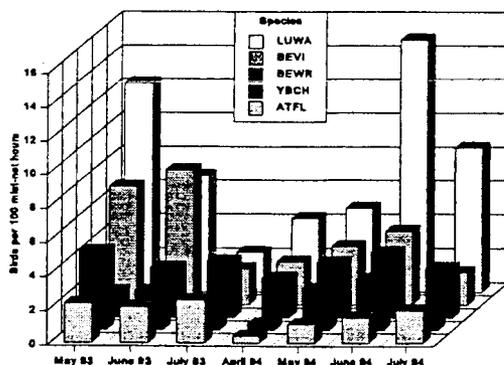


Figure 2. The number of breeding and young-of-the-year birds captured (of the five most common riparian breeding species) along the Colorado River in the Grand Canyon, May 1993 through July 1994.

LUWA=Lucy's Warbler, BEVI=Bell's Vireo, BEWR=Bewick's Wren, YBCH=Yellow-breasted Chat, ATFL=Ash-throated flycatcher.

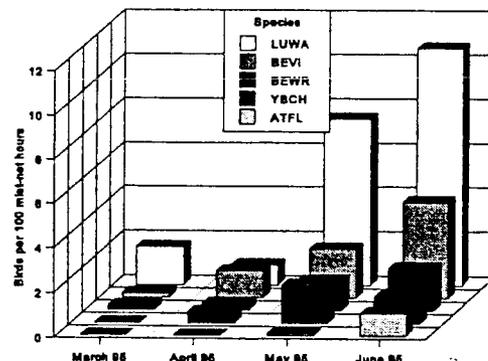


Figure 3. The number of breeding and young-of-the-year birds captured (of the five most common riparian breeding species) along the Colorado River in the Grand Canyon, 1995. LUWA = Lucy's Warbler; BEVI = Bell's Vireo; BEWR = Bewick's Wren; YBCH = Yellow-breasted Chat; ATFL = Ash-throated Flycatcher.

Annual Patterns of Species Composition: breeding versus nonbreeding species

The percentage of individuals of breeding species captured along the river corridor changes dramatically throughout the year (Table 4). During the late fall and early winter, breeding species accounted for only 15% or less of the birds caught. In fact, Bewick's Wren, Rock Wren and Canyon Wren are the only breeding species present in the Canyon during the winter. The percentage of individuals of breeding species increases during spring and early summer (peaking at 91% in June), then decreases again through late summer and fall. Thus, there is almost a complete turnover in species composition between the breeding and wintering seasons.

Table 4. The number of captured birds of breeding and nonbreeding species, 1993 - 1995.

Month	Number of individuals of nonbreeding species	Number of individuals of breeding species	Percent of captured birds that were of breeding species
January	93	3	3
February	5	1	16
March	39	20	33
April	83	63	43
May	144	294	67
June	30	289	91
July	37	130	78
August	5	15	75
September	85	29	25
October	22	2	8
November	24	5	17
December	26	1	4
TOTAL	593	852	

Breeding Status and Condition*Confirmation of breeding status*

Nineteen species of known or suspected breeding birds showed evidence of brood patches or cloacal protuberance over the course of this study. For the Northern Mockingbird, for which several females were found with brood patches but no nests were located, this provided the only verification of local breeding.

We also banded 12 nestling and 440 recently fledged and hatching birds. We began catching young birds in May, with a peak in June and July (Table 5). Young birds can account for a significant portion of the local avifauna during the breeding season, and may actually outnumber adults during some months (Table 5). We caught hatching year birds of 13 locally-breeding species (Table 6), including two fledgling Song Sparrows at Spring Canyon in May (the first verification of breeding for that species in that portion of the Canyon) and a hatch year Verdin at Spring Canyon on 26 July (first confirmed breeding record above Lake Mead).

Table 5. The number of captured hatching year and nestling birds, 1993 - 1995. Hatching year birds from May through July represent locally-produced young, while those in August and September also include southbound first-year migrants.

Month	Adults	Hatching Year (birds caught during their first year of life)	Nestlings (birds banded while in their nest)
April	146	0	0
May	353	77	8
June	161	151	4
July	68	98	0
August	8	12	0
September	24	77	0
TOTAL	440	415	12

Table 6. List of locally-breeding bird species (not limited to riparian breeders) for which hatching year (birds hatched that year) were caught from March through July of each year, 1993-1995.

Mourning Dove	Common Yellowthroat
Ash-throated Flycatcher	Yellow-breasted Chat
Bewick's Wren	Rufous-crowned Sparrow
Blue-gray Gnatcatcher	Black-throated Sparrow
Verdin	Song Sparrow
Bell's Vireo	House Finch
Yellow Warbler	

Verified local breeders versus potential migrants

For species that both breed in and migrate through the Canyon, the proportion of birds that showed evidence of breeding varied substantially among species (Table 7). The proportion of confirmed local breeders provides an index (though not an exact count) of the relative abundance of breeders versus migrants in the system. Using these criteria, a large proportion of Yellow Warblers and Common Yellowthroats that we banded were migrants, as opposed to Lucy's Warblers which were probably almost all local breeders.

Table 7. The number of captured adult birds showing physiological signs of breeding activity from March through July of each year (1993-1995). Species shown are those for which more than 20 individuals were captured.

Species	# not showing evidence of breeding	# showing evidence of breeding
Ash-throated Flycatcher	9	22
Bell's Vireo	13	34
Bewick's Wren	6	22
Blue-gray Gnatcatcher	8	18
Common Yellowthroat	15	16
Lucy's Warbler	19	122
Yellow-breasted Chat	10	35
Yellow Warbler	73	18

Timing of breeding

Netting and banding provided data on the breeding status of many species. A total of 317 individuals of known or suspected breeding species showed evidence of a brood patch or cloacal protuberance when captured. Although these signs of breeding activity were found from March through August, most individuals were in breeding condition during May and June (Table 8).

Table 8. The number of captured birds showing physiological signs of breeding activity, 1993 - 1995.

Month	Evidence of brood patch (females)	Evidence of cloacal protuberance (males)
March	0	13
April	19	29
May	47	64
June	66	54
July	14	9
August	0	2
TOTAL	146	171

Recaptures and Resightings

In 1994, we recaptured 64 different birds, representing 13 species. These included 26 return breeding birds and eight natal returns (Table 9). During 1995, we recaptured 57 different birds, representing 13 species. These included 41 return breeding birds and three natal returns (Table 10).

Overall, we recaptured nine Bell's Vireos at Parashant and four Bewick's Wrens at both Saddle and Paria. Parashant had the greatest number of returns with 18 birds belonging to five species. A Bewick's Wren, recaptured at Saddle in January 1994, was the first confirmed permanent resident of that species in the canyon. A Southwestern Willow Flycatcher (*Empidonax traillii extimus*), banded at Saddle in 1993, nested at river mile 50 in 1994. On our July trip, we saw a Bell's Vireo at Spring Canyon which had been banded at Parashant.

Overall, the nature and degree of recaptured birds suggests a high degree of breeding site fidelity and philopatry

Table 9. Breeding and natal birds banded in 1993 which returned to the same study site in 1994.

Species	Paria	Saddle	Stairway	Parashant	Total
Yellow-breasted Chat	1			2	3
Rufous-crowned Sparrow		1			1
Lucy's Warbler		2		5	7
Brown-headed Cowbird				1	1
Bewick's Wren	4	4		2	10
Bell's Vireo			1	9	10
Ash-throated Flycatcher		3			3
Total	5	10	1	19	35

Table 10. Breeding and natal birds banded in 1993 or 1994 which returned to the same study site in 1995.

Species	Paria	Saddle	Parashant	Spring	Total
Ash-throated Flycatcher		3	2		5
Bewick's Wren	3	3	2		8
Bell's Vireo			6	4	10
Lucy's Warbler		7	4	3	14
Yellow Warbler		1	1		2
Yellow-breasted Chat		1	3	1	5
Total	3	15	18	8	44

Movements

We frequently saw birds fly between habitat patches located on opposite sides of the river, even in some of its widest sections (such as near Lees Ferry). We observed many adults crossing the river to collect food that was then brought to a nest on the opposite side of the river. This occurred for both small (e.g., hummingbirds, Lucy's Warbler, Yellow Warbler) and large (Yellow-breasted Chat, Summer Tanager) species. In general, the river itself does not appear to act as a physical barrier to short-term local bird movements.

Interestingly, we found little evidence of movement upstream or downstream between relatively distant sites. Exceptions were the Southwestern Willow Flycatcher banded at Saddle in 1993 and found nesting at RM 50 in 1994, and the Bell's Vireo banded at Parashant that was observed five miles downriver at Spring Canyon in July, 1994.

Migrants

Timing and Type of Migrants

Tamarisk dominated habitats of the Colorado River are used by many migratory species. Peak numbers pass through the river corridor in May (Figures 4 and 5). Warblers are by far the most frequently captured migratory birds, with high numbers in May and again in July. Sparrows and most other migrants are highest in April and May.

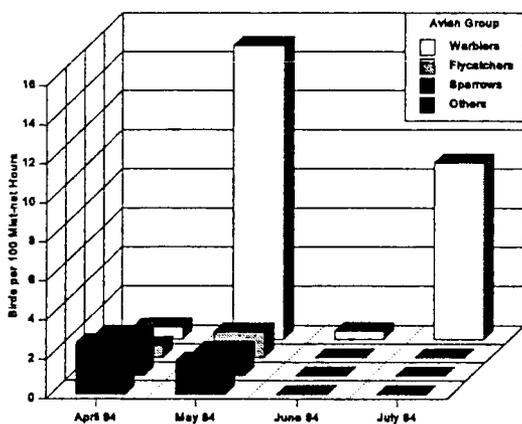


Figure 4. Migrating birds (by taxonomic group) banded along the Colorado River in Grand Canyon in 1994.

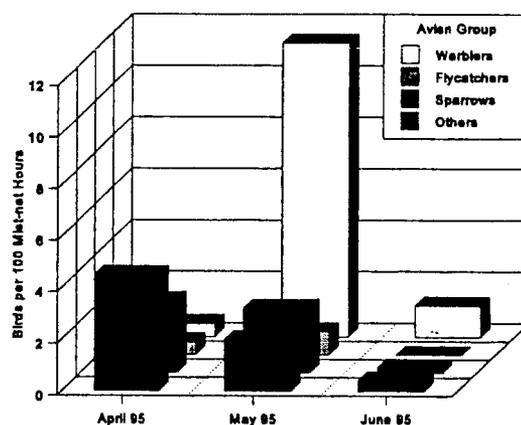


Figure 5. Migrating birds (by taxonomic group) banded along the Colorado River in Grand Canyon in 1995.

Voucher Specimens

Over the course of the study, we attempted to photograph at least one individual of each species that we captured. These photographs were to provide documentation of species identification, in essence serving as photographic "voucher specimens." We obtained good quality photographs of 55 of the species that we captured. We also photographed one snowy egret as it flew by, a recently fledged white-throated swift that was found at a base camp, and one black-chinned hummingbird nest containing two nestlings.

In July 1996, we provided Grand Canyon National Park with copies of 96 slides that document the identity of the 58 species listed Table 6. These slides were chosen specifically to illustrate the field characteristics that would allow definitive identification of the species. In many cases, more than one slide was presented for a given species, in order to show an array of diagnostic characteristics. Each slide was labeled with the common and scientific name (per the 1993 American Ornithologists' Union checklist and subsequent supplements), the site where captured or photographed, and the date (month/year) photographed.

This slide collection included photo documentation of three species that were formerly considered "hypothetical" (per the 1993 *Checklist of the Birds of the Grand Canyon Region*), as well as one species never before noted within Grand Canyon National Park.

Table 11. List of bird slides provided to Grand Canyon National Park. Birds were photographed along the Colorado River through the Grand Canyon during the Grand Canyon Avian Monitoring Project, 1993-1995. Species noted in boldface type formerly lacked specimen or photographic documentation within the canyon and were considered "hypothetical" per *Checklist of the Birds of the Grand Canyon Region*, 1993. An underlined species name denotes a record of a new species for the canyon.

Snowy Egret (<i>Egretta thula</i>)	Virginia's Warbler (<i>Vermivora virginiae</i>)
Mourning Dove (<i>Zenaidura macroura</i>)	Lucy's Warbler (<i>Vermivora luciae</i>)
White-throated Swift (<i>Aeronautes saxatalis</i>)	Yellow Warbler (<i>Dendroica petechia</i>)
Black-chinned Hummingbird (<i>Archilochus alexandri</i>)	Yellow-rumped Warbler (<i>Dendroica coronata</i>)
Red-naped Sapsucker (<i>Sphyrapicus nuchalis</i>)	<u>Blackpoll Warbler</u> (<i>Dendroica striata</i>)
Northern Flicker (<i>Colaptes auratus</i>)	Northern Waterthrush (<i>Seiurus noveboracensis</i>)
Western Wood-pewee (<i>Contopus sordidulus</i>)	MacGillivray's Warbler (<i>Oporornis tolmiei</i>)
Willow Flycatcher (<i>Empidonax traillii</i>)	Common Yellowthroat (<i>Geothlypis trichas</i>)
Hammond's Flycatcher (<i>Empidonax hammondii</i>)	Wilson's Warbler (<i>Wilsonia pusilla</i>)
Dusky Flycatcher (<i>Empidonax oberholseri</i>)	Yellow-breasted Chat (<i>Icteria virens</i>)
Gray Flycatcher (<i>Empidonax wrightii</i>)	Summer Tanager (<i>Piranga rubra</i>)
Cordilleran Flycatcher (<i>Empidonax occidentalis</i>)	Western Tanager (<i>Piranga ludoviciana</i>)
Ash-throated Flycatcher (<i>Myiarchus cinerascens</i>)	Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)
Brown-crested Flycatcher (<i>Myiarchus tyrannulus</i>)	Blue Grosbeak (<i>Guiraca caerulea</i>)
Mountain Chickadee (<i>Parus gambeli</i>)	Lazuli Bunting (<i>Passerina amoena</i>)
Verdin (<i>Auriparus flaviceps</i>) - includes recently fledged young, verifying breeding at this site	Indigo Bunting (<i>Passerina cyanea</i>)
Bushtit (<i>Psaltriparus minimus</i>)	Green-tailed Towhee (<i>Pipilo chlorurus</i>)
Rock Wren (<i>Salpinctes obsoletus</i>)	Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)
Canyon Wren (<i>Catherpes mexicanus</i>)	Rufous-crowned Sparrow (<i>Aimophila ruficeps</i>)
Bewick's Wren (<i>Thryomanes bewickii</i>)	Chipping Sparrow (<i>Spizella passerina</i>)
House Wren (<i>Troglodytes aedon</i>)	Brewer's Sparrow (<i>Spizella breweri</i>)
Marsh Wren (<i>Cistothorus palustris</i>)	Lark Sparrow (<i>Chondestes grammacus</i>)
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	Black-throated Sparrow (<i>Amphispiza bilineata</i>)
Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>)	Sage Sparrow (<i>Amphispiza belli</i>)
Hermit Thrush (<i>Catharus guttatus</i>)	Song Sparrow (<i>Melospiza melodia</i>) - includes recently fledged young, verifying breeding at this site
American Robin (<i>Turdus migratorius</i>)	Lincoln's Sparrow (<i>Melospiza lincolni</i>)
Northern Mockingbird (<i>Mimus polyglottos</i>)	Golden-crowned Sparrow (<i>Zonotrichia atricapilla</i>)
Phainopepla (<i>Phainopepla nitens</i>)	White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	Dark-eyed Junco (<i>Junco hyemalis</i>)
Bell's Vireo (<i>Vireo bellii</i>)	Great-tailed Grackle (<i>Quiscalus mexicanus</i>)
Solitary Vireo (<i>Vireo solitarius</i>)	Brown-headed Cowbird (<i>Molothrus ater</i>)
Warbling Vireo (<i>Vireo gilvus</i>)	Northern Oriole (<i>Icterus galbula</i>)
Orange-crowned Warbler (<i>Vermivora celata</i>)	House Finch (<i>Carpodacus mexicanus</i>)
Nashville Warbler (<i>Vermivora ruficapilla</i>)	Lesser Goldfinch (<i>Carduelis psaltria</i>)

DISCUSSION

Netting and banding clearly provided valuable data to our avian monitoring project, including verification of breeding status, timing and patterns of breeding and migration, and information on bird movements. Much of this data could not have been collected if we limited our project to general avian surveys. Netting also provided an index of abundance for bird species along the river corridor, and we captured all of the most common breeding and wintering species. We also captured a number of inconspicuous and less vocal species that would otherwise have been overlooked or less frequently detected. Many of these captures added significantly to what was previously known about that species in the canyon (refer to the Annotated Species List chapter). Further, mist-netting provides an effective way to capture and detect wintering and migrant birds, for which few effective census techniques have been developed (Verner 1985, Bibby et al. 1992). Banding also provided the opportunity to conduct research on bird diet (refer to the Avian Diet chapter).

However, some less common species (even those that bred in the canyon during the course of this study) were detected during surveys but were not netted, and so would have been missed had netting been the only component to the study. Locally breeding birds are more effectively surveyed by point counts or other survey methods, which gather more data points over a shorter period of time. Overall, due to the inherent biases and time-consuming nature of mist-netting (see Introduction), as well as the fact that it requires specialized skills and federal permits, we do not recommend it as a stand-alone technique for avian monitoring in the Grand Canyon. In general, we recommend netting and banding studies only where specific, objective-driven research needs that can best be met through banding.

We documented an almost complete seasonal "turnover" of species along the river corridor. During the winter, almost all of the species that breed in the canyon are gone. In fact, breeding species accounted for only about 15% or fewer of the birds captured from November through February. Only wrens (Bewick's Wren, Canyon Wren and Rock Wren) are common to both breeding and nonbreeding season. Our recapture data demonstrates that some of the Bewick's Wrens that breed along the river remain in the same habitat patch during the remainder of the year, while some also appear to leave their breeding patch and perhaps the canyon entirely (refer to Annotated Species List chapter). All other breeding species migrate south out of the canyon before the winter.

Brood patch and cloacal protuberance patterns provided excellent data on the timing of breeding activity in the canyon. Small numbers of birds (all males) begin showing signs of breeding in March. Breeding activity picks up rapidly in April, peaks in May and June, then declines rather steeply in July. Almost no breeding activity was detected in August. The peak in breeding activity may be linked to local vegetation phenology (Weins 1989a) and food availability (Stevens 1976, Wiens 1989b).

Stevens et al. (1977) and Brown et al. (1987) have noted the many migrant bird species that use the riparian habitats along the Colorado River corridor within the Grand Canyon. Our banding results support this, and added both new species and additional records of rare species.

Examination of captured birds also allowed us to look at migration patterns with regard to individual birds. For example, we documented that migrants account for a large percentage of the Yellow Warblers and Common Yellowthroats detected along the river corridor. This was most pronounced for the warbler, for which 80% of the captured individuals showed no sign of breeding.

The presence of large proportions of migrants illustrates the value of the riparian corridor as stopover habitat for migrant birds. It also has ramifications on how to interpret survey information for these and other species. For example, if local breeders and migrants are detected and tallied together as residents, the surveys inflate estimates of the number of locally breeding. In the case of the Yellow Warblers, this error could be as great as 400%. For Common Yellowthroats, estimates could be off by as much as 100%. This argues for the use of "decision rules" which estimate the number of breeding pairs in a patch by comparing detections over multiple surveys and applying species-specific criteria designed to reduce the overestimation due to migrants. Abundance estimates (e.g., Brown and Johnson 1987, Brown 1988) based on the highest number of birds counted on any survey, and that include surveys during months when many migrants are present, overestimate the number of locally breeding birds. This is especially true for groups such as warblers and flycatchers. Simple count-based estimates may still prove useful for following annual trends in species abundance, as long as it is understood that the numbers include both migrants and local breeders.

Recapture and resighting of banded birds provided useful data on movements and site fidelity. We found only limited movement of individual resident birds up and down the river corridor, and many individuals returned to the same patch (often the same territory) to breed. This is not surprising, in that most territorial birds show a fairly high degree of breeding site fidelity between years (Weins and Rotenberry 1985, Wiens 1989a). We did note that family groups (adults and fledged young) of riparian-obligate breeding birds often moved into upland areas shortly after the young left the nest. Similarly, several upland species were captured in riparian habitat after nesting was completed. Thus, as noted in other systems (Weins 1989a) the distinction between riparian and upland species may become less pronounced following breeding, and the patterns of habitat and resource use can change.

Interestingly, the river itself does not appear to function as a physical barrier to territorial birds. We commonly saw birds crossing the river, even at some of its widest spots, carrying food from a habitat patch on one side of the river to a nest or fledglings on the other side. Birds banded on one side of the river were also seen in patches opposite of where they were banded. This was noted for both large and small species. In some cases, territorial males sang from song perches on both sides of the river, and thus appeared to include both patches in their territory. In some cases, birds were nesting in large patches (such as at Saddle Canyon or Triple Alcoves), and foraging across river in patches that were too small to solely support a breeding pair.

This pattern of across-river patch use creates an interesting "meta-patch" system, whereby two (or more) close but separated patches of habitat may actually be functioning as a single patch, in terms of resource use by birds. A flight across the river is probably not energetically costly to most birds, and allows them to exploit additional resources. If the across-river patch is small and not defended by competing birds, then food may be more abundant than in patches where

competitors co-occur, and exploitation of these resources may come at a reduced energetic costs (e.g., lower vigilance and/or aggression against competitors). Concurrent use of several small patches may also allow birds to live and breed in areas devoid of large patches. Thus, even small habitat patches may play an important role in local bird community ecology.

Understanding meta-patch patterns is important in several ways. First, it reminds us that birds, being very active and highly mobile, may use and respond to habitat in different ways and at different scales than other organisms (Wiens 1989b). Birds also may perceive, use and respond to habitat at temporal and spatial scales different than those most obvious or intuitive to humans. From a practical perspective, the nature and occurrence of meta-patch patterns could affect avian survey and monitoring programs. Bird counts that include two across-river patches have some potential for double-counting the same individual as it moves between patches, which would inflate pooled abundance estimates (although it may not significantly affect population monitoring on a patch-by-patch basis). This may be especially likely where a very small patch is located across from a larger one. Detection of individuals foraging in a small patch, but actually nesting across river, could mislead investigators into believing that a small patch of that size could, alone, support breeding by that species. It could also lead to spurious density estimates; e.g., a single bird detected during a cross-river foray into a 0.05 ha patch could lead to an inaccurate density estimate of 800 pairs per 40 ha at that patch.

Mist-netting and banding also served a very useful function by allowing us to capture and photograph 55 species of birds that we captured. These photographs allow positive species identification, and serve as voucher specimens relative to this study. Such photographic vouchers require less storage space and specialized maintenance than conventional study skins. Photographic slides can also be reproduced, and used for a variety of resource and interpretive purposes.

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Appendix 1. Species and number of individuals banded at the five direct impact study sites along the Colorado River in Grand Canyon National Park, from May 1993 through July 1994. Common names are followed by standard 4-letter codes.

Species	Paria	Saddle	Stairway	Parashant	Spring	Total
Red-naped Sapsucker (RNSA)				1		1
Brown-crested Flycatcher (BCFL)				7		7
Ash-thoated Flycatcher (ATFL)	5	12	2	21	2	42
Western Wood Pewee (WWPW)				1	1	2
Gray Flycatcher (GRFL)				2		2
Dusky Flycatcher (DUFL)		1		1	1	3
Hammond's Flycatcher (HAFL)				1		1
Willow Flycatcher (WIFL)	1	2		1		4
Western Flycatcher (WEFL)					2	2
Mountain Chickadee (MOCH)	2	1				3
Verdin (VERD)					1	1
Bushtit (BUSH)	11	16				27
House Wren (HOWR)			1	2		3
Bewick's Wren (BEWR)	15	25	2	19	2	63
Marsh Wren (MAWR)	6					6
Canyon Wren (CNWR)	1	1				2
Rock Wren (ROWR)		1				1
Ruby-crowned Kinglet (RCKI)	12	7	4	7		30
Blue-gray Gnatcatcher (BGGN)	3	4	9	7	2	25
Hermit Thrush (HETH)				1		1
American Robin (AMRO)				1		1
Northern Mockingbird (NOMO)	3			4		7
Bell's Vireo (BEVI)			8	52	19	79
Solitary Vireo (SOVI)	1			1		2
Warbling Vireo (WAVI)					2	2
Orange-crowned Warbler (OCWA)	1	4				5
Virginia's Warbler (VIWA)	3	2				5
Lucy's Warbler (LUWA)	4	84	17	65	31	201
Yellow-rumped Warbler (YRWA)	3	1		1		5
Yellow Warbler (YEWA)	14	16		7	20	57
MacGillivray's Warbler (MGWA)	3	2		1	7	13
Wilson's Warbler (WIWA)	6	5		1	12	24
Northern Waterthrush (NOWA)				1		1
Common Yellowthroat (COYE)	4	4		10	11	29
Yellow-breasted Chat (YBCH)	5	6	3	24	9	47
Black-headed Grosbeak (BHGR)	1				1	2
Blue Grosbeak (BLGR)	2	1				3
Lazuli Bunting (LZBU)			1			1
Green-tailed Towhee (GTTO)	1					1
Rufous-sided Towhee (RSTO)				1		1
Song Sparrow (SOSP)				5	1	6
Lark Sparrow (LASP)		1				1
Black-throated Sparrow (BTSP)		2		2	1	5
Rufous-crowned Sparrow (RCSP)		2	1			3
Chipping Sparrow (CHSP)	1					1
Brewer's Sparrow (BRSP)	1					1
Dark-eyed Junco (DEJU)	4					4
White-crowned Sparrow (WCSP)	14					14
Lincoln's Sparrow (LISP)	3	2	1	2		8
Brown-headed Cowbird (BHCO)	2			1		3
Great-tailed Grackle (GTGR)					1	1
Northern Oriole (NOOR)				4		4
Western Tanager (WETA)	1		2		3	6
Summer Tanager (SUTA)				5		5

Species	Paria	Saddle	Stairway	Parashant	Spring	Total
Loggerhead Shrike (LOSH)				2		2
Lesser Goldfinch (LEGO)				1		1
House Finch (HOFI)	2	11		3		16
Total	135	213	51 [^]	265	129*	793
Species Total	28	25	12 [^]	35	20*	57

[^]site only mist-netted from 5/93-4/94

*site only mist-netted from 5/94-7/94

Records are 12 higher than mist-net hours reported due to nestlings banded and one bird caught in box trap.

Appendix 2. Species and number of individuals banded at the four direct impact study sites along the Colorado River in Grand Canyon National Park during 1995. Common names are followed by standard 4-letter codes.

Species	Paria	Saddle	Parashant	Spring	Total
Mourning Dove (MODO)	3				3
Ash-thoated Flycatcher (ATFL)	3	1		2	6
Western Wood Pewee (WWPW)				1	1
Gray Flycatcher (GRFL)		1	1	1	3
Dusky Flycatcher (DUFL)	1	1		1	3
Willow Flycatcher (WIFL)			1	1	2
Bushtit (BUSH)	28				28
House Wren (HOWR)	1				1
Bewick's Wren (BEWR)	3	7	6	2	18
Marsh Wren (MAWR)	7		1	3	11
Ruby-crowned Kinglet (RCKI)	12	1	4	3	20
Blue-gray Gnatcatcher (BGGN)	3	1	6	4	14
Hermit Thrush (HETH)			1		1
Northern Mockingbird (NOMO)			1	1	2
Bell's Vireo (BEVI)			18	21	39
Gray Vireo (GRVI)	1				1
Solitary Vireo (SOVI)				1	1
Orange-crowned Warbler (OCWA)	2			1	3
Virginia's Warbler (VIWA)	2	1			3
Lucy's Warbler (LUWA)	1	10	45	58	114
Yellow-rumped Warbler (YRWA)			1	1	2
Yellow Warbler (YEWA)	5	2	12	36	55
MacGillivray's Warbler (MGWA)	2		2	1	5
Wilson's Warbler (WIWA)	3	2	2	3	10
Northern Waterthrush (NOWA)	1				1
Common Yellowthroat (COYE)	7		3	2	12
Yellow-breasted Chat (YBCH)	2		4	9	15
Black-headed Grosbeak (BHGR)	1				1
Blue Grosbeak (BLGR)	1				1
Indigo Bunting (INBU)				2	2
Lazuli Bunting (LZBU)	2				2
Green-tailed Towhee (GTTO)	2				2
Song Sparrow (SOSP)	3		2	3	8
Black-throated Sparrow (BTSP)			1		1
Rufous-crowned Sparrow (RCSP)			1		1
Chipping Sparrow (CHSP)	1				1
Dark-eyed Junco (DEJU)	19	2	4		25
White-crowned Sparrow (WCSP)	22				22
Lincoln's Sparrow (LISP)	6		2	1	9
Red-winged Blackbird (RWBL)			1		1
Northern Oriole (NOOR)	1			1	2
Western Tanager (WETA)				5	5
Phainopepla (PHAI)				1	1
Lesser Goldfinch (LEGO)			2	1	3
House Finch (HOFI)		2			2
Total	145	31	121	166	463
Species Total	29	12	23	27	45

Appendix 3. The total number of male and female breeding birds banded, by site, along the Colorado River in Grand Canyon 1993-1995. Refer to appendices 1 and 2 for the common name associated with each standard 4-letter bird code. For each species, m = males and f = females.

SPECIES	Paria			Saddle			Stairway			Parashant			Spring			Total			Total	
	93	94	95	93	94	95	93	94	95	93	94	95	93	94	95	93	94	95		
ATFL m f		4	1	3	1	8	4	1	1	1	3	1		3	1	2	1	2	5	25
BEVI m f							1	1		7	5	3		4	4	8	1	7	25	25
BEWR m f		2	1	1	3	2				1	1	1				2	6	4	12	21
BGGN m f		1	1		1		2			1	2	2		1	1	3	5	3	11	8
COYE m f			3	1						2	1	2		2	1	3	3	6	12	4
LUWA m f				3	16	1	2	2		7	17	6		13	8	12	48	24	84	61
YBCH m f		1	2	1	1	1	1			3	6	3		2	5	5	1	1	25	23
YEWA m f			1	2	2	2				1	4	1		3	1	3	9	5	17	6

Appendix 4. The number of young (hy; hatching year) birds banded along the Colorado River in the Grand Canyon 1993-1995. Refer to appendices 1 and 2 for the common name associated with each standard 4-letter bird code. Some hatching year birds are locally produced, while others may be southbound migrants that were produced outside of the Grand Canyon region.

Species	Paria			Saddle			Stairway			Parashant			Spring			Total			Total
	93	94	95	93	94	95	93	94	95	93	94	95	93	94	95	93	94	95	
ATFL										5						5			5
BEVI							4			23	2	15		6	16	27	8	31	66
BEWR	5	4	1	3	13	7	2			4	7	6		2	1	14	26	15	55
BGGN		1			2		4			1		2		1	2	5	4	4	13
COYE										2	1	1		5		2	6	1	9
LUWA				5	39	2	1			15	2	34		5	47	3	46	83	159
YBCH		3					1			3		1			3	4	3	4	1
YEWA		9		3	1						2					3	12		15

Appendix 5. The number of birds of each species banded at each study site within the Grand Canyon, 1993-1995. Refer to appendices 1 and 2 for the common name associated with each standard 4-letter bird code.

Species	Paria	Saddle	Stairway	Parashant	Spring	Total
MODO	3					3
RNSA				2		2
NOFL		1				1
BCFL				7		7
ATFL	8	13	2	21	4	48
WEWP	1			1	2	4
GRFL		1		3	1	5
DUFL	1	2		1	2	6
HAFL				1		1
WIFL	2	2		2	1	7
WEFL	1				2	3
MOCH	2	1				3
VERD					1	1
BUSH	41	16				57
HOWR	1		1	2		4
BEWR	19	33	2	27	6	87
MAWR	16	1		3	3	23
CNWR	2	1				3
ROWR		1		1		2
RCKI	39	8	4	12	3	66
BGGN	8	5	9	13	7	42
HETH	1			2		3
AMRO				1		1
NOMO	3			5	1	9
BEVI			8	70	40	118
GRVI	1					1
SOVI	1			2	1	4
WAVI	2			1	3	6
OCWA	10	4		4	1	19
NAWA				1		1
VIWA	5	3				8
LUWA	5	94	17	110	89	315
BTBW	1					1
YRWA	5	1		2	1	9
YEWA	23	18		21	56	118
MGWA	8	2		4	8	22
WIWA	14	9		5	17	45
BLPW					1	1
NOWA	1			1		2
COYE	12	4		13	16	45
YBCH	8	6	3	28	18	63
BHGR	2				1	3
BLGR	3	1				4
INBU					2	2
LABU	2		1			3
GTTO	3					3
RSTO				1		1
SOSP	10			11	8	29
LASP		1				1
BTSP		2		3	1	6
SGSP	1					1
RCSP		2	1	3		6
CHSP	2					2
BRSP	5			5		10

Species	Paria	Saddle	Stairway	Parashant	Spring	Total
DEJU	47	2		4		53
WCSP	49	2		5	5	61
GCSP					1	1
LISP	10	2	1	10	6	29
RWBL				1		1
BHCO	2			1		3
GTGR					1	1
NOOR	1			4	1	6
WETA	1	1	2		8	12
SUTA				5		5
PHAI					1	1
LOSH				2		2
LEGO				3	1	4
HOFI	2	13		3		18
TOTAL	384	252	51	427	320	1434
SPP TOT	45	30	12	43	38	68

Appendix 6. The number of birds banded, by month, along the Colorado River in the Grand Canyon, 1993. Refer to appendices 1 and 2 for the common name associated with each standard 4-letter bird codes.

Species	May	Jun	Jul	Sep	Total
MODO					
RNSA					
NOFL					
BCFL		1	3		4
ATFL	3	9	12		24
WEWP					
GRFL					
DUFL					
HAFL					
WIFL		1	1		2
WEFL					
MOCH					
VERD					
BUSH					
HOWR					
BEWR	2	11	13	4	30
MAWR					
CNWR			1	1	2
ROWR			1		1
RCKI					
BGGN	3	6			9
HETH					
AMRO					
NOMO			2		2
BEVI	9	27	6	3	45
GRVI					
SOVI					
WAVI					
OCWA				1	1
NAWA					
VIWA					
LUWA	16	30	11		57
BTBW					
YRWA					
YEWA	1		3	4	8
MGWA				1	1
WIWA	1	1			2
BLPW					
NOWA					
COYE	2	2	2	1	7
YBCH	6	8	8	1	23
BHGR					
BLGR			1		1
INBU					
LABU				1	1
GTTO					
RSTO			1		1
SOSP				1	1
LASP					
BTSP			1		1
SGSP					
RCSP			1		1
CHSP					
BRSP					
DEJU					

Species	May	Jun	Jul	Sep	Total
WCSP					
GCSP					
LISP					
RWBL					
BHCO		1			1
GTGR					
NOOR			1	1	2
WETA			1	1	2
SUTA			1		1
PHAI					
LOSH					
LEGO					
HOFI		2	7		9
TOTAL	43	99	77	20	239
SPP TOT	9	12	20	12	27
BIRDS/100nh	32.3	27.3	19.1	17.0	20.6

Appendix 7. The number of birds banded, by month, along the Colorado River in the Grand Canyon, 1994. Refer to appendices 1 and 2 for the common name associated with each standard 4-letter bird codes.

Species	Jan	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
MODO												0
RNSA	1							1				2
NOFL								1				1
BCFL				1	2							3
ATFL			2	4	6	7						19
WEWP				2				1				3
GRFL			2									2
DUFL				3								3
HAFL			1									1
WIFL			1				1		1			3
WEFL				2				1				3
MOCH	3											3
VERD						1						1
BUSH	27									2		29
HOWR		1	2									3
BEWR	1	1	6	6	9	10		6				39
MAWR			4	2				4	2			12
CNWR						1		1				2
ROWR								1				1
RCKI	17	4	7	2				1	6	6	3	46
BGGN			6	6	1	3		2			1	19
HETH	1									1		2
AMRO		1										1
NOMO				3	2							5
BEVI			6	12	12	6						36
GRVI												0
SOVI		1		1				1				3
WAVI				2				4				6
OCWA				4				4	7			15
NAWA								1				1
VIWA				4			1					5

Species	Jan	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
LUWA		5	17	22	65	35						144
BTBW									1			1
YRWA		1		4						1	1	7
YEWA			3	28	4	5	9	6				55
MGWA				11	1			4				16
WIWA				21	1			11				33
BLPW								1				1
NOWA			1									1
COYE			2	14	5	1		4				26
YBCH			2	13	6	1	2	1				25
BHGR				1		1						2
BLGR					1	1						2
INBU												0
LABU												0
GTTO			1									1
RSTO												0
SOSP	2	2				1		8	2	5		20
LASP						1						1
BTSP						4						4
SGSP										1		1
RCSP	1		1			1		2				5
CHSP			1									1
BRSP							1	9				10
DEJU		4							1	8	17	30
WCSP		2	5	7				12	4	4	5	39
GCSP								1				1
LISP		4	4					11		1		20
RWBL												0
BHCO					2							2
GTGR				1								1
NOOR				1		1						2
WETA				3		1		1				5
SUTA					2	2						4
PHAI												0

Species	Jan	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
LOSH					1	1						2
LEGO			1									1
HOFI			1	2		4						7
TOTAL	53	26	76	182	120	88	14	100	24	29	27	739
Spp Total	8	11	22	28	16	21	5	27	8	9	5	61
BIRDS/ 100nh	12.0	7.8	20.4	39.2	38.5	25.6	34.4	24.6	43.3	54.0	54.7	27.5

Appendix 8. The number of birds banded, by month, along the Colorado River in the Grand Canyon, 1995. Refer to appendices 1 and 2 for the common name associated with each standard 4-letter bird codes.

Species	Jan	Feb	Mar	Apr	May	Jun	Total
MODO						3	3
RNSA							
NOFL							
BCFL							
ATFL					3	3	6
WEWP					1		1
GRFL				2	1		3
DUFL					3		3
HAFL							
WIFL				1	1		2
WEFL							
MOCH							
VERD							
BUSH	28						28
HOWR					1		1
BEWR	1		1	1	8	7	18
MAWR			4	7			11
CNWR							
ROWR							
RCKI		1	3	16			20
BGGN				7	4	3	14
HETH			1				1
AMRO							
NOMO				2			2
BEVI			1	3	12	23	39
GRVI					1		1
SOVI				1			1
WAVI							
OCWA					3		3
NAWA							
VIWA					3		3
LUWA			8	3	47	56	114
BTBW							
YRWA				2			2
YEWA					55		55
MGWA					5		5
WIWA					10		10
BLPW							
NOWA					1		1
COYE			1	3	5	3	12
YBCH				1	9	5	15
BHGR					1		1
BLGR					1		1
INBU					1	1	2
LABU				1	1		2
GTTO				1	1		2
RSTO							
SOSP		1	3	1	2	1	8
LASP							
BTSP						1	1
SGSP							
RCSP						1	1
CHSP				1			1
BRSP							
DEJU	12	3	8	2			25

Species	Jan	Feb	Mar	Apr	May	Jun	Total
WCSP	2	1	1	5	13		22
GCSP							
LISP			2	6	1		9
RWBL				1			1
BHCO							
GTGR							
NOOR					1	1	2
WETA					5		5
SUTA							
PHAI					1		1
LOSH							
LEGO				2	1		3
HOFI					2		2
TOTAL	43	6	33	69	204	108	463
SPP TOT	4	5	11	22	32	13	45
BIRDS/100nh	41.5	10.4	11.2	20.4	36.7	28.2	25.3

Appendix 9. Banding effort (in net hours) and results by patch and year for banding efforts along the Colorado River in the Grand Canyon, 1993 - 1995.

1993

Site	Mist net hours	Number of species caught	Total birds banded	Recaps/ escapees from nets	Birds per 100 net hours
Paria	221.8	4	13	5	8.1
Saddle	338.3	14	49	8	16.8
Stairway	349.6	8	38	11	14.0
Parashant	447.1	17	135	20	34.7
TOTAL	1356.0	27	235	44	20.6

1994

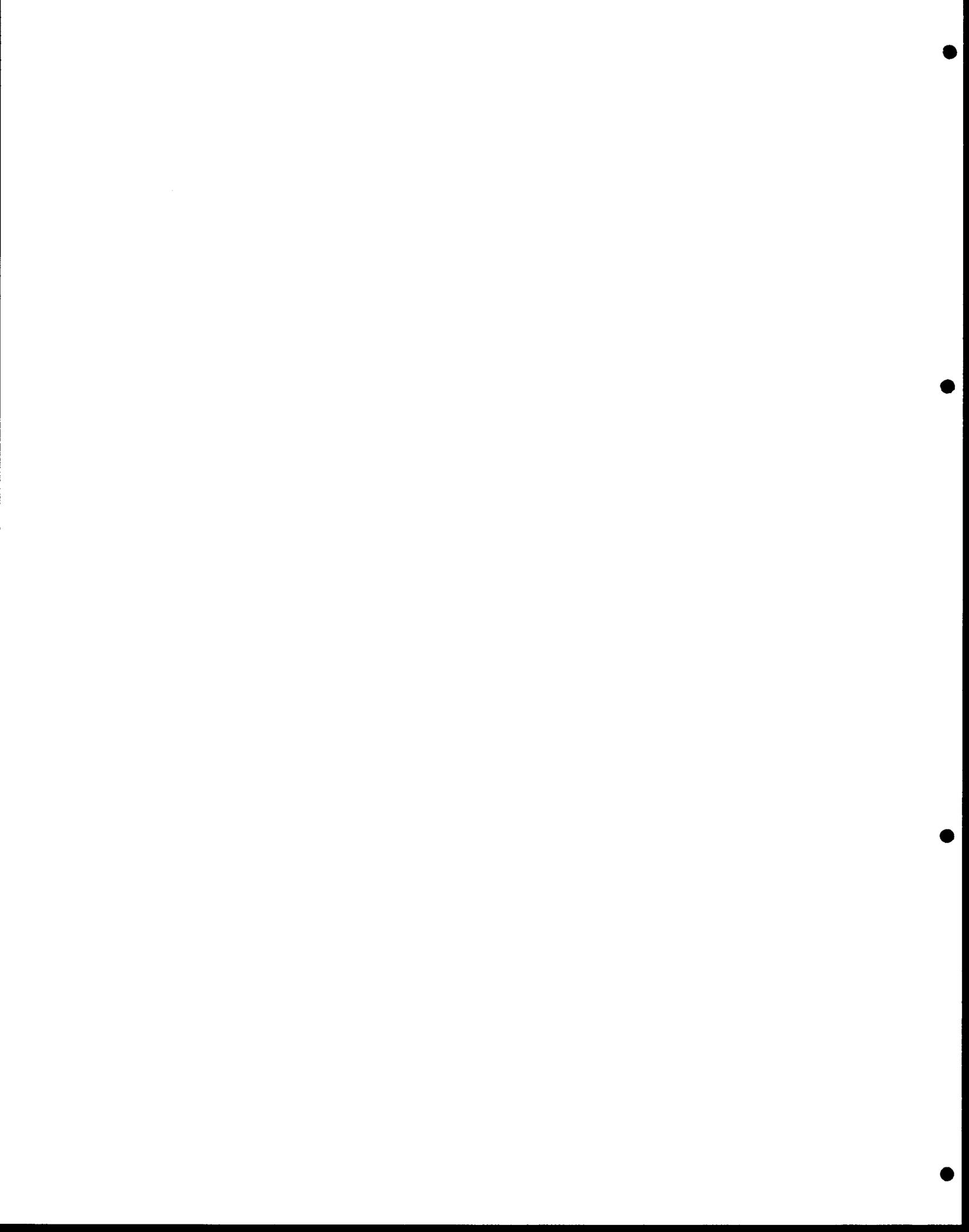
Site	Mist net hours	Number of species caught	Total birds banded	Recaps/escapees from nets	Birds per 100 net hours
Paria	1006.5	38	226	75	29.9
Saddle	916.4	25	168	41	22.8
Stairway	265.5	12	13	9	8.3
Parashant	983.4	42	171	75	25.0
Spring	328.8	25	147	38	56.3
TOTAL	3500.6	61	725	238	27.5

1995

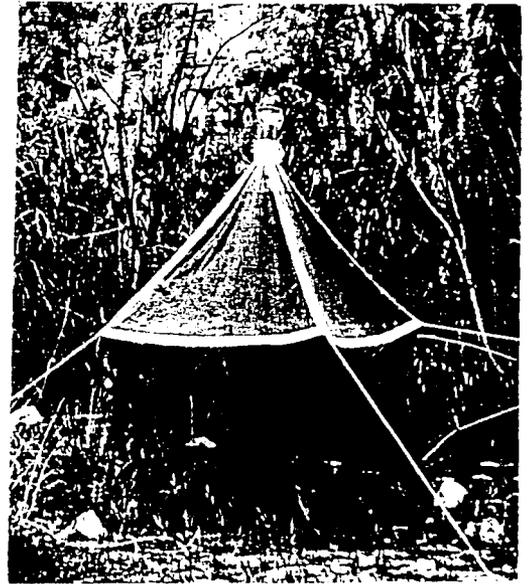
Site	Mist net hours	Number of species caught	Total birds banded	Recaps/ escapees from nets	Birds per 100 net hours
Paria	939.5	30	142	68	22.4
Saddle	475.4	14	31	38	15.5
Parashant	661.7	25	121	57	26.9
Spring	590.7	28	166	57	37.8
TOTAL	2667.3	49	460	220	25.3

1993 through 1995

Site	Mist net hours	Number of species caught	Total birds banded	Recaps/ escapees from nets	Birds per 100 net hours
Paria	2167.8	44	381	148	24.4
Saddle	1730.1	32	248	87	19.4
Stairway	615.1	13	51	20	11.5
Parashant	2092.2	44	427	152	27.8
Spring	919.5	39	313	95	44.4
TOTAL	7524.7	69	1420	502	25.5



Chapter 4: Diet Analysis



Quantitative Diet Analysis of Selected Breeding Birds along the Colorado River in Grand Canyon National Park

Cooperative Agreement: 8031-8-0002

Project Name: GRAND CANYON AVIAN COMMUNITY MONITORING

Principle Investigators: Terry May, Graduate Studies and Research, Northern Arizona University, Flagstaff, AZ 86011 and
Charles van Riper III, U.S.G.S. Biological Resources Division, Colorado Plateau Research Station, Northern Arizona University, Flagstaff, AZ 86011

Government Technical Representative: John Ray, Resources Management, Grand Canyon National Park

Short Title of Work: Riparian Bird Diet Study - Final Report

Funded By: Glen Canyon Environmental Studies, Bureau of Reclamation and U.S.G.S. Biological Resources Division, Colorado Plateau Research Station

Supported By: The Bureau of Reclamation
Glen Canyon Environmental Studies Program
P.O. Box 22459
Flagstaff, AZ 86002-2459

Submitted To: Resource Management
Grand Canyon National Park
Grand Canyon, AZ

Prepared By: Helen K. Yard, Colorado Plateau Research Station, Northern Arizona University

Recommended citation: Yard, H.K. 1996. Quantitative diet analysis of selected breeding birds along the Colorado River in Grand Canyon National Park. U.S.G.S. Colorado Plateau Research Station/Northern Arizona University Report. 41 pp.

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Prepared By: Helen K. Yard, Colorado Plateau Research Station, Northern Arizona University

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NOTE: This avian diet report is included as a chapter within the Riparian Bird Community Ecology in the Grand Canyon Final Report because the diet work was a component of the overall bird community ecology project. However, the diet report was originally released as a separate project deliverable, and information and data contained herein should be attributed to Yard 1996 (see above).

INTRODUCTION

Riparian zones in the southwest are extremely important for resident and migratory species of birds. Over 60% of neotropical migratory birds use riparian habitat in the West for stopover areas during migration or for breeding (Ehrlich *et al.* 1988). Of 166 species of nesting birds in the southwest, 77% were dependent on water associated habitats and 51 % were completely dependent upon riparian habitat (Johnson *et al.* 1977). The thick, multi-storied vegetation found in riparian areas provides more nest sites and greater arthropod production for birds than adjacent xeric habitat (Gori 1992). Steven's *et al.*(1977) reported that western riparian areas contained up to 10 times the number of neotropical migrant birds per hectare than adjacent non-riparian habitats. Knowing how important riparian areas are to birds, it is of growing concern that estimates have placed riparian habitat loss at greater than 95% in the western United States (Krueper 1992). Recent studies suggest that neotropical migrant songbird populations are declining and that these decreases have accelerated in recent years possibly due to loss of this type of available habitat (Finch 1991).

Breeding bird densities along the Colorado River corridor have increased in the last 20 years due to the increased amount of new riparian habitat (Carothers and Johnson 1975, Brown and Johnson 1985). Before Glen Canyon Dam was built to control the water flows through Grand Canyon, vegetation adjacent to the river was sparse due to annual flooding (Turner and Karpiscak 1980). The pre-dam vegetation (termed old high water zone [OHWZ]) that still exists, is comprised of a band of vegetation characterized predominately by native honey mesquite (*Prosopis glandulosa*) and catclaw acacia (*Acacia greggii*) (Carothers and Brown 1991). A new zone of riparian habitat has become established along the Colorado River after the completion of

Glen Canyon Dam in 1963. The new riparian habitat zone or, new high water zone (NHWZ) established after the completion of the dam immediately adjacent to the river and composed predominately of introduced tamarisk (*Tamarix chinensis*), native coyote willow (*Salix exigua*) and several species of seep willow (*Baccharis*). More than 500 hectares (1,235 acres) of new riparian habitat has been established along the river from Lee's Ferry to Diamond Creek in the last 20 years (Brown and Trosset 1989). Lower Grand Canyon, below river mile 170, has experienced a more dramatic increase in vegetation. The canyon is wider there due to the geomorphology (Pucherelli 1988)

Another consideration of regulated water flows through Grand Canyon since the establishment of Glen Canyon Dam is the change in temperature and sediment load in the water of the Colorado River that affects the aquatic arthropod productivity. Pre-dam water temperatures were warmer and changed seasonally as with any natural river system (Blinn and Cole 1991). High sediment loads were sporadic being associated with heavy rainfall and spring snow melt. Historically, there was an abundant and diverse assemblage of aquatic insects in the Colorado River (Ward 1976). Water presently released from the dam is clear and colder (8 to 10 degrees C) than in pre-dam times and varies very little in temperature seasonally, supporting a low diversity yet high abundance of aquatic insects (Valdez and Ryel 1995). Above the Little Colorado River (LCR) at River Mile (RM) 61.5, there is an abundance of aquatic insects emerging from the river, predominately Chironomide midges adapted to the clear, cold water of the Colorado river released from the dam. Below the LCR, which has a high sediment load varying throughout the year, aquatic insect abundance drops in a stairstep fashion an order of magnitude as you continue downstream from the LCR to Diamond Creek (Shannon 1993).

Past studies on breeding bird communities along the Colorado River corridor in the Grand Canyon have concentrated on species present, nesting habits and the effects of fluctuating flows on densities of birds in the riparian areas (Carothers and Sharber 1976, Brown 1987, Brown and Johnson 1988). Very little was known about the diet of birds that use the riparian vegetation along the river. Direct examination of avian diet is essential in gaining an understanding of avian habitat use and yet the diet of many neotropical bird species in general is poorly known (Karr 1976, Loiselle and Blake 1990). Diet studies are seldom undertaken in avian ecology due to difficulties in identifying fragmented arthropods found in diet samples of birds, but is a very effective method that can show direct habitat use and food selection by avian insectivores (Sherry 1984, Rosenberg and Cooper 1990, Johnson 1991). How several insectivorous bird species with similar foraging tactics coexist in fairly monotypic stands of exotic and native vegetation in riparian areas is poorly understood. Studies of resource partitioning among potential avian competitors are numerous, but studies that complement data on resource partitioning with dietary data are few (Rotenberry 1980, Robinson and Holmes 1982, Rosenberg et al. 1982).

Within the Grand Canyon, it is important to study avian diet for the purpose of : (1) understanding what several common songbirds are feeding upon within the riparian vegetation along the Colorado River and (2) determine if there is a link to the feeding ecology of these terrestrial bird species to aquatic resources (ie. insects emerging from the river) (Shannon 1993) and (3) to determine if the birds are feeding in the relatively recent NHWZ vegetation dominated by introduced saltcedar .

Stevens (1976, 1985) inventoried arthropods found in the NHWZ and OHWZ riparian vegetation at selected sites along the Colorado River in Grand Canyon. Information and results from these collections were invaluable for the identification of insects collected in this present study. This study is among the first to relate arthropod relative availability to actual composition of arthropods in bird diets along the Colorado River.

The specific objectives of this project were to:

- 1) Determine the similarities and/or differences in diet between six common insectivores in the riparian area along the Colorado River in Grand Canyon.
- (2) Quantify proportions of the birds diets that are insects of aquatic origin (ie. insects emerging from the Colorado River) versus terrestrial origin in order to determine if these birds rely on aquatic based food resources
- (3) Calculate the proportion of aquatic insects that emerged from the Colorado River found in the upper Grand Canyon (sites above the LCR at RM 61.5) versus sites in the lower Grand Canyon (below the LCR) related to differences in aquatic insect productivity in the upper canyon versus the lower canyon.
- (4) Determine if the prey items found in avian diet samples overlap more closely with the relative (observable) prey availability in NHWZ or OHWZ (Vegetation zone of foraging preference)

Study area:

The four study sites were chosen along the Colorado River in Grand Canyon National Park were: Paria Creek (RM 1.0); Saddle Canyon (RM 46.7); Stairway Canyon (RM 171.0); Parashant Canyon (RM 198.0). Partway through 1994, Spring Canyon (RM 204.5) was substituted for the Stairway Canyon site due to low capture rate of birds at the latter. Stairway Canyon was sampled for birds March and April of 1994, then Spring Canyon was sampled in May, June and July (Fig. 1). Two study sites were chosen above the LCR and two below the LCR in order to compare upper and lower canyon differences in emerged aquatic insect composition at the sites and in the diets of the six species of birds.

Bird Species:

Six common insectivorous bird species were selected for dietary analysis: Lucy's Warbler (*Vermivora luciae*), Bell's Vireo (*Vireo bellii*), Yellow Warbler (*Dendroica petechia*) and the Yellow-breasted Chat (*Icteria virens*), all neotropical migratory birds associated with riparian vegetation, primarily forage by gleaning insects from foliage. The Ash-throated Flycatcher (*Myiarchus cinerascens*), also a neotropical migrant, is primarily an aerial forager, but gleans insects from stems and trunks of trees as well. Bewick's Wren (*Thryomanes bewickii*), a permanent resident of Grand Canyon, forages in foliage, on the ground and in dead wood. (Ehrlich *et. al* 1988).

METHODS

Bird Capture

Birds were captured live in 8 to 10 mist nets two days per month at each study site during the breeding season (March through June) of 1994 (Sogge *et al.* 1994). Measurements taken on each bird caught in mist nets included beak length in millimeters (mm) and body weight in grams (g). These measurements were averaged for each bird species. Nets were placed in the same general locations within each study site during each month to maintain sampling consistency. The netting efforts were already underway as part of the overall Avian Community Monitoring Study in Grand Canyon in effort to band birds with US Fish and Wildlife and color bands (Sogge *et al.* 1995).

Lavage

Stomach contents from the birds were obtained by flushing the digestive tract with a fixed amount of warm water (lavage) as described by Moody (1970). This technique involves using a syringe filled with water with a 5 cm tube attached to the end. The tube is gently placed into the beak and down the esophagus of the bird. The water is then slowly pushed out of the syringe into the stomach. Lavage has a low mortality rate compared to using chemical emetics for forced regurgitation (Laursen 1978, Robinson and Holmes 1982, Gavett and Wakeley 1986). In past studies, the efficiency rate of the flushing technique (prey particles remaining in the stomach after flushing) was $52\% \pm 29\%$ (Laursen 1978). Diet samples were taken from birds caught between dawn and noon, a period when high feeding rates usually guaranteed full stomachs for sampling (Sherry 1984). Ten or fewer bird stomachs have been considered adequate for assessing

species-specific diets during a sampling period (Rosenberg and Cooper 1990). The stomach content samples were labeled with the date, location of sample, and species of bird then stored in vials with 70% alcohol and identified later in the lab.

Prey Identification and Diet Comparisons

Each prey item was identified to taxonomic order and when possible, family and genus using a variable power dissecting scope (Borror *et al.* 1982). Individual arthropods, usually fragmented, were pieced together until I accounted for all identifiable prey fragments. One prey item (arthropod) was counted for each head capsule, pair of mandibles, four wings (two for Diptera), or two elytra found in each diet sample (Anthony and Kunz 1977). For example, if I found one elytra, two Hemipteran head capsules and a Dipteran wing, I counted one Coleopteran, two Hemipterans and one Diptera. In order to make dietary comparisons between the six species of birds, arthropods found in stomach samples were grouped into eight ordinal categories: Araneae (spiders); Hemiptera (true bugs); Homoptera (mainly leafhoppers); Coleoptera (beetles); Diptera (flies and midges); Hymenoptera (wasps, bees and ants); Lepidoptera (mainly moth and butterfly larvae) and "Other" (Thysanoptera, Neuroptera, Acari and unknown). Aquatic or terrestrial origin of the arthropod was also specified when arthropods could be identified to family. Proportions (or percent) of prey orders and aquatic versus terrestrial emerging insects were calculated for each stomach sample depending on the statistical test employed to analyze the data.

In the event of rare accidental mortality, the entire stomach was removed and dissected after flushing, to determine what, if any, prey remained in the stomach after lavage.

Arthropod Samples

Arthropod sampling was conducted at each site one day per month from March through July during the same time period that birds were captured in mist nets and lavaged for diet samples. Three invertebrate sampling methods were used to obtain a better representative collection of what prey items were present at the sites during the time of diet sampling (Cooper and Whitmore 1990). In order to collect vegetation dwelling arthropods, I made 25 sweeps with a standard sweep net (37 cm in diameter) through the vegetation and 25 beats on the vegetation (collected onto a beating canvas). A passive Malaise trap was used to collect flying insects. All three sampling methods described above were used in both the NHWZ and OHWZ to compare arthropod availability between zones. Relative prey availability is very difficult to quantify because each sampling method has its own inherent biases, therefore I used the three methods described above to determine what arthropods were in *observable* abundance or availability. Arthropods were stored in 70% alcohol and later identified to order and family level, and in some cases genus using a variable power dissecting scope. They were then grouped into the same eight categories as the prey fragments found in the diet samples from the birds. At a later date, arthropods representing every family found in the bird diet samples were measured and grouped into three categories: >3 mm, 3 - 5 mm and < 5 mm. The origin (aquatic or terrestrial) of each arthropod was also recorded to determine proportion of aquatic insects collected during sampling at each site.

Statistical Analysis and Calculations

Diet Analysis. A multivariate analysis of variance (Manova) comparing the mean proportion of prey orders between the six species of birds was used to determine if the diets were significantly different between species (Sokal and Rohlf 1995). All mean proportions were arc sine transformed to correct for non-normality. Only stomach samples containing four or more prey items were used for statistical analysis to reduce the bias of finding, for example, 100% spiders in a diet sample when only one spider was found in the entire sample. A one-way analysis of variance (Anova) was used to detect if there were significant differences in the proportion of prey orders present in each species (showing what bird species had a higher proportion of what prey order) (Sokal and Rohlf 1995).

Descriptive Calculations. Descriptive calculations such as dietary overlap between bird species and dietary or prey diversity for each bird species were used to help determine similarities and differences between the diets of the six species of birds. Diet overlap between species of birds was calculated as: $O_a = \sum (P_{ia} P_{ij}) / \sqrt{(\sum P_{ia}^2)(\sum P_{ja}^2)}$, where P_{ia} and P_{ij} are the proportions of prey category and "a" in the diets of species "i" and "j" respectively (Pianka 1974). A value of zero would represent zero dietary overlap and a value of 1.0 would represent 100% overlap. Prey-type diversity was calculated of each bird species using $B = (\sum p_i^2)^{-1}$, where p_i is the proportion of taxon "i" in the diet samples of the bird species (Levins 1968). This index value is an indicator of whether the bird species has a stereotypic diet (specialization consuming a narrow range of prey taxa) or is opportunistic in their diet (a generalist consuming a wide variety of prey items) (Sherry 1990). A value of 8.0 is considered opportunistic or a generalist, a value of 1.0 is a specialist. Proportions of arthropod orders were used for both of these equations.

Aquatic insects in diet. A Kruskal-Wallis one-way analysis of variance (Anova) was used to determine if there was a significant difference in the percent of arthropods with aquatic origin versus terrestrial origins in the diets of the six species (Sokal and Rohlf 1995). A Mann-Whitney U (post hoc analysis) was used to detect significant differences in the percent of aquatic insects in the diets between species (Sokal and Rohlf 1995). A Kruskal-Wallis Anova was used to determine if the birds were consuming a higher percent of insects of aquatic origins at the two upper study sites versus the two lower sites.

Aquatic Insect availability. A G-statistic (Goodness of fit) was calculated to determine if there was a significant difference in the number of insects from aquatic origins in *observable* availability at the sites above the LCR (ie. Paria and Saddle) versus the sites below the LCR (ie. Parashant and Spring) (Sokal and Rohlf 1995).

Avian Diet and Zone of Vegetation Overlap (foraging preference). Pianka's index (Pianka 1974) for overlap was used as an indicator of foraging location (OHWZ or NHWZ) used by the six species of birds. Indices of overlap have been proven to be useful to ecologist in comparative studies of diet and habitat preference as well as a descriptor of dietary similarity between bird species (Horn 1966). This formula was described in detail in the *Descriptive Calculations* sections.

Additionally, a Manova was used to determine if there were significant differences between mean proportions of arthropod orders collected in the NHWZ and the OHWZ...

RESULTS

Diet samples were successfully obtained from 202 (92%) of 220 birds having received lavage in 1994 (Table 1). The average body weight, beak length and sample size for each bird species caught for diet sampling is shown in Table 2. To avoid sampling biases for the statistical analysis, I used 161 (73%) of the diet samples all of which contained four or more prey items.

Dietary analysis. Manova results showed that the diets of the six species of birds evaluated (fig. 2) were significantly different from each other (Wilk's Lambda approx. $F_{5,155} = 5.22$, $p < 0.001$). The "other" category of the arthropod fragments found in the diets of the six bird species represented only 2% of their overall total diet and was therefore omitted from the statistical analysis. Anova results showed that each bird species had consumed a higher proportion of one particular prey order. Lucy's Warbler had consumed a significantly higher proportion of Homopterans ($p < 0.005$) (Fig.3) averaging < 3 mm in size; Bell's Vireo had eaten a significantly higher proportion of Hemipterans ($p < 0.005$) and an higher proportion of Lepidopterans ($p < 0.01$) (Fig.4a and 4b), both prey types averaged 3 - 5 mm in size; Bewick's Wren had a higher proportion of spiders ($p < 0.01$) (Fig. 5) sizes averaging 3 - 5 mm; Yellow Warbler had a significantly higher proportion of Dipterans ($p < 0.005$) (Fig. 6) size range of 3 - 5 mm; Yellow-breasted Chat had a significantly higher proportion of Hymenopterans ($p < 0.005$) (Fig. 7) average size of < 5 mm. The diet of Ash-throated Flycatcher contained a higher proportion of Hymenopterans than four of the other bird species, having the second highest proportion compared to the Yellow-breasted Chat ($p < 0.01$) (Fig. 7) average size of < 5 mm. When I examined the Hymenopterans in the diet of the Yellow-breasted Chat, 98% consisted of wingless ants (family Formicidae) while the Hymenopterans in the diet of the Ash-throated

the diets in the six bird species analyzed. Overall diet composition of arthropods having aquatic origins in all six bird species combined was 8.7%, while arthropods of terrestrial origin comprised 91.3%.

There was a significant difference in the percent of arthropods having an aquatic origin versus terrestrial origin found in the diet of the six species of birds (Kruskal-Wallis Anova, $n = 161$, $DF = 5$, $P = 0.001$). The percent of arthropods having aquatic origins found in each species of bird were variable (Fig. 10), with the Yellow Warbler consuming the highest percent of aquatic insects (10%), and the Yellow-breasted Chat consuming the lowest percent (2%). Post hoc multiple analysis (Mann-Whitney U) revealed the Yellow Warbler had a significantly higher percent of aquatic origin arthropods in their diet when compared with the other five species ($P < 0.05$). No other significant differences in percent of aquatic origin arthropods were found in the diets between bird species.

Aquatic Insect availability. Arthropods of aquatic origins composed 46.5% of the those collected in sampling at the upper sites above the LCR. Only 13.4% of the arthropods collected at the lower sites were of aquatic origin. There was a significant difference in the number of aquatic insects found at the sites above the LCR versus the sites below the LCR ($X^2 = 228.38$, $DF = 1$, $P < 0.001$). This clearly shows that aquatic insects were in higher observable availability at the upper sites. There was no significant difference in the percent of aquatic insects consumed by the birds ($n = 68$) at the upper sites versus aquatic insects consumed by birds ($n = 93$) at the lower sites (Kruskal-Wallis Anova: $X^2 = 0.835$, $DF = 1$, $P = 0.359$).

Avian Diet and Zone of Vegetation Overlap (foraging preference). All six bird species had a high index of overlap with the OHWZ, with no species having an overlap value less than

0.76 (Table 4). Lucy's Warbler, Bewick's Wren and Yellow Warbler had similar overlap indices for both zones, where Bell's Vireo, Yellow-breasted Chat and the Ash-throated Flycatcher clearly showed a preference for the OHWZ. Before calculating the overlap of the birds diet in relationship to the two habitat types (NHWZ and OHWZ), it was necessary to determine if the arthropods were statistically different between the two zones. Malaise trap samples were omitted from the observable availability data because it appeared to have over-sampled Diptera (flies) (Table 5). All the arthropod orders were represented in the beat and sweep samples and therefore were believed to reflect a better representative sample of what was available in the habitat. Mean proportions of arthropod orders collected in each vegetation zone are shown in Figure 11. A Manova showed there was a significant difference in arthropods collected in the two zones (Wilks Lambda $F_{1,64} = 11.658$, $P < 0.001$). Anova results showed there were significantly higher proportions of Dipterans (Wilks Lambda $F_{1,64} = 16.8$, $P < .001$) and Homopterans (Wilks Lambda = $F_{1,64} = 8.30$, $P < .005$) in the NHWZ and a significantly higher proportion of Coleopterans in the OHWZ (Wilks Lambda $F_{1,64} = 21.60$, $P < .001$). No other arthropod orders were found to be significantly different between the two zones.

Only three birds out of 220 (1.4%) died of apparent stress due to lavage in 1994 and 1995. All three were Lucy's Warblers that died after using the lavage method. The stomachs of all three warblers were removed and preserved immediately after mortality. Arthropod fragments were lavaged from the stomachs of two out of the three birds, while no prey items were obtained from the third. No prey items were detected in the preserved stomachs of the three accidental mortalities when they were examined in the lab. This suggests that lavage was effective in obtaining stomach contents from birds.

DISCUSSION

Diets of the six species of birds were significantly different, each species of bird showing a preference for a particular order of arthropod. The significant difference in prey order proportions in the diets of the six species of birds is a clear indication of resource partitioning that helps shape the bird community co-existing in the riparian vegetation along the Colorado River. These dietary differences can be attributed to many reasons.

Classic foraging theory states that different bird species will tend to specialize in a different prey types if resources are abundant (Recher 1990). According to Stevens (1985), the highest standing crop of herbivores on willow and tamarisk occurs from mid June through August. This time period coincides with part of the breeding season for the bird species in the diet study. The birds, therefore, are able to specialize on different prey types because of the high availability.

Bird body weight and bill length in relation to prey size is also a known reason for dietary differences between bird species (Cambell 1989). Lucy's warbler, the smallest bird sampled in this diet study having the lowest average body weight and bill length had consumed the highest proportion of Homopterans, specifically the exotic leaf hopper *Opsius stactogalus* (averaging 2 mm in length). The Bell's Vireo, Yellow Warbler and Bewicks Wren, the "mid-sized" birds similar in average body weight and bill length, consumed prey in the mid-sized category (3 - 5 mm). The main prey items found in higher proportions in the Yellow-breasted Chat and Ash-throated Flycatcher , the largest birds sampled for diet, averaged 5 mm or greater.

Foraging tactics also play a role in dietary differences. Lucy's Warbler, Bell's Vireo, Bewick's Wren, Yellow-breasted Chat and Yellow Warbler are all foliage gleaners. With the

exception of the Yellow-breasted Chat and Lucy's Warbler, dietary overlap among these species is greater than 60%. The low dietary overlap value between Yellow-breasted Chat and Lucy's Warbler is most likely due to the size difference of the birds. The Ash-throated Flycatcher is primarily an aerial forager. The diet of the Ash-throated Flycatcher had a higher proportion of Hymenopterans, primarily flying insects as to be expected. The flycatcher and the Yellow-breasted Chat were found to be similar in the proportion of Hymenopterans with an overlap value of 93%. When the diets of the two species of birds were examined by family level, however, it was found that the chat had consumed a high proportion of non-flying Hymenopterans (ants), in contrast to the higher proportion of flying Hymenopterans found in the diet of the Ash-throated Flycatcher. The high overlap values in regards to these two species diets with the arthropods in the OHWZ for both species would indicate the difference in the diets of these two similar sized species could be explained by foraging tactics. The Yellow-breasted Chat was found to be more of a prey specialist in comparison to the other five species of birds, while the Ash-throated Flycatcher is somewhat of a generalist (refer to Table 3b).

Another consideration in prey selection is that migrant bird species will chose different prey than permanent residents. A diet study conducted on birds in Panama that showed permanent residents consumed larger proportions soft bodied arthropods having high nutritional value, such as spiders, in contrast to the migrant species found to co-exist in the same habitat. Migrants fed mostly on low quality invertebrates easy to prey upon and were found to be opportunist in regards to diet. Bewick's Wren, a permanent resident I collected diet samples from in this study, had consumed more spiders than the other five bird species, all neotropical migrants (Poulin and Lefebvre 1996). Bewick's Wren also has a slightly different foraging tactic than the

other four foliage gleaners, foraging low in the canopy and on the ground. It's bill is longer and slightly down curved allowing for probing in bark and leaves (Ehrlich *et al.* 1988). This bird species is considered a broad generalist according to the prey diversity index. This is understandable considering the bird stays in the same general area all year, being able to prey on changing insect fauna throughout the year.

Birds similar in size with similar foraging tactics have been documented to forage at different heights in forest canopies and therefore consume different prey (Morse 1989). The Yellow Warbler and Bell's Vireo have similar average body weight and bill size, and yet their diets are significantly different. These two bird species exhibit similar foraging tactics, though the Yellow Warbler is known to hawk insects as well as glean (Ehrlich *et al.* 1988). The prey type diversity in the Yellow Warbler (refer to Table 3b) was lower than the Bell's Vireo, having the highest proportion of Diptera (primarily Chironomide midges) in it's diet than any other species. The Bell's Vireo had a higher proportion of two prey taxa, Hemipterans (true bugs) and Lepidoptera larvae (caterpillars) and therefore could be considered more generalized in diet.

My findings that the Yellow Warblers had consumed a high proportion of Chironomide midges is consistent with dietary data from a study conducted in Canada (Busby and Sealy 1978). The Yellow Warblers observed there showed that overall, the birds were consuming a high proportion of midges and foraging high in the canopy. From personal observations, I have repeatedly seen Yellow Warblers foraging high in the tamarisks hawking midges that swarm above the trees.

Bell's Vireo has historically been associated with mesquite, though more current data indicates they are utilizing the tamarisk as well (Brown 1985). This vireo can be difficult to see

because of their affinity to dense shrub (Ehrlich *et al.* 1988). There is very little prior information available on the diet and foraging of Bell's Vireo. I conclude that one reason for the high proportion of Lepidoptera larvae and Hemipterans present in their diet was due to their foraging height in the vegetation. However, this is a speculation without data on arthropod availability throughout the vertical structure within the vegetation. A consideration for future diet studies would be to include observational data on foraging behavior and location.

Identification of arthropod prey remains in the diets of the six bird species revealed the main food resources selected were arthropods of terrestrial origin, comprising approximately 90% of their diet. Insects from aquatic origins only comprised approximately 8.0% of the total diet of the six species of birds analyzed. In arthropod sampling, five times as many terrestrial-origin arthropods were found in the riparian habitat as opposed to those arthropods with aquatic origin. The Colorado River has been shown to support a limited diversity of emerging arthropods because of cold water temperatures (Shannon 1993). This was supported by our finding low proportions of aquatic arthropods in invertebrate collections from the riparian vegetation. The riparian vegetation along the Colorado River supports an abundance of terrestrial-origin arthropods providing a rich food resource for riparian birds. Although, while the river is clearly important in that it supports the riparian vegetation which in turn supports arthropod food resources, its role as a direct source of arthropod prey for these species of birds is minor.

Arthropods collected at the two sites sampled above the LCR (Paria and Saddle Canyon) contained a higher percent of those from aquatic origins (46.5%) than the samples taken at sites below the LCR (Parashant and Spring Canyon with 13.4%). The six species of birds were not relying heavily on aquatic insects for a food resource, therefore, the fact that aquatic insects were

in higher abundance at the upper sites as opposed to the lower sites had no bearing on their diet. There was no significant difference in the proportion of aquatic insects in the diets of the six species of birds at the upper sites above the LCR than in the diets of the birds at the lower sites (below the LCR). This indicates the six species of birds are not interested in preying on aquatic insects during the sampling period in 1994 regardless of the observable abundance.

The arthropods identified in the diets of the six bird species showed higher overlap indices with the arthropods collected in the OHWZ vegetation as opposed to the arthropods collected in the NHWZ (refer to Table 4). I speculate that the higher overlap between the birds diets with the OHWZ is probably due to the fact this band of vegetation existed for centuries prior to the dam. The birds present in the Grand Canyon historically used this vegetation for nesting and as a food source. The predominate vegetation in the OHWZ (mesquite and acacia) has less dense foliage than tamarisk possibly allowing the birds to find prey more easily in these types of vegetation than in the dense foliage of tamarisk. In addition, tamarisk may contain biochemicals that discourage most plant herbivores (Carothers and Brown 1991).

Management considerations and recommendations:

There is strong evidence supporting that neotropical migrant birds are adjusting to the relatively recent expansion of exotic tamarisk not only for higher availability of nest sites (Brown and Trosset 1989, Hunter *et al.* 1988) but for opportunistic utilization of an abundant food resource as well. All six bird species I collected diet samples from were consuming the tamarisk specific leafhopper. Future decisions in regard to the avifauna along the Colorado River in the Grand Canyon should bear in mind that birds rely heavily on the recent band of vegetation

established along the river in the last 30 years for their food resources as well as for nesting sites (Brown and Trosset 1989). Returning flows in the Colorado River through Grand Canyon to pre-dam conditions would eliminate much of the vegetation that has been established in the river corridor and therefore would decrease avian populations along the river. Extermination of exotic tamarisk would have the same repercussions.



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Table 1. Number of individuals caught, by species, for avian diet analysis during the breeding season in 1994 at five sites along the Colorado River in Grand Canyon National Park.

SITE	Lucy Warbler	Bell's Vireo	Bewick's Wren	Yellow Warbler	Yellow-breasted Chat	Ash-throated Flycatcher	TOTAL
Paria Beach RM 1.0	4	0	11	0	3	4	22
Saddle Canyon RM 46.5	27	0	15	6	3	10	61
Stairway Canyon RM 172.0	2	2	0	0	0	0	4
Parashant RM 198.0	23	22	5	1	8	2	61
Spring Canyon RM 204.5	21	15	2	11	4	1	54
TOTAL	77	39	33	18	18	17	202

Table 2. The average body weight (grams), bill length (millimeters) and the sample size for the six bird species sampled for diet along the Colorado River in Grand Canyon during the breeding season, 1994. Measurements used were taken from adult birds.

Bird Species	Body Weight	Bill Length	Sample Size
Lucy's Warbler	6.5	8.9	62
Bell's Vireo	8.9	9.7	29
Bewick's Wren	9.3	12.8	27
Yellow Warbler	8.9	9.3	14
Yellow-breasted Chat	25.9	13.9	15
Ash-throated Flycatcher	26.4	16.8	14

Table 3a. Dietary overlap among the six species of birds sampled along the Colorado River during the breeding season 1994. A value of zero would be no overlap, a value of 1.0 would be complete overlap.

	Luwa	Bevi	Bewr	Yewa	Ybch	Atfl
Luwa		0.76	0.87	0.64	0.49	0.64
Bevi	0.76		0.85	0.71	0.69	0.76
Bewr	0.87	0.85		0.83	0.75	0.9
Yewa	0.64	0.71	0.83		0.8	0.88
Ybch	0.49	0.69	0.75	0.8		0.94
Atfl	0.64	0.76	0.9	0.88	0.94	

Table 3b. Prey-type diversity index values (B) for the six species of birds. A value of 8.0 is least specialized (a generalist), a value of 1.0 is most specialized (a narrow range of prey).

Bird Species	Luwa	Bevi	Bewr	Yewa	Ybch	Atfl
Diversity index	4.57	5.9	6.32	4.04	2.33	4.35

Luwa - Lucy's Warbler, Bevi - Bell's Vireo, Bewr - Bewick's Wren, Ybch - Yellow-breasted Chat, Atfl - Ash-throated Flycatcher

Table 4. Overlap of arthropods found in the diet of the six species of birds with the arthropods found in the New High Water Zone (NHWZ) and the Old High Water Zone (OHWZ). A value of 1.0 represents a 100% overlap.

Bird Species	NHWZ	OHWZ
Lucy's Warbler	0.63	0.76
Bell's Vireo	0.51	0.88
Bewick's Wren	0.76	0.93
Yellow Warbler	0.86	0.90
Yellow-breasted Chat	0.44	0.83
Ash-throated Flycatcher	0.65	0.93

Table 5. Frequency and percent (%) of arthropod orders collected in three sampling methods at Paria, Saddle Canyon, Parashant and Spring Canyon combined.

Order	Method of Arthropod Sampling					
	Beat		Sweep		Malaise	
	Frequency	%	Frequency	%	Frequency	%
Araneae	83	10.6	38	4.9	1	0.0
Hemiptera	45	5.8	63	8.2	3	0.1
Homoptera	123	15.7	144	18.7	25	0.9
Coleoptera	37	4.7	56	7.3	2	0.1
Diptera	194	24.8	328	42.5	2617	92.0
Hymenoptera	160	20.5	131	17.0	198	7.0
Lepidoptera	139	17.8	11	1.4	0	0

Figure 1. Location of study sites where samples were taken along the Colorado River in the Grand Canyon, 1994-1995.

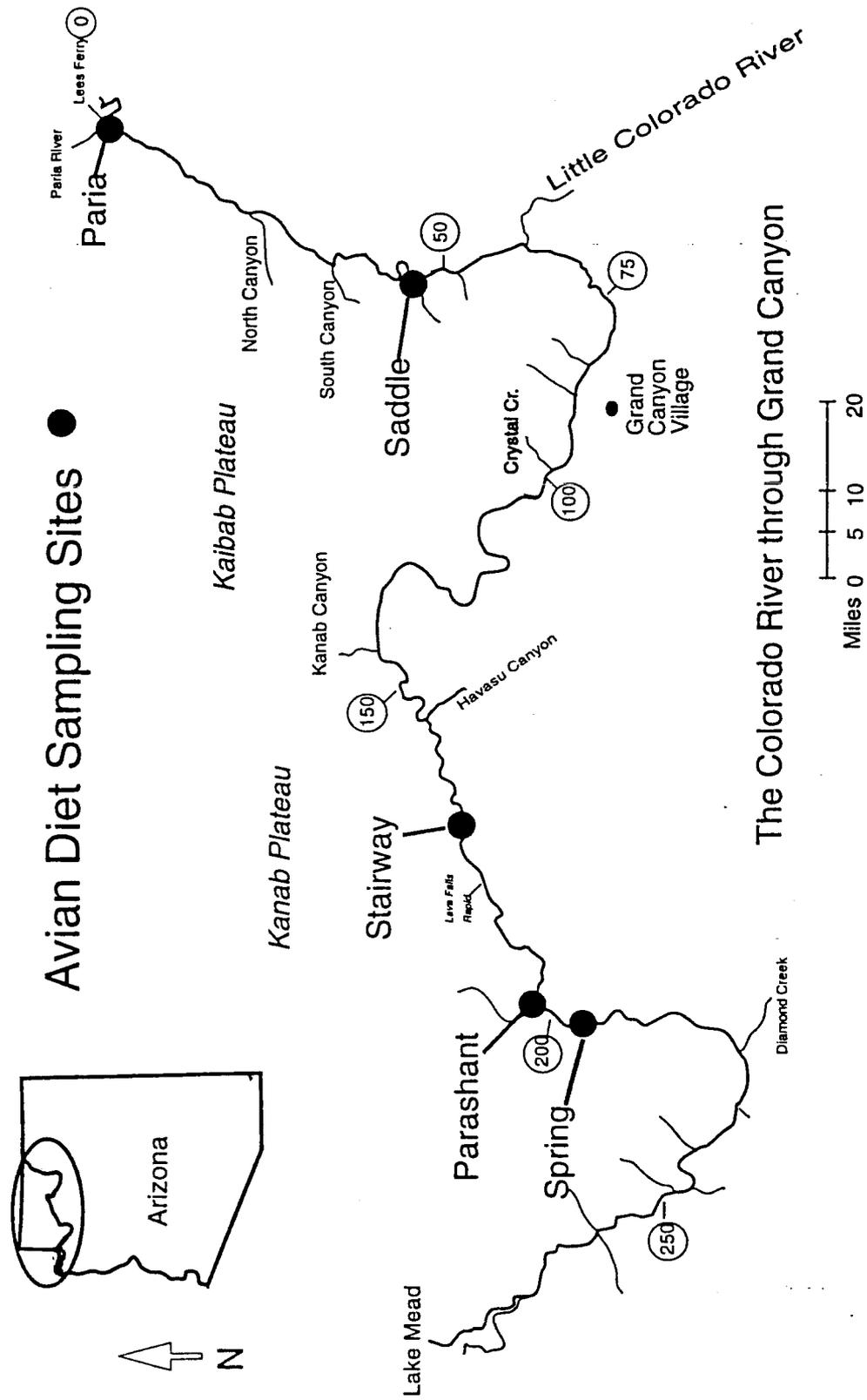
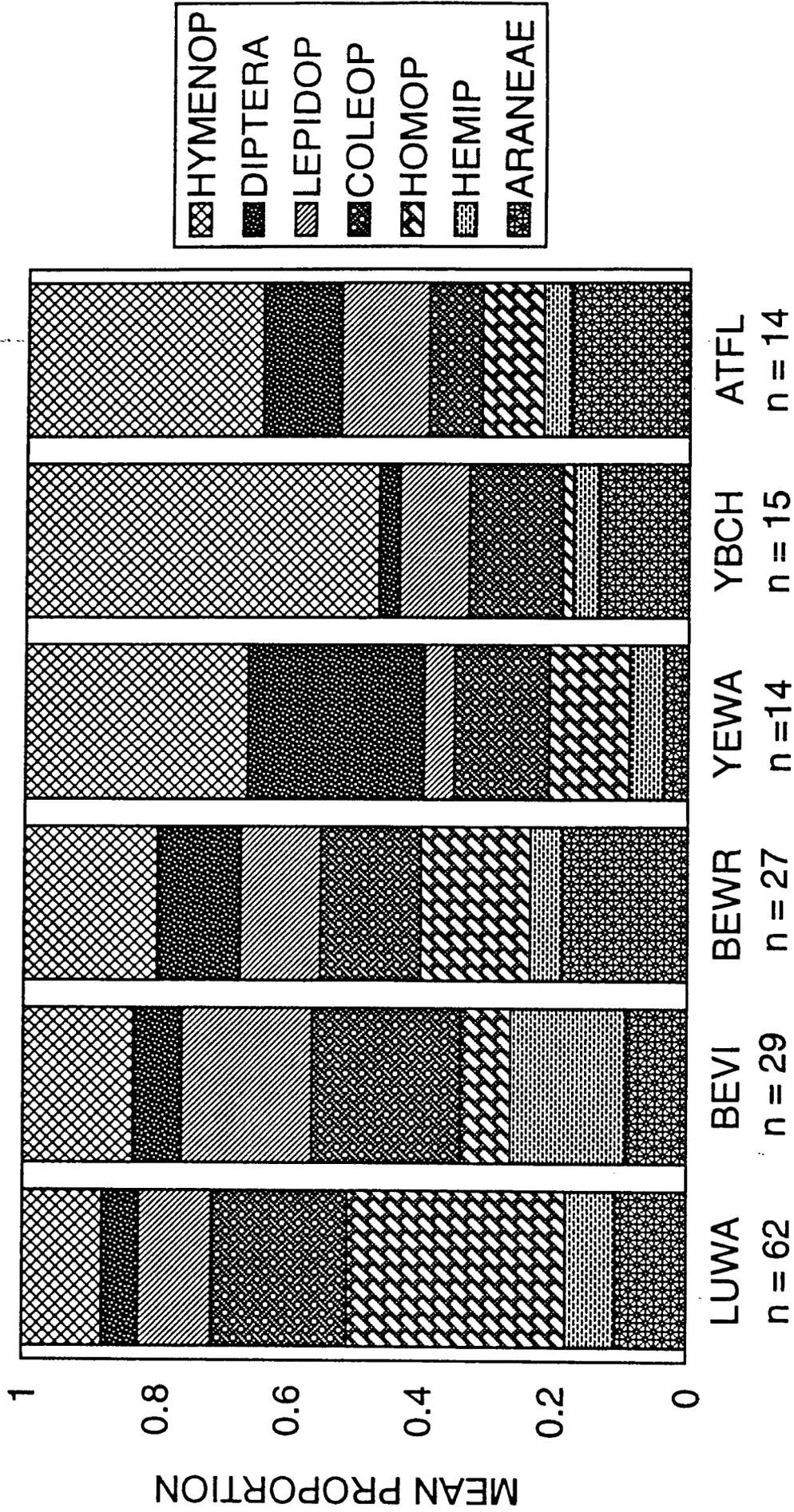


Figure 2. Mean proportion of arthropod orders found in the diets of the six species of birds.



BIRD SPECIES AND SAMPLE SIZE

Figure 3. Mean proportion of Homopterans consumed by the six species of birds. Standard error bars represent one standard deviation. Significance denoted by asterisk.

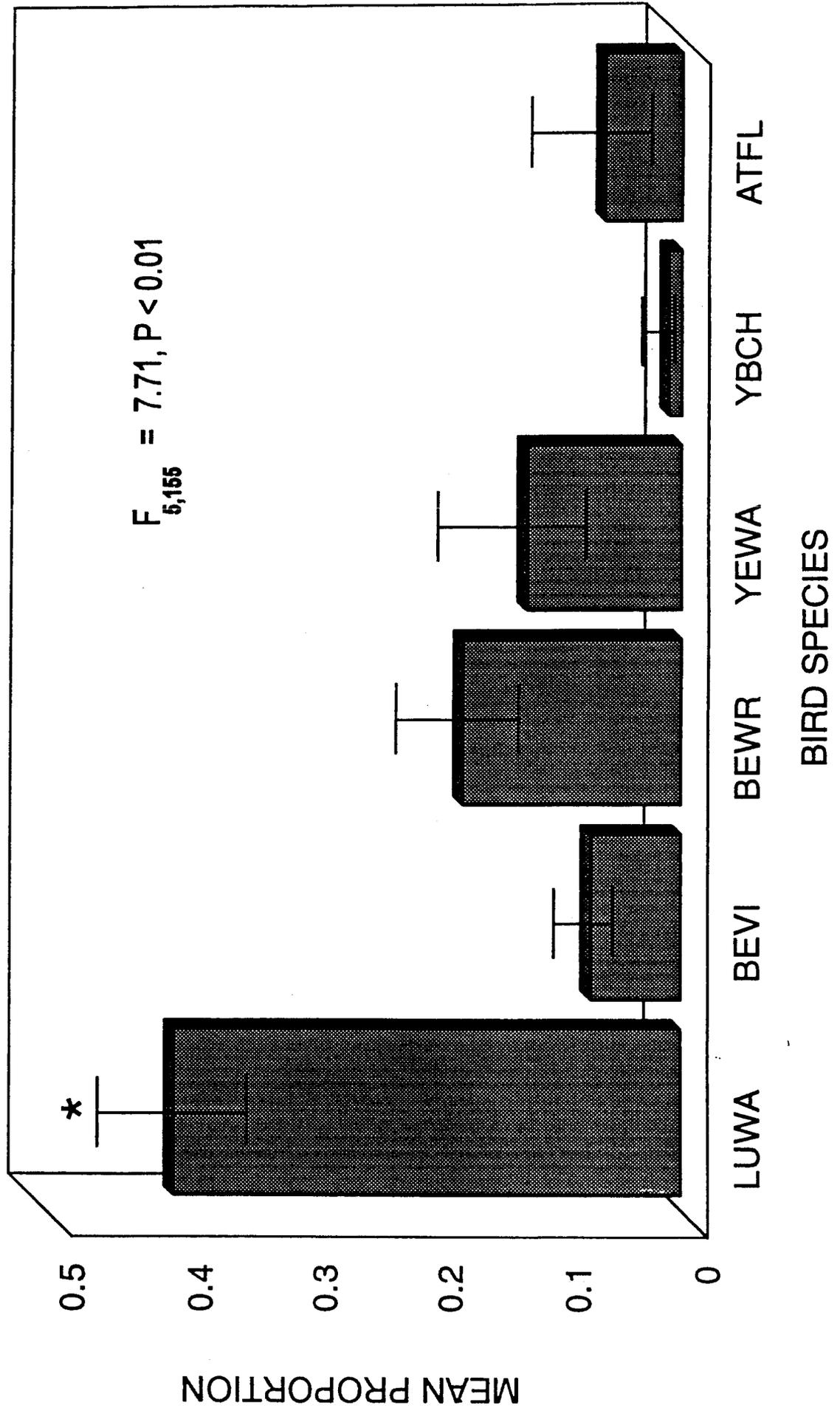


Figure 4a. Mean proportion of Hemiptera consumed by the six species of birds. Standard error bars represent one standard deviation. Significance denoted by asterisk.

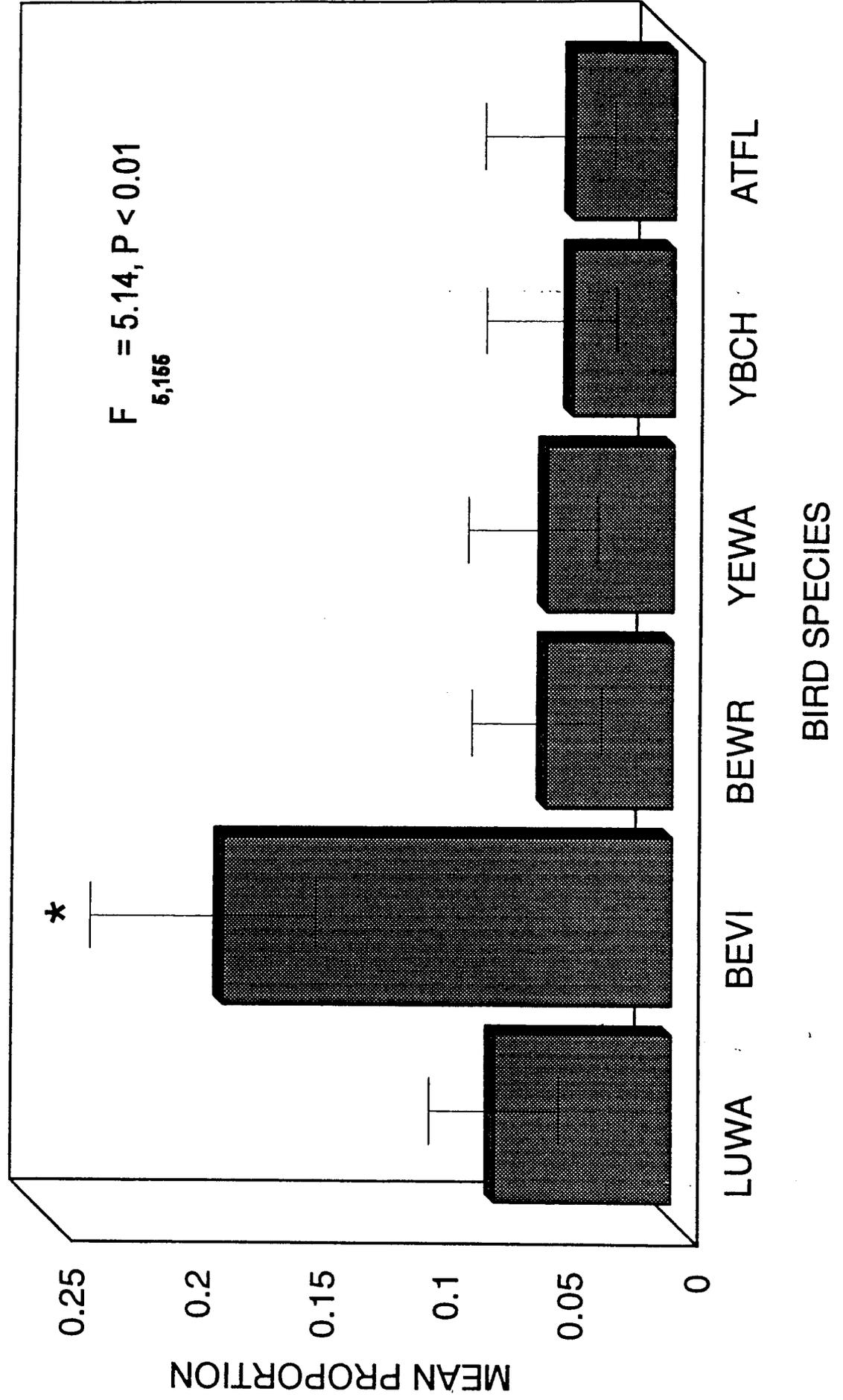


Figure 4b. Mean proportion of Lepidoptera larvae consumed by the six species of birds. Standard error bars represent one standard deviation. Significance denoted by asterisk.

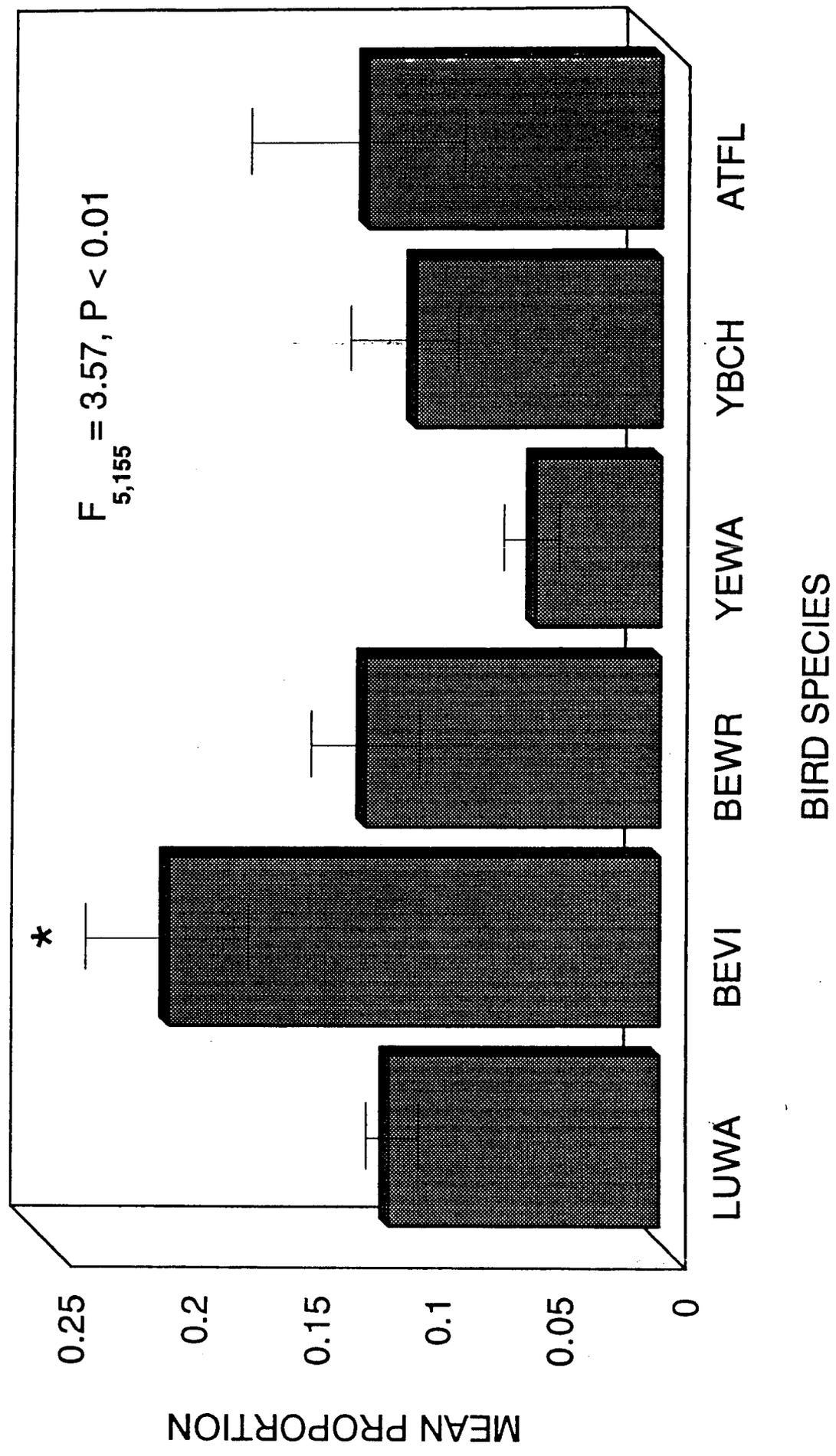


Figure 5. Mean proportion of Araneae consumed by the six species of birds. Standard error bars represent one standard deviation. Significance denoted by asterisk.

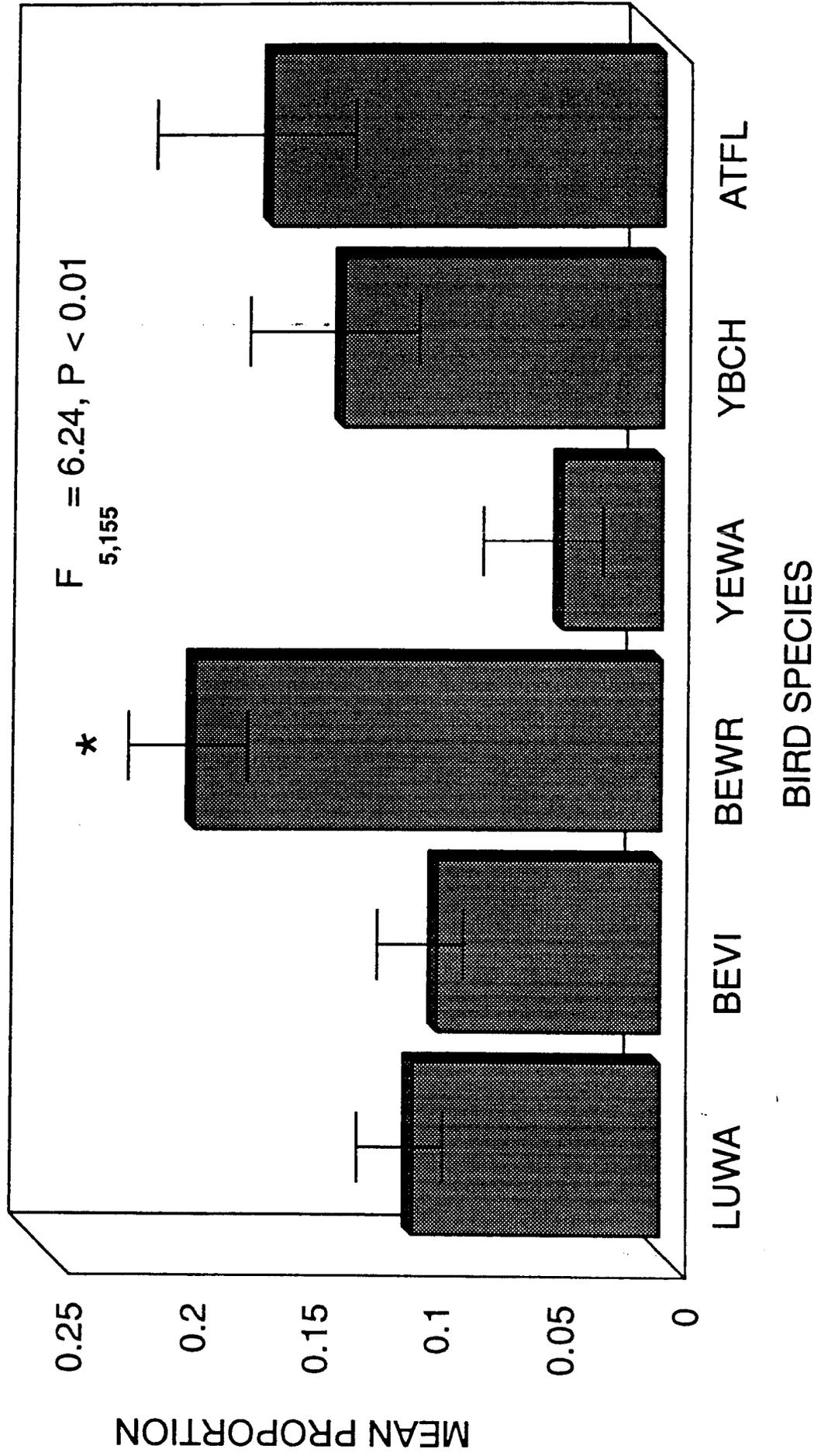


Figure 6. Mean proportion of Diptera consumed by the six species of birds. Standard error bars represent one standard deviation. Significance denoted by asterisk.

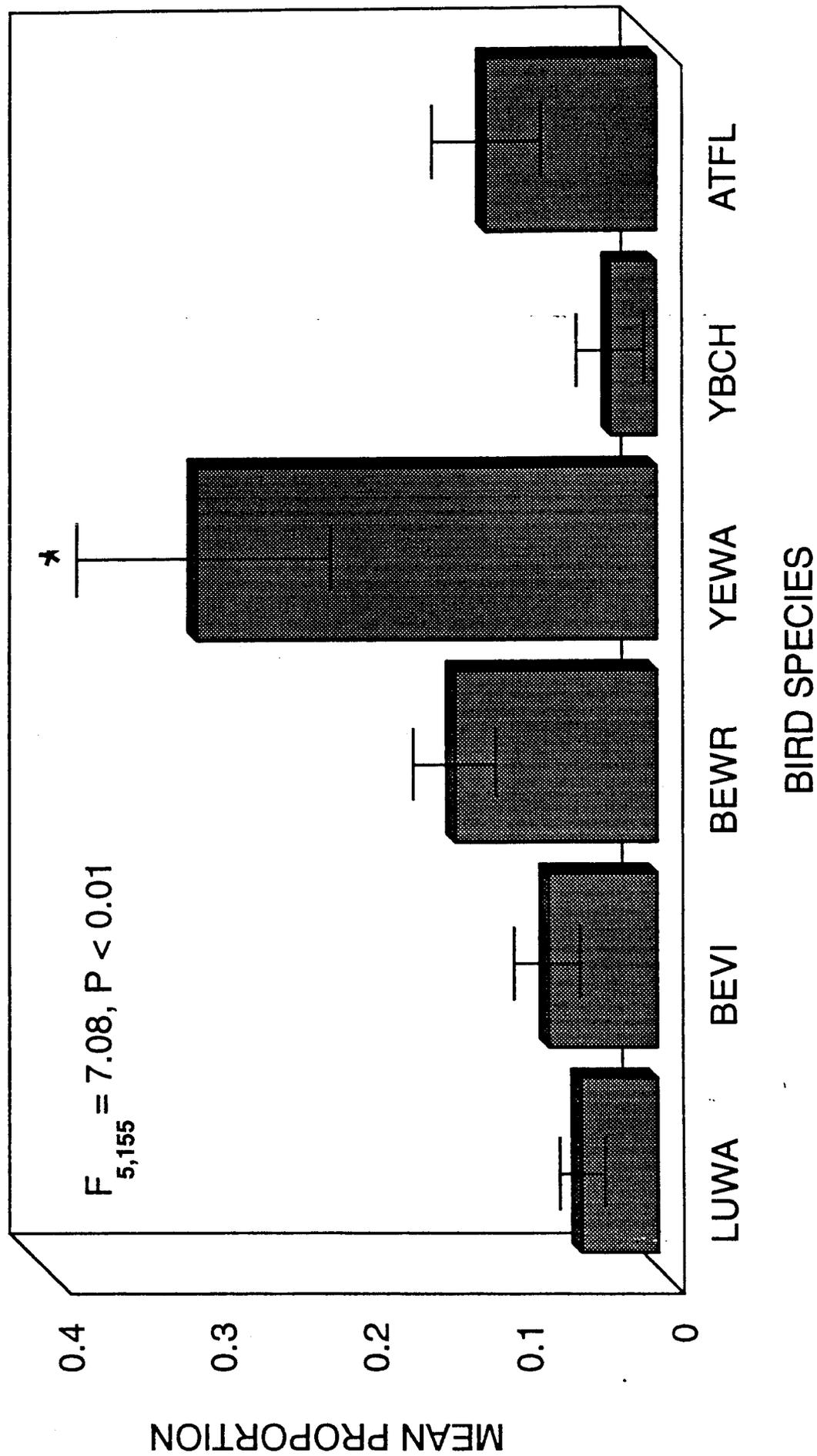


Figure 7. Mean proportion of Hymenopterans consumed by the six species of birds. Standard error bars represent one standard deviation. Significance denoted by asterisk.

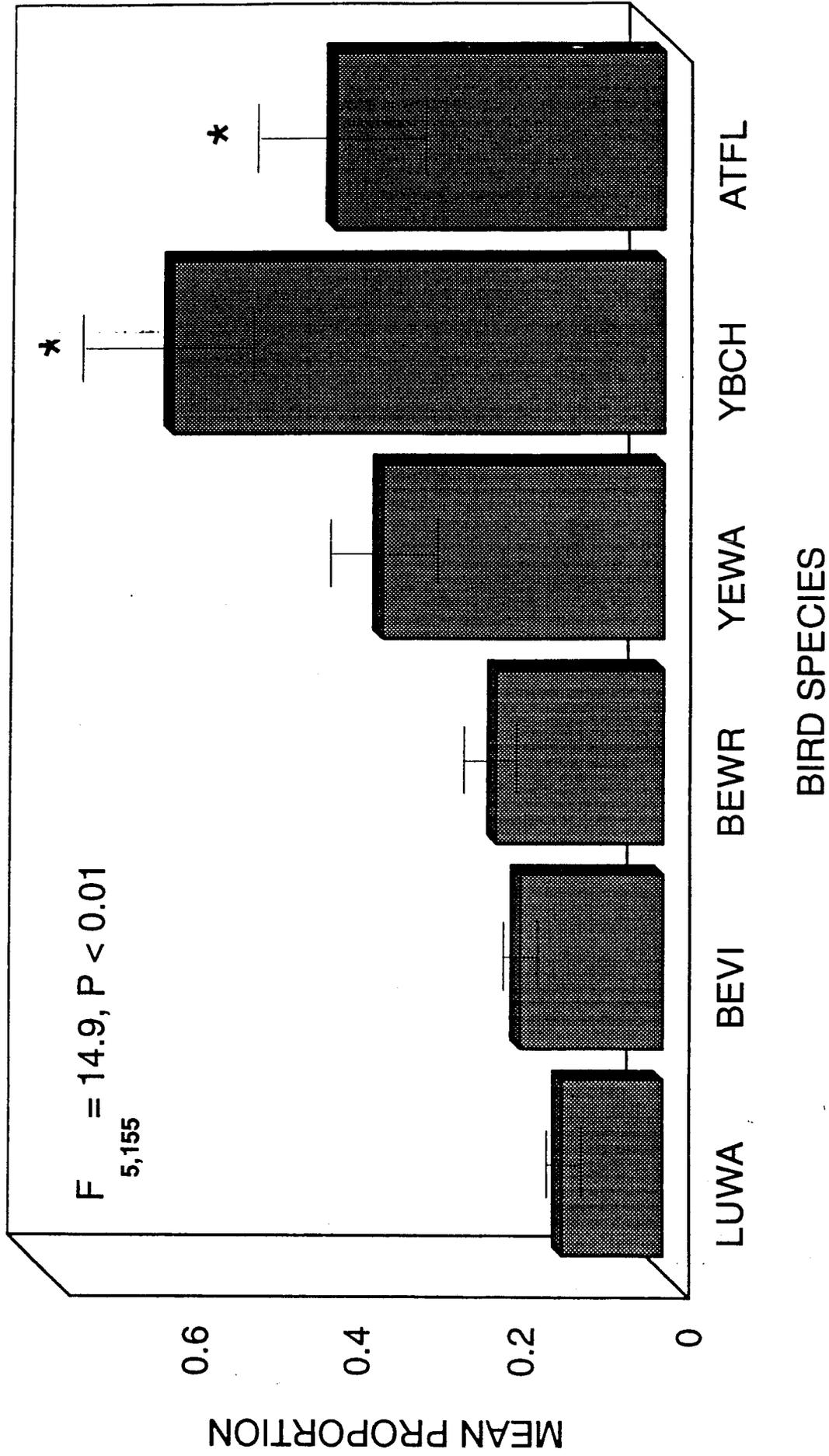


Figure 8. Mean proportion of Coleoptera consumed by the six species of birds. Standard error bars represent one standard deviation.

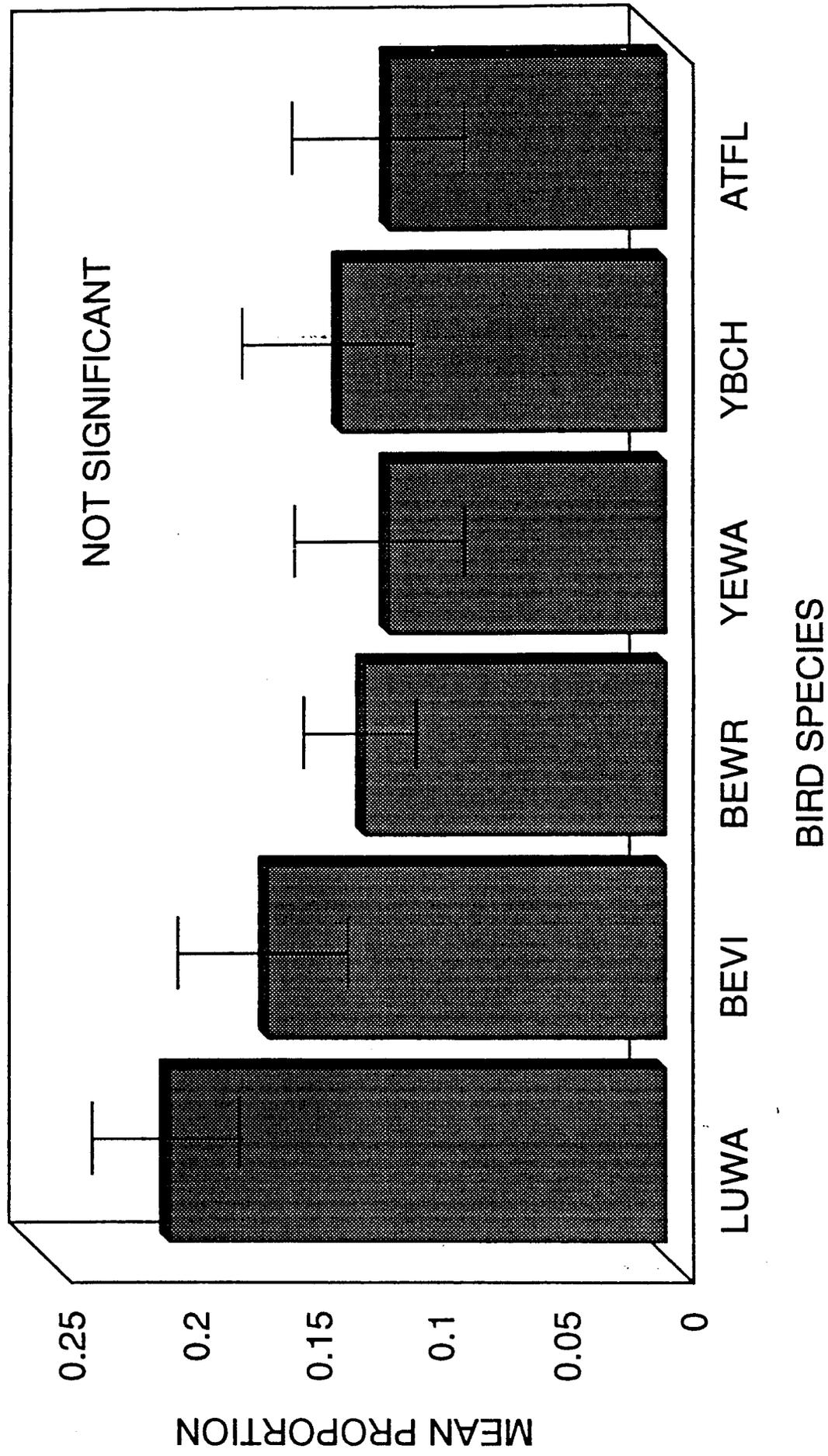


Figure 9. Proportion of leafhoppers (*Opsius stactogalus*) in the diet of the six species of birds.

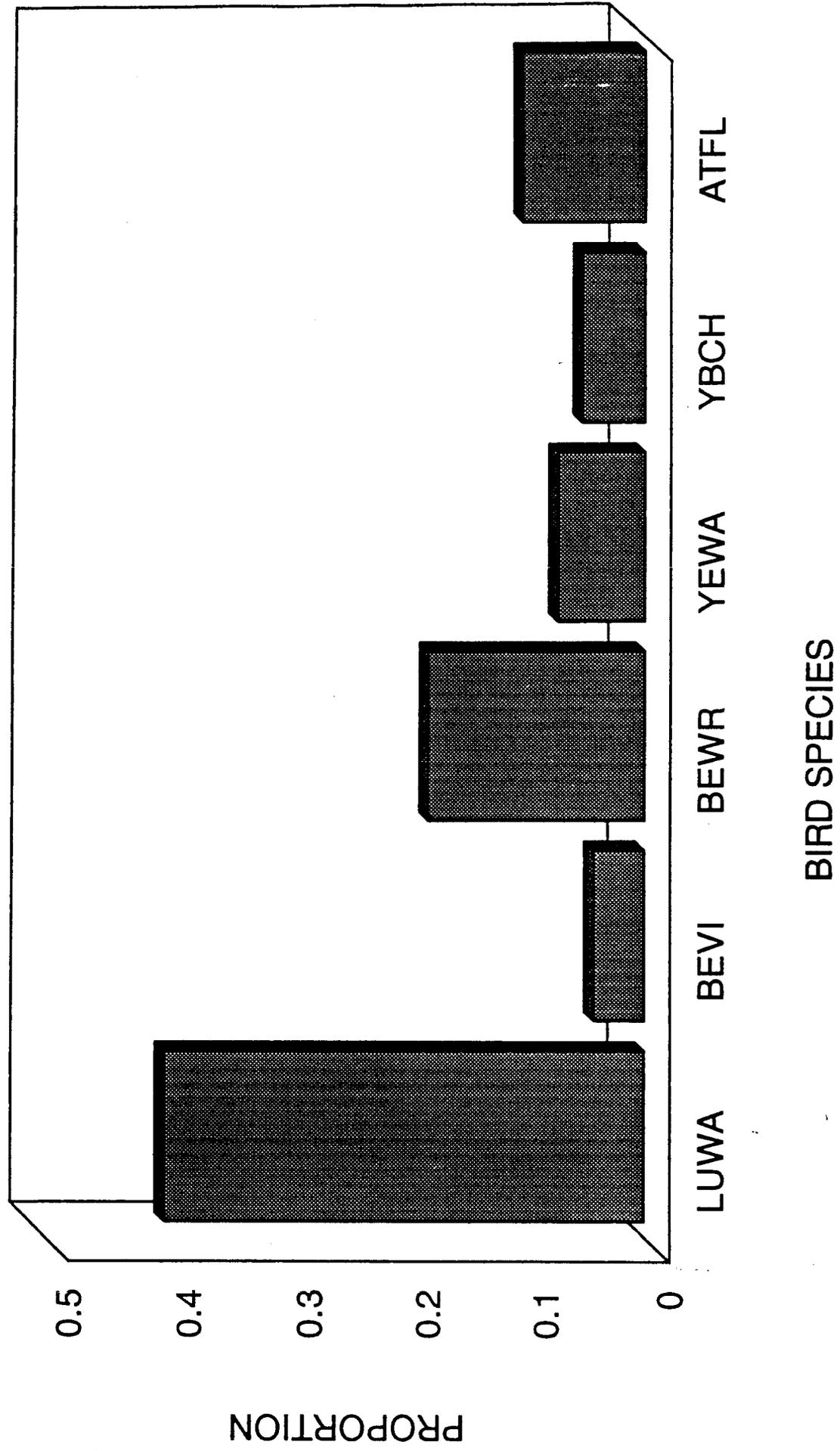


Figure 10. Percent of aquatic arthropods found in the diets of the six species of birds. Significance denoted by asterisk.

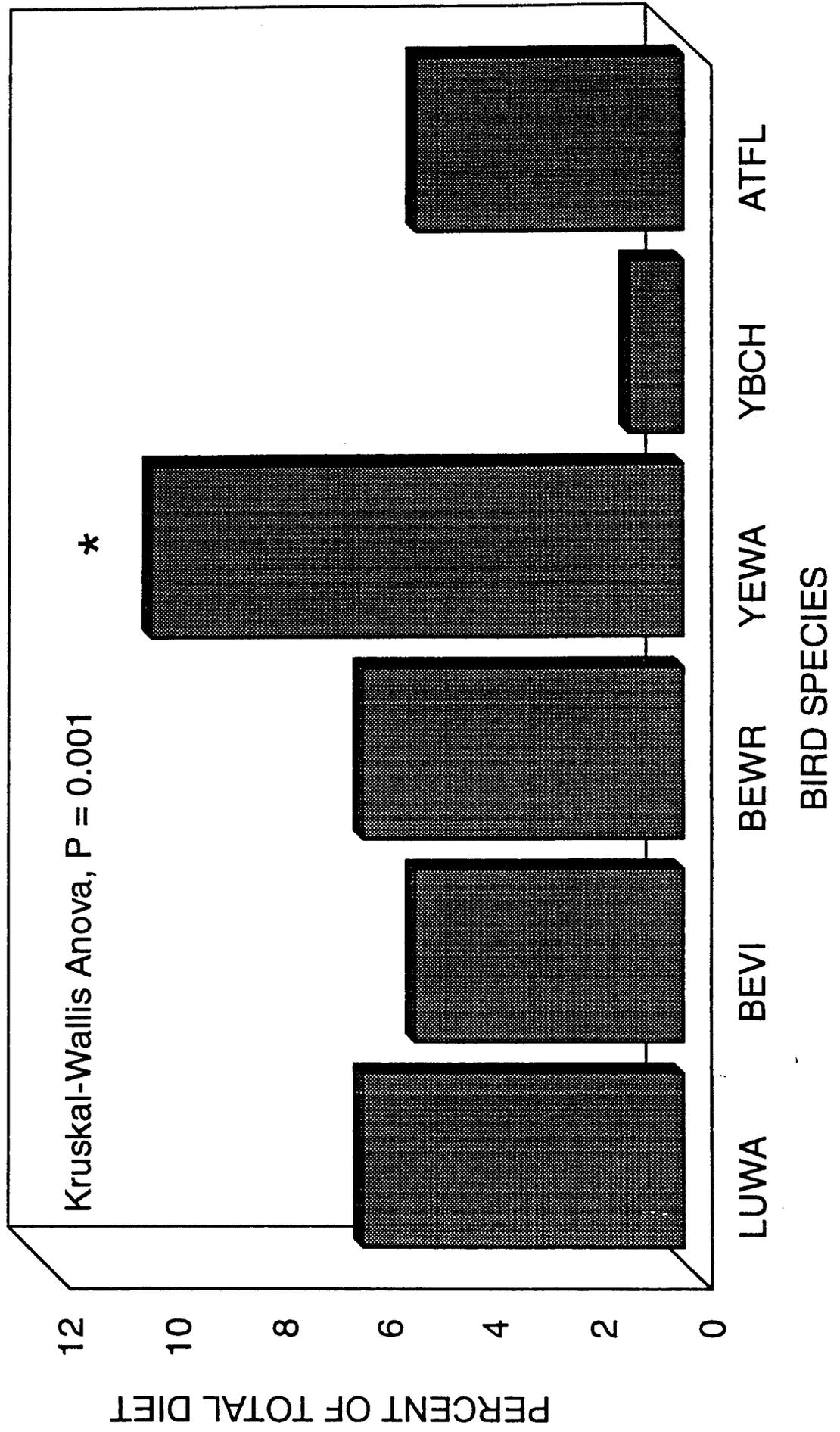
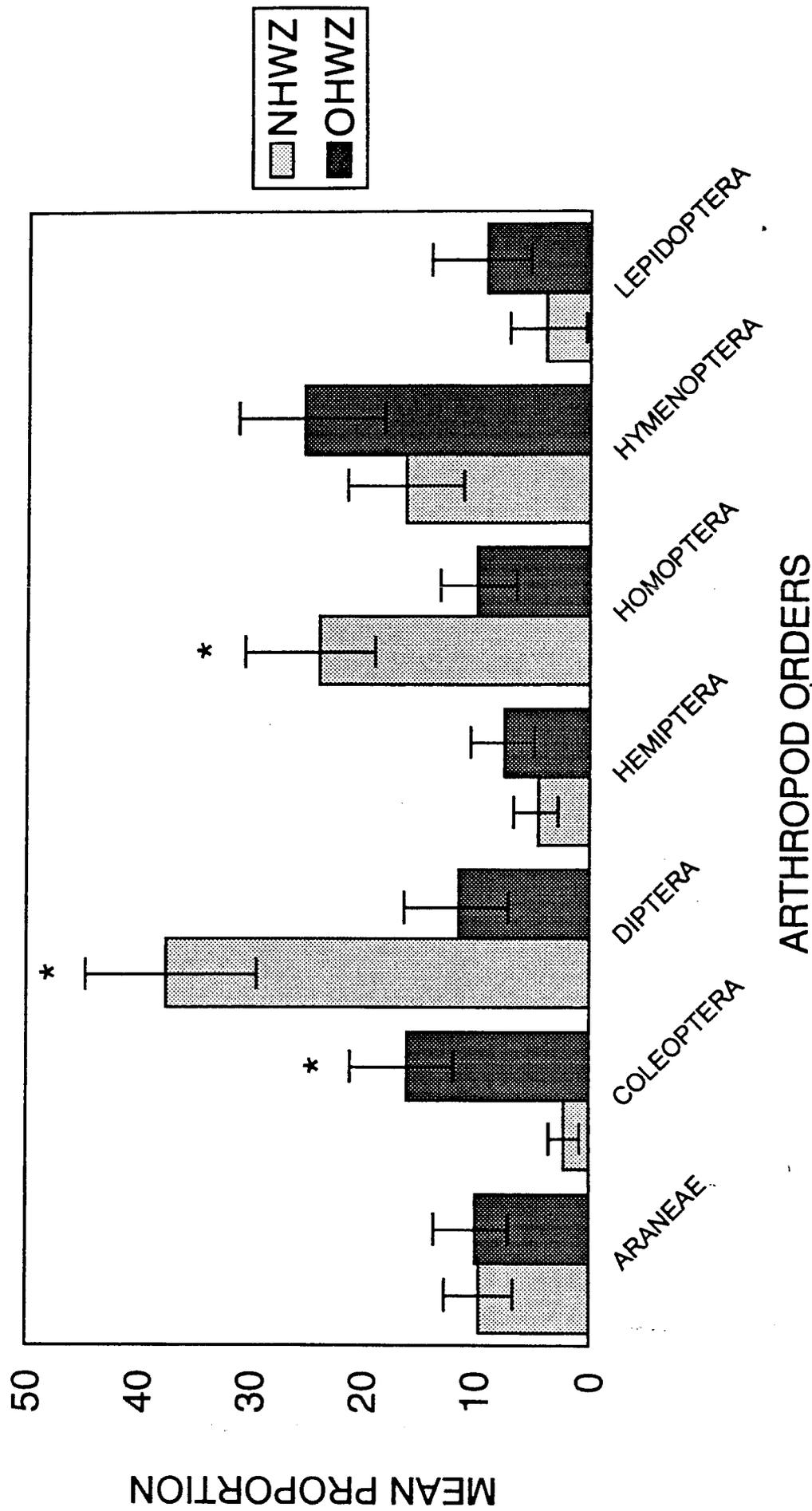
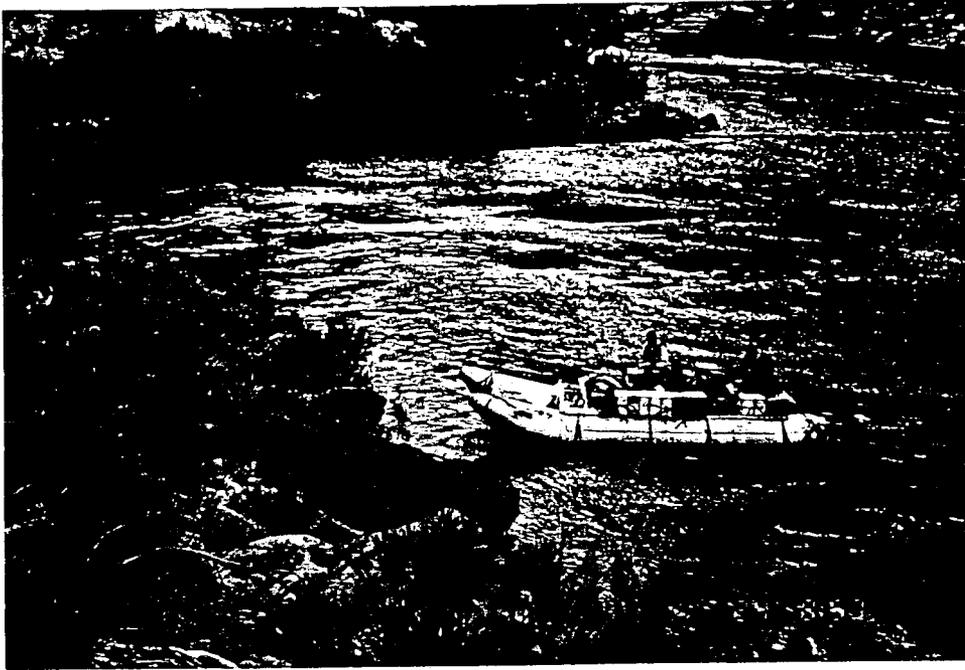


Figure 11. Mean proportion of arthropod orders collected in the old high water zone (OHWZ) and new high water zone (NHWZ). Error bars represent one standard error. Asterisks show significant differences.



Chapter 5: Survey Techniques Comparison



COMPARISON OF AVIAN SURVEY METHODS SUITABLE FOR LONG-TERM MONITORING

INTRODUCTION

As part of the Grand Canyon Avian Community Monitoring project, we studied the utility of various techniques for long-term monitoring of riparian breeding birds. We designed surveys to gather data to understand the sources of variability and bias inherent in the breeding bird surveys and to directly compare different survey methods. Understanding the accuracy and precision of the survey methods is essential for recognizing the level of resolution obtainable given finite human and financial resources.

Variability and bias are caused by many factors and have been well studied (e.g., Ralph and Scott 1981, Verner 1985). Sources of variability which can be controlled include observers, type of survey method, length of survey period, time of day, number of visits, and other parameters. Some factors, such as weather, environmental noise, species-specific behavior, natural history, and avian community complexity cannot be controlled, but their effect can be recognized and taken into account.

We conducted surveys of the breeding bird community to determine species richness and abundances, then compared survey results to determine methodological and observer variability and daily changes in study site occupancy. We used four different techniques to survey breeding birds: floating counts (Carothers and Sharber 1976), total-count walking surveys (Brown and Johnson 1987), point counts (Ralph et al. 1993), and spot maps (I.B.C.C. 1970). Total count walking surveys were paired with each technique because the total count walking survey method has been used more than others in Grand Canyon National Park in the past.

METHODS

We conducted surveys from 1993-95 at 71 study sites, each a discrete patch of riparian vegetation, between Lee's Ferry and Diamond Creek (Figure 1. Appendix 1). Sites were selected to represent a wide range of the sizes, shapes, geomorphology, and floristic composition of patches of riparian vegetation found along the river. Sites were located in seven of the 11 geomorphic reaches (Schmidt and Graf 1986). All surveys were conducted between one-half hour before sunrise and 10:00 AM. With the exception of some floating surveys designed to compare observer variability, all observers had >2 years of avian survey experience.

These analyses consider only the riparian breeding birds, excluding migrants, extremely rare (< 3 detections during the entire project) and upland breeders. The species included were: Black-chinned Hummingbird [bchu], Costa's Hummingbird [cohu], Mourning Dove [modo], Ash-throated Flycatcher [atfl], Brown-crested Flycatcher [bcfl], Bewick's Wren [bewr], Bell's Vireo [bevi], Blue-gray Gnatcatcher [bggn], Northern Mockingbird [nomo], Yellow Warbler [yewa], Lucy's Warbler [luwa], Common Yellowthroat [coye], Yellow-breasted Chat [ybch], Lazuli Bunting [labu], Blue Grosbeak [blgr], Hooded Oriole [hoor], Northern Oriole [noor], Brown-headed Cowbird [bhco], Great-tailed Grackle [gtgr], Summer Tanager [suta], Lesser Goldfinch [lego], and House Finch [hofi]. Statistical significance was defined as $P \leq 0.05$. All means are shown \pm SE.

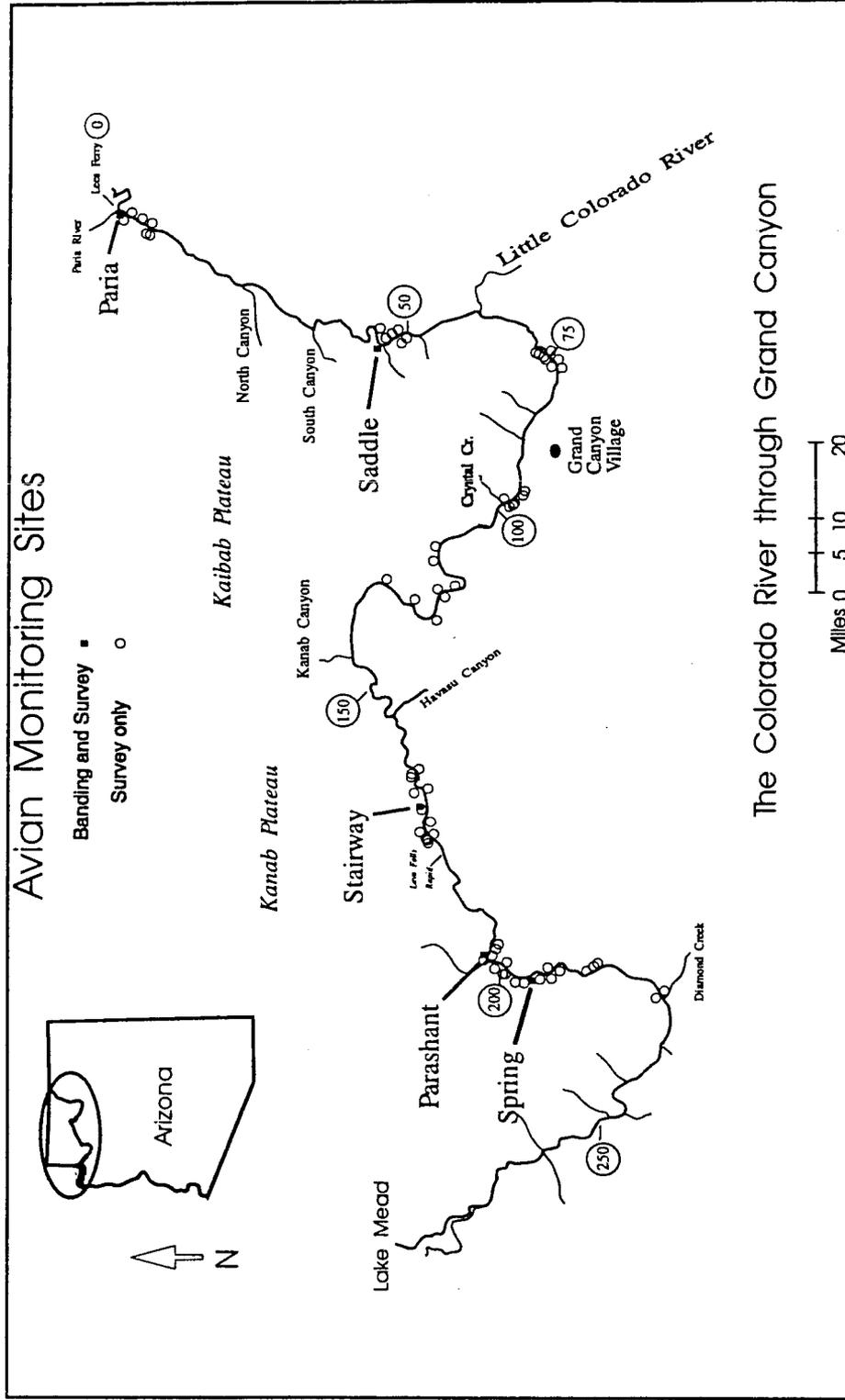


Figure 1. Location of Grand Canyon avian community monitoring direct study sites (black squares) and survey sites (open circles) in the Grand Canyon.

Walking surveys

Walking surveys were the standard against which we compared all other survey methods. These consisted of one observer walking slowly through the riparian habitat, recording species and numbers of all birds observed at the study site (Brown 1988, Sogge et al. 1994, Sogge et al. 1995). The survey was considered complete when all parts of the site had been visited, taking from 15 to 120 minutes depending on total area. Walking surveys were made at all study sites surveyed from 1993-95. To control observer bias, observers were rotated between visits so that no one observer conducted the majority of surveys at any one site.

Floating surveys

One or two observers floated past each study site in a raft ahead of the walking surveyor. Observers silently recorded all birds observed while floating with the current in a 22- or 37-foot motorboat with the motor off. We compared the number of species detected on simultaneous walking and floating surveys by comparing data from one walking observer to data from the most experienced floating observer.

We compared the abundance of different species detected by each technique with a linear regression of data summed from all surveys with simultaneous walking and floating observers for each of the ten most abundant species. For example, all the Lucy's Warblers counted on walking surveys in 1993 were regressed against all those counted on paired floating surveys making one data point on the walk-float regression for 1993. We also compared the number of species and total count of birds observed on individually paired walking and floating surveys with Wilcoxon signed-rank test and regression. Finally, we analyzed the effects of patch shape and the presence of noise-producing riffles nearby. Sites were subjectively defined as linear if vegetation was nowhere more than three meters thick and nonlinear otherwise. To standardize counts from species-rich and species-poor sites we used the difference between walking and floating results divided by the walking results.

Territory Mapping

We made territory maps of breeding species at the major study sites in 1994 only. Methods closely followed internationally accepted guidelines (I.B.C.C. 1970) except, due to trip logistics, we were forced to make fewer visits than the ten recommended by these guidelines (six to nine, depending on study site). Observations of territorial behavior, (e.g., singing males and border disputes) and nest sites were registered on enlarged xerox copies of aerial photos (one per visit) taken into the field. After all the data were collected, registrations were combined onto one map for each species and study site and territorial boundaries were drawn in accordance with observations. Visits were made from mid-March through the end of July. One person was responsible for all territory mapping and interpreting territorial boundaries.

Point counts

We conducted paired point counts and walking surveys at 11 study sites. Point counts were conducted once per month at each site, March-June 1995. On each visit to a site, a walking survey was conducted on one morning and a point count survey was conducted on the next, or vice versa. Point count survey methods generally follow the recommendations of Ralph et al. (1993). A 50-meter radius was used to separate bird detections into two classes -- detections $\leq 50\text{m}$ (50m point count), and detections \leq or $> 50\text{m}$ (unbounded point count). Point counts began as soon as the observer reached the point count station.

Points were placed systematically, 125 to 150 meters apart, half way between the river and the upland habitat. We surveyed as many points as would fit into each site using these criteria. Number of points varied from one to five per site depending on area and there were 37 points altogether. Point counts lasted for 10 minutes in March and 5 minutes from April-June. The total time from the start of the first point count to the end of the last in each site was recorded for comparison of survey effort with walking surveys.

To determine the most efficient point count duration (balancing completeness with diminishing returns), we calculated the accumulation of new species and new individuals in successive 2-minute intervals of a 10-minute count period in March (Hutto et al. 1986).

Observer Variability

We had two observers on some floating surveys. Thus, each observer was exposed to the same survey environment while minimally influencing the other observer. Both observers silently recorded data on birds present and did not share observations. We compared the number of species and number of observations for each observer, and number of species in common for each paired survey.

Study site variability

We repeatedly conducted walking surveys of major study sites on consecutive days on each monthly visit. To reduce observer variability when estimating site variability, we only compared surveys made by the same observer on different days. We compared the number of species detected and the total number of observations.

Comparisons

Comparisons were made between the different methods: walking surveys, territory maps, floating surveys, 50m point counts, and unbounded point counts. The mean number of species observed per survey and the mean number of species in common were compared using paired t-tests (when data were normally distributed) or Wilcoxon tests (when data were non-normally distributed). We estimated the reliability of walking surveys and point counts, defining reliability as the number of surveys in which a species was detected by a given method divided by the total number of survey pairs in which that species was detected by any method (including casual observations). Reliability was compared using the Wilcoxon test. We used linear regression to

quantify the relationships between abundance estimates of the three methods.

To compare the variability of results obtained from the different survey methods with observer and daily site variability, we used the Bray-Curtis dissimilarity metric (Clifford and Stephenson 1975). This metric provides an index of dissimilarity of species lists and abundance produced by different methods. The index scales from 0 (complete similarity) to 1 (complete dissimilarity). To make comparisons of all techniques, we limited analyses to two study sites (RM 46.7R and 198.0R), the only sites adequately territory mapped. We further limited analyses to those species for which we were able to produce territory maps: Bewick's Wren, Blue-gray Gnatcatcher, Bell's Vireo, Lucy's Warbler, Yellow Warbler, Common Yellowthroat, and Yellow-breasted Chat.

RESULTS

Floating surveys

Simultaneous floating and walking surveys were conducted in 1993 and 1994 only, and showed several important things. In 1993, the overall species lists (pooled for all surveys) produced by the two techniques were very similar: 20 species on walking surveys and 18 on floating surveys, with only 3 species (Willow Flycatcher, Hooded Oriole, and Lazuli Bunting) not common to both lists. Rank abundance of the 10 most common species from these two lists was similar with two exceptions (Table 1).

Table 1. Rank abundance of the ten most common species of riparian breeding birds from simultaneous walking and floating surveys on the Colorado River through Grand Canyon National Park, 1993. n = number of birds observed. **Bold** = species ranked differently by the two techniques.

Species Abundance: Walking		Species Abundance: Floating	
	n		n
Lucy's Warbler	389	Lucy's Warbler	141
Bell's Vireo	120	Bell's Vireo	70
House Finch	95	House Finch	45
Blue-gray Gnatcatcher	82	Yellow Warbler	40
Yellow Warbler	71	Ash-throated Flycatcher	32
Ash-throated Flycatcher	69	Yellow-breasted Chat	31
Yellow-breasted Chat	42	Blue-gray Gnatcatcher	24
Bewick's Wren	41	Bewick's Wren	21
Black-chinned Hummingbird	30	Common Yellowthroat	16
Common Yellowthroat	12	Black-chinned Hummingbird	7

Results from paired walking and floating surveys in 1994 were somewhat different. Two more species were added in 1994 -- Northern Mockingbird and Song Sparrow. Again, the species lists produced by the two techniques were very similar. Of 22 species detected on floating surveys, all were detected on walking surveys as well. Two additional species, Blue Grosbeak and Northern Oriole, were unique to walking surveys. Rank abundances of the 10 most common species were more different than in 1993, with three species in different rank orders (Table 2). The Black-chinned Hummingbird, ranked sixth on the walking surveys, did not even make the top ten species on the floating surveys, and the Blue-gray Gnatcatcher was further displaced than in 1993.

Table 2. Rank abundance of the ten most common species of riparian breeding birds from simultaneous walking and floating surveys on the Colorado River through Grand Canyon National Park, 1994. n = number of birds observed. **Bold** = species ranked differently by the two techniques.

Species walking	n	Species floating	n
Lucy's Warbler	540	Lucy's Warbler	278
Blue-gray Gnatcatcher	129	Bell's Vireo	89
Bell's Vireo	128	House Finch	80
Bewick's Wren	121	Bewick's Wren	61
House Finch	105	Ash-throated Flycatcher	58
Black-chinned Hummingbird	93	Blue-gray Gnatcatcher †	53
Ash-throated Flycatcher *	70	Yellow Warbler †	53
Yellow Warbler *	70	Say's Phoebe	47
Say's Phoebe	36	Yellow-breasted Chat	22
Yellow-breasted Chat	28	Black-chinned Hummingbird	19

* Ranks tied. † Ranks tied.

We also compared the number of species and total counts from paired walking and floating surveys. We detected significantly more species on walking surveys, on average, than on paired floating surveys (mean difference = 1.03 ± 0.09 species; Wilcoxon test; $Z = 9.72$, $P < 0.001$). We also counted significantly more birds on walking surveys (mean difference = 3.56 ± 0.31 ; $Z = 11.19$, $P < 0.001$). We measured the accuracy of the abundance estimate from floating surveys with a regression. Regression of floating versus walking counts from paired data show slope (symbolized by "b") $b = 0.44$ ($R^2 = 0.58$) in 1993 and $b = 0.40$ ($R^2 = 0.53$) in 1994.

Regression of counts summed for the 11 most common species from walking vs. floating surveys displays some interesting species-specific patterns. The slope of the regression line in 1993 is $b = 0.38$ ($R^2 = 0.94$), and in 1994, $b = 0.51$ ($R^2 = 0.94$) (Figs. 2 and 3).

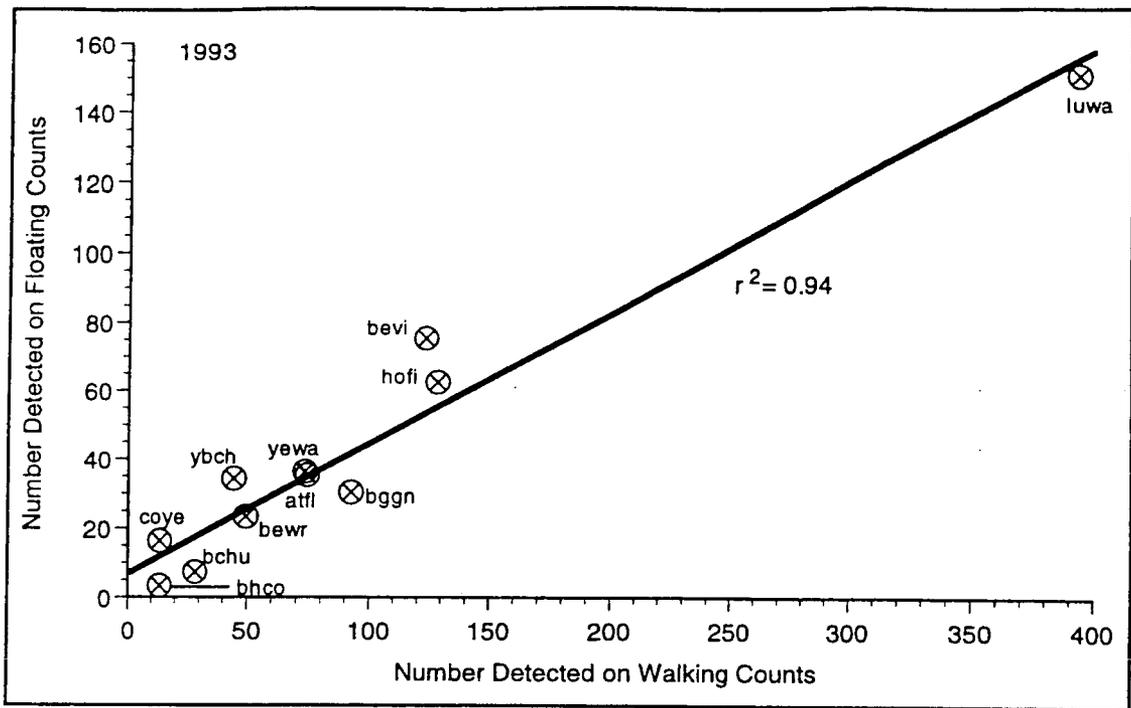


Figure 2. The number of detections made during simultaneous walking and floating bird surveys along the Colorado River in the Grand Canyon, 1993.

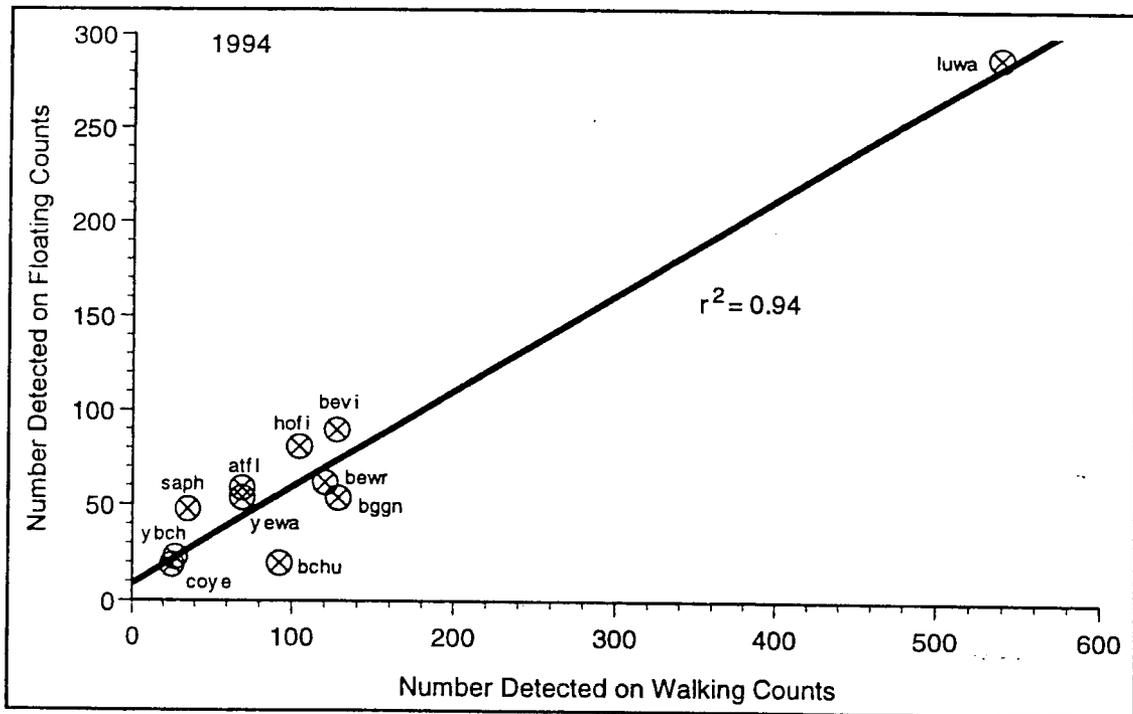


Figure 3. The number of detections made during simultaneous walking and floating bird surveys along the Colorado River in the Grand Canyon, 1994.

Comparisons of standardized count and species differences $[(\text{walk} - \text{float}) / \text{walk}]$ for linear versus non-linear patches showed that floating surveys were significantly more accurate at linear sites for count differences (Wilcoxon test, $Z = -4.17$, $P < 0.001$) but not for species differences ($Z = -1.18$, $P = 0.22$). The presence of riffle noise at a study site significantly reduced floating survey accuracy for both count differences ($Z = -3.08$, $P = 0.002$) and species differences ($Z = -2.80$, $P = 0.005$).

Territory mapping

Because of the logistics of river travel, we only obtained enough data to accurately map the territories of breeding birds at two sites in 1994: RM 46.7R and 198.0R. We mapped territories on nine visits to these two sites. Because this small sample size precludes detailed analyses, only general comments can be made in comparing results from territory maps and walking surveys. Results appear generally in good agreement between these two techniques (Table 3) for those species which can be recognized advertising and defending a breeding territory. Note that territories of Lucy's Warblers are hard to quantify, being under-estimated on walking surveys. Also, the Blue-gray Gnatcatcher was over-estimated on walking surveys compared to territory mapping. Territory mapping could not be compared with point counts because the two techniques were not used in the same year.

Table 3. Comparisons of population estimates of riparian breeding birds from absolute-count walking surveys and territory mapping from two sites on the Colorado River in Grand Canyon National Park, 1994. RM = river miles below Lee's Ferry (Stevens 1983).

Species	Saddle Canyon (RM 46.7R)		Parashant (RM 198.0R)	
	# territories walking	# territories mapped	# territories walking	# territories mapped
Lucy's Warbler	5	6-7	4	4-8
Bewick's Wren	3	2-3	2	2
Yellow Warbler	2	2	1	1
Common Yellowthroat	2	2	1	1
Yellow-breasted Chat	1	2	2	2
Blue-gray Gnatcatcher	2	1	5	2-3
Bell's Vireo			6	7

Point counts

We calculated the rate of addition of new species and individuals on ten minute point counts in March. Average numbers of new species decreased from 2.4 (53% of cumulative total) in the first 2-minute interval and continued to taper off gradually during successive intervals (Fig.4). The same pattern was evident for April-June. The total number of new individuals also declined in the same manner, from 2.1 (55% of cumulative total) in the first 2 minutes. Based on this, we adopted a standard 5-minute count period.

We obtained a sample of 40 paired surveys in 1995 for comparing methods. Average length of walking surveys (45 ± 3.8 minutes) and point count surveys (44 ± 4.1 minutes) were not significantly different ($T = 0.15$, 77 df, $P = 0.88$).

The mean number of species detected on walking surveys (7.2 ± 0.5) was greater than on 50m point counts (5.5 ± 0.4 ; $T = -4.25$, 39 df, $P < 0.001$), but not on unbounded point counts (6.7 ± 0.5 ; $T = -1.1$, 39 df, $P = 0.25$). Not surprisingly, fewer species were detected on 50m point counts than on unbounded point counts ($T = -5.51$, 39 df, $P < 0.001$). Number of species common to paired walking and point count surveys was low; 4.3 species (60% overlap) for 50m point counts, and 4.8 species (67% overlap) for unbounded point counts. Regression of the number of species detected in point counts against paired walking surveys gave $b = 0.57$ ($R^2 = 0.49$) for 50 m point counts and $b = 0.87$ ($R^2 = 0.71$) for unbounded point counts.

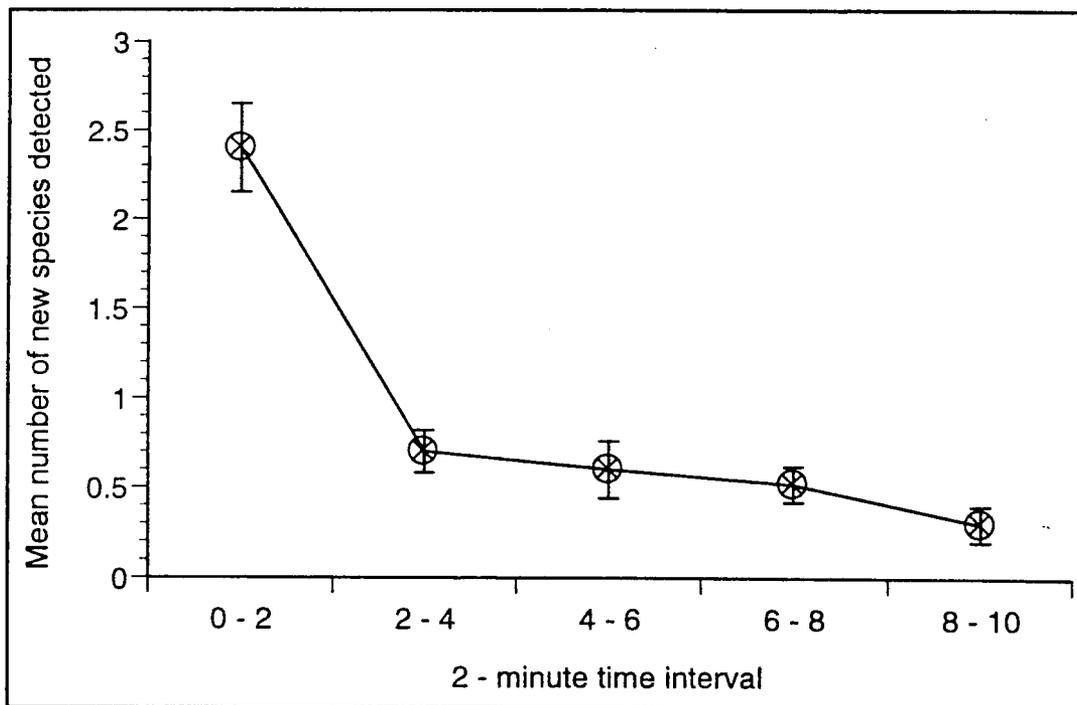


Figure 4. The mean number (\pm SE) of new species detected in each 2-minute interval of 10-minute point counts along the Colorado River in the Grand Canyon

Of the 22 riparian breeding species present, ten were observed on less than 5% of all point counts. These were the Costa's Hummingbird, Brown-crested Flycatcher, Phainopepla, Northern Mockingbird, Blue Grosbeak, Indigo Bunting, Lazuli Bunting, Brown-headed Cowbird, Northern Oriole, and Summer Tanager.

Regression of total abundance for each species (summed from all paired surveys) from walking versus 50m point counts were highly correlated and gave similar estimates ($R^2 = 0.98$, $b = 0.88$; Fig. 5). Regression of abundance estimates from walking versus unbounded point counts were also correlated and gave similar estimates ($R^2 = 0.99$, $b = 1.14$; Fig. 5).

Overall walking survey reliability was 0.82, ranging from 1.0 to 0.62 for different species (Table 4). Fifty meter point count survey reliability was 0.61, ranging from 0.83 to 0.23 for different species, significantly different from walking surveys (Wilcoxon signed-rank test, $Z = -2.66$, $P = 0.01$). Unbounded point count survey reliability was 0.80, ranging from 1.0 to 0.46, not significantly different from walking surveys ($Z = -0.10$, $P = 0.92$).

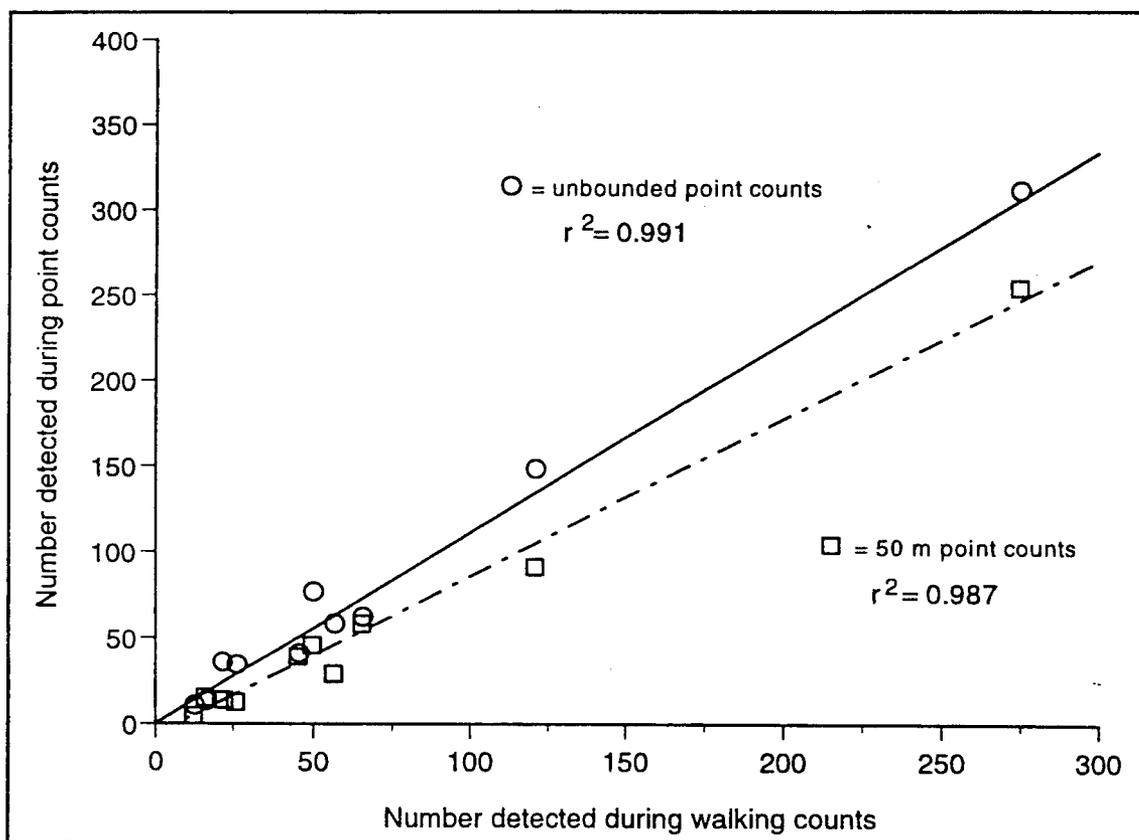


Figure 5. Regression of total abundance for each species (summed from all paired surveys) from walking counts versus 50-m point counts (open boxes and dashed line) and unbounded point counts (open circles and solid line). Data are from 1995 bird surveys along the Colorado River in the Grand Canyon.

Table 4. Reliability of walking and point count surveys to detect bird species. Reliability = # of surveys the on which the species was detected by given method / # of survey pairs on which the species was detected by any method.

Species	Walking	50m point count	Unbounded point count
Lucy's Warbler	1.0	0.83	1.0
Bell's Vireo	1.0	0.77	0.85
Ash-throated Flycatcher	0.67	0.24	0.71
Yellow-breasted Chat	0.81	0.38	0.81
Yellow Warbler	0.64	0.64	0.64
Common Yellowthroat	0.85	0.23	0.46
Mean	0.82	0.61	0.80

Observer Variability

We obtained data from 256 floating survey pairs to compare observer variability. We paired five observers (three experienced and two amateur avian surveyors) in eight combinations. Thirty-eight paired surveys, or 15% of the total were identical. Identical surveys averaged 1.5 species, significantly less than 2.8 on nonidentical paired survey (Mann-Whitney $U = 2281$, $Z = -4.54$, $P < 0.001$). The mean number of species per survey was significantly different for three of eight surveyor pairs, one from a pair of two experienced observers (mean difference = 0.59, $T = 4.70$, 20 df, $P < 0.001$) and two from amateur and experienced observer pairs (mean difference = 0.85, $T = 2.74$, 19 df, $P = 0.01$; mean difference = 0.53, $T = 2.09$, 31 df, $P = 0.04$). The difference in number of species for survey pairs ranged from 0 to 5 species. The mean number of species in common to the two lists ranged from 1.6 to 3.0, or 75-84% of the average number of species from the paired lists.

The mean number of birds observed per survey ranged from 2.8 to 8.0, and was significantly different for two of eight pairs, one between two experienced observers (mean difference = 0.73, $T = -2.52$, 21 df, $P = 0.02$) and one between an experienced and amateur observer (mean difference = 1.55, $T = 2.16$, 19 df, $P = 0.04$). The range of differences was from 0 to 11 observations/survey.

Daily Survey Variability

Consecutive daily walking surveys were conducted at the major study sites, but data useful for this analysis were only obtained from four: RM 0.0R, 1.0R, 46.7R, and 198.0R. There were 34 surveys, making 17 pairs, conducted by the same observer within two days. The mean number of species recorded on all surveys was 6.7 ± 0.39 (median = 6.5), ranging from 3 to 11. The difference in species recorded within paired surveys ranged from 0 to 4 and averaged 1.4 ± 0.21 .

The difference between mean number of species on one day or another was 0.24 ± 0.36 , not significantly different (paired T-test; $T = 0.66$, 16 df, $P = 0.52$). There were 17 riparian breeding species found on one survey but not the other. The most numerous omission was the Yellow-breasted Chat, missed on six of the 34 surveys. Five species were missed four times: Ash-throated Flycatcher, Black-chinned Hummingbird, Bewick's Wren, Common Yellowthroat, and Mourning Dove. The Brown-headed Cowbird and House Finch were each missed three times.

The number of birds on these walking surveys ranged from 3 to 47 and the mean number counted was 17.7 ± 1.5 . The mean difference between paired counts was 5.2 ± 1.2 (median = 4) and ranged from 0 to 17, much more right skewed than the distribution of species number. The difference between mean counts of one day or the other was 2.4 ± 1.6 , not significantly different (Wilcoxon test; $Z = -1.29$, $P = 0.20$).

Dissimilarity Comparisons

We compared the variability introduced by different methods, observers, years, and daily variability. We found that differences in the bird community between years at the same site produced the least variability (B-C as low as 0.03, Table 5), while daily differences at the same site were great (B-C as great as 0.56). Observer differences were also very important (B-C as great as 0.48). It should be noted, however, that observer pairs used for these Bray-Curtis comparisons were all of one experienced and one inexperienced observer, probably accentuating observer variability. The survey method most different from walking surveys was the floating surveys, and the least different was the point count. Territory maps were the most consistently the same, but with only two comparisons, the importance of these results are questionable.

Table 5. Range of Bray-Curtis dissimilarity metric values for survey results compared between survey methods and other sources of variability. N = number of pairs for comparison.

Methods	Range of Bray-Curtis values	N
Year differences	0.03-0.20	6
Walk-Map	0.12-0.12	2
Walk-float	0.33-0.64	4
Walk-point	0.09-0.20	4
Observer differences	0.08-0.48	8
Daily differences	0.15-0.56	5

DISCUSSION

Floating surveys

Floating surveys provided the least labor-intensive index of the composition of the riparian breeding bird community. Our results show that they provide a fairly accurate estimate of relative abundance, though for some species results are seriously biased. As one would expect, walking surveys detect significantly more species, at a ratio of 2.5:1 (count from walking survey: count from floating survey).

Species-specific differences were fairly obvious (Figs. 2 and 3). Population estimates from floating survey tended to be closer to estimates from walking surveys (falling above the regression line) for especially loud species and those more closely associated with NHWZ habitats. These were Bell's Vireo, House Finch, Yellow Warbler, Yellow-breasted Chat, Common Yellowthroat, and Blue Grosbeak (though note the total absence of the Blue Grosbeak from floating surveys in 1994). Populations of quiet or more upland-associated species (Lucy's Warbler, Blue-gray Gnatcatcher, Black-chinned and Costa's Hummingbird) were more seriously underestimated by floating surveys (falling below the regression line).

For an index of abundance this would be acceptable, unless comparisons between species are desirable. Clearly, floating surveys provide different results depending on the species habitat choice, singing frequency, and loudness. Further, accuracy of the floating survey varies between sites, depending on physical characteristics. In some areas, especially reaches 4 and 10, most available habitat occur on large debris fans. These large, non-linear habitat patches have high interior-to-edge ratios making floating surveys less accurate. Worse, these debris fans are often associated with noise-producing riffles. Even a small riffle may produce enough noise to significantly interfere with surveying. These two factors contribute to severely decrease the accuracy of floating surveys in these reaches, and increase the variability of accuracy between sites, making comparisons of data from floating surveys between reaches invalid.

Territory maps

When comparing walking and floating surveys, we assumed that population estimates from walking surveys would be closest to the true avian abundances. To test whether walking surveys produced reliable population estimates, we compared our estimates from walking surveys with estimates obtained from territory mapping - a highly accurate method for avian population estimation (Franzreb 1981). Comparisons at two of the major study sites showed good correlation between the two techniques for the species we were able to map. Data from Lucy's Warblers, however, showed a poor match between the two methods. We believe this is because many pairs were nesting in nearby cliffs off the study sites, and only spent a portion of their time in the study sites.

Though useful for testing the accuracy of the walking surveys, as a general monitoring method territory mapping has several draw-backs. First, ten visits over the breeding season are recommended as a minimum adequate sample (I.B.C.C. 1970). Given the logistics of river trips,

this is very difficult to attain. We only reached nine visits at two sites, severely limiting the our ability to generalize from these results. Second, territory mapping is only effective for species which defend breeding territories, and which sing or display to advertise territorial boundaries. This severely limits the ability to monitor species which do not sing distinct territorial songs or defend breeding territories (e.g. Ash-throated Flycatcher, Black-chinned Hummingbird, Lesser Goldfinch, House Finch, swallows and swifts).

Point counts

A primary variable of point counts is the time length of the counting period. The appropriate time length must be a compromise between efficiency (to maximize sample size) and return on effort (based on abundance of the species of interest). Hutto et al. (1986) recommended a period long enough to detect 75-80% of all species present. Ralph et al. (1993) recommend 10-minute counts for general inventory surveys when distances between points are large. We detected 81% of the species observed at a site in the first five minutes of 10-minute counts. While this may not represent 81% of all species present, given the relatively low number of breeding species in the canyon's riparian environment and the great extent and remote nature of habitat in the canyon, we feel that 5-minute counts represent a good compromise between completeness and efficiency. Because the time to get between points is usually >15 minutes, 10-minute counts recommended by Ralph et al. (1993), would be preferable if manpower and river logistics permit.

As expected, point count observations within the 50m fixed radius were significantly fewer than observations within and beyond 50m. Despite this, there are several advantages to using a fixed radius. First, it helps reduce observer variability. Most competent observers will hear birds equally well within a small fixed distance, while beyond this distance individual differences cause variability to increase rapidly (Ramsey and Scott 1981). Given the small size of most habitat patches in the canyon, we believe that 50m is appropriate for most riparian breeders.

Second, a crucial assumption to all survey methods is that individuals are not counted more than once. When the distance separating survey points is not large relative to the fixed detection radius, a fixed radius can reduce the subjectivity of deciding whether an individual was counted at a previous counting station. To decrease double-counting and increase the statistical independence of adjacent points, Hutto et al. (1986) placed points 200m apart, and Ralph et al. (1993) recommend 250m separation. In this study, the distance between survey points, 125-150m, increased the possibility of double counting, especially for birds with large territories, and decreases the statistical independence of adjacent points. In the small riparian patches of the canyon where counting stations may need to be closely spaced, use of a 50m detection radius can help control these factors.

The few differences between walking survey and point count results were probably not due to differences in survey effort, since there was no significant difference between mean survey length for the two methods. Similar numbers of species were observed during walking surveys and unbounded point counts. However, the number of species in common for the walking and point count surveys was low. This lack of agreement was probably due to observations of rare species. A statistically powerful test to compare the ability of these methods to detect rare species would require many more detections than we obtained (i.e., more surveys; Dawson 1981), therefore we

excluded these rarer species when comparing the reliability of the methods. Also because of this limitation, monitoring population trends of rare species in the Grand Canyon may require species-specific methods, rather than a general monitoring effort.

Excluding rare species, the reliability of the unbounded point counts and walking surveys to detect a species were similar overall, and higher than the reliability of 50m point counts. Also, certain species-specific differences were evident (Table 4). Common species with small territories (Lucy's Warbler and Bell's Vireo) were equally well detected by all three methods, because their territories were likely to fall entirely into the 50 m detection radius. Loud species with larger territories (Yellow-breasted Chat and Ash-throated Flycatcher) were poorly detected by 50m point counts only. This may be because individuals within their territories were likely to be beyond the 50m radius during the count period. Relatively quiet and rare species (Yellow Warbler and Common Yellowthroat) were equally poorly detected by all methods. Finally, the Common Yellowthroat, a habitat specialist nesting in emergent vegetation, was especially poorly detected by both point count methods due to a methodological bias. We located point count stations half way between the river and the uplands, shifting survey attention away from the river's edge where this species is usually found. Thus, survey methodology must be tailored to reflect the life history of the species to be monitored.

The preceding analyses dealt only with presence-absence data. While this may provide the most accurate way to monitor population trends, it is not as precise as abundance estimates. However, both walking and point count methods can provide only an index of abundance rather than an accurate estimate (Verner 1985). The question is whether point counts provide as good an index of abundance as walking surveys. Results of regression of counts from paired walking and point count surveys for 50m point counts ($b = 0.52$) showed no better correlation than for paired walking and floating surveys and slightly better correlation for unbounded point counts ($b = 0.87$). However, this analysis includes observations from the rare species already discussed above.

Linear regression analyses of abundance data summed for the ten most common species showed that abundance estimates from walking and point count surveys were highly correlated and strikingly similar. Both point count methods were near one-to-one with the walking surveys, with 50m point counts undercounting and unbounded point counts over-counting relative to walking surveys. The overestimate of abundance by the unbounded point counts may be due to double-counting and could be decreased by moving count stations further apart (Hutto et al. 1986, Ralph et al. 1993). Refer to Felley and Sogge (1997) for additional comparison of point counts and walking counts.

Observer Variability

Except when only a few birds were present at a site, observers recorded different things. This was true whether pairs were both highly experienced or one observer was less experienced. Obviously, the range of observer variability is greater in more complex communities (Cyr 1981). "Sensory overload", when stimuli are coming much faster than the observer's ability to observe and record data, exacerbates this problem. Observer variability may be minimized by avoiding the period of greatest activity, the dawn chorus (Bart and Schoultz 1984). However, this comes

at the expense of reduced sample sizes. Because of the relatively simple communities of the Grand Canyon's riparian habitat, observer variability may not be an important factor in survey accuracy overall. However at large sites, with a rich and abundant bird community, observer variability is among the most important sources of variability, as shown by the Bray-Curtis comparisons. If such sites are of special management interest, then observer variability must be carefully controlled. Potential ways to control this variability are to maintain the same observers between years or through training programs for observers (Faanes and Bystrak 1981, Kepler and Scott 1981).

Though mean difference in number of species detected was generally small, the overall range of differences was sometimes large (up to five species). This may be due to misidentification or omission. Misidentification can be minimized through training and field experience (Ramsey and Scott 1981). Omission is more often the result of differences in observers' hearing ability, power of concentration, or survey length. Omissions can best be minimized by training observers and maintaining the same observers over time, while standardizing survey length will help standardize the rate of omission.

The total number of birds observed was more variable than number of species observed. This is expected simply because the number of birds observed was often much greater than the number of species. More important, differences between observers were smaller, presumably because it takes less skill and judgement to detect that a bird is present than to correctly identify it.

Study site variability

Because we could look at daily variability at only the largest study sites with the richest bird community, this analysis probably overestimates this source of variability in general. Most study sites were generally much smaller, with less diverse and presumably less variable bird communities.

The Bray-Curtis analysis showed the greatest source of variability arose from daily differences. Differences between days at the same site were more due to the abundance estimate than the number of species recorded. Hence, as with any survey technique, the ability to detect population change will more affected by this source of variability than the ability to detect species occupancy at a site.

Some of this variability was due to species-specific natural history differences. The Yellow-breasted Chat, most frequently missed on one of the paired surveys, seemed to have a highly variable singing rate, making detection on a survey of relatively short duration difficult. Many species, including the chat, Bewick's Wren, and Common Yellowthroat often did not start singing until relatively late in the morning, (8:00-9:00 AM), frequently after the surveys were complete. Difficulty in counting the quiet but numerous Black-chinned Hummingbird has been discussed elsewhere (Brown 1992). The Ash-throated Flycatcher is a large species and often maintained a territory extending outside our study sites. If it was outside the study site during a survey, it was missed. The Brown-headed Cowbird, House Finch, and Mourning Dove wandered even more widely, making them even more likely to be missed during a survey. The detection rate of all these species is sensitive to the survey period, underlining the importance of standardizing survey length for controlling variability.

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Appendix 1. Listing and location of avian community monitoring study sites in Grand Canyon National Park, 1993-95. Direct impact study sites are named in brackets. Photograph number refers to the aerial photograph/negative number on which the patch may be seen (based on U.S. Bureau of Reclamation GCES photographs taken 5-29-95). Unless otherwise noted, UTM's were gathered from a point at each patch with Garmin hand-held GPS units and differentially corrected to ± 10 m estimated horizontal accuracy.

River Mile	Aerial Photograph Negative Number	UTM X	UTM Y
1.0 R [Paria]	11-8	446151	4078815
1.6 R	11-10	445643	4078236
2.0 L	11-10	445247	4078043
3.7 L	12-10	444089	4075305
5.1 L	12-14	443564	4073900
5.2 R	12-16	443243	4073660
5.6 R	12-16	442821	4073325
46.0 L	36-10	420656	4025948
46.7 R [Saddle]	37-1	420037	4025506
47.5 L	37-4	420610	4024523
48.5 L	37-6	420905	4024148
49.1 R	37-9	421529	4023259
49.2 L	37-9	421764	4023087
50.0 R	37-14	422682	4021505
73.9 R	50-5	420577	3991654
74.1 R	50-6	420185	3991553
74.3 R	50-6	419919	3991549
74.4 R	50-8	419672	3991167
74.4 L	50-8	419717	3991486
75.9 R	51-8	418468	3989321
76.0 L	51-8	418322	3989192
76.5 L	52-3	417909	3989064
95.7 L	60-8	389857	3996287
95.9 L	60-8	389752	3996433
97.4 R	62-3	388816	3999060
97.4 L	62-3	388707	3999019
97.5 L	62-3	388613	3999123
97.6 L	62-3	388483	3999217
110.0 R ²	67-4	377058	4011521
112.0 R ²	68-4	374083	4011465
117.5 R	71-5	369335	4008293
119.5 R	72-5	368564	4011022
119.6 L	72-5	368247	4011123
122.8 L	73-13	363760	4011928
125.5 R	75-7	364012	4015582

River Mile	Aerial Photograph Negative Number	UTM X	UTM Y
131.3 R	78-3	369568	4022539
167.0 R	96-2	329128	4013663
167.2 L	96-2	328873	4013584
167.6 R	96-4	328180	4013826
168.5 L	97-6	326805	4012909
168.8 R	97-6	326619	4012825
171.0 R [Stairway]	98-9	323963	4011871
171.1 R	98-9	323833	4011799
172.2 L	99-1	322233	4011250
173.1 R	99-5	320659	4011754
174.2 L	99-8	319606	4012064
174.4 R	100-3	319085	4012119
174.5 R	100-3	318956	4012072
174.7 R	100-5	318290	4011745
197.3 L	113-5	292050	3997262 ¹
197.6 L	113-5	291886	3997267
198.0 R [Parashant]	114-2	291448	3997252
198.2 L ²	114-2	291512	3997109
198.3 R	114-2	291120	3996962
199.5 R	114-6	290684	3995807
200.0 L	114-8	290517	3994434
200.4 R	115-2	290140	3994014
200.5 R	115-2	290036	3993850
202.5 R	115-10	288072	3991594
204.1 R	116-8	288176	3989015
204.5 R [Spring]	116-10	288197	3988204
205.8 R	117-4	289092	3986389
206.5 L	117-7	289057	3985398
206.6 R	117-7	288980	3985094
208.7 R	119-2	290622	3983579
213.6 L	123-3	289849	3976256
214.0 L	123-6	290265	3975733
214.2 L ²	123-6	290421	3975253
224.0 L ²	127-8	287561	3961944
224.1 R ²	127-8	287521	3961964

1 = interpolated from points adjacent to patch

2 = coordinates taken from USGS topo map digital raster graphic (DRG)



Chapter 6: Survey Summary



AVIAN SURVEY SUMMARY

INTRODUCTION

Bird surveys have the potential of providing useful information regarding the abundance, distribution, and ecology of bird species and bird communities. However, different survey techniques have different biases and provide particular types of data, therefore, survey techniques must be matched to project objectives and survey data must always be analyzed and interpreted with survey techniques and data biases in mind (Bibby et al. 1992).

One of the simplest objectives to develop and fulfill is to conduct surveys in order to determine what bird species are present. This is typically the minimum level of data necessary for virtually all avian ecology studies. Most studies also include developing an estimate of the abundance of each species, even though true abundance and/or density is almost impossible to determine in most cases (Verner 1985, Bibby et al. 1992). If surveys are conducted using scientifically sound, robust and standardized protocols and in a consistent manner over a period of years, the resulting data can provide the foundation for an avian monitoring program that species occurrence and distribution over time.

In this chapter, we provide a summary of the results of the bird surveys we conducted in riparian habitats along the Colorado River corridor from 1993 to 1995. The data we gathered and the results we present are shaped by the overall goals of our project, which were: (1) to relate bird community composition and abundance to riparian habitat characteristics along the river corridor; and (2) test and evaluate different survey and monitoring techniques. Our surveys were not designed to provide a complete inventory of all possible species found along the river, nor did we attempt to develop a standardized monitoring program to track bird populations from year to year. Therefore, our survey sites, techniques, and efforts varied from year to year as needed to meet our objectives, but in such a way as to limit their use for between-year comparisons and long-term avian monitoring. However, our data provide much useful information on bird species and community patterns. This is particularly true for 1994 and 1995, when field work included the full avian breeding season. Surveys in 1993 did not begin until May, missing the early portion of the breeding season and limiting their value for comparisons with other years. This project also included winter surveys which provided new information on wintering species.

The survey data that we collected, although not designed as a long-term monitoring program, may nonetheless be useful to future avian monitoring programs. Our patch-by-patch survey results can be used by future researchers to help select avian monitoring sites and as comparative data at any sites which are incorporated into an avian monitoring program.

Although we performed point counts, walking surveys, and floating surveys, this chapter focuses (unless otherwise noted) on results from walking surveys and point counts, which provide better survey data than floating counts (refer to the Survey Technique Comparison chapter for details). We include here all records of birds we detected during surveys, including non-riparian species such as waterfowl, waders and shorebirds, raptors, upland-associated songbirds, and any accidental and casual visitors to the patch. More detailed discussions of riparian breeding bird habitat associations, study of survey methods, banding results, and avian diet can be found in other sections of the report.

METHODS

We located study sites to form a representative sample of riparian habitats between Lee's Ferry (River Mile (RM) 0) and Diamond Creek (RM 225; river mile designations per Stevens 1983). At the largest geographic scale, canyon-wide, the river corridor follows an elevation gradient with changing vegetation communities from Great Basin desert-scrub to Sonoran desert-scrub (Turner and Karpiscak 1980). Also, characteristics of riparian vegetation relate naturally to the geomorphology of the 11 reaches of the river (as defined by Schmidt and Graf 1988). For these reasons, we tried to locate some sites in each reach, within the constraints of river logistics. We conducted surveys from 1993-95 at 71 study sites, each a discrete patch of riparian vegetation, between Lee's Ferry and Diamond Creek (Figure 1). Sites were selected to represent a wide range of the sizes, shapes, geomorphology, and floristic composition of patches of riparian vegetation found along the river. Sites were located in seven of the 11 geomorphic reaches. All surveys were conducted between one-half hour before sunrise and 10:00 AM. We located sites in groups so each group could be completely surveyed in one morning.

In 1993, we ran trips in May, June, July, and September. In 1994, we ran trips in January, March, April, May, June, July, and September. In 1995 we ran trips in February, March, April, May, and June. Though the focus of this project was to survey riparian breeding birds, trips in September allowed us to document use of the river corridor by fall migrants, and January and February trips allowed us to add to the small amount of information on winter bird use in the canyon.

Walking surveys

Walking surveys consisted of one observer walking slowly through the riparian habitat, recording species and numbers of all birds observed at the study site (Brown and Johnson 1987, Brown 1988, Sogge et al. 1994, Sogge et al. 1995). The survey was considered complete when all parts of the site had been visited, taking from 15 to 120 minutes depending on total area. Walking surveys were made at all study sites surveyed from 1993-95. To control observer bias, observers were rotated between visits so that no one observer conducted the majority of surveys at any one site.

Floating surveys

One or two observers floated past each study site in a raft ahead of the walking surveyor. Observers silently recorded all birds observed while floating with the current in a 22- or 37-foot motorboat with the motor off. We compared the number of species detected on simultaneous walking and floating surveys by comparing data from one walking observer to data from the most experienced floating observer.

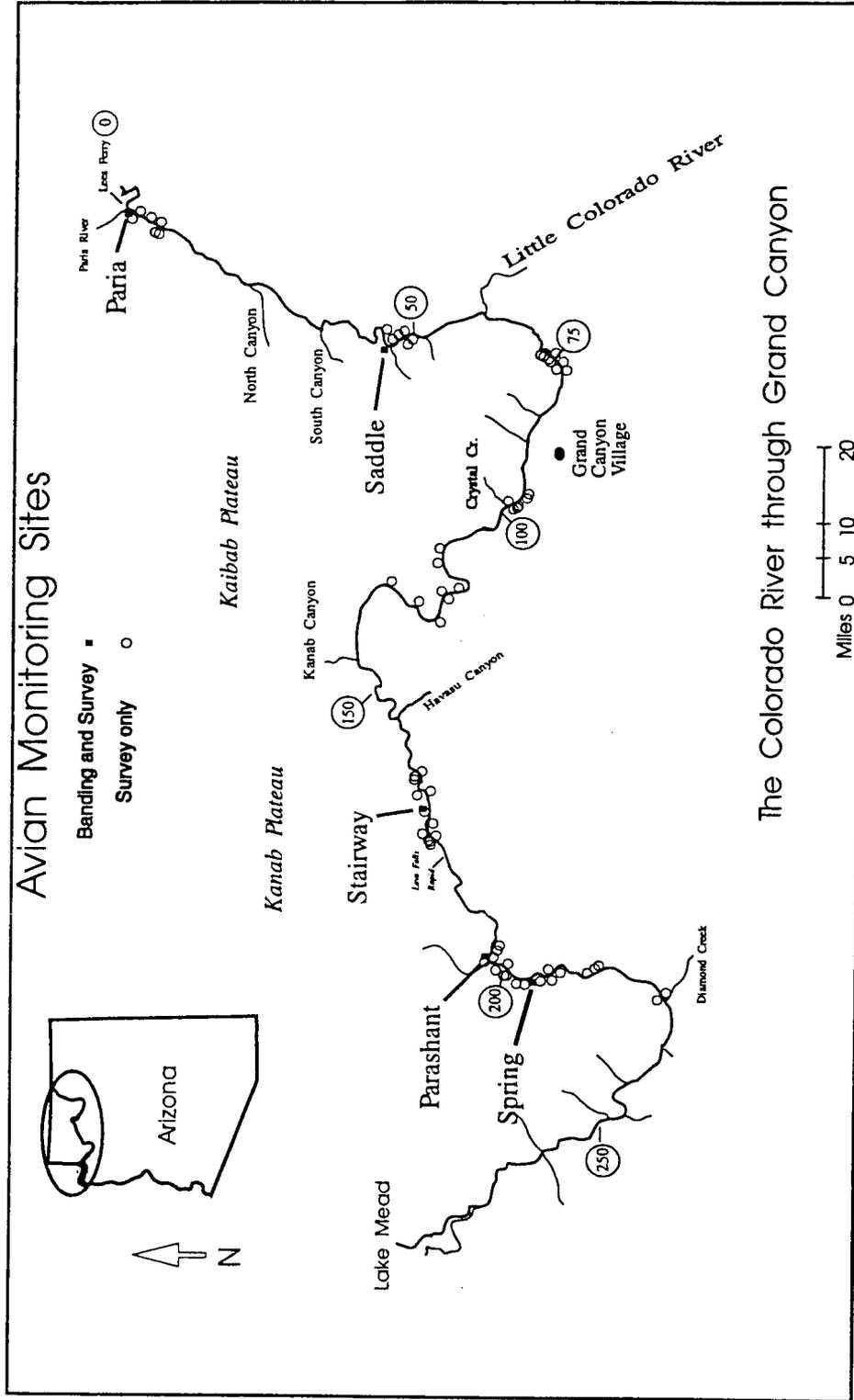


Figure 1. Location of Grand Canyon avian study sites, 1993 - 1995. Black squares are sites where surveys and banding were conducted, and open circles are sites where surveys, but no banding, were conducted.

Point counts

We conducted paired point counts and walking surveys at 11 study sites. Point counts were conducted once per month at each site, March-June 1995. On each visit to a site, a walking survey was conducted on one morning and a point count survey was conducted on the next, or vice versa. Point count survey methods generally follow the recommendations of Ralph et al. (1993). A 50-meter radius was used to separate bird detections into two classes -- detections $\leq 50\text{m}$ (50m point count), and detections \leq or $> 50\text{m}$ (unbounded point count). Point counts began as soon as the observer reached the point count station.

Points were placed systematically, 125 to 150 meters apart, half way between the river and the upland habitat. We surveyed as many points as would fit into each site using these criteria. Number of points varied from one to five per site depending on area and there were 37 points altogether. Point counts lasted for 10 minutes in March and 5 minutes from April-June.

Decision rules for determining breeding status and abundance

Raw data from surveys provides information on the total number of species and birds detected. However, even during the breeding season, these totals include migrants as well as local breeders (refer to the Banding Studies chapter for details). Therefore, totals and/or high counts are subject to potential high variability caused by yearly or seasonal changes in the number of migrants, even if the number of local breeders remains nearly constant. Inclusion of migrants can also inflate calculated values for species richness and abundance, and alter avian community/habitat relationship models (Weins 1989, Morrison et al. 1992). These considerations led us to develop a set of "decision rules" (Table 1), tailored to each species, that allow us to develop the most conservative and accurate estimate of the type of breeding species and the number of breeding pairs in each patch. In some cases, these decision rules involved using information gathered from nest searches and/or banding.

Table 1. Decision rules used to determine whether a species was considered a breeder at a particular patch and to estimate the number of breeding pairs of that species.

Species	Criteria for Breeder Status in Patch	Calculation of Number of Breeding Pairs
Ash-throated Flycatcher	observed on two visits, excluding July	highest count from April or May divided by two.
Brown-crested Flycatcher	observed	highest count divided by two
Black-chinned Hummingbird	observed	highest count of any sex or highest count divided by two
Bell's Vireo	observed on two visits	highest count of singing males, obvious pairs, or nests found
Bewick's Wren	observed on two visits	highest count of singing males, obvious pairs, or nests found
Blue-gray Gnatcatcher	observed on two visits	highest count from April or May, divided by two
Brown-headed Cowbird	observed	highest count of males or females
Blue Grosbeak	observed on two visits	highest count of singing males or obvious pairs
Costa's Hummingbird	observed	highest number of males observed
Common Yellowthroat	observed on two visits	highest count of singing males or obvious pairs common to two months
House Finch	observed on two visits	highest count of singing males or obvious pairs common to two months
Hooded Oriole	observed on two visits, not in July	highest number males or females from any survey
Lesser Goldfinch	observed in April or May	highest number of singing males or total count, divided by two
Lucy's Warbler	observed on two visits	highest number of singing males, obvious pairs, or count divided by two, except June or July
Mourning Dove	observed on two consecutive visits	highest number of singing males or obvious pairs
Northern Mockingbird	observed on two consecutive visits	highest number of singing males or obvious pairs from two surveys
Northern Oriole	observed on two visits, not in July	highest number of males or females from any survey, not July
Phainopepla	observed on two visits	highest number of males or obvious pairs from any survey
Rufous-crowned Sparrow	observed on two visits	highest number of males or obvious pairs from any survey
Say's Phoebe	observed on two consecutive visits	highest count common to two surveys, divided by two
Summer Tanager	observed on two visits	highest number of singing males or obvious pairs
Yellow-breasted Chat	observed on two visits	highest number of singing males common to two surveys
Yellow Warbler	observed on two visits	highest number of singing males common to two surveys, excluding may

RESULTS

OVERALL SURVEY RESULTS

We detected 112 species during our walking, floating, and point count surveys from 1993 to 1995 (see Appendices 1 and 2). Most of these were not locally breeding species, and included many migrants, winter visitor, raptors and waterfowl. Many of these species were detected in areas outside of the riparian zone such as on the river (waterfowl), flying overhead (typically ravens, raptors and swifts), or in upland or cliff habitat (e.g., rock wrens, canyon wrens). It is critical to remember that these surveys were not designed to provide standardized data for between-year comparisons, especially with regard to the number of species and number of detections. However, the data are useful for a variety of analyses as presented below.

Type of Detections

During a survey, birds can be detected aurally (by being heard) or visually. In each year, over two thirds of the birds counted in walking surveys were first detected by hearing their song or call, rather than by sight (Table 2). The percentage of aural detections was even higher for point counts. Overall, only four percent of birds detected by song or call were also seen later during the survey period. The percentage of visual detections was greater during the non-breeding season (Table 2).

Table 2. Summary of the percent of bird detections made aurally and visually, by year and season. Aural detections include birds that were heard but never seen, as well as a few birds that were first heard and later seen. A "w" indicates results of walking surveys, and "pc" indicates point counts. Breeding and non-breeding comparisons are based only on walking counts, because no point counts were conducted during the non-breeding season.

Type of Detection	1993 w n=912	1994 w n=2139	1995 w n=2217	1995 pc n=875	Breeding Season (April - July) n=4024	Non-breeding Season (Sept - Feb) n=552
Aural	76	71	78	91	77	56
Visual	23	29	22	9	23	44

Habitat Where Detected

Detections were not equally divided among habitat types (Table 3). During 1993 and 1994 walking counts, half or more of the birds detected were in the New High Water Zone (NHWZ: tamarisk-dominated riparian habitat closest to the river), while only approximately a third were detected in the Old High Water Zone (OHWZ: mesquite and cat-claw acacia-dominated habitat generally higher up on the banks). During 1995, most birds were detected in the OHWZ, reflecting increased survey emphasis in this habitat (particularly among point counts, which were placed to include OHWZ habitat). Overall, NHWZ habitat provided the greatest number of bird detections during breeding and non-breeding seasons.

Table 3. The percentage of birds detected in each of five major habitat types. OHWZ = Old High Water Zone; NHWZ = New High Water Zone; Upland = non-riparian vegetation upslope of the OHWZ; Air = flying by or overhead, not associated with a particular habitat; Water = in the river; Other = beach, rock, or unrecorded. A "w" indicates results of walking surveys, and "pc" indicates point counts. Breeding and non-breeding comparisons are based only on walking counts, because no point counts were conducted during the non-breeding season.

Habitat Where Detected	1993 w n=912	1994 w n=2139	1995 w n=2217	1995 pc n=875	Breeding Season (April - July) n=4024	Non-breeding Season (Sept - Feb) n=552
NHWZ	57	50	38	30	48	43
OHWZ	30	34	39	41	37	26
Upland	9	9	15	17	9	12
Air (flying over)	2	4	5	6	3	9
Water	1	1	1	0	1	3
Other	1	2	2	6	2	7

Gender of Birds Detected

In many cases, especially during the breeding season, it is possible to determine the gender of a bird by plumage (usually brighter and more conspicuous in males) and/or behavior (e.g., in many species, only the male sings). Overall, between 40 and 46 percent of the birds we detected could be determined as males, with fewer than five percent definite females (Table 4). We could not determine gender for approximately half of the birds we found, even during the breeding season. The number of unknown gender birds rose dramatically in the non-breeding season, when gender-specific behavioral cues such as singing are absent.

Table 4. Summary of the percent of male and female birds detected, by year and season. A "w" indicates results of walking surveys, and "pc" indicates point counts. Breeding and non-breeding comparisons are based only on walking counts, because no point counts were conducted during the non-breeding season.

Gender	1993 w n=912	1994 w n=2139	1995 w n=2217	1995 pc n=875	Breeding Season (April - July) n=4025	Non-breeding Season (Sept - Feb) n=552
Male	46	40	40	49	44	4
Female	3	3	4	2	4	8
Unknown	51	57	56	49	52	88

Activity when detected

Overall, more than two-thirds of birds were singing or calling when first detected (Table 5). During point counts, the proportion of singing and calling birds was even greater. The other most commonly observed behaviors were feeding, reacting to observer (e.g., flushing or flying away, perching attentively giving alarm calls), perching and flying, and together accounted for about one-fourth of detected birds during walking counts. Point counts, which utilize a stationary observer, detected even fewer non-singing birds. Less than one percent of birds were seen engaged in any nesting behavior (e.g., carrying nest material or food), even during the breeding season.

Table 5. The percentage of birds engaged in different activities when first detected. A "w" indicates results of walking surveys, and "pc" indicates point counts. Breeding and non-breeding comparisons are based only on walking counts, because no point counts were conducted during the non-breeding season.

Bird Activity When Detected	1993 w n=912	1994 w n=2139	1995 w n=2217	1995 pc n=875	Breeding Season (April - July) n=4024	Non-breeding Season (Sept - Feb) n=552
Singing/calling	72	71	72	85	74	50
Feeding	6	12	9	3	8	21
Reacting to Observer (e.g., flushing)	6	6	8	2	7	8
Perching	5	5	5	2	5	5
Flying	5	2	3	5	2	8
Nesting behavior	>1	>1	>1	>1	>1	0
Not noted	6	4	3	3	4	8

Species Detections - Overall and between years

We detected between 35 and 93 species of birds each year (Table 6). The fewest species were detected in 1993, when survey efforts were lowest and included only a portion of the breeding season. The most species were detected in 1994 and 1995, when survey efforts were greatest and included breeding and non-breeding surveys. We detected roughly the same number of species during the breeding and non-breeding season.

Far more birds were detected in breeding and non-breeding seasons, even though the number of species was almost the same. The greater number of detections was a function of much greater survey effort, as well as increased bird abundance during the breeding season. The pattern of fewer individuals but similar number of species shows that the winter bird community includes proportionately fewer individuals per species than the breeding season community.

Table 6. Summary of the number of bird species detected, by year and season. A "w" indicates results of walking surveys, and "pc" indicates point counts. Breeding and non-breeding comparisons are based only on walking counts, because no point counts were conducted during the non-breeding season.

	1993 w	1994 w	1995 w	1995 pc	Breeding Season (April - July)	Non-breeding Season (Sept - Feb)
Number of Species Detected	35	93	82	49	76	72
Total number of detections	912	2139	2217	875	4025	552

Relative abundance between breeding seasons

Given that survey effort, timing and location changed between years, it is inappropriate to directly compare the number of detections for each species each year. However, it is useful to look at patterns of rank order and relative abundance, particularly of the most common species, among years and techniques. The following analyses are restricted to breeding season (April - July) surveys, as they were the most consistent between years.

Overall, the list of the 15 most frequently detected species was very similar among years and techniques (Table 7). Each year, the five most frequently detected species accounted for over 50 percent of the detections (range = 53-58%), with Lucy's Warbler accounting for 19 to 26 percent of all detections. Lucy's Warbler, Bell's Vireo, Blue-Gray Gnatcatcher, and House Finch were always among the five most common species, and the same 10 species were found in the top 15 every year. Common Yellowthroat was among the 15 most frequently detected during walking counts in all three years, but not based on point count data. Collectively, 22 species are included in Table 7, with two non-breeding species (Ruby-crowned Kinglet and Townsend's Solitaire) among the top 15 during at least one breeding season.

The relative abundance (percent of detections) was very similar among years for most of the common species, but varied widely for some such as Ash-throated Flycatcher (range = 7.3% - 3.3%) and Yellow Warbler (range = 7.3% - 1.6%).

Table 7. The 15 most commonly detected species during the breeding season (April - July), 1993 - 1995. Bold font indicates a species found among the top 15 in all columns. A "w" indicates results of walking surveys, and "pc" indicates point counts.

Species and Percentage of Detections (n=807) 1993 w	Species and Percentage of Detections (n=1618) 1994 w	Species and Percentage of Detections (n=1600) 1995 w	Species and Percentage of Detections (n=875) 1995 pc
Lucy's Warbler (19.2%)	Lucy's Warbler (24.6%)	Lucy's Warbler (25.6%)	Lucy's Warbler (25.3%)
Bell's Vireo (12.0%)	Blue-gray Gnatcatcher (8.8%)	Bell's Vireo (9.4%)	Bell's Vireo (12.1%)
Blue-gray Gnatcatcher (8.4%)	Bell's Vireo (8.5%)	Blue-gray Gnatcatcher (9.1%)	Bewick's Wren (7.7%)
House Finch (7.8%)	Bewick's Wren (6.7%)	House Finch (6.9%)	Blue-gray Gnatcatcher (7.3%)
Ash-throated Flycatcher (7.3%)	House Finch (5.3%)	Black-chinned Hummingbird (6.6%)	House Finch (5.1%)
Yellow Warbler (7.3%)	Yellow Warbler (5.0%)	Bewick's Wren (5.0%)	Black-chinned Hummingbird (4.8%)
Bewick's Wren (5.2%)	Black-chinned Hummingbird (4.8%)	Ash-throated Flycatcher (3.3%)	Yellow-breasted Chat (4.1%)
Yellow-breasted Chat (4.3%)	Ash-throated Flycatcher (4.5%)	Canyon Wren (3.2%)	Ash-throated Flycatcher (3.5%)
Canyon Wren (3.8%)	Canyon Wren (3.2%)	Rock Wren (2.8%)	Canyon Wren (3.4%)
Black-chinned Hummingbird (2.9%)	Yellow-breasted Chat (3.1%)	Lesser Goldfinch (2.7%)	Lesser Goldfinch (2.5%)
Violet-green Swallow (2.6%)	Common Yellowthroat (3.2%)	Yellow Warbler (2.4%)	Song Sparrow (2.4%)
Rock Wren (2.4%)	Black-throated Sparrow (1.4%)	Yellow-breasted Chat (2.3%)	Common Raven (1.9%)
Mourning Dove (2.2%)	Say's Phoebe (1.3%)	Common Yellowthroat (1.5%)	Ruby-crowned Kinglet (1.7%)
Common Yellowthroat (1.6%)	Violet-green Swallow (1.3%)	Song Sparrow (1.4%)	Yellow Warbler (1.6%)
Brown-headed Cowbird (1.4%)	Ruby-crowned Kinglet (1.2%)	Mourning Dove (1.3%)	Townsend's Solitaire (1.5%)

Relative abundance between seasons

Relative abundance data from walking surveys conducted during the breeding (April - July) and non-breeding (September - February) seasons provide for interesting seasonal comparisons (Table 8). During the breeding season, five species were so prevalent that they account for over half of the total detections. However, during the non-breeding season, there was no such numerical dominance by a suite of common species: the 15 most common species collectively accounted for just under half of the total detections.

Species composition and abundance differed between seasons. Only one species (Bewick's Wren) was among the five most common during both the breeding and non-breeding seasons, and only five were found among the top 15 during both periods. This demonstrates a major turnover of species between breeding and non-breeding seasons.

Table 8. The 15 most commonly detected species during the breeding and non-breeding seasons, 1993 - 1995 combined, based on walking surveys. Species in bold font are among the top 15 in breeding and non-breeding season.

Species	Percentage of Breeding Season Detections (n=4025)	Species	Percentage of Non-breeding Season Detection (n=552)
Lucy's Warbler	23.9	Ruby-crowned Kinglet	13.6
Bell's Vireo	9.6	Bewick's Wren	8.7
Blue-gray Gnatcatcher	8.8	Canyon Wren	8.0
House Finch	6.5	White-crowned Sparrow	4.5
Bewick's Wren	5.7	Dark-eyed Junco	4.2
Black-chinned Hummingbird	5.1	Rock Wren	3.3
Ash-throated Flycatcher	4.6	Common Raven	2.9
Yellow Warbler	4.4	House Finch	2.9
Canyon Wren	3.3	Song Sparrow	2.4
Yellow-breasted Chat	3.0	Red-naped Sapsucker	2.2
Rock Wren	2.0	Say's Phoebe	1.8
Common Yellowthroat	1.8	Orange-crowned Warbler	1.6
Lesser Goldfinch	1.7	Common Yellowthroat	1.4
Violet-green Swallow	1.5	Mallard	1.4
Mourning Dove	1.3	Yellow-rumped Warbler	1.4

BREEDING SPECIES PATTERNS

Because (1) simply detecting a species in a patch during the breeding season does not prove that it is a local breeder, and (2) counting migrant individuals of locally-breeding species can inflate local population estimate, we used species-specific decision rules (refer to Methods section) to more accurately determine what species and how many pairs were breeding in each patch.

Appendices 3 and 4 present more detailed data on the number of breeding pairs of each breeding species during 1994 and 1995. Here we present only summary information on observed patterns of species richness (the number of breeding species), abundance (the number of breeding pairs) and diversity, which may be useful for future researchers designing or conducting avian monitoring programs. Further analysis of species patterns can be found in the Bird Community and Habitat Relationships chapter.

The number of breeding species in a patch (Table 9) ranged from 0 (at the smallest patches) to 14, with most patches having between two and nine breeding species. Spring Canyon (RM 204.5R), one of our largest patches, had the highest species richness. The number of breeding species detected was relatively stable among years at many patches, but varied substantially at others.

The number of breeding pairs of all species combined (Table 9) ranged from 0 to 57, generally lower at smaller patches. Only five of the patches we surveyed supported more than 20 breeding pairs, and most had 10 or fewer. Spring Canyon had the greatest number of breeding pairs (50 and 57, in 1994 and 1995 respectively). Much as with species richness, the number of breeding pairs was similar between years at some patches, but varied widely at others.

Shannon Diversity Indices were calculated per MacArthur and MacArthur (1961), and varied from 0 to 2.39 (Table 9; SDI), though most were between 1.0 and 2.0. The dominance of values in the range of 1.0 to 2.0 suggest that, in most patches, there were similar numbers of breeding pairs among the different breeding species. At many of the patches with high SDI values (e.g., Parashant, Spring Canyon), a small number of species such Bell's Vireo, Lucy's Warbler and/or Black-chinned Hummingbird contributed a large proportion of the number of breeding pairs.

Table 9. The total number of breeding species, the number of breeding pairs (all species combined), and the Shannon Diversity Index (SDI) for each surveyed patch, 1993 -1995. Determination of status as a breeding species, and calculation of the number of breeding pairs, was based on a set of "decision rules" (refer to the chapter text). Shannon Diversity Index was calculated per MacArthur and MacArthur (1961). Data for 1993 are not directly comparable with 1994 and 1995 because surveys did not cover the entire breeding season of that year. Not all sites were surveyed in all years. River mile designations follow Stevens (1983).

Site: River Mile	1993			1994			1995		
	# breeding species	# breeding pairs	SDI	# breeding species	# breeding pairs	SDI	# breeding species	# breeding pairs	SDI
1.0 R [Paria]	8	8	2.08	11	14	2.34	9	10	2.16
1.6 R	2	2	0.69	6	6	1.79	2	2	0.69
2.0 L							3	4	1.04
3.7 L							3	3	1.10
5.1 L	4	5	1.33	5	5	1.61	3	3	1.10
5.2 R	5	6	1.56	5	7	1.55	8	9	2.04
5.6 R	1	1	0	2	2	0.69			
46.0 L							8	13	1.93
46.7 R [Saddle]	11	22	2.28	11	22	2.24	11	23	2.12
47.5 L	0	0	na	5	6	1.56	2	6	0.69
48.5 L	6	7	1.75	3	5	1.05	4	5	1.33
49.1 R				6	13	1.52	8	16	1.81
49.2 L	3	3	1.10	4	6	1.24	8	9	2.04
50.0 R	8	13	1.84	10	15	2.15	7	20	1.73
73.9 R	6	6	1.79	8	10	2.02	3	4	1.04
74.1 R	2	2	0.69	5	6	1.56	3	4	1.04
74.3 R	2	2	0.69	4	5	1.33	3	3	1.10
74.4 R	2	2	0.69	3	3	1.10			
74.4 L						1.10	9	15	2.06
75.9 R				3	3				
76.0 L				2	2	0.69			
76.5 L							9	9	2.04
95.7 L				2	2	0.69			
95.9 L				3	3	1.10			
97.4 R				4	1	1.39			
97.4 L				1	4	0			
97.5 L				1	1	0			
97.6 L				1	1	0			
110.0 R	1	1	0						
112.0 R	3	3	1.1						
117.5 R	1	1	0				3	3	1.1
119.5 R	0	0	na				1	1	0
119.6 L	1	2	0						

Site: River Mile	1993			1994			1995		
	# breeding species	# breeding pairs	SDI	# breeding species	# breeding pairs	SDI	# breeding species	# breeding pairs	SDI
122.8 L				6	9	1.67	8	2	2.08
125.5 R				1	2	0	2	4	0.69
131.3 R				5	7	1.47	1	5	0
167.0 R				5	5	1.61	5		1.61
167.2 L				6	8	1.73			
167.6 R	3	5	1.05	9	11	2.15			
168.5 L	4	6	1.33	6	6	1.79			
168.8 R	8	11	1.97	10	16	2.13			
171.0 R [Stairway]	7	14	1.75	11	14	2.34	8	13	1.99
171.1 R	9	12	2.14	10	13	2.24	6	7	1.75
172.2 L	5	5	1.61	6	9	1.74	9	13	2.10
173.1 R	5	7	1.55	7	10	1.75	6	8	1.67
174.2 L				11	16	2.3			
174.4 R	5	7	1.55	6	9	1.68	7	11	1.85
174.5 R	4	6	1.33				5	7	1.55
174.7 R	2	3	0.64	5	5	1.61	4	4	1.39
197.3 L							11	17	2.26
197.6 L							9	12	2.09
198.0 R [Parashant]	14	29	2.31	13	29	2.34	14	30	2.34
198.2 L							12	20	2.32
198.3 R							9	12	2.14
199.5 R				10	10	2.30	5	5	1.61
200.0 L				5	7	1.55	6	9	1.74
200.4 R				5	6	1.56	8	12	1.98
200.5 R				12	16	2.39	10	16	2.19
202.5 R				7	10	1.83	7	12	1.82
204.1 R							13	30	2.37
204.5 R [Spring]				18	50	2.51	15	57	2.36
205.8 R				4	4	1.39			
206.5 L				3	5	1.05	6	8	1.67
206.6 R									
208.7 R				7	11	1.85	9	14	2.07
213.6 L							7	10	1.83
214.0 L							10	13	2.25
214.2 L							2	2	0.69
224.0 L							7	8	1.91
224.1 R							3	4	1.04

DISCUSSION

The number, type and location of our surveys varied between years so that we could maximize the number of sampled points (for habitat modeling) and compare different techniques. Such a variable sampling design precludes the use of these survey data for detailed quantitative and statistical comparisons between years, sites and seasons. However, these data do highlight considerations that must be kept in mind when designing, conducting, and interpreting avian surveys in the Grand Canyon, and illustrate seasonal patterns in the riparian bird communities.

Avian survey considerations

Based on type of detection and the activity of detected birds, surveyors can expect to hear approximately 75 - 90 percent of the birds found during walking surveys or point counts. Of these, only a few will also be seen. This emphasizes the importance of using only highly skilled and trained survey personnel who can accurately identify species based on songs and calls. This is critical during the breeding season, when song rates are high and dense vegetation inhibits seeing the bird that is vocalizing (often, even if it is close). Point-counts are even more reliant upon aural detections, because the surveyor is stationary and (1) does not flush birds into view, and (2) can not move to get the bird into view. Point-counts are probably more effective when in surveys that rely heavily on aural detections because the surveyor is not generating noise during the count, as opposed to walk counts where travel through the vegetation can be noisy.

Surveyors must be familiar with the songs and calls of the many species expected on canyon surveys. Among agencies there is often a tendency to use biologists or other staff with limited avian survey experience to conduct bird surveys. Doing so almost certainly results in fewer species detected, and a greater rate of misidentified species. Therefore, both data quantity and quality are negatively affected. Even a trained and experienced avian surveyor may require several "tune up" surveys or trips to the appropriate habitat in order to relearn bird songs and calls at the beginning of each year.

Our data on detections also suggests that walking counts may be preferable to point counts when conducting winter surveys. Because point counts are heavily biased toward detecting birds that are singing or calling, they become less efficient during winter when vocalization rates are lower. Non-vocalizing birds may be easily overlooked unless flushed, such as during walking counts. Point counts also work best where it can be assumed that birds are territorial and not moving in or out of the survey radius (Verner 1985, Bibby et al. 1992). This is often the case during the breeding season, but most migrant and wintering species display no such territorial behavior.

General surveys (both walking and point counts) do not appear to an effective technique to detect or quantify actual nesting behavior. Fewer than 1% of breeding season detections involved observations of breeding behavior such as copulation, nest building, or food carrying. Thus, absolute proof of nesting is best determined through nest searches (see Direct Impacts chapter) or mist-netting and banding (see Banding Studies chapter).

Our comparisons of annual and seasonal survey results show that the details of survey timing,

technique, efforts, and locations will greatly affect estimates of species richness (the number of species) and abundance (the number of individuals detected), as well as patterns of relative abundance (the percent of detections attributable to each species). Variables such as species presence/absence and rank abundance of common species appear to be more robust to inconsistencies in surveys, though potentially of lower management value.

Inconsistencies in surveys may not be a problem if the objective is simply to inventory the species present, without regard for tracking trends. However, comparisons among sites, regions or years requires that uniform techniques and efforts are used, and constant and repeatable survey sites are monitored. Given the length (over 200 miles) and linear nature of the Colorado River riparian system within the Grand Canyon, it is not simply enough to keep the number of sites constant between years. Major changes in the sizes or location of survey sites could greatly affect the resultant data. For example, increasing or decreasing the number of survey sites along the upper or lower portions of the corridor could affect the absolute numbers and ratios of particular species (such as Bell's Vireo, Lucy's Warbler, Brown-crested Flycatcher, and others) that are not uniformly distributed throughout the corridor (Brown et al. 1983, 1987). Similarly, expanding the survey area to include sites below Diamond Creek (where we stopped) would change the absolute and relative numbers of detections for many species. For example, Song Sparrow, Blue Grosbeak, Common Yellowthroat, Yellow Warbler and Marsh Wren, that are all much more common in the large, often willow-dominated patches of the lower river than they are in the more upstream reaches.

Bird community patterns

Clearly, the riparian and upland habitats along the river corridor are used by a large number of bird species. Although abundance was highest during the breeding season (partly due to a large number of migrating birds), species richness was high and similar during both the breeding and non-breeding seasons.

During the breeding season, Lucy's Warbler, Bell's Vireo, Bewick's Wren were the most common and widely distributed species between Lees Ferry and Diamond Creek. They, as well as two other species (Blue-gray Gnatcatcher and House Finch) accounted for over half of the birds detected. The most frequently detected species during this study were also noted to be the most common species during the 1970s and 1980s (Brown and Johnson 1987, Brown 1988, Brown and Trossett 1990), so there does not appear to have been a major shift in the numeric dominance and ecological importance the most common breeding-season species.

The pattern was somewhat different during the non-breeding season. Although the most common species (Ruby-crowned Kinglet) accounted for almost 20 percent of detections, the remainder of species present during this season were found in low abundance, such that the 15 most common species failed to provide even 50% of the detections.

Only a few of the common breeding species were also common during the non-breeding season, illustrating a major change in bird community composition and ecology during these two times. Similar patterns have been shown along the lower Colorado River downstream of the Grand

Canyon (Rosenberg et al. 1991). This is not surprising, given that most of the riparian breeding species in the Southwest neotropical migrants that winter elsewhere (Phillips et al. 1964, Monson and Phillips 1981, Brown et al. 1987), such as Central and South America, where food resources are higher.

The use of "decision rules" to determine which species bred in a given patch and to estimate the number of breeding pairs resulted in different species composition and abundance values than if we had simply taken the highest number of birds detected during breeding season surveys. The latter approach has been used by previous researchers (e.g., refer to Brown and Johnson 1987, Brown 1988), but this almost certainly overestimates the abundance (and therefore calculated density) of breeding birds in each patch. Such overestimations are probably considerable for species that both breed in, and migrate through, the canyon (refer to Banding Studies chapter for further details).

For decision rules to be effective, they must take into account the breeding chronology and migration chronology of each breeding or potentially-breeding species within the survey region. Even when carefully developed and applied, the results obtained when applying decision rules are still completely dependent upon the quantity and quality of survey data. Surveys must be of high quality, sufficient number, and appropriate timing to provide good raw data that can be filtered through a decision rule process. Application of decision rules can be greatly augmented by using nest searching and protocols, which can provide direct, unequivocal proof of breeding as well as help improve estimates of the breeding population size (e.g., Brown 1992, 1994; refer also to Direct Impact and Banding Studies chapters).

Survey timing is another factor important in minimizing variation in the breeding bird counts. Breeding community surveys are best conducted during the months of April, May and June (although the large influx of migrants in May needs to be taken into account). Surveys before April are too early to detect many locally breeding birds. By July, most local nesting activity has ended and recently fledged and hatching year individuals can inflate species counts, resulting in an overestimate of breeding pairs (young birds can not always be differentiated from adults during surveys). Although they have limited utility for breeding surveys, censuses conducted before April and after June may be useful in investigating migrant and wintering bird communities.

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Appendix 1 (section a). The maximum number of individuals detected during any one survey (all techniques combined) at patches 1.0R through 95.9L during 1994. Refer to Appendix 5 for the key to standard 4-letter species codes.

PATCH	1.0R	1.6R	5.1L	5.2R	5.6R	46.7R	47.5L	48.5L	49.1R	49.2L	50.0R	73.9R	74.1R	74.3R	74.4R	75.9R	76.0L	95.7L	95.9L
AMKE											1								
AMRO	1			1															
AMWI		2																	
ATFL	1		1	3	1	4	1	2	2		2		1	1	1	1	3	1	1
BCFL																			
BCHU	1	1	1	1	1	3	4	2	4	1	2	1	1	1		1			1
BEVI																			
BEWR	5	1	1	2		4	1	3	3	1	3	2	1	1	1				
BGGN	3	2	1	1	1	3	1	1	2		3	1	1	1				1	1
BHCO	1			1							1								
BHGR																			
BLGR	1	1	1	1		3	1												
BLPH		2									2	1		1					
BRBL																			
BRSP	5																		
BTSP							1						1	1	1				
BUFF	3	1																	
BUSH	2	2	2	15		5													
CAGO		16																	
CAKI															1				
CHSP																			
CNWR	1	1	2	4	1	2	4	1	3	4	4	2			1				
COGO		16																	
COHA																			
COHU																			
CORA	2			2		1	1	2	1	1						1			
COYE	3	1				3			2		1								
CRTH																			
DEJU	9	1				1		2			3			1					
GADW		6																	
GAQU																			
GBHE	1		1	1															
GRFL	1																		
GRHE		1																	

Appendix 1 - continued

PATCH	1.0R	1.6R	5.1L	5.2R	5.6R	46.7R	47.5L	48.5L	49.1R	49.2L	50.0R	73.9R	74.1R	74.3R	74.4R	75.9R	76.0L	95.7L	95.9L
GTGR																			
GTTO						2			1										
HAWO			1																
HETH																			
HOFI	3	5	4	7	2	3		1	2	1	1	3	2	1	3	1			
HOOR															1				
HOSP						1													
HOWR																			
KILL	3																		
LASP																			
LBWO																			
LEGO									1			1	1						
LISP	1	1	1			1					1				2				
LOSH																			
LUWA	2					25	2	4	12	5	9	2	4	3	2	1	1	1	2
LABU	1	3							1										
MALL						2		1	7	2									
MAWR	1								1										
MGWA	1																		
MOCH	1														1				
MODO	2			1		2			2		1	1							
NAWA																			
NOFL																			
NOMO																			
NOOR																	1		
NRWS	1																		
OCWA	1									3									
OSFL																			
PEFA			2			1		1											
PHAI																			
RBGU																			
RCKI	3	2	2	1		2	1	2	2		4			1	3				
RCSP		1					1		1					1	2				
RNSA	1					1													
ROWR		1		1	1	1		1	1	1	1	1	1	1	1				1

Appendix 1 - continued

PATCH	1.0R	1.6R	5.1L	5.2R	5.6R	46.7R	47.5L	48.5L	49.1R	49.2L	50.0R	73.9R	74.1R	74.3R	74.4R	75.9R	76.0L	95.7L	95.9L
RSTO						1													
RTHA					1	1													
RUHU																			
SAPH		2	2	1		2	1			1	2	1							
SCJA																			
SORA																			
SOSP	1			1		2						1							
SPSA		1	1		1	1						2							
SSHA																			
SUTA											1								
TOSO																			
TUVU																			
VASW	1																		
VGSW	13	5	5	6		7					15			1					
WAVI								1	3										
WCSP	11	1		2		1				4	2								
WEBL																			
WEFL									1										
WEKI			1	1											1				
WETA						1													
WFIB																			
WFL	2	1																	
WITU											1								
WIVA	1					2													
WTSW						5													
WWPE	1								1										
YBCH	1			1		1		1			1				1				
YEWA	2		1	1		3	1		1	1	1								
YRWA	3	3	2		1				1	1									
TOTAL-MAX	95	81	31	55	10	97	19	25	55	26	62	19	13	14	24	4	8	4	5

Appendix 1 (section b). The maximum number of individuals detected during any one survey (all techniques combined) at patches 97.4R through 174.7R during 1994. Refer to Appendix 5 for the key to standard 4-letter species codes.

PATCH	97.4R	97.4L	97.5L	97.6L	97.6R	97.6L	97.6R	167.0R	167.0L	167.2L	167.2R	167.6R	168.5L	168.8R	171.0R	171.1R	172.2L	173.1R	174.2L	174.4R	174.5R	174.7R	
AMKE																							
AMRO																							
AMWI																							
ATFL			2	1	1			2				1	1	2			1				1	2	
BCFL																							
BCHU	1								1	2		1	1	1	2	1	2		2	1			
BEVI								1		2		2	1	2	2	3	3	1	2	2	1	2	
BEWR	1								1	1		1	1	1	1			1	1				
BGGN								1				2	2	2	3	2	1	1	3	3		1	
BHCO																							
BHGR															1								
BLGR																			2				
BLPH										1					1	1	5				3		
BRBL																							
BRSP																							
BTSP																				1			
BUFF										2	1												
BUSH																							
CAGO																							
CAKI																							
CHSP																							
CNWR																							
COGO										2	1	2	1	1	1	1	1	1	1	1	1		
COHA																							
COHU																							
CORA												1	1	1	1	1				1			
COYE	2											1			1				1				
CRTH																							
DEJU																							
GADW																							
GAQU																							
GBHE																							
GRFL																							
GRHE																							
GTGR																							

Appendix 1 - continued

PATCH	97.4R	97.4L	97.5L	97.6L	122.8L	125.5R	131.3R	167.0R	167.2L	167.6R	168.5L	168.8R	171.0R	171.1R	172.2L	173.1R	174.2L	174.4R	174.5R	174.7R
GTTO																				
HAWO																				
HETH																				
HOFI	1	1				2			1	1	1	1	1			1				
HOOR										1	1	1	1			1				
HOSP													2							
HOWR												1	1							
KILL																				
LASP																				
LBWO																				
LEGO				1			1						2		1		1			
LJSP									1				2		1	1		1		
LOSH																				
LUWA	3		2		4	5	4	2	3	3	2	4	5	4	12	4	6	5	1	7
LABU					1															
MALL																				
MAWR													1					1		
MGWA																				
MOCH																				
MODO				1				1					1				2	1		
NAWA																				
NOFL																				
NOMO																				
NOOR	1																			
NRWS																				
OCWA											1									
OSFL																				
PEFA													1							
PHAI												1								
RBGU														1						
RCKJ						1		1	1	1		1	2	1	1	1		2		
RCSP						1						2								
RNSA												1								
ROWR						1		1	1	1				1	1	2		1		1
RSTQ					4															

Appendix I - continued

PATCH	97.4R	97.4L	97.5L	97.6L	122.8L	125.5R	131.3R	167.0R	167.2L	167.6R	168.5L	168.8R	171.0R	171.1R	172.2L	173.1R	174.2L	174.4R	174.5R	174.7R	
RTHA																					
RUHU							1														
SAPH					1			1	2		1	1	1	1	1	1	1	2			1
SCJA																	1				
SORA																					
SOSP							1			1	1										
SFSA					1									1		2					
SSHA																					
SUTA																					
TOSO																					
TUVU																	1				
VASW																					
VGSW																					
WAVI																					
WCSP							2			1			2		2		1	1			
WEBL																					
WEFL																					
WEKI																					
WETA																					
WFIB										3											
WIFL																					
WITU																					
WIWA					1																
WTSW																					
WWPE																					
YBCH																					
YEWA	1	1						1	2	1	1	1	2	2	2	1	2				
YRWA																	1				
TOTAL MAX	10	2	2	4	27	11	21	13	21	22	13	27	31	30	35	21	30	31	7		14

Appendix 1 (section c). The maximum number of individuals detected during any one survey (all techniques combined) at patches 1.980R through 214.0L during 1994. Refer to Appendix 5 for the key to standard 4-letter species codes.

PATCH	198.0R	199.5R	200.0L	200.4R	200.5R	202.5R	204.5R	205.8R	206.5L	208.7R	213.6L	214.0L
AMKE												
AMRO												
AMWI												
ATFL	2	1	2	1	1	1	2		1	2	1	1
BCFL	3											
BCHU	5	2			3	1	4		1	2		
BEVI	7	1	2	2	2	5	20	3		3		2
BEWR	3	1		1	1	1	2					
BGGN	5	1	1		2	3	6		1	1		
BHCO												
BHGR	1											
BLGR		1			1		1			2		
BLPH							1					1
BRBL						16						
BRSP	3											
BTSP	2			1		1	4		3	1	2	
BUFF												
BUSH							3					
CAGO												
CAKI												
CHSP							2					
CNWR	1	1			1	1						
COGO												
COHA							1					
COHU	1	1			1	1						
CORA	1						1					
COYE	1				2		2					1
CRTH												
DEJU												
GADW												
GAQU	3									13		
GBHE												
GRFL							2					
GRHE							1					
GTGR												

Appendix I - continued

PATCH	198.0R	199.5R	200.0L	200.4R	200.5R	202.5R	204.5R	205.8R	206.5L	208.7R	213.6L	214.0L
GTTO												
HAWO												
HIETH								1				
HOFI					1	2	3			1		1
HOOR					1	2	3			1		1
HOSP												
HOWR												
KILL												
LASP							2					
LBWO	1						1					
LEGO	1	2		2	2	1	3			1		
LISP	3						1					
LOSH	1								1			1
LUWA	12	6	3	16	4	8	16	3	2	7	1	5
LABU							1			1		
MALL												
MAWR	1						1					
MGWA	1						1					
MOCH												
MODO												
NAWA	1						3					
NOFL	1											
NOMO		1					2	1			1	
NOOR							1				1	
NRWS												
OCWA	3											
OSFL										1	2	
PEFA										1		
PHAI												
RBGU							4					
RCKI	3											
RCSP												
RNSA	2				1	1					1	1
ROWR	1						1					
ESTO	1											

Appendix I - continued

PATCH	198.0R	199.5R	200.0L	200.4R	200.5R	202.5R	204.5R	205.8R	206.5L	208.7R	213.6L	214.0L
RTHA				1	1							
RUHU												
SAPH	1					1						
SCJA	1						1					
SORA						1						
SOSP	1						1					
SPSA						2						
SSHA	1					1						
SUTA	1		1			1						
TOSO						1						
TUVU												
VASW												
VGSW												
WAVI												
WCSP	3						4		1	1		3
WEBL	10											
WEFL												
WEKI							1					
WETA							1				1	
WFIB												
WIFL												
WITU												
WTWA												
WTSW												
WWPE							1					
YBCH	3		1	1	1	10		2				
YEWA	2	1			1	6		1	1			
YRWA	1					2					1	
TOTAL MAX	94	19	11	26	26	46	127	11	11	39	11	17

Appendix 2 (section a). The maximum number of individuals detected during any one survey (all techniques combined) at patches 1.0R to 76.5L during 1995. Refer to Appendix 5 for the key to standard 4-letter species codes.

SPECIES	1.0R	1.6R	2.0L	3.7L	5.1L	5.2R	46.0L	46.7R	47.5L	48.5L	49.1R	49.2L	50.0R	73.9R	74.1R	74.3R	74.4L	76.5L
AMCO	1																	
AMCR								13			2			1				
AMKE											1							
AMRO										7								
AMWI																		
ATFL	2		2	1	1	2	4	2		1	1	2	1			1	1	2
BAEA													1					
BCFL																		
BCHU						1	4	4	3	1	3	1	4	1	1	1		1
BCNH						1												
BCSP																		
BEKI																		
BEVI									1									
BEWR	2	1			2	1	9	7	1	2	6	2	7	1	1		5	2
BGGN	2	1				1	2	4	1	2	5	3	5				4	4
BHCO	3	2									1	1	1					
BLGR			1			1		1									1	
BLPH																		
BRTO																1		
BTSP																	1	
BUFF																	2	
CAKI			1		1	1												
CEWA																		
CHSP		2																
CNWR		3	1	2	1	2	4	2	3	5	1	5	3	1	2		4	3
COGO					4							8	5			2		
COHU							2											
COME												3						
CORA	1				1	2	2	4					1					2
COYE							2	2						1			1	
CRTH																		
DEJU	4	8			3		2	6			2	4	12	3	1	1		
GBHE	1																	
GRFL							1											
GRVI																		

Appendix 2 - continued

SPECIES	1.0R	1.6R	2.0L	3.7L	5.1L	5.2R	46.0L	46.7R	47.5L	48.5L	49.1R	49.2L	50.0R	73.9R	74.1R	74.3R	74.4L	76.5L
GTGR	8																	
HETH																		
HOFI	4	2	4	4	1	7	2	3		1	2	2	2	1	1	2	4	2
HOOR																		
HOWR	1												1					1
INBU																		
KILL	1	2		1	1													
LBWO																		
LEGO											1						5	1
LISP		2	1				1											
LUWA	2			1	1		8	8	5	4	12	2	8	6	4	3	8	7
LZBU			1					1				1						1
MALL		2	1				1	3		3	1							
MAWR								1										
MODO	2				3	1						1	1				1	1
NOFL																		
NOMO																		
NOOR											1							
NOPI		10																
OCWA		1																
PEFA							1		2									
PHAI																		
RCKI	1	3	1	2	3	3	3	3	2	1	2		3	1	1	1	3	1
RCSP							4					2					5	1
RNSA																		
ROWR	1	1	1	1	1	2	3	2	1			2		1	1	2	2	1
RSTO								1										
RTHA		1																
RWBL												1						
SAPH	2		1			1		1			1	1	1	1		1	2	1
SCJA																		
SNEG																		
SOSP	2	3	1		2			1			1							
SFSA	2	1	2															
SSHA								1										

Appendix 2 - continued

SPECIES	1.0R	1.6R	2.0L	3.7L	5.1L	5.2R	46.0L	46.7R	47.5L	48.5L	49.1R	49.2L	50.0R	73.9R	74.1R	74.3R	74.4L	76.5L
SUTA											1							
TOSO																		
TUVU																		
VGSW	6	3	14	7		2		15			16		30	4			1	3
WCSP	5					3												
WEBL																		
WETA									1				1					
WTU											1							
WVA													1					
WTSW						2	3	12				20						
WWPE											1							
YBCH	1					1	1	1	1									
YEWA	3		2	1	1	1	1	2			1		1					
YRWA	1	1		2	1	4					1							
TOTAL-MAX	58	49	34	26	27	39	60	101	21	27	64	61	89	22	11	15	50	34

Appendix 2 (section b). The maximum number of individuals detected during any one survey (all techniques combined) at patches 117.5R to 198.3R during 1995. Refer to Appendix 5 for the key to standard 4-letter species codes.

SPECIES	117.5R	119.5R	122.8L	125.5R	131.3R	167.0R	171.0R	171.1R	172.2L	173.1R	174.4R	174.5R	174.7R	197.2L	197.6L	198.0R	198.2L	198.3R
AMCO																		
AMCR																		
AMKE													1					
AMRO			1	1												5		
AMWI																		
ATFL						1	1	1	2		2		2	1	1	1	1	
BAEA																		
BCFL														1	1	1	1	1
BCHU			1			1	4	2	2	1	2		2	2	1	2	2	1
BCNH																		
BCSP																		
BEKI																		
BEVI							6	4	8	3	2	2	1	3	7	8	7	4
BEWR			1			1				1						3	2	
BGGN			1			2	4	5	4		3	1		1	2	5	2	2
BHCO																		
BLGR																		
BLPH							1					2						
BRTO																		
BTSP			2	1	1				1									1
BUFF																		
CAKI																		
CEWA																		
CHSP			1															
CNWR	1	1	1		1	1	1			1				1	1	1	1	
COGO																		
COHU						1				1	1	1						
COME																		
CORA			1				1				1	2		1	1	1	1	
COYE	3		1					1						1	1	1	1	1
CRTH																		
DEJU			3	3		4											3	
GBHE			1															
GRFL																		
GRVI																		

Appendix 2 - continued

SPECIES	117.5R	119.5R	122.8L	125.5R	131.3R	167.0R	171.0R	171.1R	171.1R	172.2L	173.1R	174.4R	174.5R	174.7R	197.2L	197.6L	198.0R	198.2L	198.3R	
GTGR											1									
HETH			1														1			
HOFI			1	1			6	1	1	1	1			1	4	3	4	5	4	
HOOR																				
HOWR																				
INBU																				
KILL																				
LBWO																				
LEGO			1			2	1	3	1	1		1			2	3	1	4	1	
LISP			1																	
LUWA	2	2	13	1	4	3	16	3	5	12	12	5	8	3	12	10	12	10	4	
LZBU			3						1				1							
MALL																				
MAWR			1																	
MODO			2												1	1				
NOFL																				
NOMO																	1			
NOOR																	2			
NOPI																				
OCWA																				
PEFA				2																
PHAI																				
RCKI				1	1	1	1	2							2		2	1		
RCSP			1												1					
RNSA																	1			
ROWR	2	1	2		2	1	3	1	2	2	2	1		2				2		
RSTO																				
RTHA				1																
RWBL																				
SAPH	1		1	1	2	1	1	1		1					1		1			
SCJA				1																
SNEG																				
SOSP			2				1								2	2	2	3		
SPSA																				
SSHA																				

Appendix 2 - continued

SPECIES	117.5R	119.5R	122.8L	125.5R	131.3R	167.0R	171.0R	171.1R	172.2L	173.1R	174.4R	174.5R	174.7R	197.2L	197.6L	198.0R	198.2L	198.3R
SUTA									1						1			
TOSO							1									1		
TUVU											1		1					
VGSW																		
WCSP																		
WEBL																4		
WETA																		
WITU																		
WIWA																	1	
WTSW																		
WWPE																		
YBCH	1						1		1				2			6	4	2
YEWA			3				1	1	2	2	1	2	1	2		1	2	
YRWA																1		
TOTAL MAX	9	4	46	14	11	18	51	25	31	26	20	19	16	37	35	73	49	21

Appendix 2 - continued

SPECIES	199.5R	200.0L	200.4R	200.5R	202.5R	204.1R	204.5R	206.5L	208.7R	213.6L	214.0L	214.2L	224.0L	224.1R
HETH														
HOFI	1	4	2	6	3	8	2		2	4	3	1	3	3
HOOR											1			
HOWR														
INBU							1							
KILL								1						
LBWO						1								
LEGO		3	3	1	2	6	7	1	2	5	1		1	
LISP								1						
LUWA	9	6	6	19	10	15	15	5	8	5	11	1	3	4
LZBU						1	1							
MALL														
MAWR							1	3	1					
MODD				1			1		1					
NOFL														
NOMO														
NOOR							2							
NOPI														
OCWA														
PEFA														
PHAI												1		
RCKI		2	1		1	2	6	1	2	2	1			
RCSP							1							
RNSA														
ROWR		2	1	1	3	3	1	1	1		1		1	1
RSTO														
RTHA														
RWBL														
SAPH	1	3	1		1	2	1	1	1	1	1		1	
SCJA														
SNEG											1			
SOSP				2		1	2							
SPSA														
SSHA														
SUTA				1			1							

Appendix 2 - continued

SPECIES	199.5R	200.0L	200.4R	200.5R	202.5R	204.1R	204.5R	206.5L	208.7R	213.6L	214.0L	214.2L	224.0L	224.1R
TOSO						1	10			1				
TUVU														
VGSW									6					
WCSP				5	1	2	5		1					
WEBL							6							
WETA														
WITU														
WIWA														
WTSW														
WWPE						1	1							
YBCH		1	1	3		2	5		2		2			
YEWA				1		1	5							
YRWA														
TOTAL MAX	18	32	26	58	35	79	120	26	49	29	34	8	14	9

Appendix 3. The number of pairs of each breeding species detected during 1994, based on "decision rules" as outlined in the Methods section of this chapter. Refer to Appendix 5 for the key to standard 4-letter species codes.

PATCH	ATFL	BCFL	BCHU	BEVI	BEWR	BGGN	BHCO	BLGR	COHU	COYE	HOFT	HOOR	LEGO	LUWA	MODO	NOMO	NOOR	PHAI	SAPH	SUTA	YBCH	YEWA	Total
1.0R	1		1		2	2	1	1		1	2			1							1	1	14
1.6R			1		1	1		1			1								1				6
5.1L			1					1		1	1								1			1	5
5.2R					2		1	1			2											1	7
5.6R			1								1												2
46.7R	1		3		3	1	1	1		2	2		5					1		1	2	2	22
47.5L			2				1	1					1									1	6
48.5L			2								1			2									5
49.1R			4		1	1				1	1		5										13
49.2L			1		1						1		3										6
50.0R	1		2		2	1	1	1			1		4					1		1	1	1	15
73.9R			1		2	1	1				1		1	2					1				10
74.1R			1		1						1		1	2									6
74.3R			1		1						1		2										5
74.4R					1						1		1										3
75.9R									1		1		1										3
76.0L			1										1										2
95.7L						1							1										2
95.9L			1			1							1										3
97.4R			1		1					1			1										4
97.4L											1												1
97.5L													1										1
97.6L													1										1
122.8L	1		2		1	1			1				3										9
125.5R													2										2
131.3R			1		1				1		1		3										7
167.0R	1			1		1			1				1										5
167.2L			2		1						1		2					1				1	8

Appendix 4. The number of pairs of each breeding species detected during 1995, based on "decision rules" as outlined in the Methods section of this chapter. Refer to Appendix 5 for the key to standard 4-letter species codes.

PATCH	ATFL	BCFL	BCHU	BEVI	BEWR	BCGN	BHCO	BLGR	COHU	COYE	HOFI	HOOR	LABU	LEGO	LUWA	MODO	NOOR	PHAJ	SAPH	SOSP	SUTA	YBCH	YEWA	Total
1.0R	1		1		1	1	1				2				1	1						1		10
1.6R							1				1													2
2.0L	1							1			2													4
3.7L								1			1				1									3
5.1L					1						1					1								3
5.2R	1		1		1	1		1			2					1						1		9
46.0L	2		4		1	1				1	1				2							1		13
46.7R	1		4		2	2	1	1		1	2				7							1	1	23
47.5L			3												3									6
48.5L			1		1	1									2									5
49.1R	1		3		2	1	1				1			1	6									16
49.2L	1		1		1	1	1						1		2				1					9
50.0R			4		3	2	1				2				7	1								20
73.9R			1		1										2									4
74.1R			1		1										2									4
74.3R			1								1				1									3
74.4L	1				1	2		1			2			2	4	1				1				15
76.5L	1		1		1	1					1		1	1	2									9
117.5R										1					1					1				3
119.5R															1									1
122.8L			1		1	1				1			1	1	1	1								8
125.5R											1				1									2
131.3R															4									4
167.0R			1			1			1					1	1									5
171.0R	1		2	2		1					2			1	3							1		13
171.1R	1		1	1		1							1	1	2									7
172.2L	1		2	2		1					1			1	3							1	1	13
173.1R			1	1					1						3				1					8
174.4R	1		2	1		2			1					3									1	11

Appendix 4 - continued

PATCH	ATFL	BCFL	BCBU	BEVI	BEWR	BGGN	BHCO	BLGR	COHU	COYE	HOFI	HOOR	LABU	LEGO	LUWA	MODO	NOOR	PHAI	SAPH	SOSP	SUTA	YBCH	YEWA	Total
174.5R				2		1			1				1		2									7
174.7R	1		1	1											1									4
197.2L		1	2	1		1			1	1	2			2	4					1			1	17
197.6L	1	1	1	1		1			1					2	3							1		12
198.0R		1	2	7	3	2	1		1	1	1			1	6				1	1	1		2	30
198.2L	1	1	2	2	2	1					2			1	5						1		1	20
198.3R		1	1	2	1	1				1	2				2								1	12
199.5R				1		1					1				1				1					5
200.0L			1	2		1			1		2				2									9
200.4R			2	1		1			1	1	1			3	2									12
200.5R			2	2	1	1				1	3			1	3						1		1	16
202.5R			3	3		1			1		1			1	2									12
204.1R	2		5	5	2	1		1		1	2			2	5				1	1		2		30
204.5R			7	12	1	3		2	2	2	1		2	5	11		1	2			1	5		57
206.5L	1		1	1		1			1						3									8
208.7R	1		3	1				1	2		1			1	3							1		14
213.6L			1	1		1					2			3	1				1					10
214.0L	1		1	2		1			1		2	1		1	2				1					13
214.2L				1											1									2
224.0L			1			1			1		1			1	2				1					8
224.1R									1		1				2									4

Appendix 5. Key to standard 4-letter bird codes. Codes and common names are standardized per the American Ornithologists' Union (1983 and subsequent revisions) convention.

AMCO	American Coot	LOSH	Loggerhead Shrike
AMCR	American Crow	LUWA	Lucy's Warbler
AMKE	American Kestrel	LZBU	Lazuli Bunting
AMRO	American Robin	MALL	Mallard
AMWI	American Widgeon	MAWR	Marsh Wren
ATFL	Ash-throated Flycatcher	MGWA	MacGillivray's Warbler
BAEA	Bald Eagle	MOCH	Mountain Chickadee
BCFL	Brown-crested Flycatcher	MODO	Mourning Dove
BCHU	Black-chinned Hummingbird	NAWA	Nashville Warbler
BCNH	Black-crowned Night Heron	NOFL	Northern Flicker
BCSP	Black-chinned Sparrow	NOMO	Northern Mockingbird
BEKI	Belted Kingfisher	NOOR	Northern Oriole
BEVI	Bell's Vireo	NOPI	Northern Pintail
BEWR	Bewick's Wren	NRWS	Northern Rough-winged Swallow
BGGN	Blue-gray Gnatcatcher	OCWA	Orange-crowned Warbler
BHCO	Brown-headed Cowbird	OSFL	Olive-sided Flycatcher
BHGR	Black-headed Grosbeak	PEFA	Peregrine Falcon
BLGR	Blue Grosbeak	PHAI	Phainopepla
BLPH	Black Phoebe	RBGU	Ring-billed Gull
BRBL	Brewer's Blackbird	RCKI	Ruby-crowned Kinglet
BRSP	Brewer's Sparrow	RCSP	Rufous-crowned Sparrow
BRTO	Brown Towhee	RNSA	Red-naped Sapsucker
BTSP	Black-throated Sparrow	ROWR	Rock Wren
BUFF	Bufflehead	RSTO	Rufous-sided Towhee
BUSH	Bushtit	RTHA	Red-tailed Hawk
CAGO	Canada Goose	RUFU	Rufous Hummingbird
CAKI	Cassin's Kingbird	RWBL	Red-winged Blackbird
CEWA	Cedar Waxwing	SAPH	Say's Phoebe
CHSP	Chipping Sparrow	SCJA	Scrub Jay
CNWR	Canyon Wren	SNEG	Snowy Egret
COGO	Common Goldeneye	SORA	Sora
COHA	Cooper's Hawk	SOSP	Song Sparrow
COHU	Costa's Hummingbird	SPSA	Spotted Sandpiper
COME	Common Merganser	SSHA	Sharp-shinned Hawk
CORA	Common Raven	SUTA	Summer Tanager
COYE	Common Yellowthroat	TOSO	Townsend's Solitaire
CRTH	Crissal Thrasher	TUVU	Turkey Vulture
DEJU	Dark-eyed Junco	VASW	Vaux's Swift
GADW	Gadwall	VGSW	Violet-green Swallow
GAQU	Gambel's Quail	WAVI	Warbling Vireo
GBHE	Great-blue Heron	WCSP	White-crowned Sparrow
GRFL	Gray Flycatcher	WEBL	Western Bluebird
GRHE	Green Heron	WEFL	Western (Cordilleran?) Flycatcher
GRVI	Gray Vireo	WEKI	Western Kingbird
GTGR	Great-tailed Grackle	WETA	Western Tanager
GTTO	Green-tailed Towhee	WFIB	White-faced Ibis
HAWO	Hairy Woodpecker	WIFL	Willow Flycatcher
HETH	Hermit Thrush	WITU	Wild Turkey
HOFI	House Finch	WIWA	Wilson's Warbler
HOOR	Hooded Oriole	WTSW	White-throated Swift
HOSP	House Sparrow	WWPE	Western Wood-pewee
HOWR	House Wren	YBCH	Yellow-breasted Chat
INBU	Indigo Bunting	YEWA	Yellow Warbler
KILL	Killdeer	YRWA	Yellow-rumper Warbler
LASP	Lark Sparrow		
LBWO	Ladder-backed Woodpecker		
LEGO	Lesser Goldfinch		
LISP	Lincoln Sparrow		

Chapter 7: Avian Community and Habitat Relationships



Avian Community and Habitat Relationships

INTRODUCTION

Riparian habitats in the western United States, especially those dominated by native vegetation, typically support a disproportionately large number of birds as compared to adjacent non-riparian habitats, both in terms of bird abundance and species richness. The Colorado River corridor in the Grand Canyon is no exception and provides important habitat to a large number of wintering, migrant, and breeding birds (Brown et al. 1987, Carothers and Brown 1991, this study), even though much of the habitat is dominated by introduced tamarisk (*Tamarix ramosissima*).

Knopf et al. (1988) calculated that riparian habitat covers less than one percent of the land area of the western United States, and much of this is subject to the influence of water management activities (Collier et al. 1996). The rarity and importance of riparian habitats highlights the uniqueness and value of the Colorado River corridor through the Grand Canyon, one of the largest protected riparian areas in the West. The operation of Glen Canyon Dam has affected riparian habitats in the Grand Canyon (Turner and Karpiscak 1980, Anderson and Ruffner 1988, Stevens and Ayers 1994) and the associated bird communities in the past (Carothers and Brown 1991, Brown et al. 1987, Brown 1988a), and will continue to do so in the future. It is incumbent upon the resource- and land-management entities responsible for the corridor to determine and understand how dam operations could affect local birds and their habitats.

Understanding the relationship between riparian vegetation and the habitat of a bird species or community is central to informed river management and conservation of avian resources. This is especially true of the breeding bird community in the Grand Canyon, which includes many riparian-obligate breeding species (Brown et al. 1987, this study). The avifauna of the riparian corridor in the Grand Canyon has received much study, and a number of researchers have looked at bird - habitat relationships in the past (Brown and Johnson 1985, 1987, 1988; Brown et al. 1987, Brown and Trosset 1989). These studies have provided much useful information for some research and management questions, but are generally hard to apply to broader questions of bird communities. For example, studies of single species (e.g., Brown 1988b, Sogge et al. 1997) or indicator species (Brown and Johnson 1987, Brown 1988a) have limited application to community-level questions. The use of avian indicator species has been the subject of much debate and criticism in general (Verner 1985, Morrison 1986), and Brown (1988) found that indicator species were not useful for predicting long-term trends in the breeding bird community along riparian areas in the Grand Canyon. Therefore, bird community studies should include all species within the community of interest (e.g., migrants, breeders, insectivores, etc.). Furthermore, bird-habitat relationship models can be greatly affected by the type and scale of habitat measurements (Wiens 1989a, Morrison et al. 1992). Studies involving a small number of study sites (Brown and Johnson 1987, Brown 1988) can provide accurate information for these particular sites but may not include a variety of sites representative of the diversity within a region (Wiens 1989a). Habitat measurements that are fine-scale and/or focus on nest-centered measurements (Brown and Trosset 1989) may provide different results or models than studies conducted at different habitat scales (Morrison et al. 1992, Block and Brennan 1993). The nature of the bird survey techniques used can also influence bird - habitat models (Verner 1985, Wiens

1989a, Block and Brennan 1993). Some survey techniques and data summaries can introduce potential biases that could affect bird - habitat relationship patterns (refer to Survey Summary and Techniques Comparison chapters; see Felley and Sogge 1997).

Our objective was to quantify the relationship between riparian vegetation/habitat characteristics and measures of the resident breeding bird community, which in turn could be used to evaluate possible indirect impacts of dam operations. In order to do so we needed to use bird counting techniques that would provide robust, unbiased data on the entire breeding bird community (see Techniques Comparison and Survey Summary chapters). We wanted to base our habitat measurements on protocols that could be applied quickly and parameters that could be quantified easily, using remote sensing (aerial photography) to the greatest degree possible. We also emphasized patch-scale parameters, rather than nest-based measurements, in order to more easily relate our bird - habitat models to larger-scale patterns and future dam-induced habitat changes.

METHODS

Study Sites

We selected study sites to form a representative sample of riparian habitats between Lee's Ferry (River Mile [RM] 0) and Diamond Creek (RM 225; river mile designations per Stevens 1983). At the largest geographic scale, the river corridor follows a 540 m elevation gradient with changing vegetation communities from Great Basin desert-scrub (elevation 950 m at Lees Ferry) to Sonoran desert-scrub (elevation 410 m at Diamond Creek) (Turner and Karpiscak 1980), and characteristics of riparian vegetation relate naturally to the geomorphology of the 11 reaches of the river (as defined by Schmidt and Graf 1988). For these reasons, we located sites in a variety of reaches, within the constraints of river logistics.

We conducted bird surveys and measured habitat parameters at 50 study sites in 1995. We had conducted bird surveys at 32 of these sites in 1994. Each sites was a discrete patch of riparian vegetation, with most sites located above RM 75 or below RM 150 (Figure 1). Site selection was stratified to include a wide range of the sizes, shapes, geomorphology, and floristic composition of patches of riparian vegetation found along the river. All surveys were conducted between one-half hour before sunrise and 10:00 AM. We located sites in groups so each group could be completely surveyed in one morning.

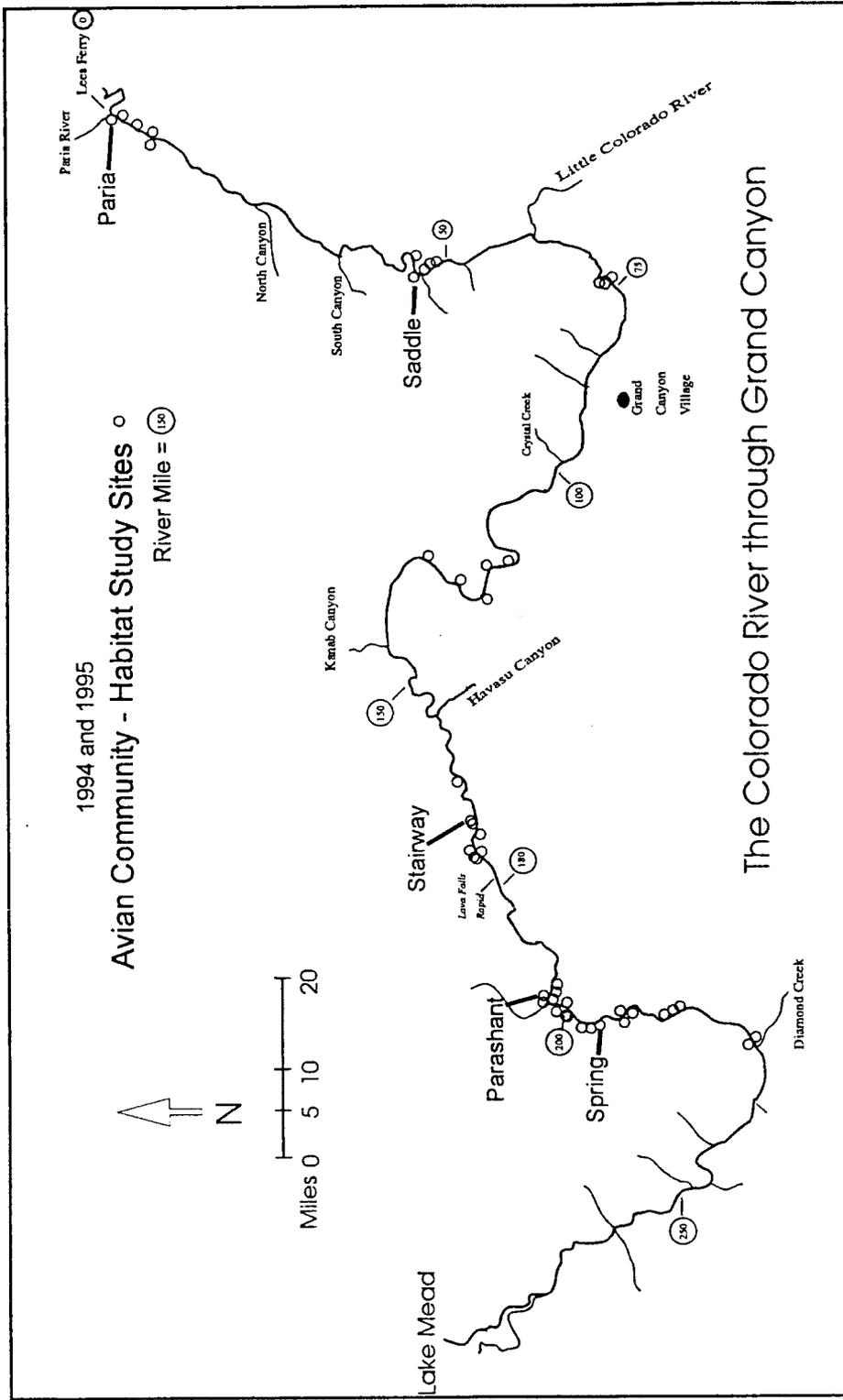


Figure 1. Location of Grand Canyon avian community - habitat study sites, 1994 - 1995. Open circles are sites where bird surveys and habitat measurements were conducted.

Bird Surveys

In 1994, we conducted monthly bird surveys from April through July. In 1995, surveys were conducted monthly from March through June. We integrated information from walking count, floating count, and point count techniques in order to develop a composite data set on the number and types of birds detected in each patch.

Walking surveys: Walking surveys consisted of one observer walking slowly through the riparian habitat, recording species and numbers of all birds observed at the study site (Brown and Johnson 1987, Brown 1988, Sogge et al. 1994, Sogge et al. 1995). Walking surveys were made at all study sites surveyed during 1994-95.

Floating surveys: Observers floated past each study site in a raft ahead of the walking surveyor and recorded all birds heard or observed. Floating surveys were conducted only in 1994.

Point counts: We conducted point count surveys at 11 study sites (37 total point count stations) where walking counts were also conducted. Point counts were made once per month at each site, March-June 1995. Point count survey methods generally follow the recommendations of Ralph et al. (1993). The number of points varied from one to five per site depending on patch size.

Refer to the Survey Comparison and Survey Summary chapters for additional details on survey methods. We integrated the data from all survey techniques by combining survey information into a composite list of species detections and abundance estimates for each day of survey for each patch. This was done by pooling species lists (e.g., species were included as present in the patch if they were found during any of the surveys) and using the highest abundance estimate for each species from any one technique. These results, in turn, were aggregated to provide a composite data set of species presence and abundance for each patch, by month. These data sets were then fine-tuned through the decision rule process outlined below.

Decision rules for determining breeding status and abundance

Raw data from surveys provides information on the total number of species and birds detected. However, even during the breeding season, these totals include migrants as well as local breeders (refer to the Banding Studies chapter for details). Therefore, survey totals and/or high counts are subject to potentially high variability due to yearly or seasonal changes in the number of migrants, even if the number of local breeders remains nearly constant. Inclusion of migrants can also inflate calculated values for species richness and abundance, and alter avian community/habitat relationship models (Wiens 1989a, Morrison et al. 1992). These considerations led us to develop a set of "decision rules" (Table 2), tailored to each species, that allow us to develop the most conservative and accurate estimate of the type of breeding species and the number of breeding pairs in each patch. In some cases, these decision rules involved using information gathered from nest searches and/or banding.

Table 1. Decision rules used to determine whether a species was considered a breeder at a particular patch and to estimate the number of breeding pairs of that species.

Species	Criteria for Breeder Status in Patch	Calculation of Number of Breeding Pairs
Ash-throated Flycatcher	observed on two visits, excluding July	highest count from April or May divided by two.
Brown-crested Flycatcher	observed	highest count divided by two
Black-chinned Hummingbird	observed	highest count of any sex or highest count divided by two
Bell's Vireo	observed on two visits	highest count of singing males, obvious pairs, or nests found
Bewick's Wren	observed on two visits	highest count of singing males, obvious pairs, or nests found
Blue-gray Gnatcatcher	observed on two visits	highest count from April or May, divided by two
Brown-headed Cowbird	observed	highest count of males or females
Blue Grosbeak	observed on two visits	highest count of singing males or obvious pairs
Costa's Hummingbird	observed	highest number of males observed
Common Yellowthroat	observed on two visits	highest count of singing males or obvious pairs common to two months
House Finch	observed on two visits	highest count of singing males or obvious pairs common to two months
Hooded Oriole	observed on two visits, not in July	highest number males or females from any visit
Lesser Goldfinch	observed in April or May	highest number of singing males or total count, divided by two
Lucy's Warbler	observed on two visits	highest number of singing males, obvious pairs, or count divided by two, except June or July
Mourning Dove	observed on two consecutive visits	highest number of singing males or obvious pairs
Northern Mockingbird	observed on two consecutive visits	highest number of singing males or obvious pairs from two visits
Northern Oriole	observed on two visits, not in July	highest number of males or females from any visit, not July
Phainopepla	observed on two visits	highest number of males or obvious pairs from any visit
Rufous-crowned Sparrow	observed on two visits	highest number of males or obvious pairs from any visit
Say's Phoebe	observed on two consecutive visits	highest count common to two visits, divided by two
Summer Tanager	observed on two visits	highest number of singing males or obvious pairs
Yellow-breasted Chat	observed on two visits	highest number of singing males common to two visits
Yellow Warbler	observed on two visits	highest number of singing males common to two visits, excluding may

Habitat Mapping and Measurements

The standardized habitat measurement techniques often used for vegetation studies are not always the most appropriate protocols for characterizing habitat parameters important for animals (Morrison et al. 1992). This is particularly true in avian habitat studies, which have generally found that most birds are not responding to fine-scale habitat features (Wiens 1989a). Therefore, it is best to select or develop habitat variables and measurement protocols tailored to the objectives of a particular study. We developed our own methodology to measure macro-habitat scale features including patch size, vegetative structure and composition. In order to do so, we delineated vegetation types and structure on aerial photographs of each patch, estimated density and height of shrub and tree vegetation, georeferenced the aerial photographs using GPS and GIS, and determined the aerial extent and/or volume of different vegetation and structural types.

Delineating vegetation and structural types: We procured color xerox copies of 1:2400 aerial photographs (GCES photo series 5-29-95; see Aerial Photograph section of report) for each survey site. While at each site, we delineated and labeled polygons of visually distinct vegetation types and nonvegetated areas. The classifications used to delineate vegetation/habitat categories are described in Table 2.

Estimating vegetation height and density: For each vegetation/habitat polygon, we recorded Braun-Blanquet cover estimates (Bonham 1989) for the major dominant plant species in each of three structural layers; tree (woody vegetation >2 m tall), shrub (woody vegetation < 2 m tall) and herb (nonwoody vegetation). We also estimated the mean height of the top and bottom of the tree and shrub layers.

Georeferencing aeriels: While at each site, we used Trimble Pathfinder GPS units to record (as waypoints) the coordinates of three to four points at or near each patch. These coordinate were taken at sites that could be easily recognized on each aerial photograph. At each georeference point, we collected a minimum of 100 data points, to provide for effective differential correction once we returned from the field. Georeference locations were dispersed across the patch and/or photograph in order to minimize the proportional spatial error during georeferencing. The GPS points were later differentially corrected using data from Trimble base station located at the Colorado Plateau Field Station. We used a digitizing pad to trace the delineated vegetation polygons and created ArcView coverages of the vegetation at each study site. The differentially corrected GPS points were transferred to these coverages, creating a georeferenced habitat theme.

Determining area and volume: We used ArcView to calculate the aerial extent (in square meters) of each of the delineated polygons for a patch. In order to calculate volume indices, we multiplied the areal extent of the vegetation or structural type (e.g., tamarisk, tree, etc.) by the vertical thickness (mean height of top minus mean height of bottom) of the vegetation layer. This was weighted by the Braun-Blanquet cover estimate (weighting factor ranging from 0 - 1). This produced a unitless volume index that increased with increasing area, density, or vertical thickness of that habitat type. In order to characterize different habitat and structural types, we combined the habitat types listed in Table 2 into a variety of categories which were used as covariates in further analyses (Table 3).

Table 2. Description of habitat types used to classify and characterize vegetation components at avian community - habitat study sites along the riparian corridor in the Grand Canyon during 1995.

Code	Description	Life form ^a	Water zone ^b
a	ARROWWEED: Monotypic arrowweed. Pioneer on beach/sandy sites. Always a shrub. Canyon-wide.	S	N
abt	ARROWWEED - BACCHARIS - TAMARISK: mixture of a, b, and t; shrub form, linear along river, no obvious dominant	S	N
ag	ARROWWEED - GRASS: a and g mix, a seral stage where grass has moved into arrowweed, shrub form, relatively open with % cover dominated by grass, linear along river.	S	N
ax	ARROWWEED - DESERT BROOM: shrub form, usually a linear stretch between OHWZ and NHWZ, usually dominated by arrowweed but relative amounts vary	S	N
b	BACCHARIS: monotypic or dominant seepwillow, tall shrubby form, deep and relatively wet soil	S	N
bmt	BACCHARIS - MESQUITE - TAMARISK: large area of shrubby b and t, with scattered larger mesquites, mesquite is minor component. Everything but mesquite is shrub form.	S	N
bt	BACCHARIS - TAMARISK: Mixture of b and t, no obvious or consistent dominant; shrub form, linear along river in wet sites	S	N
btw	BACCHARIS - TAMARISK - WILLOW: Mixture of b, w and t, no obvious or consistent dominant - usually an even mix (at least 20% of any one); shrub form, linear along river in wet sites	S	N
bw	BACCHARIS - WILLOW: Mixture of b and w, no obvious or consistent dominant - usually an even mix; shrub form, linear along river in wet sites	S	N
btx	BACCHARIS - TAMARISK - DESERT BROOM: Mixture of b, t and x, usually a mix with no obvious dominant; shrub form, linear along river, only along lower river	S	N
c	ACACIA: Basically OHWZ with a northern exposure where mesquite does not grow. Acacia dominated, but never monotypic (usually with some upland species). Rocky substrate, dry sites. Varies from shrub to low trees. Open stands, low density.	T	O
d	SAND / BEACH / DUNE / ROCK / TALUS: no vegetation	N/A ^c	N/A
e	EQUISETUM / SEDGE / SHORE: No woody vegetation, very wet sites within the inundation zone. Generally dominated by Equisetum, but sometimes with other wetland species	H	N/A
f	DEBRIS FAN: rocky/boulder substrate with very sparse, dispersed shrubby vegetation (usually a mix of species such as desert broom, tamarisk, seepwillow, willow).	S	N/A
g	GRASS: monotypic grass (predominantly Bermuda grass and red brome)	H	O
h	HACKBERRY (<i>Celtis reticulata</i>): monotypic hackberry, small stands in shady sites of OHWZ, tree form, possibly important for some birds such as summer tanager	T	O
k	CLIFFROSE: monotypic cliffrose, shady sites in OHWZ along upper canyon, shrub form	S	O
m	MESQUITE: monotypic or dominant mesquite, often in savannah landscape; tree forms typically in deeper well watered soil; shrub form usually higher in slopes in dryer/rockier sites with higher stem density (but high canopy cover) than tree form.	T	O
p	MARSH / REEDS / CATTAIL: Wetland vegetation dominated by or with monotypic emergent vegetation; dominated by phragmites (usually) or cattail; often in return channel configuration	H	N
t	TAMARISK: monotypic tamarisk, almost always a tree form when monotypic. Overwhelmingly NHWZ.	T	N
tw	TAMARISK - WILLOW: mixture of t and w, no consistent dominant, only one site.	S	N
tx	TAMARISK - DESERT BROOM: mixture of t and x, only in lower canyon. Shrub form. No consistent dominant. Usually linear between NHWZ and OHWZ. Structurally similar to ax.	S	N
w	WILLOW: monotypic coyote willow, usually shrub form. In wetter sites, usually not linear.	S	N
x	DESERT BROOM: monotypic but not closed canopy/total cover. Intermediate band between OHWZ and NHWZ much like ax and tx. Shrub form.	S	N
xy	DESERT BROOM - shrub: Desert broom component but not overwhelmingly dominant; Intermediate band, similar to x category.	S	N
y	Shrub - <i>Baccharis</i> ?: Very short shrub form, similar to <i>Baccharis</i> , dispersed in sandy/rocky substrate.	S	N

^a T = tree; S = shrub; H = herb;^b N = new high water zone; O = old high water zone^c N/A = Not applicable

Data Integration

Integrating two years (1994 and 1995) of bird survey data with the one year (1995) of vegetation data required several assumptions:

- 1) There were no between-year differences in the area of a given surveyed patch (e.g. due to changes in the bird survey route between years). This assumption was met because survey patches were relocated during each visit, such that the same patch was surveyed each visit and/or year.
- 2) There were no between-year differences in the size or location of any given patch (e.g. due to different observers delineating boundaries differently between years). This assumption was met because survey boundaries were standardized and indicated on aerial photographs of each site, and we surveyed the entire patch area on each visit.
- 3) There were no between-year differences in the proportion or location of the 1995 vegetation classes (e.g. due to major changes in the actual vegetation; e.g., a new moist-soil vegetation type emerges between years in response to water level fluctuations or bank erosion). We based this assumption with our familiarity with each survey patch, and by comparison of aerial photographs between 1994 and 1995.

General Analysis Methods

Variables

Variables of interest include three response variables, two factors and 17 covariates (Table 3). The number of breeding pairs per patch (ABUND) was \log_{10} transformed and the Shannon diversity index (SDI) was squared to meet the assumptions of general linear models. No transformations were necessary for the number of breeding species (RICH). Covariates were calculated from original vegetation type classifications as noted in Table 3.

Table 3. Response variables, factors, and covariates used in analyzing breeding bird community and habitat relationships along the riparian corridor in the Grand Canyon, 1994 and 1995. Refer to Table 2 for descriptions of habitat type codes noted under "Covariates" below.

Name	Description
RESPONSE VARIABLES	
ABUND	Number of breeding pairs for each patch.
RICH	Number of breeding species for each patch.
SDI	Shannon diversity index for each patch, calculated per MacArthur and MacArthur (1961)
FACTORS	
YEAR	1994 or 1995.
SEG	River segment: A = RM 0 - 77; B = RM 117-132; C = RM 171 - 224 (River miles per Stevens 1983)
COVARIATES	
AREA	Total patch area (m ²).
VEG	Total vegetation area (m ²) for each patch; AREA minus area of habitat type d.
TREE	Tree area (m ²) for each patch; sum of the areas for vegetation types c + h + m + t.
SHRB	Shrub area (m ²) for each patch for each patch; sum of the areas for vegetation types shrub=a + ag + ax + abt + bw + btw + btx + bt + b + tw + tx + x + xy + y + w + bmt + f + k.
HERB	Herb area (m ²) for each patch; sum of the areas for vegetation types e + g + p.
NHWZ	Total tree area (m ²) for each patch; sum of the areas for vegetation types a + ag + ax + abt + bw + btw + btx + bt + b + tw + tx + x + xy + y + w + bmt + p + t.
OHWZ	Total tree area (m ²) for each patch; sum of the areas for vegetation types c + h + g + k + m.
TREEVOL	Tree volume per patch calculated as per text.
SHRBVOL	Shrub volume per patch calculated as per text.
TAMVOL	Tamarisk volume per patch calculated as per text.
MESQVOL	Mesquite volume per patch calculated as per text.
ARROW	Patch area (m ²) that contained arrowweed; sum of the areas for vegetation types a + abt + ag + ax.
BACH	Patch area (m ²) that contained Baccharis spp.; sum of the areas for vegetation types abt + b + bmt + bt + btw + bw + btx.
GRASS	Patch area (m ²) that contained grass; sum of the areas for vegetation types ag + g.
MESQ	Patch area (m ²) that contained mesquite; sum of the areas for vegetation types bmt + m.
TAM	Patch area (m ²) that contained tamarisk; sum of the areas for vegetation types abt + bmt + bt + btw + btx + t + tw + tx.
WILLOW	Patch area (m ²) that contained willow spp.; sum of the areas for vegetation types btw + bw + tw + w.

The non-parametric Spearman's correlation coefficient was used for all bivariate correlations of untransformed variables. Techniques associated with general linear models (analysis-of-variance, ANOVA and analysis-of-covariance, ANCOVA) were used to evaluate factors and covariates. Similar analyses were conducted separately for each response variable. The factors were evaluated first using ANOVA in a step-down approach beginning with a full-factorial model which included YEAR, SEG and their interaction. The covariates were then added to the full-factorial model and evaluated using ANCOVA in the presence of the factors.

Analyses were conducted separately for each covariate as follows: The data were fit to a series of 7 models beginning with the most general model (MODEL 1: YEAR, SEG, the covariate, and their interactions), and proceeded in a step-down approach analogous to backwards multiple regression. The 3-way interaction was tested first and dropped from the model if it was not significant ($P < 0.05$). Next, each 2-way interaction was sequentially dropped from the model (MODELS 2-4), beginning with the least significant (highest P-value). Then, each main effect was dropped from the model (MODELS 5-6), beginning with the least significant (highest P-value), until all main effects were significant ($P < 0.05$). Finally, the interaction of the remaining main effects were added back to the model (MODEL 7). A "best" model was determined for each covariate. Consequently, the relative importance of each covariate (in the presence of the factors) was noted for each response variable. This approach was feasible because most of the covariates were significantly and highly correlated with each other.

RESULTS

OVERALL BIRD COMMUNITY PARAMETERS

Because simply detecting a species in a patch during the breeding season does not prove that it is a local breeder, we used species-specific decision rules (refer to Methods section) to more accurately determine what species and how many pairs were breeding in each patch. This minimizes the likelihood of including non-breeding species or migrant individuals, and thereby inflating resident breeding population estimates. Appendices 1 and 2 present more detailed data on the number of breeding pairs of each breeding species during 1994 and 1995.

Abundance (number of breeding pairs of all species combined) ranged from 0 to 57 (Table 4), and was generally lower at smaller patches. Only five of the patches we surveyed supported more than 20 breeding pairs, and most had 10 or fewer. Spring Canyon had the greatest number of breeding pairs (50 and 57, in 1994 and 1995 respectively). The number of breeding pairs was similar between years at some patches, but varied widely at others (Table 4).

Richness (number of breeding species in a patch) ranged from 0 (at the smallest patches) to 14 (Table 4), with most patches having between two and nine breeding species. Spring Canyon, one of our largest patches, had the highest species richness. The number of breeding species detected was relatively stable among years at many patches, but varied substantially at others (Table 4).

Shannon Diversity Indices varied from 0 to 2.39, though most were between 1.0 and 2.0 (Table 4). The dominance of values in the range of 1.0 to 2.0 suggest that, in most patches, there were similar numbers of breeding pairs among the different breeding species. At many of the patches with high SDI values (e.g., Parashant, Spring Canyon), a small number of species contributed a large proportion of the number of breeding pairs (refer to Survey Summary chapter).

For a more detailed description and analysis of bird results, refer to the Survey Summary chapter.

Table 4. The total number of breeding species, the number of breeding pairs (all species combined), and the Shannon Diversity Index (SDI) for each avian community - habitat survey patch, 1994 -1995. Determination of status as a breeding species, and calculation of the number of breeding pairs, was based on a set of "decision rules" (refer to the chapter text). Shannon Diversity Index was calculated per MacArthur and MacArthur (1961). River mile designations follow Stevens (1983). River segments are sections of the river that responded differently in the bird community - habitat models (refer to text for details).

Site: River Mile	1994			1995		
	# breeding species	# breeding pairs	SDI	# breeding species	# breeding pairs	SDI
River Segment A						
1.0 R [Paria]	11	14	2.34	9	10	2.16
1.6 R	6	6	1.79	2	2	0.69
2.0 L				3	4	1.04
3.7 L				3	3	1.10
5.1 L	5	5	1.61	3	3	1.10
5.2 R	5	7	1.55	8	9	2.04
46.0 L				8	13	1.93
46.7 R [Saddle]	11	22	2.24	11	23	2.12
47.5 L	5	6	1.56	2	6	0.69
48.5 L	3	5	1.05	4	5	1.33
49.1 R	6	13	1.52	8	16	1.81
49.2 L	4	6	1.24	8	9	2.04
50.0 R	10	15	2.15	7	20	1.73
73.9 R	8	10	2.02	3	4	1.04
74.1 R	5	6	1.56	3	4	1.04
74.3 R	4	5	1.33	3	3	1.10
74.4 L				9	15	2.06
76.5 L				8	9	2.04
River Segment B						
117.5 R				3	3	1.1
119.5 R				1	1	0
122.8 L	6	9	1.67	8	8	2.08
125.5 R	1	2	0	2	4	0.69
131.3 R	5	7	1.47	1	5	0
River Segment C						
167.0 R	5	5	1.61	5	5	1.61
171.0 R [Stairway]	11	14	2.34	8	13	1.99
171.1 R	10	13	2.24	6	7	1.75
172.2 L	6	9	1.74	9	13	2.10
173.1 R	7	10	1.75	6	8	1.67
174.4 R	6	9	1.68	7	11	1.85
174.5 R				5	7	1.55
174.7 R	5	5	1.61	4	4	1.39

Site: River Mile	1994			1995		
	# breeding species	# breeding pairs	SDI	# breeding species	# breeding pairs	SDI
197.3 L				11	17	2.26
197.6 L				9	12	2.09
198.0 R [Parashant]	13	29	2.34	14	30	2.34
198.2 L				12	20	2.32
198.3 R				9	12	2.14
199.5 R	10	10	2.30	5	5	1.61
200.0 L	5	7	1.55	6	9	1.74
200.4 R	5	6	1.56	8	12	1.98
200.5 R	12	16	2.39	10	16	2.19
202.5 R	7	10	1.83	7	12	1.82
204.1 R				13	30	2.37
204.5 R [Spring]	18	50	2.51	15	57	2.36
206.5 L	3	5	1.05	6	8	1.67
208.7 R	7	11	1.85	9	14	2.07
213.6 L				7	10	1.83
214.0 L				10	13	2.25
214.2 L				2	2	0.69
224.0 L				7	8	1.91
224.1 R				3	4	1.04

OVERALL VEGETATION/HABITAT PARAMETERS

The characteristics of the habitat patches used in this study varied widely. Patches ranged from very small (0.002 ha) to large (7.4 ha), with most between 0.5 and 2 ha. The absolute and relative amounts of different habitat types (e.g., OHWZ, NHWZ, tamarisk, mesquite, etc.) and vegetative structure (e.g., area and volume of tree, shrub, etc.) also varied widely at each patch. Larger patches in the upper portion of the river tended to be dominated by tamarisk vegetation, while many larger patches in the lower segment included a major mesquite component.

All but one patch included tree or shrub habitat, usually tamarisk and/or mesquite. Herbaceous understory was present to some degree in every patch. Overall, the variety of habitats, configurations, sizes, and geographic locations provides for a wide range of habitat characteristics to consider in modeling bird community - habitat relationships.

Table 5. Select habitat variables for each avian community - habitat survey patch, 1994 -1995. Habitat variables are described in detail in the text. River mile designations follow Stevens (1983). River segments are sections of the river that responded differently in the bird community - habitat models (refer to text for details).

Site:	Total Vegetated Area (m ²)	Area NHWZ (m ²)	Area OHWZ (m ²)	Tree Area (m ²)	Shrub Area (m ²)	Tree Volume Index	Shrub Volume Index	Tamarisk Volume Index	Mesquite Volume Index
River Segment A									
1.0 R [Paria]	19,004	18,552	0	15,665	2,857	40,154	17,685	53,261	0
1.6 R	7,692	7,321	153	0	7,321	11,257	6,617	0	0
2.0 L	9,804	1,614	7,644	1,110	3,391	1,624	4,049	1,776	0
3.7 L	10,575	4,111	2,078	3,728	2,016	9,472	1,911	10,345	0
5.1 L	4,095	1,807	571	1,807	0	7,228	367	7,589	0
5.2 R	7,891	6,910	346	4,567	2,343	12,960	1,274	9,796	0
46.0 L	24,914	13,023	11,891	13,768	11,146	33,226	10,140	6,710	11,296
46.7 R [Saddle]	41,346	25,045	14,237	29,629	7,405	80,794	14,259	65,845	13,528
47.5 L	6,982	2,530	2,842	3,854	2,974	8,219	2,349	3,127	0
48.5 L	6,556	3,093	3,396	3,396	3,093	11,956	1,916	0	7,556
49.1 R	38,978	10,337	25,298	29,168	7,969	51,587	18,180	15,056	39,148
49.2 L	16,714	4,342	10,855	9,433	5,794	20,512	7,939	0	18,394
50.0 R	55,303	20,303	26,254	39,865	15,276	106,086	23,142	58,868	45,944
73.9 R	3,485	3,177	0	896	2,282	5,514	2,053	2,890	0
74.1 R	6,173	2,003	0	1,684	4,489	7,478	2,245	4,842	0
74.3 R	2,102	2,009	0	0	2,009	1,356	2,232	0	0
74.4 L	37,882	19,431	15,354	18,217	19,369	47,138	27,964	8,088	31,476
76.5 L	16,842	3,917	12,925	12,925	3,917	14,727	7,520	0	14,217

Site:	Total Vegetated Area (m ²)	Area NHWZ (m ²)	Area OHWZ (m ²)	Tree Area (m ²)	Shrub Area (m ²)	Tree Volume Index	Shrub Volume Index	Tamarisk Volume Index	Mesquite Volume Index
River Segment B									
117.5 R	217	203	0	0	161	326	74	0	0
119.5 R	3,471	734	2,556	2,556	734	2,761	984	0	2,556
122.8 L	8,424	4,703	0	935	7,195	8,456	3,796	2,688	0
125.5 R	1,171	305	0	305	865	1103	612	831	0
131.3 R	6,973	2,257	4,198	4,198	2,257	3,830	3,555	0	0
River Segment C									
167.0 R	5,628	2,848	2,634	2,634	2,848	937	2,982	0	1,870
171.0 R [Stairway]	29,985	7,822	7,220	8,426	20,614	25,303	17,175	3,437	19,675
171.1 R	12,478	5,305	2,092	2,092	10,046	9,825	2,861	0	3,400
172.2 L	14,970	10,154	4,622	6,122	8,653	13,702	9,215	4,050	7,626
173.1 R	10,487	2,845	2,758	3,078	7,296	17,043	6,717	672	9,308
174.4 R	22,775	5,713	7,288	11,037	11,738	26,826	12,768	10,558	13,665
174.5 R	14,594	5,457	6,819	6,267	4,280	12,849	7,693	9,087	4,089
174.7 R	6,119	1,735	4,203	4,203	1,735	6,815	3,984	0	8,196
197.3 L	9,727	3,692	5,579	7,251	2,020	16,341	4,424	10,654	6,805
197.6 L	7,112	2,873	4,005	5,049	1,829	9,153	3,413	2,798	6,174
198.0 R [Parashant]	23,576	6,895	16,267	16,214	3,400	41,689	15,918	18,853	34,800
198.2 L	4,828	2,381	2,593	3,978	596	9,970	2,759	4,819	6,872
198.3 R	8,829	3,079	4,872	6,708	1,243	13,056	6,781	6,426	11,206
199.5 R	10,204	3,260	4,850	4,850	5,354	16,666	7,343	9,393	8,730
200.0 L	21,247	11,658	9,588	11,985	9,262	14,360	19,486	6,829	15,341
200.4 R	10,195	3,288	5,719	6,593	2,864	10,400	4,466	744	8,864
200.5 R	17,453	9,182	6,124	10,217	6,268	23,155	13,091	15,758	10,717
202.5 R	17,614	5,024	12,297	12,297	5,024	25,024	15,437	0	34,432
204.1 R	41,429	16,256	23,699	29,120	10,834	48,560	22,526	17,834	48,857
204.5 R [Spring]	74,133	24,868	46,924	48,961	19,252	112,860	41,835	12,110	120,315
206.5 L	14,993	7,686	7,308	7,308	7,686	14,889	10,711	0	14,249
208.7 R	8,785	4,050	4,337	6,086	2,302	15,180	3,469	6,549	9,108
213.6 L	5,654	3,374	2,280	3,453	2,135	12,270	3,416	6,041	4,332
214.0 L	5,993	3,050	2,943	5,609	384	13,543	4,151	11,597	5,886
214.2 L	777	396	382	382	396	465	544	0	745
224.0 L	1,278	246	48	0	340	396	289	228	0
224.1 R	1,390	508	103	279	1,057	710	347	739	0

BIRD COMMUNITY AND HABITAT RELATIONSHIPS

Breeding Pair Abundance and Habitat

Differences between years. Overall mean breeding pair abundance at sites did not differ (one-way ANOVA; $F = 0.425$; $df = 1$; $P = 0.516$) between 1994 (10.8 ± 1.6) and 1995 (10.7 ± 1.3). Additionally, the lack of year differences was consistent among river segments (test of YEAR*SEG interaction in full factorial model; $F = 0.596$; $df = 2$; $P = 0.554$).

There was also no evidence of year differences in the abundance of breeding pairs per patch for any analysis which included a single covariate. For each series of the 7 models that we ran for each covariate, there was no significant 3-way interaction ($P \geq 0.217$) among YEAR, SEG, and the covariate (see MODEL 1 of Table 6). Likewise, we found no significant 2-way interactions ($P \geq 0.061$) between YEAR and SEG, or YEAR and the covariate (see MODELS 2-4 of Table 6). Finally, there was no significant contribution by YEAR ($P \geq 0.319$) in the main effects only models (see MODEL 5 of Table 6). We therefore conclude that the abundance of breeding pairs per patch did not differ between 1994 and 1995 for any segment of the river.

Differences among river segments. Abundance differed by river segment (one-way ANOVA; $F = 9.6$; $df = 2$; $P < 0.001$). Abundance for river segment B (4.5 ± 1.1) was lower than that for river segment A (9.0 ± 1.0) and river segment C (13.2 ± 1.7) (Bonferroni's multiple comparisons; $P = 0.021$ and < 0.001 respectively), while river segment A did not differ from river segment C ($P = 0.084$).

Among the series of 7 models we ran for each covariate, SEG was a significant factor in the "best" model. The main effect SEG and/or the SEG*covariate interaction was always highly significant ($P \leq 0.021$; see shaded cells in Table 6). We therefore conclude that the abundance of breeding pairs per patch differed by river segment.

Covariates. All covariates were positively correlated with abundance of breeding pairs and all except BACH, GRASS, and WILLOW were highly and significantly correlated with ABUND (Spearman's $\rho \geq 0.426$; $P < 0.01$). Each individual covariate that we considered, in the presence of SEG, accounted for a significant proportion of the variation in abundance ($P \leq 0.021$; see shaded cells in Table 6). Among the series of models considered for each covariate, the "best" model contained the main effects SEG and the covariate for 7 of the covariates (see MODEL 6 in Table 6), and contained the additional SEG*covariate interaction term for the remaining 10 covariates (see MODEL 7 in Table 6). Covariates AREA, VEG, TREE, NHWZ, TREEVOL, SHRBVOL, and TAM (in the presence of SEG) accounted for the greatest proportion of the variation in abundance ($0.605 \leq R^2 \leq 0.685$; see MODELS 6 and 7 in Table 6). Among the significant interactions, abundance increased with AREA, VEG, HERB, NHWZ, TREEVOL, and SHRBVOL, at a greater rate for river segment B than for river segments A and C (e.g. see Figure 2). Abundance increased with TAM and TAMVOL at a lesser rate for river segment A than for river segments B and C (e.g. See Figure 3). For covariates MESQ and MESQVOL, the interaction term was not meaningful since mesquite was found at only one patch in segment B.

We therefore conclude that covariates associated with total patch size (total area and vegetated area), and covariates associated with areas and volumes composed primarily of large vegetation structures (tree area, new-high-water-zone area, tamarisk area, tree volume and shrub volume) have the greatest potential, among those considered, to predict abundance. Additionally, abundance increased at the greatest rate with most of the vegetation variables for river segment B, but increased at a lesser rate for tamarisk area and volume for river segment A.

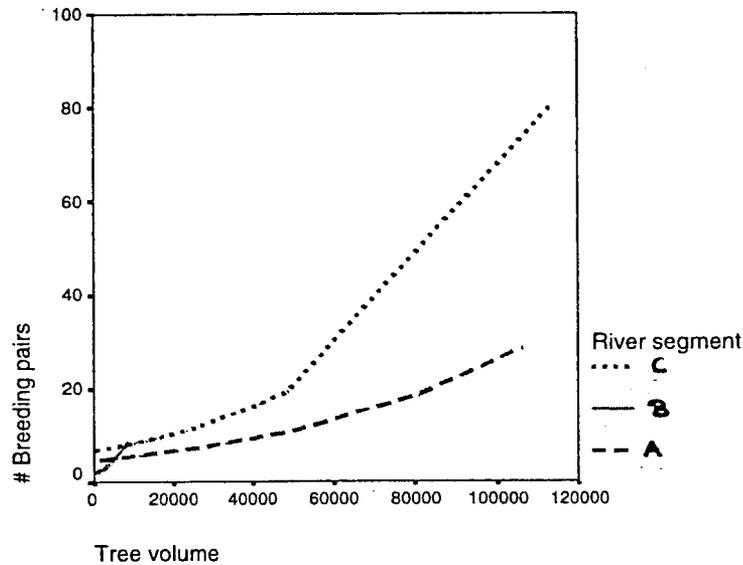


Figure 2. Predicted values of model $\log_{10}(\text{ABUND}) = \text{SEG} + \text{TREEVOL} + (\text{SEG} * \text{TREEVOL})$. Tree volume index calculations are described in the text.

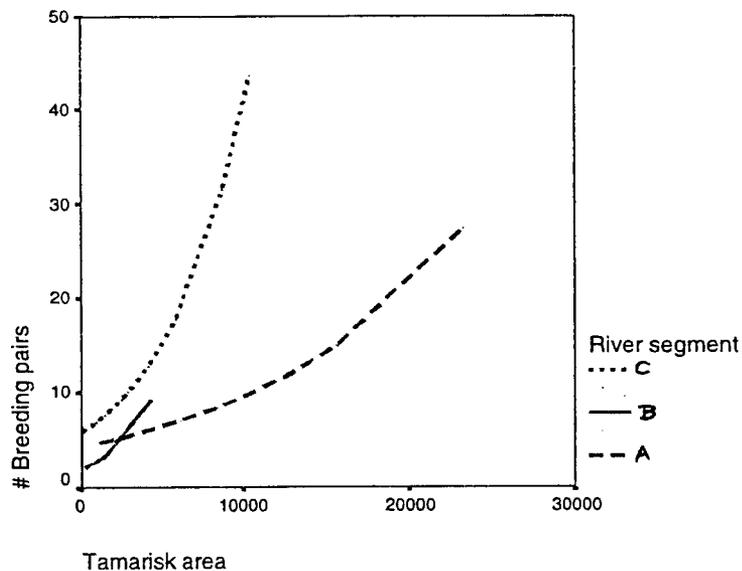


Figure 3. Predicted values from model $\log_{10}(\text{ABUND}) = \text{SEG} + \text{TAM} + (\text{SEG} * \text{TAM})$. Tamarisk area is in square meters.

Table 6. Response variable: $\log_{10}(\text{ABUND})$. Correlation coefficients and results of hypothesis tests of the effective contribution of terms used during the step-down modeling approach to evaluate the significance of individual covariates in the presence of factors YEAR and SEG on the transformed response variable $\log_{10}(\text{ABUND})$. The first line in each cell is the model correlation coefficient. The second line is the term in the model that had the highest P-value within the class of the specified term. Model 7 contains 2 main effects and their interaction, and differs from model 4 which has all 3 main effects and the single interaction. Outlined cells contain P values < 0.1, while shaded cells indicate a good model for inference for each covariate. Comparisons within columns allow for selecting the best covariates for a given model.

Covariate	Models with 2-Way interactions							Models with only main effects		MODEL 7: Model 6 with interaction added
	MODEL 1: Full factorial model	MODEL 2: All three 2-way interactions			MODEL 3: Two 2-way interactions		MODEL 4: One 2-way interaction	MODEL 5: All 3 main effects only	MODEL 6: Two main effects	
	7 parameters	6 parameters	5 parameters	4 parameters	4 parameters	3 parameters	3 parameters	2 parameters		
AREA	$R^2 = 0.673$ 3-way P = 0.493	$R^2 = 0.666$ YEAR*SEG P = 0.293	$R^2 = 0.655$ YEAR*AREA P = 0.205	$R^2 = 0.647$ SEG*AREA P = 0.017	$R^2 = 0.607$ YEAR P = 0.576	$R^2 = 0.605$ SEG & AREA P < 0.001	$R^2 = 0.646$ SEG*AREA P = 0.015			
VEG	$R^2 = 0.688$ 3-way P = 0.404	$R^2 = 0.679$ YEAR*SEG P = 0.269	$R^2 = 0.667$ YEAR*VEG P = 0.162	$R^2 = 0.658$ SEG*VEG P = 0.019	$R^2 = 0.620$ YEAR P = 0.563	$R^2 = 0.619$ SEG & VEG P < 0.001	$R^2 = 0.658$ SEG*VEG P = 0.017			
TREE	$R^2 = 0.668$ 3-way P = 0.368	$R^2 = 0.658$ SEG*TREE P = 0.934	$R^2 = 0.657$ YEAR*SEG P = 0.267	$R^2 = 0.645$ YEAR*TREE P = 0.061	$R^2 = 0.628$ YEAR P = 0.468	$R^2 = 0.625$ SEG & TREE P < 0.001	$R^2 = 0.627$ SEG*TREE P = 0.896			
SHRB	$R^2 = 0.454$ 3-way P = 0.917	$R^2 = 0.453$ YEAR*SHRB P = 0.886	$R^2 = 0.452$ YEAR*SEG P = 0.348	$R^2 = 0.436$ SEG*SHRB P = 0.076	$R^2 = 0.396$ YEAR P = 0.673	$R^2 = 0.395$ SEG & SHRB P < 0.001	$R^2 = 0.435$ SEG*SHRB P = 0.076			
HERB	$R^2 = 0.474$ 3-way P = 0.831	$R^2 = 0.472$ YEAR*SEG P = 0.499	$R^2 = 0.461$ YEAR*HERB P = 0.252	$R^2 = 0.452$ SEG*HERB P = 0.025	$R^2 = 0.395$ YEAR P = 0.319	$R^2 = 0.387$ SEG & HERB P < 0.001	$R^2 = 0.446$ SEG*HERB P = 0.021			
NHWZ	$R^2 = 0.655$ 3-way P = 0.481	$R^2 = 0.655$ YEAR*NHWZ P = 0.343	$R^2 = 0.651$ YEAR*SEG P = 0.307	$R^2 = 0.639$ SEG*NHWZ P = 0.012	$R^2 = 0.594$ YEAR P = 0.571	$R^2 = 0.593$ SEG & NHWZ P < 0.001	$R^2 = 0.639$ SEG*NHWZ P = 0.010			
OHWZ	$R^2 = 0.591$ 3-way P = 0.324	$R^2 = 0.578$ SEG*OHWZ P = 0.882	$R^2 = 0.577$ YEAR*SEG P = 0.307	$R^2 = 0.563$ YEAR*OHWZ P = 0.094	$R^2 = 0.546$ YEAR P = 0.414	$R^2 = 0.542$ SEG & OHWZ P < 0.001	$R^2 = 0.544$ SEG*OHWZ P = 0.906			
TREEVOL	$R^2 = 0.707$ 3-way P = 0.787	$R^2 = 0.705$ YEAR*SEG P = 0.314	$R^2 = 0.695$ YEAR*TREEVOL P = 0.122	$R^2 = 0.685$ SEG*TREEVOL P = 0.004	$R^2 = 0.635$ YEAR P = 0.582	$R^2 = 0.634$ SEG & TREEVOL P < 0.001	$R^2 = 0.685$ SEG*TREEVOL P = 0.003			

Covariate	Models with 2-Way interactions				Models with only main effects		
	MODEL 1: Full factorial model 7 parameters	MODEL 2: All three 2-way interactions 6 parameters	MODEL 3: Two 2-way interactions 5 parameters	MODEL 4: One 2-way interaction 4 parameters	MODEL 5: All 3 main effects only	MODEL 6: Two main effects	MODEL 7: Model 6 with interaction added
SHRBVOL	$R^2 = 0.37$ 3-way $P = 0.783$	$R^2 = 0.634$ YEAR*SHRBVOL $P = 0.529$	$R^2 = 0.632$ YEAR*SEG $P = 0.251$	$R^2 = 0.618$ SEG*SHRBVOL $P = 0.008$	$R^2 = 0.565$ YEAR $P = 0.628$	$R^2 = 0.564$ SEG & SHRBVOL $P \leq 0.003$	$R^2 = 0.617$ SEG*SHRBVOL $P = 0.007$
TAMVOL	$R^2 = 0.568$ 3-way $P = 0.790$	$R^2 = 0.565$ YEAR*SEG $P = 0.667$	$R^2 = 0.560$ YEAR*TAMVOL $P = 0.612$	$R^2 = 0.559$ SEG*TAMVOL $P < 0.001$	$R^2 = 0.437$ YEAR $P = 0.482$	$R^2 = 0.434$ SEG & TAMVOL $P < 0.001$	$R^2 = 0.555$ SEG*TAMVOL $P < 0.001$
MESQVOL	$R^2 = 0.591$ 3-way $P = 0.217$	$R^2 = 0.582$ YEAR*SEG $P = 0.620$	$R^2 = 0.577$ YEAR*MESQVOL $P = 0.140$	$R^2 = 0.564$ SEG*MESQVOL $P = 0.012$	$R^2 = 0.510$ YEAR $P = 0.529$	$R^2 = 0.507$ SEG & MESQVOL $P \leq 0.002$	$R^2 = 0.563$ SEG*MESQVOL $P = 0.011$
ARROW	$R^2 = 0.371$ 3-way $P = 0.546$	$R^2 = 0.360$ YEAR*ARROW $P = 0.976$	$R^2 = 0.360$ SEG*ARROW $P = 0.530$	$R^2 = 0.349$ YEAR*SEG $P = 0.327$	$R^2 = 0.329$ YEAR $P = 0.506$	$R^2 = 0.325$ SEG & ARROW $P \leq 0.004$	$R^2 = 0.341$ SEG*ARROW $P = 0.402$
BACH	$R^2 = 0.365$ 3-way $P = 0.976$	$R^2 = 0.364$ YEAR*BACH $P = 0.776$	$R^2 = 0.364$ YEAR*SEG $P = 0.524$	$R^2 = 0.352$ SEG*BACH $P = 0.140$	$R^2 = 0.317$ YEAR $P = 0.459$	$R^2 = 0.312$ SEG & BACH $P = 0.001$	$R^2 = 0.349$ SEG*BACH $P = 0.126$
GRASS	$R^2 = 0.297$ 3-way $P = 0.998$	$R^2 = 0.297$ SEG*GRASS $P = 0.763$	$R^2 = 0.296$ YEAR*SEG $P = 0.455$	$R^2 = 0.281$ YEAR*GRASS $P = 0.265$	$R^2 = 0.269$ YEAR $P = 0.358$	$R^2 = 0.261$ SEG & GRASS $P \leq 0.011$	$R^2 = 0.263$ SEG*GRASS $P = 0.648$
MESQ	$R^2 = 0.604$ 3-way $P = 0.306$	$R^2 = 0.598$ YEAR*SEG $P = 0.541$	$R^2 = 0.591$ YEAR*MESQ $P = 0.100$	$R^2 = 0.575$ SEG*MESQ $P = 0.018$	$R^2 = 0.527$ YEAR $P = 0.440$	$R^2 = 0.524$ SEG & MESQ $P \leq 0.001$	$R^2 = 0.574$ SEG*MESQ $P = 0.015$
TAM	$R^2 = 0.663$ 3-way $P = 0.892$	$R^2 = 0.662$ YEAR*TAM $P = 0.412$	$R^2 = 0.658$ YEAR*SEG $P = 0.350$	$R^2 = 0.648$ SEG*TAM $P < 0.001$	$R^2 = 0.558$ YEAR $P = 0.455$	$R^2 = 0.555$ SEG & TAM $P < 0.001$	$R^2 = 0.647$ SEG*TAM $P < 0.001$
WILLOW	$R^2 = 0.347$ 3-way $P = 0.852$	$R^2 = 0.344$ YEAR*WILLOW $P = 0.684$	$R^2 = 0.343$ YEAR*SEG $P = 0.646$	$R^2 = 0.335$ SEG*WILLOW $P = 0.104$	$R^2 = 0.293$ YEAR $P = 0.386$	$R^2 = 0.286$ SEG & WILLOW $P < 0.002$	$R^2 = 0.330$ SEG*WILLOW $P = 0.094$

Bird Species Richness and Habitat

Differences between years. Overall mean bird species richness per patch did not differ (one-way ANOVA; $F = 0.300$; $df = 1$; $P = 0.585$) between 1994 (8.0 ± 0.6) and 1995 (6.6 ± 0.5). Additionally, the lack of year differences was consistent among river segment (test of YEAR*SEG interaction in full factorial model; $F = 0.073$; $df = 2$; $P = 0.929$).

There was also no evidence of year differences in the richness of breeding pairs per patch for any analysis which included a single covariate. For each series of the 7 models we ran for each covariate, there was no significant 3-way interaction ($P \geq 0.271$) among YEAR, SEG, and the covariate (see MODEL 1 of Table 7). Likewise, we found no significant 2-way interactions ($P \geq 0.099$) between YEAR and SEG, or YEAR and the covariate (see MODELS 2-4 of Table 7). Finally, there was no significant contribution by YEAR ($P \geq 0.371$) in the main effects only models (see MODEL 5 of Table 7). We therefore conclude that the richness of breeding pairs per patch did not differ between 1994 and 1995 for any segment of the river.

Differences among river segments. Species richness differed by river segment (one-way ANOVA; $F = 8.7$; $df = 2$; $P < 0.001$). Species richness for river segment C (8.0 ± 0.5) was greater than that for river segment A (6.0 ± 0.5) and river segment B (3.4 ± 0.9) (Bonferroni's multiple comparisons; $P = 0.026$ and $= 0.001$ respectively), while river segment A did not differ from river segment B ($P = 0.128$).

Among the series of 7 models run for each covariate, SEG was a significant factor in the "best" model. The main effect SEG and/or the SEG*covariate interaction was always highly significant ($P \leq 0.019$; see shaded cells in Table 7). We therefore conclude that species richness of breeding pairs per patch differed by river segment.

Covariates. All covariates were positively correlated with bird species richness and all except BACH, GRASS, and WILLOW were highly significantly correlated with richness (Spearman's $\rho \geq 0.401$; $P < 0.01$). Each individual covariate considered, in the presence of SEG, accounted for a significant proportion of the variation in richness ($P \leq 0.019$; see shaded cells in Table 7). Among the series of models considered for each covariate, the "best" model contained the main effects SEG and the covariate for 14 of the covariates (see MODEL 6 in Table 7), and contained the additional SEG*covariate interaction term for the remaining 3 covariates (see MODEL 7 in Table 7). Covariates TREEVOL, TAM, and TAMVOL (in the presence of SEG) accounted for the greatest proportion of the variation in richness for the interaction models ($0.569 \leq R^2 \leq 0.611$; see MODEL 7 in Table 7), while covariates TREEVOL, TREE and NHWZ accounted for the greatest proportion of the variation in richness for the main effects models ($0.533 \leq R^2 \leq 0.562$; see MODEL 6 in Table 7). Richness increased with TREEVOL, TAM, and TAMVOL at the greatest rate for river segment B, then C, and at the lowest rate for river segment A (e.g. see Figure 4).

We therefore conclude that covariates associated with tamarisk and trees (tree area and volume, tamarisk area and volume, and new-high-water-zone area) have the greatest potential, among those considered, to predict species richness. Additionally, species richness increased at the greatest rate with tamarisk area and volume, and tree volume, for river segment B.

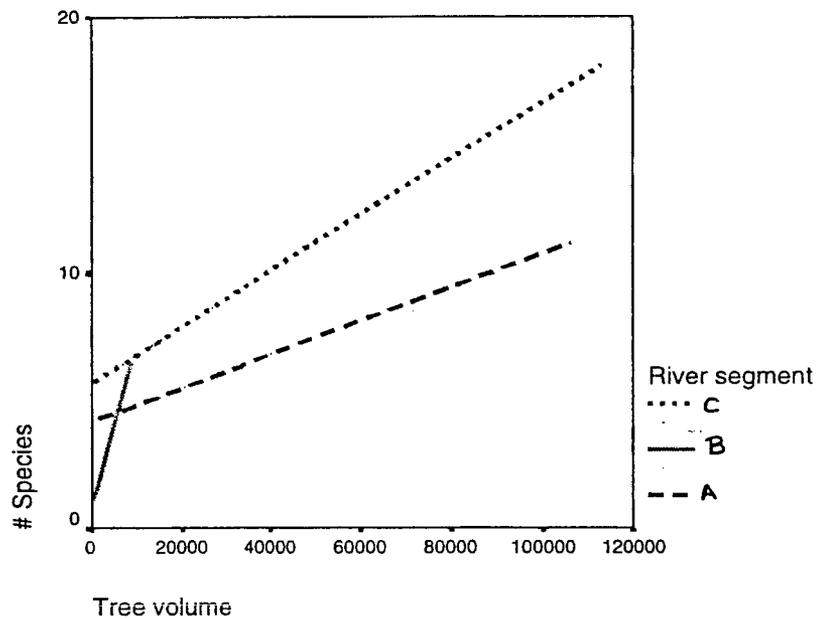


Figure 4. Predicted values for model $RICH = SEG + TREEVOL + (SEG * TREEVOL)$. Tree volume index calculations are described in the text. RICH showed similar patterns with TAM and TAMVOL.

Table 7. **Response variable: RICH.** Correlation coefficients and results of hypothesis tests of the effective contribution of terms used during the step-down modeling approach to evaluate the significance of individual covariates in the presence of factors YEAR and SEG on the transformed response variable RICH. The first line in each cell is the model correlation coefficient. The second line is the term in the model that had the highest P-value within the class of interaction (3-way, 2-way, or main effect), and this was the term that was dropped prior to running the model in the next column. The last line in each cell is the P-value of the specified term. Model 7 contains 2 main effects and their interaction, and differs from model 4 which has all 3 main effects and the single interaction. Outlined cells contain P values < 0.1, while shaded cells indicate a good model for inference for each covariate. Comparisons within columns allow for selecting the best covariates for a given model.

Covariate	Models with 2-Way interactions				Models with only main effects	
	MODEL 1: Full factorial model 7 parameters	MODEL 2: All three 2-way interactions 6 parameters	MODEL 3: Two 2-way interactions 5 parameters	MODEL 4: One 2-way interaction 4 parameters	MODEL 5: All 3 main effects only	MODEL 6: Two main effects
AREA	R ² = 0.522 3-way P = 0.547	R ² = 0.545 YEAR*AREA P = 0.658	R ² = 0.543 YEAR*SEG P = 0.630	R ² = 0.538 SEG*AREA P = 0.182	R ² = 0.516 YEAR P = 0.660	R ² = 0.515 SEG*AREA P < 0.001
VEG	R ² = 0.557 3-way P = 0.472	R ² = 0.548 YEAR*VEG P = 0.720	R ² = 0.547 YEAR*SEG P = 0.614	R ² = 0.541 SEG*VEG P = 0.291	R ² = 0.526 YEAR P = 0.650	R ² = 0.524 SEG*VEG P < 0.001
TREE	R ² = 0.568 3-way P = 0.345	R ² = 0.554 YEAR*TREE P = 0.884	R ² = 0.554 YEAR*SEG P = 0.713	R ² = 0.550 SEG*TREE P = 0.301	R ² = 0.535 YEAR P = 0.568	R ² = 0.535 SEG*TREE P < 0.001
SHRB	R ² = 0.360 3-way P = 0.764	R ² = 0.355 YEAR*SEG P = 0.596	R ² = 0.346 YEAR*SHRB P = 0.450	R ² = 0.341 SEG*SHRB P = 0.366	R ² = 0.323 YEAR P = 0.708	R ² = 0.322 SEG*SHRB P < 0.002
HERB	R ² = 0.462 3-way P = 0.745	R ² = 0.458 YEAR*SEG P = 0.870	R ² = 0.456 YEAR*HERB P = 0.099	R ² = 0.435 SEG*HERB P = 0.044	R ² = 0.386 YEAR P = 0.371	R ² = 0.380 SEG*HERB P < 0.001
NHWZ	R ² = 0.574 3-way P = 0.900	R ² = 0.573 YEAR*NHWZ P = 0.715	R ² = 0.572 YEAR*SEG P = 0.678	R ² = 0.568 SEG*NHWZ P = 0.146	R ² = 0.545 YEAR P = 0.659	R ² = 0.544 SEG*NHWZ P < 0.001
OHWZ	R ² = 0.497 3-way P = 0.271	R ² = 0.478 YEAR*OHWZ P = 0.860	R ² = 0.478 YEAR*SEG P = 0.675	R ² = 0.472 SEG*OHWZ P = 0.274	R ² = 0.454 YEAR P = 0.508	R ² = 0.451 SEG*OHWZ P < 0.001
TREEVOL	R ² = 0.618 3-way P = 0.783	R ² = 0.615 YEAR*TREEVOL P = 0.817	R ² = 0.615 YEAR*SEG P = 0.740	R ² = 0.612 SEG*TREEVOL P = 0.012	R ² = 0.563 YEAR P = 0.673	R ² = 0.562 SEG & TREEVOL P < 0.001
						MODEL 7: Model 6 with interaction added
						R ² = 0.537 SEG*AREA P = 0.167
						R ² = 0.540 SEG*YEAR P = 0.271
						R ² = 0.548 SEG*TREE P = 0.292
						R ² = 0.340 SEG*SHRB P = 0.360
						R ² = 0.430 SEG*HERB P = 0.040
						R ² = 0.567 SEG*NHWZ P = 0.134
						R ² = 0.470 SEG*OHWZ P = 0.259
						R ² = 0.611 SEG*TREEVOL P = 0.011

Covariate	MODEL 1: Full factorial model 7 parameters	Models with 2-Way interactions				Models with only main effects		MODEL 7: Model 6 with interaction added
		MODEL 2: All three 2-way interactions 6 parameters	MODEL 3: Two 2-way interactions 5 parameters	MODEL 4: One 2-way interaction 4 parameters	MODEL 5: All 3 main effects only	MODEL 6: Two main effects		
SHRBVOL	R ² = 0.525 3-way P = 0.794	R ² = 0.522 YEAR*SEG P = 0.528	R ² = 0.513 YEAR*SHRBVOL P = 0.613	R ² = 0.512 SEG*SHRBVOL P = 0.382	R ² = 0.499 YEAR P = 0.704	R ² = 0.498 SEG & SHRBVOL P < 0.005	R ² = 0.511 SEG*SHRBVOL P = 0.367	
TAMVOL	R ² = 0.579 3-way P = 0.621	R ² = 0.573 YEAR*SEG P = 0.994	R ² = 0.573 YEAR*TAMVOL P = 0.583	R ² = 0.571 SEG*TAMVOL P < 0.001	R ² = 0.420 YEAR P = 0.554	R ² = 0.417 SEG & TAMVOL P < 0.001	R ² = 0.569 SEG*TAMVOL P < 0.001	
MESQVOL	R ² = 0.476 3-way P = 0.274	R ² = 0.467 YEAR*MESQVOL P = 0.946	R ² = 0.467 YEAR*SEG P = 0.758	R ² = 0.463 SEG*MESQVOL P = 0.598	R ² = 0.456 YEAR P = 0.607	R ² = 0.454 SEG & MESQVOL P < 0.006	R ² = 0.462 SEG*MESQVOL P = 0.568	
ARROW	R ² = 0.346 3-way P = 0.277	R ² = 0.322 SEG*ARROW P = 0.985	R ² = 0.322 YEAR*SEG P = 0.538	R ² = 0.310 YEAR*ARROW P = 0.700	R ² = 0.309 YEAR P = 0.572	R ² = 0.306 SEG & ARROW P < 0.013	R ² = 0.307 SEG*ARROW P = 0.960	
BACH	R ² = 0.297 3-way P = 0.856	R ² = 0.294 YEAR*BACH P = 0.974	R ² = 0.294 YEAR*SEG P = 0.815	R ² = 0.290 SEG*BACH P = 0.365	R ² = 0.271 YEAR P = 0.523	R ² = 0.267 SEG & BACH P < 0.003	R ² = 0.288 SEG*BACH P = 0.336	
GRASS	R ² = 0.258 3-way P = 0.752	R ² = 0.257 YEAR*SEG P = 0.898	R ² = 0.255 SEG*GRASS P = 0.557	R ² = 0.251 YEAR*GRASS P = 0.345	R ² = 0.243 YEAR P = 0.419	R ² = 0.236 SEG & GRASS P < 0.019	R ² = 0.241 SEG*GRASS P = 0.482	
MESQ	R ² = 0.482 3-way P = 0.369	R ² = 0.473 YEAR*MESQ P = 0.821	R ² = 0.472 YEAR*SEG P = 0.741	R ² = 0.468 SEG*MESQ P = 0.365	R ² = 0.453 YEAR P = 0.526	R ² = 0.450 SEG & MESQ P < 0.002	R ² = 0.466 SEG*MESQ P = 0.332	
TAM	R ² = 0.622 3-way P = 0.526	R ² = 0.615 YEAR*SEG P = 0.828	R ² = 0.613 YEAR*TAM P = 0.602	R ² = 0.612 SEG*TAM P < 0.001	R ² = 0.522 YEAR P = 0.539	R ² = 0.520 SEG & TAM P < 0.001	R ² = 0.611 SEG*TAM P < 0.001	
WILLOW	R ² = 0.286 3-way P = 0.784	R ² = 0.281 YEAR*WILLOW P = 0.757	R ² = 0.278 YEAR*SEG P = 0.845	R ² = 0.275 SEG*WILLOW P = 0.328	R ² = 0.253 YEAR P = 0.454	R ² = 0.247 SEG & WILLOW P < 0.010	R ² = 0.270 SEG*WILLOW P = 0.320	

Shannon Diversity Index and Habitat

Differences between years. As with abundance and species richness, the overall mean Shannon diversity index per site did not differ between 1994 (1.7 ± 0.09) and 1995 (1.6 ± 0.08) (one-way ANOVA; $F = 0.449$; $df = 1$; $P = 0.505$). Additionally, the lack of year differences was consistent among river segment (test of YEAR*SEG interaction in full factorial model; $F = 0.157$; $df = 2$; $P = 0.855$).

There was also no evidence of year differences in the Shannon diversity index per patch for any analysis which included a single covariate. For each series of the 7 models we ran for each covariate, there was no significant 3-way interaction ($P \geq 0.271$) among YEAR, SEG, and the covariate (see MODEL 1 of Table 8). Likewise, we found no significant 2-way interactions ($P \geq 0.099$) between YEAR and SEG, or YEAR and the covariate (see MODELS 2-4 of Table 8). Finally, we found no significant contribution by YEAR ($P \geq 0.371$) in the main effects only models (see MODEL 5 of Table 8). We therefore conclude that diversity per patch, as measured by the Shannon diversity index, did not differ between 1994 and 1995 for any segment of the river.

Differences among river segments. The Shannon diversity index differed by river segment (one-way ANOVA; $F = 10.193$; $df = 2$; $P < 0.001$). The Shannon diversity index for river segment C (1.9 ± 0.06) was greater than that for river segment A (1.6 ± 0.09) and river segment B (0.9 ± 0.3) (Bonferroni's multiple comparisons; $P = 0.018$ and < 0.001 respectively), while river segment A did not differ from river segment B (February 2, 1998 ($P = 0.066$)).

Among the series of 7 models run for each covariate, SEG was a significant factor in the "best" model. The main effect SEG and/or the SEG*covariate interaction was always highly significant ($P \leq 0.036$; see shaded cells in Table 8). We therefore conclude that avian diversity per patch, as measured by the Shannon diversity index, differed by river segment.

Covariates. Interpretation of covariates for the Shannon diversity index was almost identical to that for species richness. All covariates were positively correlated with SDI and all except BACH, GRASS, and WILLOW were highly and significantly correlated with SDI (Spearman's $\rho \geq 0.406$; $P < 0.01$). In all but one case (GRASS), each individual covariate we considered, in the presence of SEG, accounted for a significant proportion of the variation in SDI ($P \leq 0.013$; see shaded cells in Table 8). Among the series of models considered for each covariate, the "best" model contained the main effects SEG and the covariate for 13 of the covariates (see MODEL 6 in Table 8), and contained the additional SEG*covariate interaction term for 3 of the remaining covariates (see MODEL 7 in Table 8). Covariates TAM, TAMVOL, and NHWZ (in the presence of SEG) accounted for the greatest proportion of the variation in SDI for the interaction models ($0.504 \leq R^2 \leq 0.545$; see MODEL 7 in Table 8), while covariates TAM, NHWZ, and TREEVOL accounted for the greatest proportion of the variation in SDI for the main effects models ($0.435 \leq R^2 \leq 0.486$; see MODEL 6 in Table 8). SDI increased with TREEVOL, TAM, and TAMVOL at the greatest rate for river segment B, then C, and at the lowest rate for river segment A (e.g. see Figures 5 and 6).

We therefore conclude that covariates associated with tamarisk and trees (tamarisk area and volume, tree volume, and new-high-water-zone area) have the greatest potential, among those considered, to predict species diversity as measured by the Shannon diversity index. Additionally, the Shannon diversity index increased at the greatest rate with tamarisk area and volume, and tree volume, for river segment B.

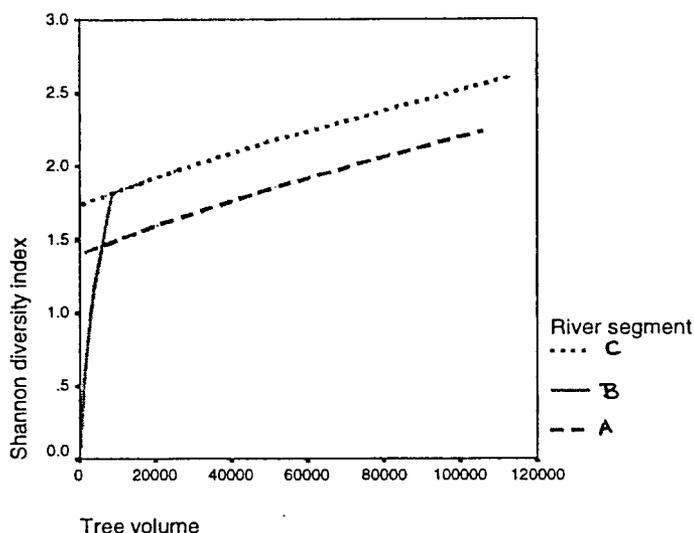


Figure 5. Predicted values for model: $SDI^2 = SEG + TREEVOL + (SEG * TREEVOL)$. Tree volume index calculations are described in the text.

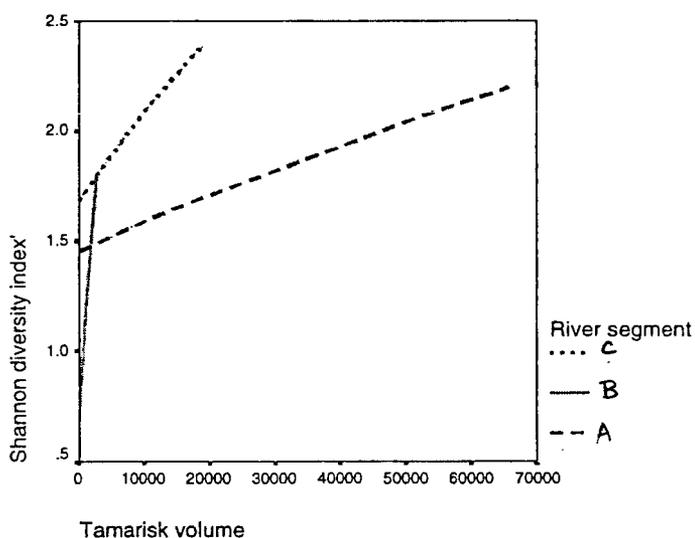


Figure 6. Predicted values of model: $SDI^2 = SEG + TAMVOL + (SEG * TAMVOL)$. Tamarisk volume index calculations are described in the text.

Table 8. **Response variable: SDI².** Correlation coefficients and results of hypothesis tests of the effective contribution of terms used during the step-down modeling approach to evaluate the significance of individual covariates in the presence of factors YEAR and SEG on the transformed response variable SDI². The first line in each cell is the model correlation coefficient. The second line is the term in the model that had the highest P-value within the class of interaction (3-way, 2-way, or main effect), and this was the term that was dropped prior to running the model in the next column. The last line in each cell is the P-value of the specified term. Model 7 contains 2 main effects and their interaction, and differs from model 4 which has all 3 main effects and the single interaction. Outlined cells contain P values < 0.1, while shaded cells indicate a good model for inference for each covariate. Comparisons within columns allow for selecting the best covariates for a given model.

Covariate	MODEL 1: Full factorial model 7 parameters	Models with 2-Way interactions			Models with only main effects		
		MODEL 2: All three 2-way interactions 6 parameters	MODEL 3: Two 2- way interactions 5 parameters	MODEL 4: One 2- way interaction 4 parameters	MODEL 5: All 3 main effects only	MODEL 6: Two main effects	MODEL 7: Model 6 with interaction added
AREA	R ² = 0.446 3-way P = 0.777	R ² = 0.446 YEAR*AREA P = 0.777	R ² = 0.442 YEAR*SEG P = 0.614	R ² = 0.435 SEG*AREA P = 0.153	R ² = 0.406 YEAR P = 0.519	R ² = 0.403 SEG & AREA P < 0.001	R ² = 0.433 SEG*AREA P = 0.139
VEG	R ² = 0.449 3-way P = 0.682	R ² = 0.443 YEAR*VEG P = 0.857	R ² = 0.443 YEAR*SEG P = 0.612	R ² = 0.435 SEG*VEG P = 0.193	R ² = 0.410 YEAR P = 0.512	R ² = 0.407 SEG & VEG P < 0.001	R ² = 0.433 SEG*VEG P = 0.180
TREE	R ² = 0.440 3-way P = 0.376	R ² = 0.424 SEG*TREE P = 0.784	R ² = 0.420 YEAR*SEG P = 0.725	R ² = 0.415 YEAR*TREE P = 0.542	R ² = 0.412 YEAR P = 0.462	R ² = 0.408 SEG & TREE P < 0.001	R ² = 0.412 SEG*TREE P = 0.797
SHRB	R ² = 0.367 3-way P = 0.727	R ² = 0.362 YEAR*SHRB P = 0.576	R ² = 0.359 YEAR*SEG P = 0.584	R ² = 0.349 SEG*SHRB P = 0.096	R ² = 0.307 YEAR P = 0.565	R ² = 0.304 SEG & SHRB P = 0.001	R ² = 0.346 SEG*SHRB P = 0.093
HERB	R ² = 0.345 3-way P = 0.767	R ² = 0.340 YEAR*SEG P = 0.833	R ² = 0.337 SEG*HERB P = 0.296	R ² = 0.315 YEAR*HERB P = 0.212	R ² = 0.300 YEAR P = 0.344	R ² = 0.292 SEG & HERB P < 0.003	R ² = 0.318 SEG*HERB P = 0.242
NHWZ	R ² = 0.513 3-way P = 0.968	R ² = 0.513 YEAR*NHWZ P = 0.937	R ² = 0.513 YEAR*SEG P = 0.616	R ² = 0.506 SEG*NHWZ P = 0.062	R ² = 0.468 YEAR P = 0.522	R ² = 0.465 SEG & NHWZ P < 0.001	R ² = 0.504 SEG*NHWZ P = 0.057
OHWZ	R ² = 0.378 3-way = 0.260	R ² = 0.354 YEAR*SEG P = 0.735	R ² = 0.348 SEG*OHWZ P = 0.550	R ² = 0.337 YEAR*OHWZ P = 0.461	R ² = 0.333 YEAR P = 0.426	R ² = 0.327 SEG & OHWZ P < 0.001	R ² = 0.338 SEG*OHWZ P = 0.541
TREEVOL	R ² = 0.491 3-way P = 0.927	R ² = 0.489 YEAR*TREEVOL P = 0.882	R ² = 0.489 YEAR*SEG P = 0.714	R ² = 0.485 SEG*TREEVOL P = 0.040	R ² = 0.438 YEAR P = 0.527	R ² = 0.435 SEG & TREEVOL P < 0.001	R ² = 0.483 SEG*TREEVOL P = 0.036

Covariate	Models with 2-Way interactions				Models with only main effects	
	MODEL 1: Full factorial model 7 parameters	MODEL 2: All three 2-way interactions 6 parameters	MODEL 3: Two 2-way interactions 5 parameters	MODEL 4: One 2-way interaction 4 parameters	MODEL 5: All 3 main effects only	MODEL 6: Two main effects
						MODEL 7: Model 6 with interaction added
SHRBVOL	R ² = 0.447 3-way P = 0.850	R ² = 0.444 YEAR*SHRBVOL P = 0.930	R ² = 0.444 YEAR*SEG P = 0.562	R ² = 0.435 SEG*SHRBVOL P = 0.099	R ² = 0.400 YEAR P = 0.548	R ² = 0.433 SEG*SHRBVOL P = 0.095
TAMVOL	R ² = 0.550 3-way P = 0.449	R ² = 0.540 YEAR*SEG P = 0.973	R ² = 0.539 YEAR*TAMVOL P = 0.494	R ² = 0.536 SEG*TAMVOL P < 0.001	R ² = 0.418 YEAR P = 0.446	R ² = 0.532 SEG*TAMVOL P < 0.001
MESQVOL	R ² = 0.358 3-way P = 0.777	R ² = 0.347 YEAR*SEG P = 0.792	R ² = 0.343 SEG*MESQVOL P = 0.540	R ² = 0.332 YEAR*MESQVOL P = 0.503	R ² = 0.328 YEAR P = 0.480	R ² = 0.336 SEG*MESQVOL P = 0.490
ARROW	R ² = 0.319 3-way P = 0.170	R ² = 0.284 SEG*ARROW P = 0.796	R ² = 0.279 YEAR*ARROW P = 0.798	R ² = 0.278 YEAR*SEG P = 0.678	R ² = 0.271 YEAR P = 0.458	R ² = 0.267 SEG*ARROW P = 0.913
BACH	R ² = 0.318 3-way P = 0.874	R ² = 0.315 YEAR*BACH P = 0.833	R ² = 0.315 YEAR*SEG P = 0.719	R ² = 0.309 SEG*BACH P = 0.142	R ² = 0.272 YEAR P = 0.428	R ² = 0.304 SEG*BACH P = 0.131
GRASS	R ² = 0.245 3-way P = 0.760	R ² = 0.244 YEAR*SEG P = 0.847	R ² = 0.241 SEG*GRASS P = 0.750	R ² = 0.240 YEAR*GRASS P = 0.456	R ² = 0.234 YEAR P = 0.368	R ² = 0.228 SEG*GRASS P = 0.672
MESQ	R ² = 0.368 3-way P = 0.327	R ² = 0.359 YEAR*SEG P = 0.748	R ² = 0.354 SEG*MESQ P = 0.547	R ² = 0.343 YEAR*MESQ P = 0.406	R ² = 0.337 YEAR P = 0.436	R ² = 0.344 SEG*MESQ P = 0.488
TAM	R ² = 0.556 3-way P = 0.765	R ² = 0.553 YEAR*TAM P = 0.998	R ² = 0.553 YEAR*SEG P = 0.652	R ² = 0.548 SEG*TAM P = 0.011	R ² = 0.490 YEAR P = 0.432	R ² = 0.545 SEG*TAM P = 0.009
WILLOW	R ² = 0.341 3-way P = 0.696	R ² = 0.334 YEAR*SEG P = 0.556	R ² = 0.323 YEAR*WILLOW P = 0.699	R ² = 0.322 SEG*WILLOW P = 0.081	R ² = 0.275 YEAR P = 0.369	R ² = 0.314 SEG*WILLOW P = 0.079

Correlation among covariates

Among the 136 bivariate correlations from the 17 covariates, only 2 were negative (BACH vs. TAMVOL and WILLOW vs. ARROW), neither of which were significant ($P > 0.05$). Most covariates were significantly ($P < 0.01$ for 106 pairs; $P < 0.05$ for 9 pairs) and highly (Spearman's $\rho > 0.5$ for 86 pairs) correlated with one-another. Non-significant correlations included covariates HERB (5 pairs), BACH (6), GRASS (5), and/or WILLOW (6) and the ARROW vs. TAMVOL pair. Consequently, the covariates BACH, GRASS, and WILLOW represented a group that tended to be correlated with each other, but were uncorrelated with most other covariates (including HERB). Small significant correlations (Spearman's $\rho < 0.5$) were primarily associated with HERB (10 pairs), ARROW (10), BACH (6), GRASS (10), WILLOW (8), TAMVOL (7), TAM (6), and MESQ (3).

DISCUSSION

Habitat and Habitat Selection Theory

Birds and bird communities have played a major role in the development of the concept of habitat, yet specific definitions of the term habitat are often vague and/or differ from one another (Block and Brennan 1993). However, a common theme among different definitions and terms is that "habitat" includes the physical and biological environmental attributes that influence the presence or absence of a bird species (Morrison et al. 1992). A bird community is an assemblage of individuals of several species that occur together, and community ecology is concerned with identifying patterns in species assemblages, understanding the causes of these patterns, and determining how general they are (Wiens 1989a).

Habitat involves many components other than the vegetation composition and structure at a site. Environmental features (climate, food, size/area), predation, competition, parasitism, disease, disturbance, past history and even chance influence the distribution and abundance of species, and thus community attributes (Wiens 1989b). Research is usually focused on those habitat components that are most easily or reliably quantified and/or considered most likely to influence the bird community, and no single study can address all of the factors that may influence bird species or community use in a system.

The abilities of a habitat to provide the necessary resources for survival and reproduction are unequal across space and time (Block and Brennan 1993). Further, many factors underlie habitat selection and these factors do not act equally for all species or even for all populations of a single species, and most bird species are distributed largely independently of one another (Wiens 1989a, 1989b). A species' morphological and physiological traits allow them to exploit certain subsets of possible resources and hence certain habitats (Morrison et al. 1992). Life-history traits such as foraging behavior, and mating strategies are also mechanisms that underlie habitat selection in a species (Hansen and Urban 1992).

Proximate factors such as song perches, nest sites, and the structure and composition of the vegetation determine whether a bird settles in a habitat. These are part of a habitat selection "template" (Wiens 1989) that results from both genetics (for that species) and learning (for that individual). Ultimate factors, including survival, reproduction, and mating success determine suitability of the habitat and long-term survival and evolution of that species in that habitat (Hilden 1965). Wiens (1985, 1989a) summarized the factors influencing habitat selection in birds (Figure 7), which can be studied at a variety of spatial scales (Figure 8).

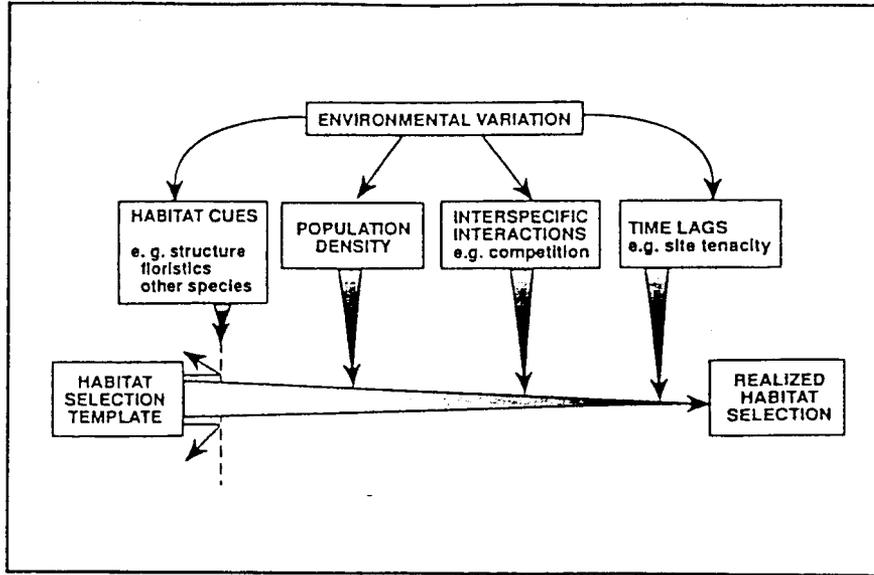


Figure 7. Factors influencing habitat selection by birds (from Wiens 1985, 1989a).

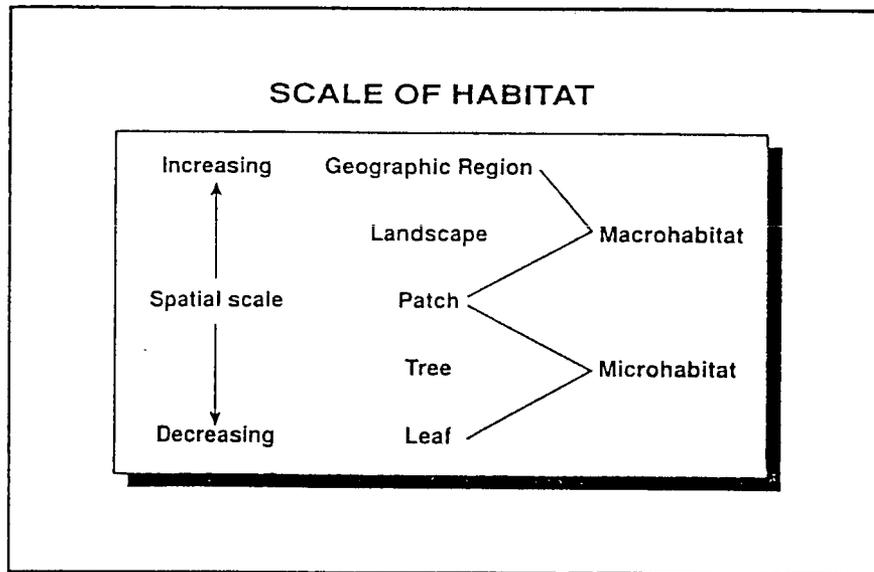


Figure 8. Continuum of spatial scales for the study of bird habitats. From Block and Brennan (1993).

Bird communities are dynamic and can vary temporally, even in the same region and/or site (Wiens 1989a, Morrison et al. 1992). Some of these changes may be due to regional and local changes in habitat distribution or characteristics, but others may be due to factors intrinsic to the bird species (such as increasing abundance, dispersal, etc.). Riparian corridors in particular facilitate faunal mixing on a broad, regional level (and Samson 1994), especially at the interface of different biomes or ecoregions (as occurs between the upper and lower portions of the Grand Canyon).

Study Design Considerations

As evidenced by the preceding discussion, when embarking on this Grand Canyon avian community - habitat relationship study we were faced with a concept of considerable complexity. Study design challenges included deciding what spatial scales to use, what variables to consider, and what methods to use. For scale, we selected a macro-habitat approach that included patch characteristics (e.g., size, structure, composition, etc.) and landscape factors (e.g., river segment). We used a larger number of study sites than any previous Grand Canyon bird study in order to increase confidence in our model and capture a wide variety of patch/habitat attributes. There is almost always an increasing relationship between the number of bird species and individuals and the amount of habitat present or surveyed (Wiens 1989a, Morrison et al. 1992), so we included a wide range of patch sizes rather than focus only on larger patches.

In terms of response variables, we selected bird species richness, abundance, and diversity for the entire riparian breeding community, rather than for a subset of species (e.g., indicator species). These variables are readily determined, reliably measured, easily understood, and can be used when developing or measuring management objectives and actions. Use of more basic data such as comparisons of simple species lists among sites is often flawed and inappropriate (Remsen 1994), while more complex and derived information such as density estimates are subject to major methodological problems (Verner 1985) and may be misleading in terms of habitat quality (Vickery et al. 1992). Although virtually all bird census techniques are subject to biases and errors, we used and integrated a variety of methods in order to maximize the likelihood of detecting those species that were present, and used decision rules to avoid overestimating the abundance of local breeders. Observers and methods were standardized in order to minimize sampling inconsistencies.

With regard to habitat, we selected from among an almost limitless number of parameters and sampling methods. Given our objective of quantifying the relationship between the riparian breeding bird community and vegetation/habitat characteristics, we focused on vegetative structure and composition, both of which have and will respond directly to dam operations. Factors such as predators, competitors, disease, etc. are difficult to study and impossible to directly relate to river flow, and hence not appropriate for this study. Given our scale of interest (macro-habitat), we focused on patch-scale vegetation area and structure, and de-emphasized fine-scale floristics (other than major tree/shrub community dominants and components) and vegetation measurements (e.g., number of stems, etc.). Releve or point-based vegetation measurement are often very time consuming (and hence expensive in terms of river-based

logistics) and can negatively impact the vegetation at a site (especially where they require entry into dense or fragile habitats). To avoid this, we used aerial photographs and rapid ocular-estimation techniques to estimate habitat parameters we thought (based on a review of the literature) would influence the bird community along the river corridor.

Bird Community - Habitat Patterns in the Grand Canyon

The discussion that follows relates only to the breeding bird community, and excludes migrants, wintering species, and vagrants. For discussion of non-breeding birds, refer to the Banding Studies, Survey Summary, and Annotated Species List chapters.

Bird species abundance, species richness, and diversity (SDI) per patch did not differ between 1994 and 1995. This allowed us to use bird community data from both years in our models, thereby increasing the sample size and improving the power of the analyses. Lack of a significant difference in these parameters is not surprising; significant changes would not be expected over such a short period as long as major habitat changes have not occurred. The interim flow guidelines governing Glen Canyon Dam operations during this period limited the likelihood and occurrence of major short-term habitat changes (such as those that occurred during the 1983 flood).

There was a strong positive correlation among the three response variables (richness, abundance, and SDI) and 14 of the 17 covariates. Eleven covariates were considered good predictors (Table 9). Covariates associated with large vegetation structures (e.g. tree area and volume, new-high-water zone area) and tamarisk species (e.g., tamarisk area and volume) were the best predictors for each of the three bird community response variables. Additionally, total area and vegetated area also had good potential as predictors for abundance of breeding pairs. Thus, the overall pattern is that as patch size increased, the number of breeding bird species and individuals increased. This is one of the most universal and generally noted relationships between habitat and bird community patterns (Wiens 1989a, Block and Brennan 1993). SDI also increased with patch size.

Our best predictive models worked better for bird abundance than for species richness or diversity (Table 9). This is interesting in that many bird community studies find better correlations between habitat parameters and species richness than with bird abundance or density (Wiens 1989a). This is generally assumed to occur because the number of bird species is often more accurately determined than the actual number of breeding pairs. In our study, the use of species-specific decision rules, seldom used in other studies, may have produced relatively accurate estimations of the actual number of breeding pairs, thereby increasing the fit of our models relative to habitat parameters.

For all bird community variables, the lowest average values were found in river-segment B. This is not surprising, given that patches in segment B were generally small and isolated, and often bordered bare rock rather than upland vegetation. The highest bird abundance, richness and diversity values were generally found in river-segment C, where patches are largest and most

contiguous, and often bordered by extensive OHWZ and upland vegetation. This region of the canyon is also adjacent to the species-rich Sonoran desert biome.

Table 9. The best models (based on correlation coefficients and significant tests) in terms of individual covariates for predicting the response variables ABUND, RICH, and SDI. Only the best model is presented for each covariate and community response variable pair, from those given in Tables 6, 7 and 8. Graphs of these predictive models are presented in Appendix 4. The first line in each cell is the model correlation coefficient and P-value. The second line is the term in the model that had the highest P-value within each covariate - response variable pair. Comparisons within columns allow for selecting the best covariates for predicting a given response variable. Models are only given for those covariates considered to be good predictors, defined as $R^2 \geq 0.50$ for ABUND and RICH, and $R^2 \geq 0.4$ for SDI. Models are not given for SHR, HERB, ARROW, BACH, GRASS, and WILLOW as no models were considered good predictors.

Covariate	Best Models for:		
	ABUND = number of breeding pairs	RICH = number of breeding species	SDI = Shannon Diversity Index
AREA	$R^2 = 0.646$; $P = 0.015$ AREA & SEG & SEG*AREA	$R^2 = 0.515$; $P < 0.001$ AREA & SEG	$R^2 = 0.403$; $P < 0.001$ AREA & SEG
VEG	$R^2 = 0.658$; $P = 0.017$ VEG & SEG & SEG*VEG	$R^2 = 0.524$; $P < 0.001$ VEG & SEG	$R^2 = 0.407$; $P < 0.001$ VEG & SEG
TREE	$R^2 = 0.625$; $P < 0.001$ TREE & SEG	$R^2 = 0.533$; $P < 0.001$ TREE & SEG	$R^2 = 0.408$; $P < 0.001$ TREE & SEG
NHWZ	$R^2 = 0.639$; $P = 0.010$ NHWZ & SEG & SEG*NHWZ	$R^2 = 0.544$; $P < 0.001$ NHWZ & SEG	$R^2 = 0.465$; $P < 0.001$ NHWZ & SEG
OHWZ	$R^2 = 0.542$; $P < 0.001$ OHWZ & SEG		
TREEVOL	$R^2 = 0.685$; $P = 0.003$ TREEVOL & SEG & SEG*TREEVOL	$R^2 = 0.611$; $P = 0.011$ TREEVOL & SEG & SEG*TREEVOL	$R^2 = 0.483$; $P = 0.011$ TREEVOL & SEG & SEG*TREEVOL
SHRBVOL	$R^2 = 0.617$; $P = 0.007$ SHRBVOL & SEG & SEG*SHRBVOL	$R^2 = 0.498$; $P < 0.005$ SHRBVOL & SEG	
TAMVOL	$R^2 = 0.555$; $P < 0.001$ TAMVOL & SEG & SEG*TAMVOL		$R^2 = 0.532$; $P < 0.005$ TAMVOL & SEG & VOL & SEG
MESQVOL	$R^2 = 0.563$; $P = 0.011$ MESQVOL & SEG & SEG*MESQVOL		
MESQ	$R^2 = 0.574$; $P = 0.015$ MESQ & SEG & SEG*MESQ		
TAM	$R^2 = 0.647$; $P < 0.001$ TAM & SEG & SEG*TAM	$R^2 = 0.611$; $P < 0.001$ TAM & SEG	$R^2 = 0.545$; $P < 0.01$ TAM & SEG & SEG*TAM

The area and volume of tree habitat (defined as woody vegetation 2 m or higher) was a much better predictor of bird community response variables than were shrub (woody vegetation >2 m high) and herb habitat (nonwoody vegetation, usually ground cover). This suggests that larger woody vegetation plays a more important role in structuring the riparian bird community than do shrub and herb. The older, dense tamarisk and mesquite vegetation that comprises most of the tree-structured habitat is heavily used by breeding birds, and provides more nesting substrate, song perches, and environmental buffering than shrub habitat.

Of the major dominant plant species, only mesquite and tamarisk functioned as good predictors of bird community parameters. Areas of arrowweed, baccharis, and grass vegetation types contributed less predictive value, as might be expected based on general observations of lower relative use by birds. We were surprised that area of willow was not a stronger predictor, given the generally higher value of native riparian habitats as compared to introduced habitats (Wiens 1989a, Morrison et al. 1992). This may be because NHWZ vegetation in our study sites were overwhelmingly dominated by tamarisk, which may have overshadowed any bird community patterns relative to willow.

Several of our models accounted for approximately two-thirds of the variation in bird communities along the canyon. We feel this is a remarkably strong model response given that we addressed primarily vegetation-related habitat components, and did not measure a number of other potential influencing factors such as predators, competitors, and environmental characteristics that also function to shape the breeding bird community.

The remaining bird community variation not accounted for in our models is likely influenced by a number of regional and local factors. For example, the Colorado River through the Grand Canyon stretches for over 360 km (280 river miles) and across an elevation gradient of 540 m. This entails changes in environment (e.g., temperature) and geomorphology that in turn influence vegetation differences (both patch-scale and floristically) such that patches in the upper canyon are often very different than similar-sized patches in the lower end. Also, the adjacent upland habitat is very different in different portions of the canyon, and avian assemblages in riparian tracts and adjoining uplands are not independent (Knopf and Sansom 1994).

Factors such as species range limits and recent range expansions by some species also affect the bird communities of an area. For example, the northern range limit of the Brown-crested Flycatcher occurs along the lower section of the Grand Canyon, and this flycatcher has not moved upstream as a breeding species (and may never do so) even as major habitat changes have occurred. Conversely, Brown and Johnson (1988) noted that some species (Bell's Vireo and Hooded Oriole) are moving into and up the Grand Canyon in recent years, and the Summer Tanager is recorded in ever-increasing numbers. It is unknown whether these species will eventually breed as far upstream as Lees Ferry, but this illustrates the temporal and spatial dynamics that are on-going and can be expected to continue within the canyon.

Brown-headed cowbird nest parasitism greatly affects some species along the river in the Grand Canyon (Brown 1994, Sogge et al. 1997). Cowbird parasitism has the potential of affecting host distribution and abundance in some systems (Lowther 1993, Robinson et al. 1995), and may be

playing a significant role in determining abundance and breeding distribution of some of the commonly parasitized hosts in the Grand Canyon.

Most of the riparian breeding birds along the river are neotropical migrants, and many of them spend half or more of the year migrating and wintering outside of the canyon. There has been increasing attention and research (e.g., Keast and Morton 1980, Martin and Finch 1995, Rappole 1995) directed toward understanding the importance of nonbreeding habitats to avian survival. Although much remains to be known, it has become clear that factors such as the quality and quantity of migratory stopover areas and wintering habitat can have major effects on overwinter survival of birds. Therefore, factors outside the Grand Canyon can be affecting the survival of locally breeding neotropical birds, and can add temporal and spatial variability to habitat use patterns that can not be accounted for in models.

Our study looked at overall bird community patterns, and not individual bird species. However, species-specific life history traits can be expected to affect at least some community-wide patterns. For example, the presence of marshy vegetation is relatively unimportant to the overall breeding bird community because most species currently present do not require it or nest in it, but it is an absolute determinant of Common Yellowthroat presence/absence. Large birds such as Brown-crested Flycatchers and Summer Tanagers may require larger patches and the presence of at least some very large trees in order to breed in a patch, even though most of the other, smaller bird species do not. Thus, individual life-history traits play a role in habitat use in the Grand Canyon.

It is also critical to remember that the results and models of this study are specific for the portion of the river corridor that we sampled, from Lees Ferry downstream to Diamond Creek. If our sampling had extended downstream below Separation Canyon to the Lake Mead interface, different and/or additional patterns would likely have emerged. Much of the habitat below Separation Canyon differs greatly from that upstream, being wider, more contiguous, with more marsh areas, and dominated by native willows, many of which are very tall and dense. As a result, the riparian bird community below Separation differs in having higher abundance of breeding Brown-crested Flycatchers, Song Sparrows, Common Yellowthroats, Blue Grosbeaks, and Summer Tanagers. Also, some birds such as the Yellow-billed Cuckoo, Red-winged Blackbird, and Black-crowned Night Heron breed below Separation but not above. These differences in bird community and habitat would have affected the details of our models, although the broad patterns of more species and individuals with increasing patch size would probably have been the same. This emphasizes the point made by Wiens (1989a), Hansen and Urban (1992) and Morrison et al. (1992) that care must be used in extrapolating habitat models from one area to another, even in what might be considered a single riparian system along the Colorado River.

Relationship to flow-induced vegetation changes

The general pattern that emerged is one whereby increasing patch size leads to increased bird abundance, richness, and diversity. This is true whether the vegetation responsible for the increase is NHWZ (dominated by tamarisk) or OHWZ (dominated by mesquite). Thus, the floristic details of habitat change are generally less important than changes in size, structure and/or life form.

Flow patterns that result in smaller, more isolated patches can be expected to decrease bird numbers, richness and diversity. If flow patterns create larger and more contiguous patches of habitat, regardless of the tree or shrub species, bird abundance and richness will increase in each patch. However, patch size in the Grand Canyon is strongly affected by local topography and geomorphology (Turner and Karpiscak 1980), and it may not be possible under any management strategy to greatly increase the size of many existing patches. Instead, future vegetation changes may take the form of loss of habitat (e.g., the gradual loss of mesquite in the OHWZ), increased number of patches (of a variety of sizes), and/or shifts in dominant species composition (e.g., from tamarisk to willow). Loss of mesquite vegetation will clearly decrease bird abundance, as it was a major factor in the habitat models. Increases in the number of patches will increase the overall number of birds and bird species in the canyon, and the exact size, width, and structure will determine which species will colonize and breed in the new patches. Patch size and structure can also affect predation, brood parasitism, and other habitat factors. Based on our models, floristic changes such as from tamarisk shrub/tree to willow shrub/tree are not likely to greatly affect the bird abundance and species richness, although it may result in some changes in the actual species composition at the patch level.

Implications to Future Monitoring

We found a strong positive correlation among most of the pairs of covariates. Some of these correlations are simply due to one covariate being a component of another covariate (e.g., tamarisk is the major component of NHWZ, and mesquite of OHWZ). Other correlations reflect the relatively simple vegetation community structure of the riparian corridor, which is dominated by only a few types of trees and shrubs. It also reflects the fact that patch size in this riparian system is strongly affected by geomorphology, and many areas that are topographically and geologically suitable for development of large patches of NHWZ are also suitable for large areas of OHWZ.

This correlation among covariates allows us to simplify our habitat model by excluding most covariates and focusing on those that are responsible for the most variation in the bird abundance and richness. For a given level of predictive ability, estimation and measurement of fewer variables decreases research time and study costs. Given the choice between model parameters that can be measured relatively quickly, as opposed to those taking much more time, the manager and researcher may be best served by choosing the former. In our case, useful predictive covariates such as the total patch area and total vegetated area, as well the area of NHWZ, OHWZ, mesquite and tamarisk can be readily estimated on aerial photographs and rapidly

ground-truthed. Tree volume produced the best predictive model, but the additional field effort needed to gather data to estimate volume (as opposed to area) may not be worthwhile given that several other area covariates produce very good models with nearly as high correlation coefficients. The use of remote sensing techniques holds great promise in simplifying habitat measurements, but may not work well in all systems or for all habitat questions (Sader et al. 1991).

Diversity indices have been widely used and provide interesting information; however, most diversity indices have severe analytical and statistical drawbacks (Wiens 1989a). For example, use of different indices on the same data sets may produce different patterns, and each diversity index is influenced somewhat differently by different aspects of the bird community. For example, the SDI is particularly sensitive to the presence of rare species. Although diversity indices can be expected to change with changes in the bird community, diversity index patterns can only be interpreted by looking at changes in each individual species and determining how these changes affect the diversity values (Wiens 1989a, Morrison et al. 1992). Such analyses are beyond the scope of our study, but we present SDI values because they are based on the most widely used index and may be useful for future comparative purposes.

Because SEGMENT was a significant factor in the models, future bird inventories, research and management must take into account the different bird community-habitat relationships throughout the river corridor. In order to do so, survey sites should be placed throughout the river corridor. In addition, bird abundance and richness patterns may have to be analyzed and interpreted separately for different segments of the river.

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Appendix 1. The number of pairs of each breeding species detected during 1994, based on "decision rules" as outlined in the Methods section of this chapter. Refer to Appendix 3 for the key to standard 4-letter species codes.

PATCH	ATFL	BCFL	BCHU	BEVI	BEWR	BCCGN	BHCO	BLGR	COHU	COYE	HOFI	HOOR	LEGO	LUWA	MODO	NOMO	NOOR	PHAI	SAPH	SUTA	YBCH	YEWA	Total
1.0R	1		1		2	2	1	1		1	2			1							1	1	14
1.6R			1		1	1		1			1								1				6
5.1L			1					1			1								1			1	5
5.2R					2		1	1			2											1	7
5.6R			1								1												2
46.7R	1		3		3	1	1	1		2	2		5				1		1		1	2	22
47.5L			2				1	1					1									1	6
48.5L			2								1		2										5
49.1R			4		1	1				1	1		5										13
49.2L			1		1						1		3										6
50.0R	1		2		2	1	1	1			1		4					1		1	1	1	15
73.9R			1		2	1	1				1		1	2			1		1				10
74.1R			1		1						1		1	2									6
74.3R			1		1						1		2										5
122.8L	1		2		1	1		1					3										9
125.5R													2										2
131.3R			1		1			1			1		3										7
167.0R	1			1		1		1					1										5
171.0R	1		2	2	1	1				1	1		2						1		1	1	14
171.1R	1		2	2		1			1		1		1	2							1	1	13
172.2L			2	2		1					1		2										9
173.1R			1	1		1			1			1	4									1	10
174.4R			1	2		1		1					3						1				9
174.7R	1			1		1					1		1										5
198.0R	1	2	5	6	2	2			1	1	1		1	4							2	1	29
199.5R	1		1	1		1		1	1		1		1	1								1	10
200.0L	1			2		1					1		2										7
200.4R				2	1								1	1								1	6
200.5R	1		3	2	1	1		1	1	1	1		1	2							1		16
202.5R	1		1	2		1			1		1		1	3									10
204.5R	1		5	10	2	2		1	1	2	1	1	2	9	1	1	1	2		1	6	2	50
206.5L	1		2										2										5
208.7R	1		2	2		1		1			1		3										11

Appendix 2. The number of pairs of each breeding species detected during 1995, based on "decision rules" as outlined in the Methods section of this chapter. Refer to Appendix 3 for the key to standard 4-letter species codes.

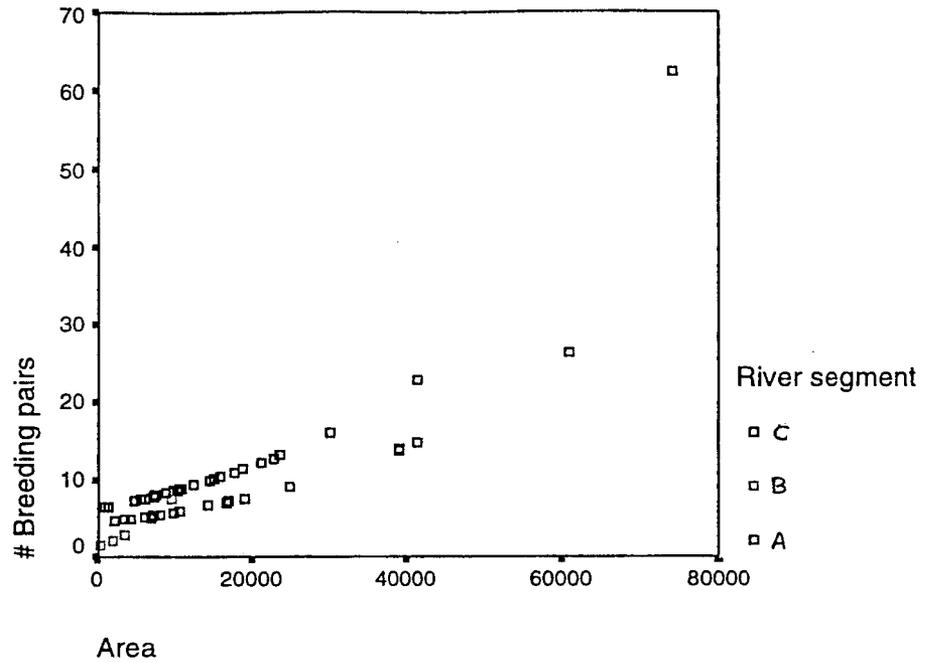
PATCH	A TEL	BCFL	BCHU	BEVI	BEWR	BGGN	BHCO	BLGR	COHU	COYE	HOFI	HOOR	LABU	LEGO	LUWA	MODO	NOOR	PHAI	SAPH	SOSP	SUTA	YBCH	YEWA	Total
1.0R	1		1		1	1	1				2				1	1						1		10
1.6R							1				1													2
2.0L	1							1			2													4
3.7L								1			1				1									3
5.1L					1						1					1								3
5.2R	1		1		1	1		1			2					1						1		9
46.0L	2		4		1	1				1	1				2							1		13
46.7R	1		4		2	2	1	1		1	2				7							1	1	23
47.5L			3												3									6
48.5L			1		1	1									2									5
49.1R	1		3		2	1	1				1			1	6									16
49.2L	1		1		1	1	1						1		2				1					9
50.0R			4		3	2	1				2				7	1								20
73.9R			1		1										2									4
74.1R			1		1										2									4
74.3R			1								1				1									3
74.4L	1				1	2		1			2			2	4	1				1				15
76.5L	1		1		1	1					1		1	1	2									9
117.5R										1					1				1					3
119.5R															1									1
122.8L			1		1	1				1			1	1	1	1								8
125.5R											1				1									2
131.3R															4									4
167.0R			1			1			1					1	1									5
171.0R	1		2	2	1	1					2			1	3							1		13
171.1R	1		1	1	1	1							1	2										7
172.2L	1		2	2	1	1					1			1	3							1	1	13
173.1R			1	1					1					3					1					8
174.4R	1		2	1		2			1					3									1	11
174.5R				2		1			1				1	2										7

PATCH	ATFL	BCFL	BCBU	BEVI	BEWR	BGGN	BHCO	BLGR	COHU	COYE	HOFI	HOOR	LABU	LEGO	LUWA	MODO	NOOR	PHAI	SAPH	SOSP	SUTA	YBCH	YEWA	Total
174.7R	1		1	1											1									4
197.2L		1	2	1		1			1	1	2			2	4						1			17
197.6L	1	1	1	1		1			1					2	3							1		12
198.0R		1	2	7	3	2	1		1	1	1			1	6				1	1		2		30
198.2L	1	1	2	2	2	1					2			1	5					1		1	1	20
198.3R		1	1	2	1	1				1	2				2							1		12
199.5R				1		1					1				1				1					5
200.0L			1	2		1			1		2				2									9
200.4R			2	1		1			1	1	1			3	2									12
200.5R			2	2	1	1			1	1	3			1	3						1		1	16
202.5R			3	3		1			1		1			1	2									12
204.1R	2		5	5	2	1		1		1	2			2	5			1	1			2		30
204.5R			7	12	1	3		2	2	2	1		2	5	11		1	2			1	5		57
206.5L	1		1	1		1			1						3									8
208.7R	1		3	1				1	2		1			1	3							1		14
213.6L			1	1		1					2			3	1				1					10
214.0L	1		1	2		1			1		2			1	2				1					13
214.2L				1											1									2
224.0L			1			1			1		1			1	2				1					8
224.1R									1		1				2									4

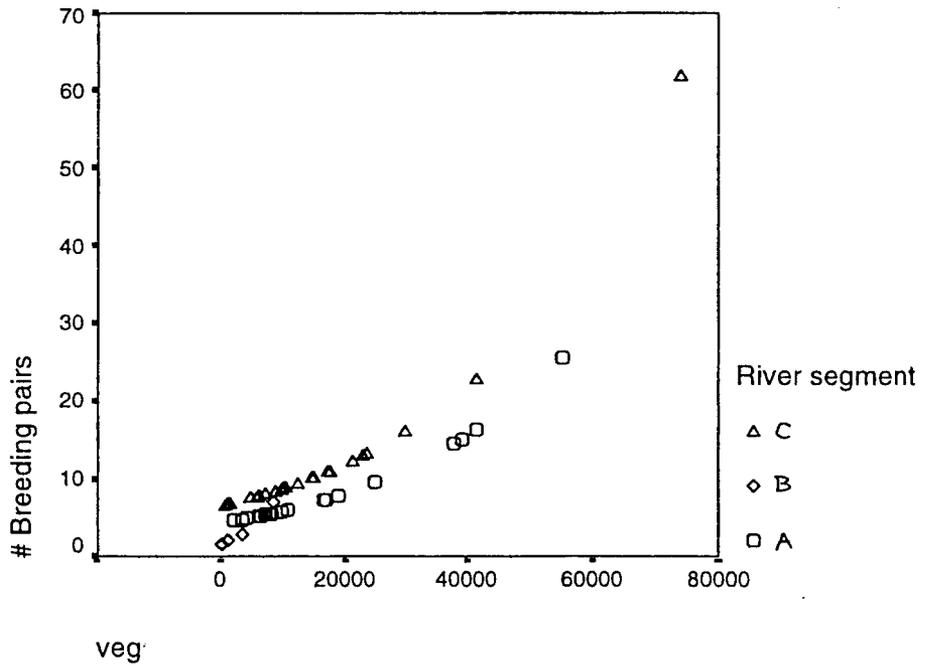
Appendix 3. Key to standard 4-letter bird codes used in Appendices 1 and 2. Codes and common names are standardized per the American Ornithologists' Union (1983 and subsequent revisions) convention. Refer to the General Appendix section for scientific names of bird species.

<u>CODE</u>	<u>COMMON NAME</u>
ATFL	Ash-throated Flycatcher
BCFL	Brown-crested Flycatcher
BCHU	Black-chinned Hummingbird
BEVI	Bell's Vireo
BEWR	Bewick's Wren
BGGN	Blue-gray Gnatcatcher
BHCO	Brown-headed Cowbird
BLGR	Blue Grosbeak
COHU	Costa's Hummingbird
COYE	Common Yellowthroat
HOFI	House Finch
HOOR	Hooded Oriole
LABU	Lazuli Bunting
LEGO	Lesser Goldfinch
LUWA	Lucy's Warbler
MODD	Mourning Dove
NOMO	Northern Mockingbird
NOOR	Northern Oriole
PHAI	Phainopepla
SOSP	Song Sparrow
SAPH	Say's Phoebe
SUTA	Summer Tanager
YBCH	Yellow-breasted Chat
YEWA	Yellow Warbler

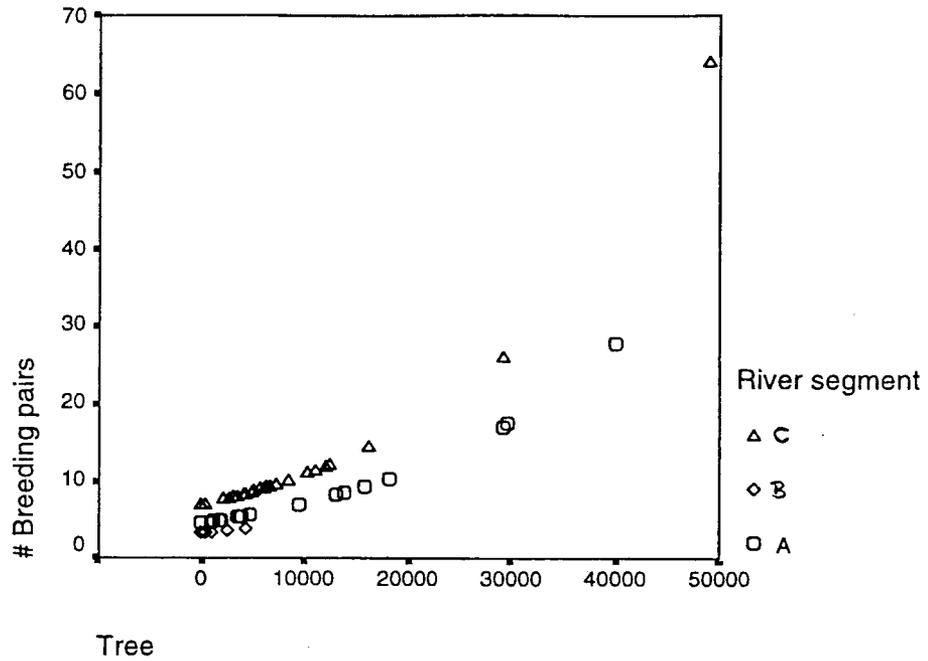
Appendix 4. Predictive graphs for the best bird community-habitat models (based on correlation coefficients and significant tests) in terms of individual covariates for predicting the response variables ABUND, RICH, and SDI. Graphs are presented only for those models given in Table 9. Models are only given for those covariates considered to be good predictors, defined as $R^2 \geq 0.50$ for ABUND and RICH, and $R^2 \geq 0.4$ for SDI. Models are not given for SHRB, HERB, ARROW, BACH, GRASS, and WILLOW as no models were considered good predictors.



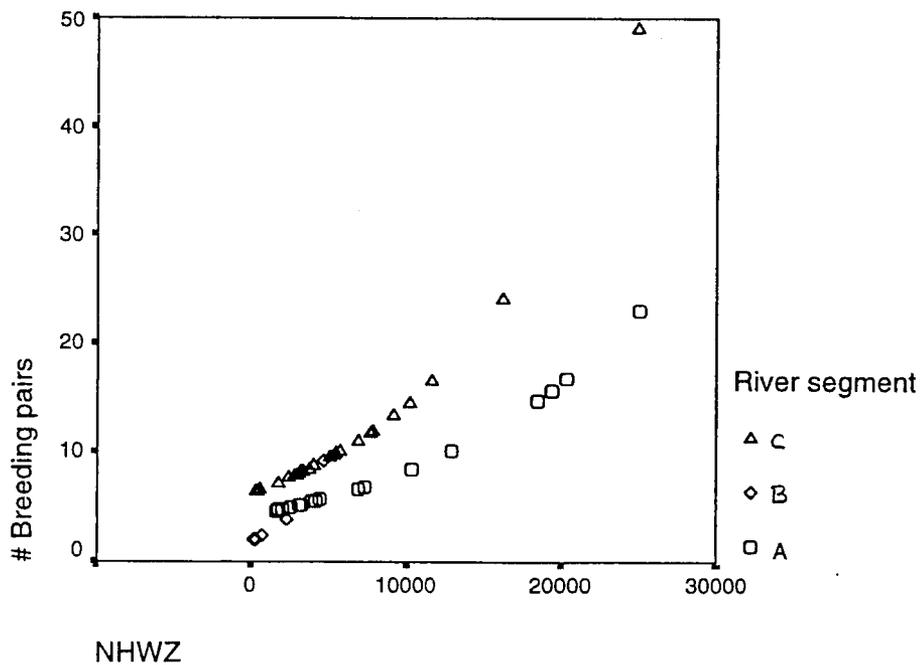
Graph of predicted values for ABUND (the total number of breeding pairs per patch) for the model AREA & SEG & SEG*AREA. Area is the total area of the patch, in square meters.



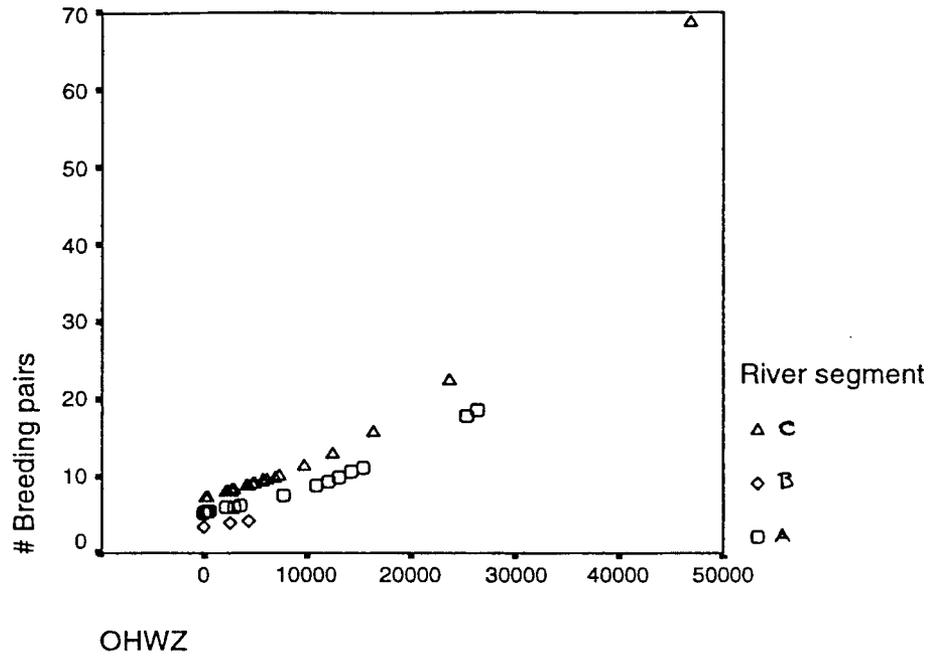
Graph of predicted values for ABUND (the total number of breeding pairs per patch) for the model VEG & SEG & SEG*VEG. VEG is total vegetated area, in square meters.



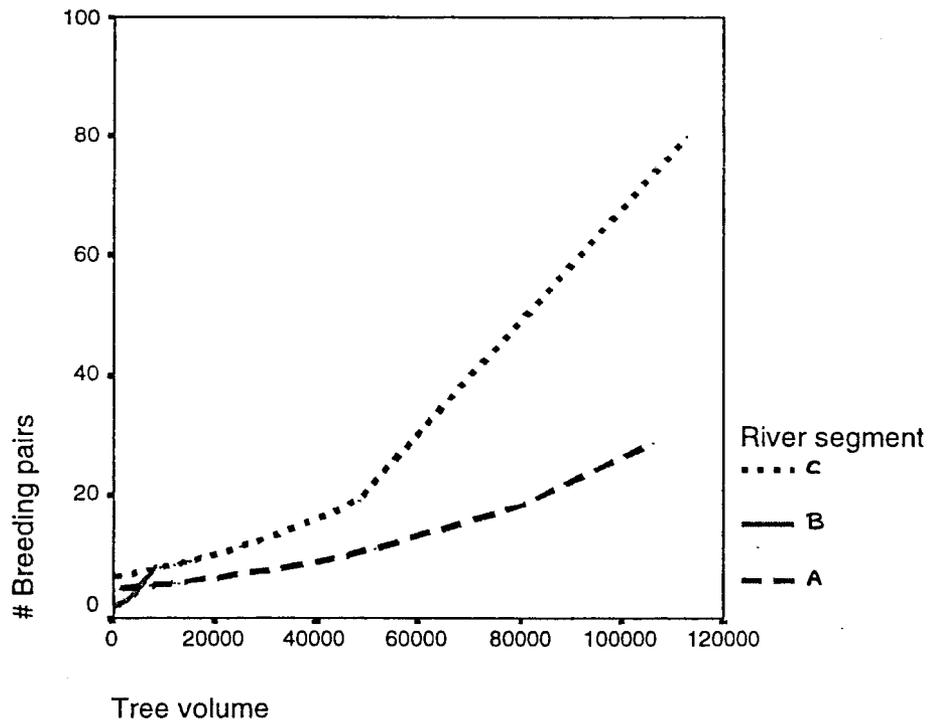
Graph of predicted values for ABUND (the total number of breeding pairs per patch) for the model TREE & SEG. TREE is total area of tree-form vegetation, in square meters.



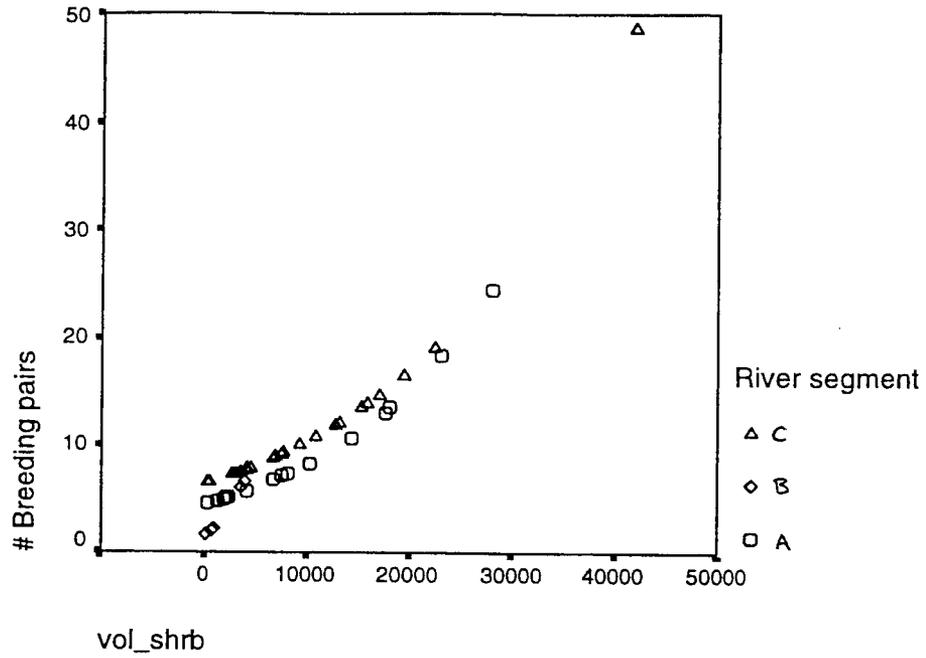
Graph of predicted values for ABUND (the total number of breeding pairs per patch) for the model NHWZ & SEG & SEG*NHWZ. NHWZ is total area of NHWZ vegetation, in square meters.



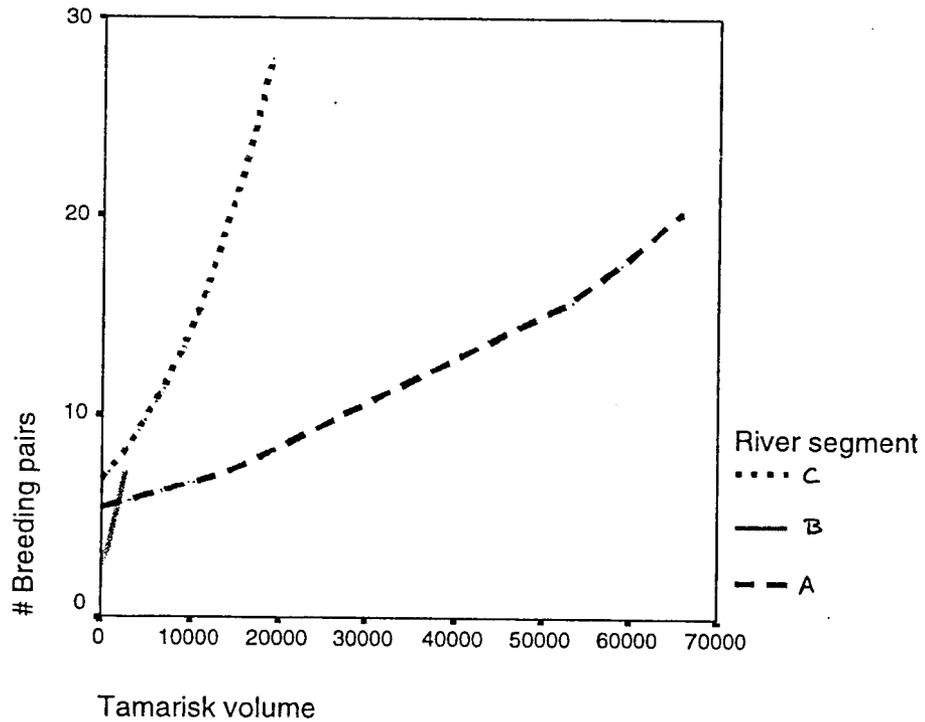
Graph of predicted values for ABUND (the total number of breeding pairs per patch) for the model OHWZ & SEG. OHWZ is total area of OHWZ vegetation, in square meters.



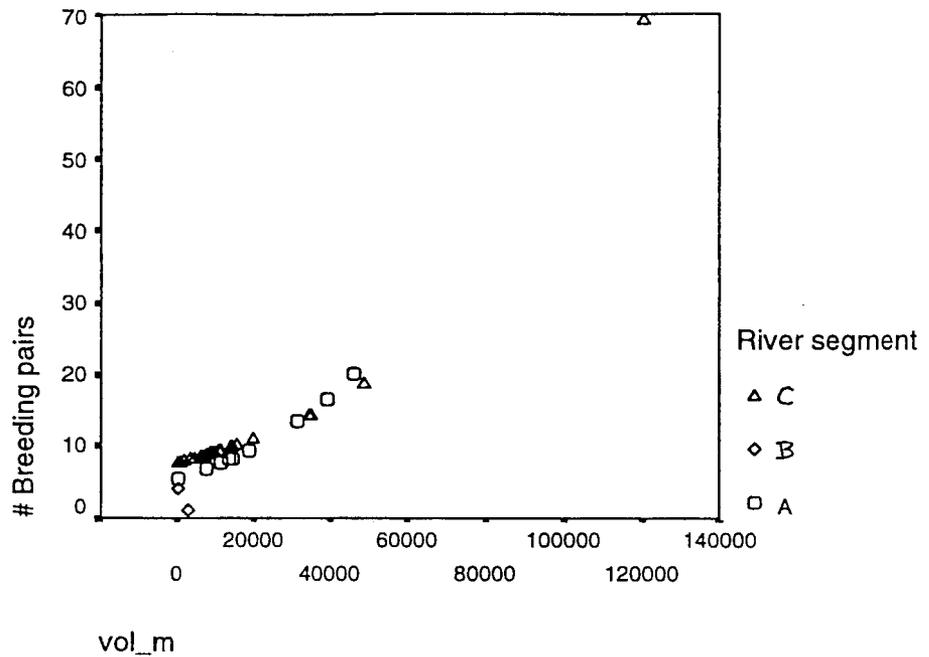
Graph of predicted values for ABUND (the total number of breeding pairs per patch) for the model TREEVOL & SEG & SEG*TREEVOL. TREEVOL is a tree-volume index as described in the text.



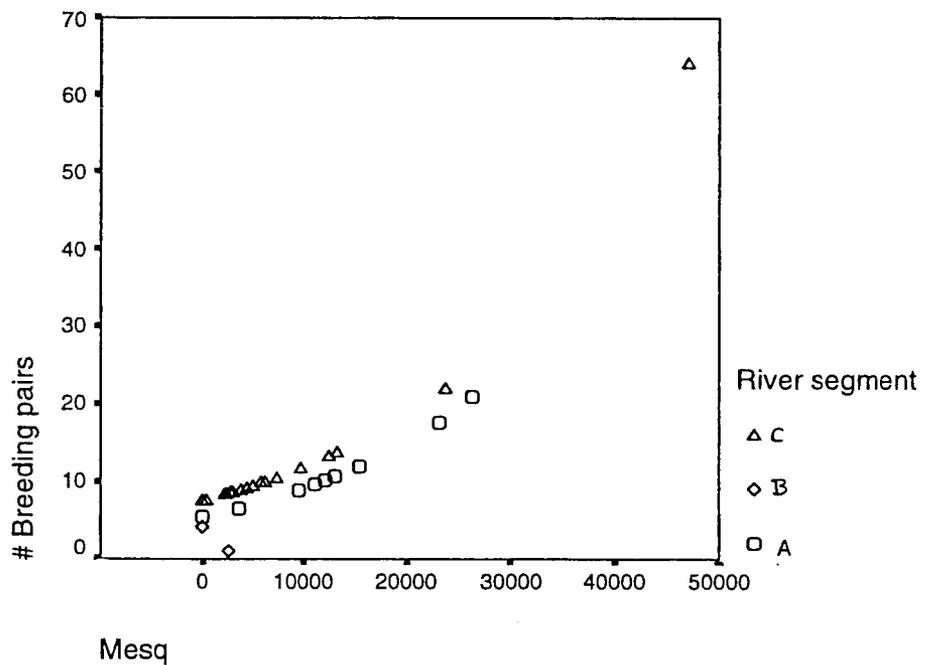
Graph of predicted values for ABUND (the total number of breeding pairs per patch) for the model SHRUVOL & SEG & SEG*SHRUVOL. SHRUBVOL is a shrub-volume index as explained in the text.



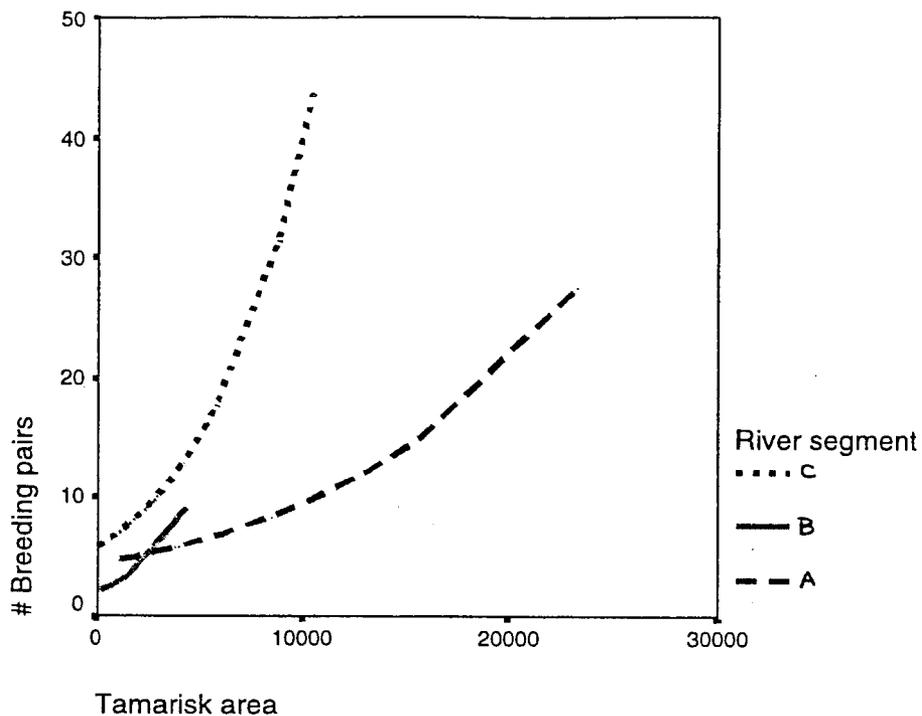
Graph of predicted values for ABUND (the total number of breeding pairs per patch) for the model TAMVOL & SEG & SEG*TAMVOL. TAMVOL is a tamarisk-volume index, as explained in the text.



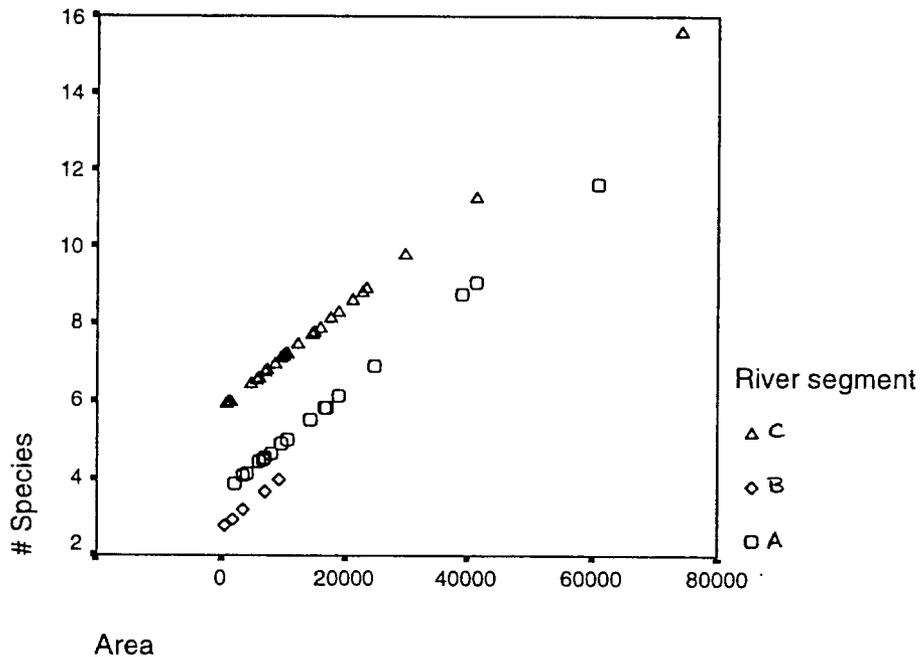
Graph of predicted values for ABUND (the total number of breeding pairs per patch) for the model MESQVOL & SEG & SEG*MESQVOL. MESQVOL is a mesquite-volume index, as explained in the text.



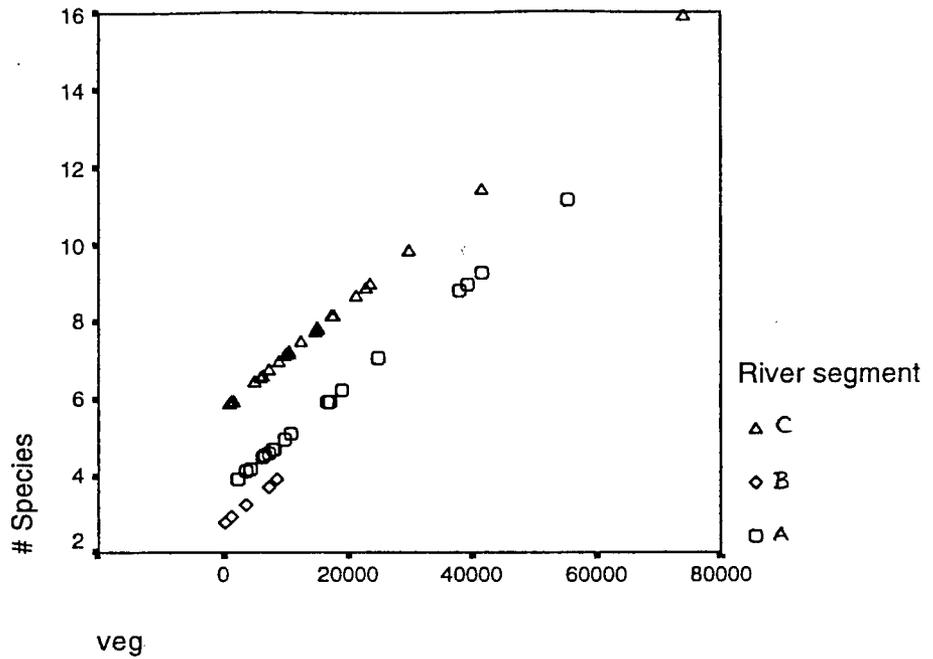
Graph of predicted values for ABUND (the total number of breeding pairs per patch) for the model MESQ & SEG & SEG*MESQ. MESQ is the total area of mesquite vegetation, in square meters.



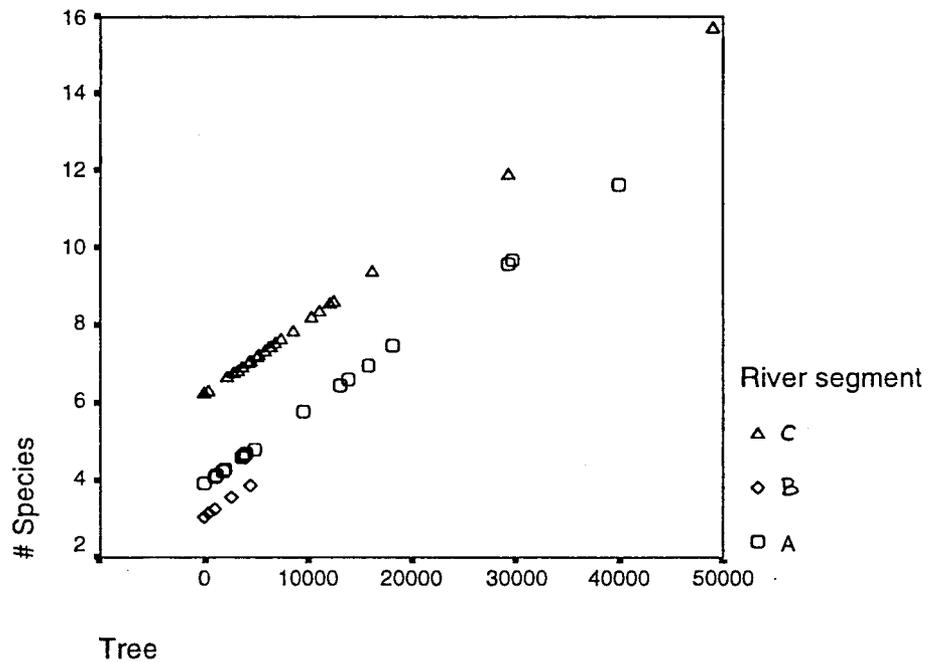
Graph of predicted values for ABUND (the total number of breeding pairs per patch) for the model TAM & SEG & SEG*TAM. TAM is the total area of tamarisk vegetation, in square meters.



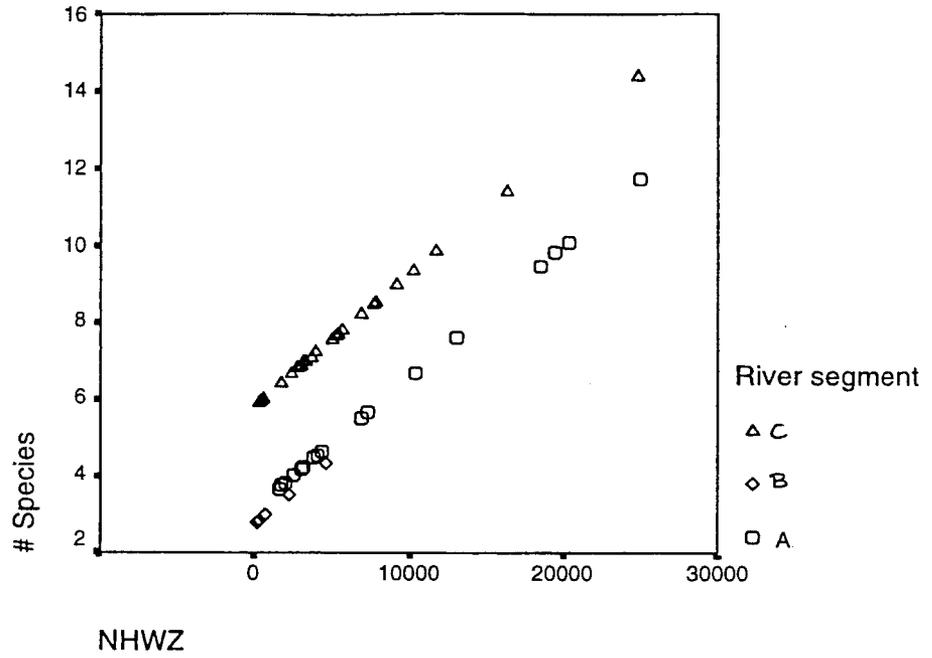
Graph of predicted values for RICH (the total number of breeding species per patch) for the model AREA & SEG. AREA is the total area of the patch, in square meters.



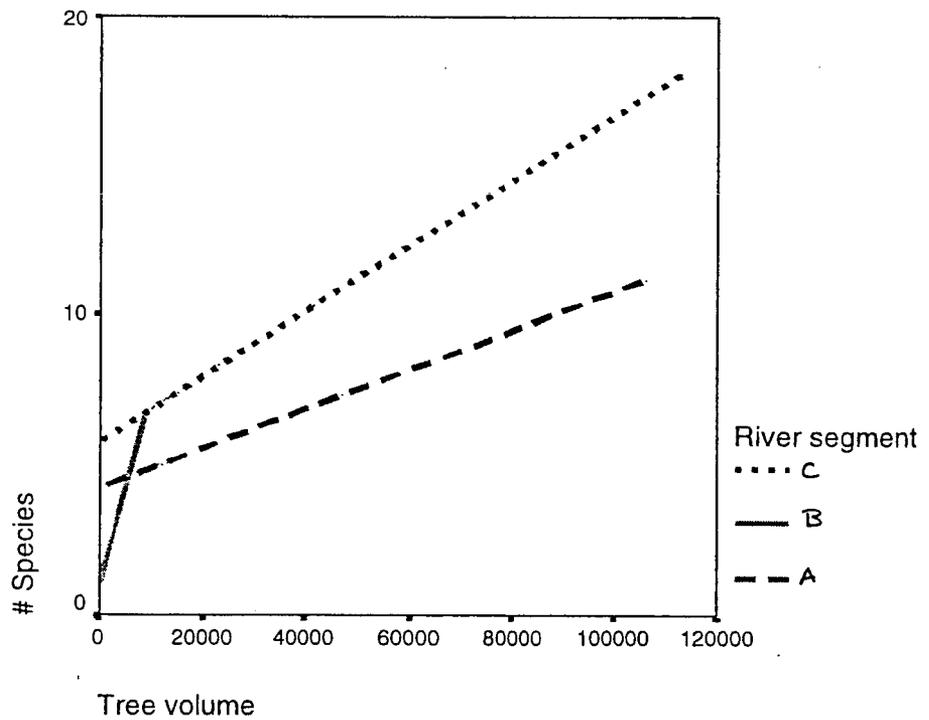
Graph of predicted values for RICH (the total number of breeding species per patch) for the model VEG & SEG. VEG is the total vegetated area of the patch, in square meters.



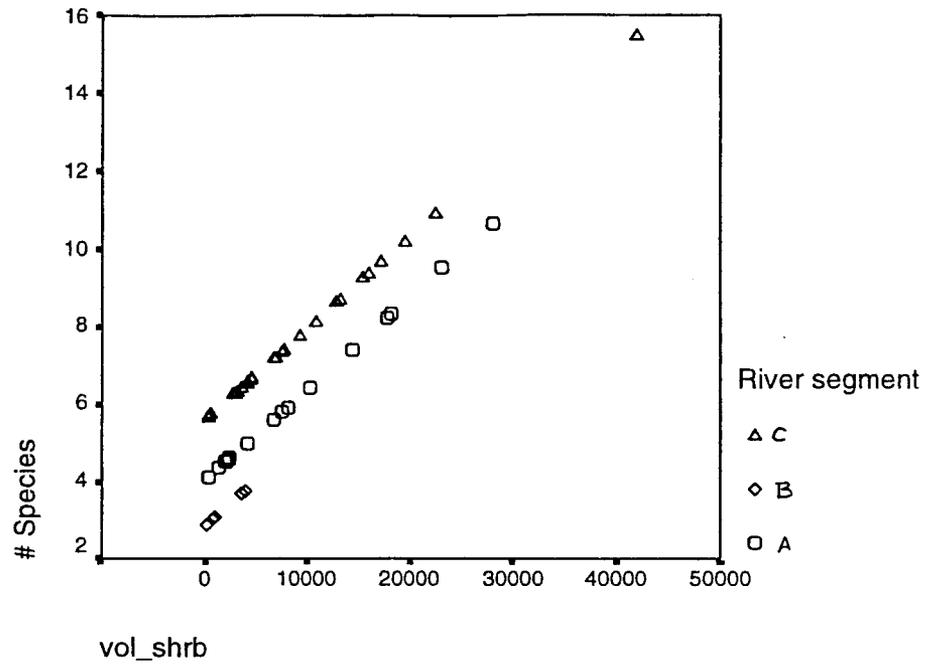
Graph of predicted values for RICH (the total number of breeding species per patch) for the model TREE & SEG. TREE is the total area of tree-form vegetation in the patch, in square meters.



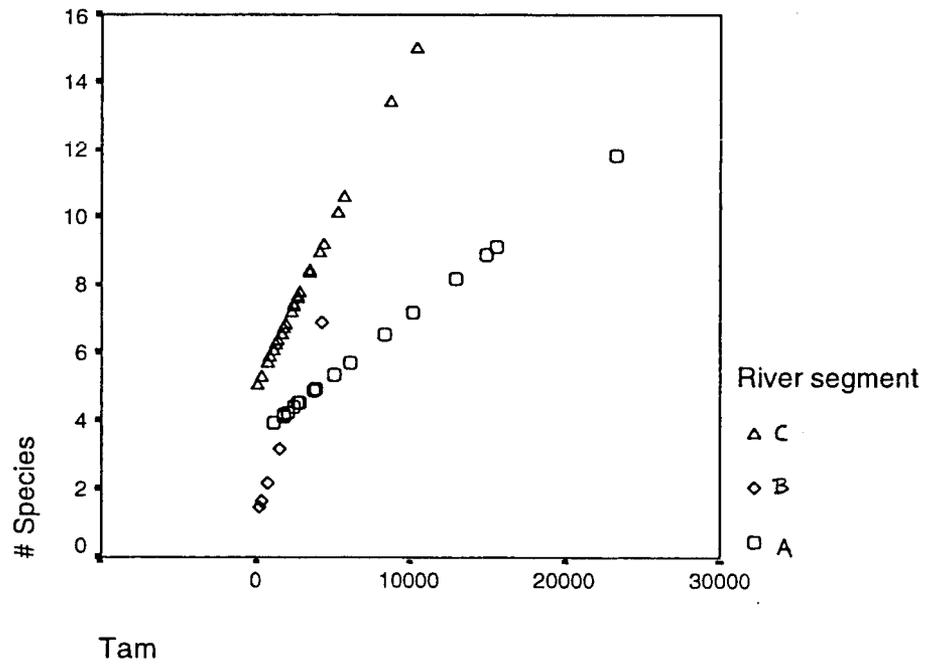
Graph of predicted values for RICH (the total number of breeding species per patch) for the model NHWZ & SEG. NHWZ is the total area of NHWZ vegetation in the patch, in square meters.



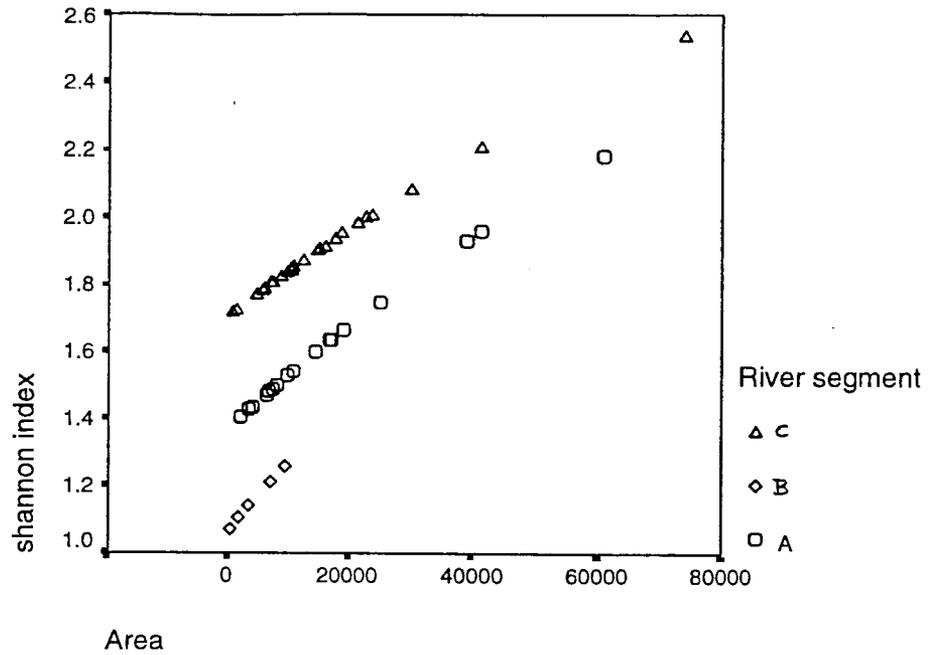
Graph of predicted values for RICH (the total number of breeding species per patch) for the model TREEVOL & SEG & SEG*TREEVOL. TREEVOL is a tree-volume index, as explained in the text.



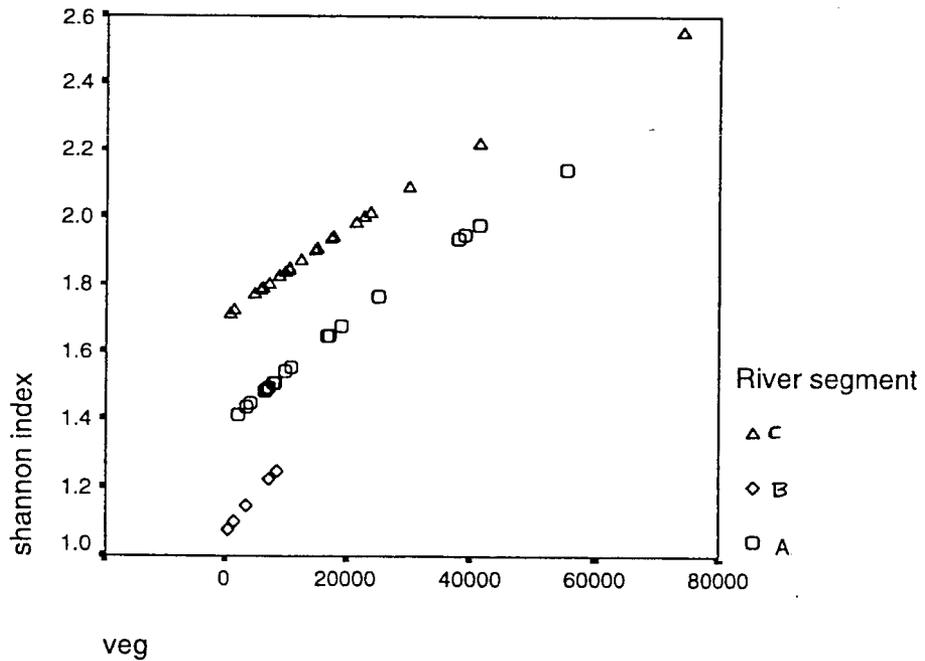
Graph of predicted values for RICH (the total number of breeding species per patch) for the model SHRBVOL & SEG. SHRBVOL is a shrub-volume index, as explained in the text.



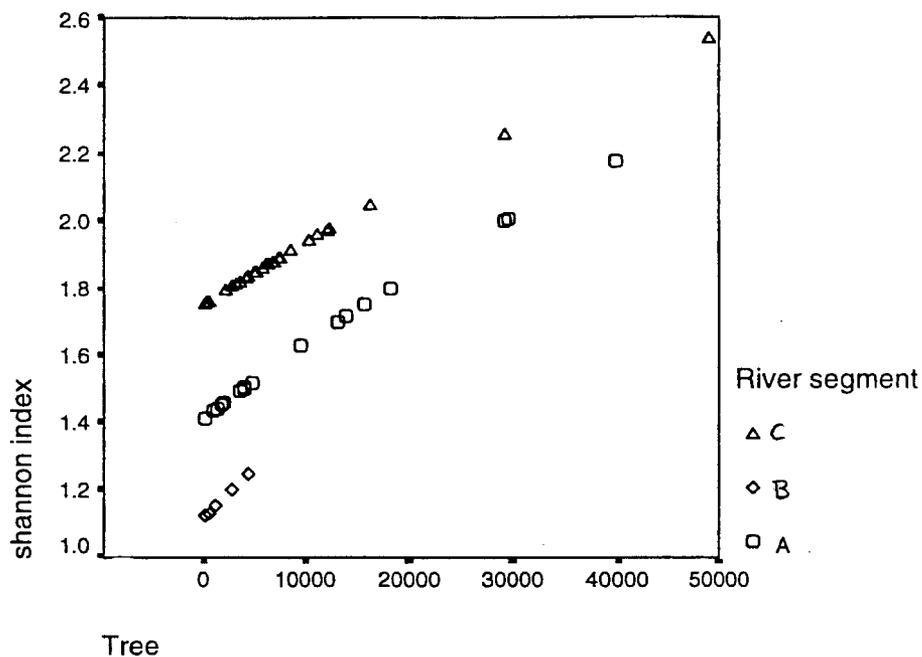
Graph of predicted values for RICH (the total number of breeding species per patch) for the model TAM & SEG & SEG*TAM. TAM is the amount of tamarisk vegetation, in square meters.



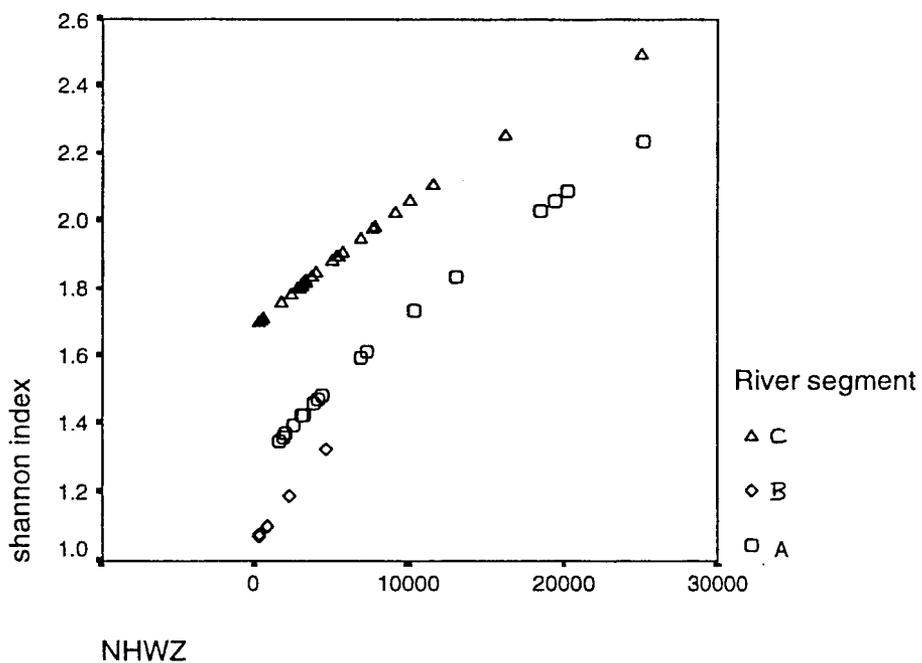
Graph of predicted values for SDI (the Shannon Diversity Index of a patch) for the model AREA & SEG. AREA is the total area of the patch, in square meters.



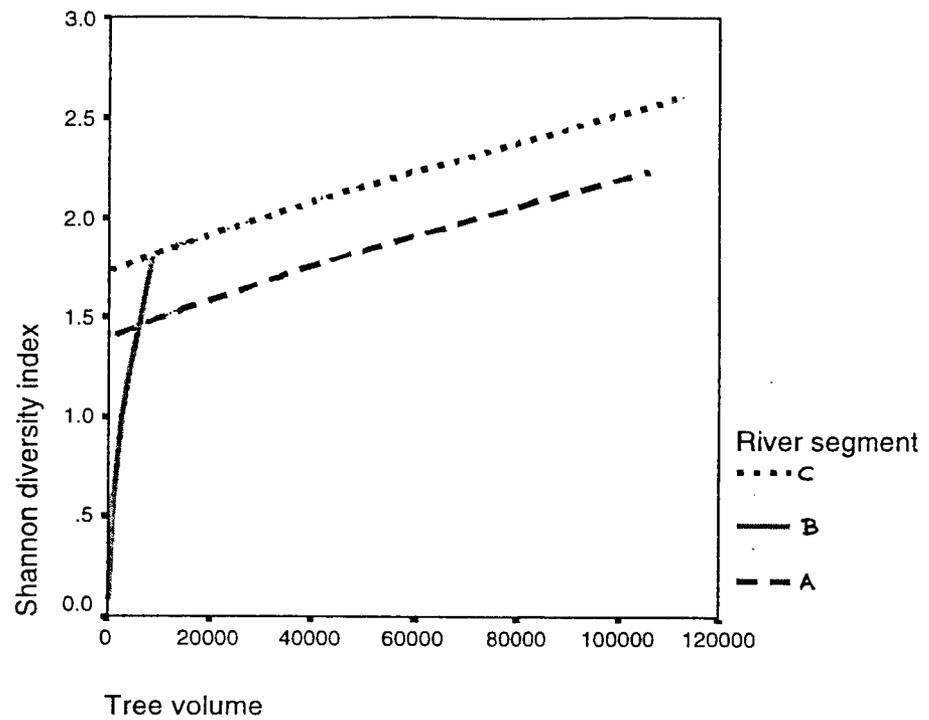
Graph of predicted values for SDI (the Shannon Diversity Index of a patch) for the model VEG & SEG. VEG is the total vegetated area of the patch, in square meters.



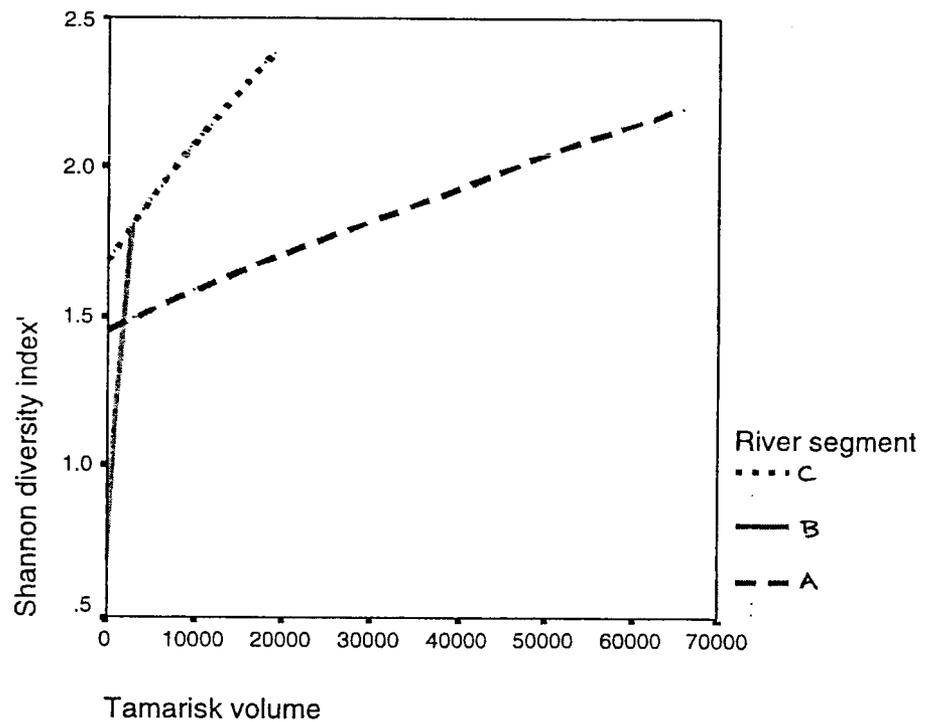
Graph of predicted values for SDI (the Shannon Diversity Index of a patch) for the model TREE & SEG. TREE is the total area tree-form vegetation in the patch, in square meters.



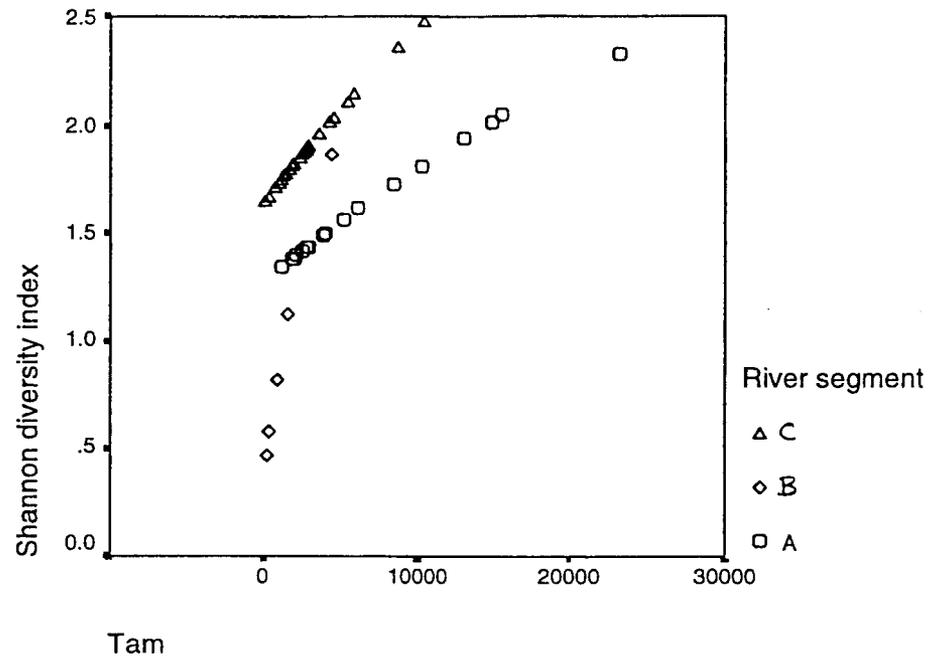
Graph of predicted values for SDI (the Shannon Diversity Index of a patch) for the model NHWZ & SEG. NHWZ is the total area of NHWZ vegetation in the patch, in square meters.



Graph of predicted values for SDI (the Shannon Diversity Index of a patch) for the model TREEVOL & SEG & SEG*TREEVOL. TREEVOL is a tree-volume index, as explained in the text.



Graph of predicted values for SDI (the Shannon Diversity Index of a patch) for the model TAMVOL & SEG & SEG*TAMVOL. TAMVOL is a tamarisk-volume index, as explained in the text.



Graph of predicted values for SDI (the Shannon Diversity Index of a patch) for the model TAM & SEG & SEG*TAM. TAM is the amount of tamarisk vegetation, in square meters.

Chapter 8: Annotated Species List



ANNOTATED SPECIES LIST AND SUMMARY

OVERVIEW

This is an overview of our study of the avian community of Colorado River riparian habitats. We also include here all records of birds we saw, including non-riparian species such as waterfowl, waders and shorebirds, raptors, upland-associated songbirds, and any accidental and casual visitors to the canyon. More detailed discussions of riparian breeding bird habitat associations, study of survey methods, banding results, and avian diet can be found in other chapters of the report.

Trip Itinerary and Methods

We located study sites to form a representative sample of riparian habitats between Lee's Ferry and Diamond creek. At the largest geographic scale, canyon-wide, the river corridor follows an elevation gradient with changing vegetation communities from Great Basin desert-scrub to Sonoran desert-scrub (Turner and Karpiscak 1980). Also, characteristics of riparian vegetation relate naturally to the geomorphology of the 11 reaches of the river (as defined by Schmidt and Graf 1988). For these reasons, surveyed sites in each reach, within the constraints of river logistics. We adjusted the number of survey sites according to the abundance of riparian vegetation in a reach. For example, we spent more time in the Lower Canyon than the Upper Granite Gorge. At the intermediate scale, within each reach, we selected survey sites in a non-random fashion to obtain a broad distribution of patch size and shape, geomorphological, and vegetative characteristics. We located sites in groups so each group could be completely surveyed in one morning.

Four major study sites were selected, first to revisit sites surveyed by Brown et al. (1987) for direct flow-related impacts to riparian breeding birds, and second, to provide areas with large and diverse bird communities for banding and diet studies. We spent 3-4 concurrent days at major study sites on each trip to band birds, monitor direct impacts, and conduct consecutive daily surveys.

In 1993, we ran trips in May, June, July, and September. In 1994, we ran trips in January, March, April, May, June, July, and September. In 1995 we ran trips in February, March, April, May, and June. Though the focus of this project was to survey riparian breeding birds, trips in September allowed us to document use of the river corridor by fall migrants, and January and February trips allowed us to add to the small amount of information on winter bird use in the canyon.

WINTER BIRDS

Though we made only two winter visits, amounting to 23 days, because of the paucity of information on wintering birds of the canyon these observations will be discussed in detail. In 1994, the trip ran from 17 January to 1 February. We conducted surveys from Lee's Ferry to Parashant Wash and banded birds at major sites: River Mile (RM) 1.0R, 46.7R, 171.0R, and 198.0R. In 1995, the trip ran from 9 February to 18 February. We conducted surveys from Lee's Ferry to RM 214 but did no banding at the major study sites.

The largest number of species wintering in riparian habitats in the canyon belong to the order Passeriformes, the perching or song birds. Besides passerines, we found Red-naped Sapsucker, Red-shafted Flicker, and Gambel's Quail. In January 1994, data from surveys, banding, and casual observations include records of 13 species of passerines using riparian habitat: Say's Phoebe, Bewick's Wren, Winter Wren, Common Raven, Bushtit, Mountain Chickadee, Ruby-crowned Kinglet, Western Bluebird, Hermit Thrush, Yellow-rumped Warbler, Rufous-crowned Sparrow, Dark-eyed Junco, and Song Sparrow. The Canyon Wren and Rock Wren were present but rarely used riparian habitats.

In February 1995, we detected 23 passerine species from surveys and casual observations. In addition to those already listed, these were: Phainopepla, American Pipit, Crissal Thrasher, American Robin, Townsend's Solitaire, Scrub Jay, Canyon Towhee, Lincoln's Sparrow, and White-crowned Sparrow. The Mountain Chickadee and Winter Wren were the only species present in January 1994 but absent in February 1995.

From our surveys, we found birds to be more rare in January than February. In January surveys, we counted 74 riparian birds belonging to 12 species compared with 126 birds belonging to 17 species at those same sites in February 1995. Granivorous species were much more common in winter than in other seasons, and insectivorous species were correspondingly rare. All species observed in February 1995 but not January 1994 were found in the lower canyon, with the exception of the White-crowned Sparrow.

It is tempting to attribute the additional species observed in February to species beginning their migration, and in some cases this is probably true. However, we surveyed more sites in 1995 and surveyed further down the river to RM 214. We may have observed more wintering species in 1995 due to both of these factors. Also, more survey effort will always increase the species list of a study area. Finally, winter distribution of birds can be highly dependent on winter weather, and a milder winter in 1994-95 could have brought more wintering species into the canyon.

MIGRATORY BIRDS

We found 54 strictly migratory species using riparian habitat in the canyon. These can be separated into short-distance and long-distance migrants. Short-distance migrants winter elsewhere in the state, or in northern Mexico. They typically arrive earlier in the spring, as early as February for the Costa's Hummingbird, and many return later in the fall, even in November. A few, such as the Phainopepla, fall between winter resident and short-distance migrant in different years. Short-distance migrants include the Mourning Dove, Common Poor-will, White-throated Swift, Costa's Hummingbird, Belted Kingfisher, Ash-throated Flycatcher, Say's and Black phoebes, Scrub Jay, House, Winter, and Marsh wrens, Northern Mockingbird, most thrushes, Blue-gray Gnatcatcher, American Pipit, Phainopepla, Loggerhead Shrike, Lucy's Warbler, Yellow-rumped Warbler, most sparrows, Lesser Goldfinch, and House Finch.

Long-distance migrants winter from southern Mexico into South America. Most of these species pass through the canyon in late April and May, with fall migration starting in late July or August. In the canyon, this group includes the Vaux's Swift, Black-chinned and Broad-tailed Hummingbirds, Western and Cassin's kingbirds, Empidonax flycatchers, swallows, vireos, most warblers, blackbirds and orioles, tanagers, and grosbeaks. Species such as the Lazuli Bunting fall between the categories of short- and long-distance migrants (Phillips et al. 1964).

Several species are represented in the canyon by both migrant and breeding populations, which presents a problem for surveying. From our findings, it was clear that counts of some breeding species made in May were artificially inflated by migrants. These included the Common Yellowthroat, Yellow-breasted Chat, and especially Yellow Warbler. By conducting repeated surveys of the same sites we identified migratory peaks of abundance in May. Capturing birds with mist nets allowed us to look at the breeding condition of the birds caught and, in many cases, differentiate breeders from migrants. Future surveys of riparian breeders must take this into account when timing surveys and developing population models.

Mist nets provided an invaluable tool for studying migratory species. In addition to separating breeders from migrants, it provided the best means of detecting typically furtive migrants. Unlike breeders, many of these species make no sounds, or only quiet and non-descript call notes, and stay low in thick brush. This makes them difficult to find and identify, while making netting more effective. Eight species of migrants were observed only through mist net capture: Dusky Flycatcher, Hammond's Flycatcher, Solitary Vireo, Virginia's Warbler, Northern Waterthrush, Black-throated Blue Warbler (one previous canyon record), Blackpoll Warbler (a new species for the canyon), and Golden-crowned Sparrow.

BREEDING BIRDS

The breeding bird community in the canyon is fairly typical of riparian areas in the Southwest. We found 30 species breeding in riparian habitat in our study areas. Only a very few of these species were year-round residents of the canyon: the Bewick's Wren (but see below), Song Sparrow, Verdin, Gambel's Quail, and Wild Turkey. These last four species occur as localized populations of relatively few individuals.

Hence, the breeding community is dominated by species that migrate south during the non-breeding season. The breeding season starts in the lower canyon as early as February with the arrival of the Costa's Hummingbird, and is in full swing throughout the canyon by March with the arrival of short-distance migrants, most notably the Lucy's Warbler. Ash-throated Flycatchers, Yellow Warblers, Common Yellowthroats, and Yellow-breasted Chats start arriving in April. Most of the rest of the breeders arrive in May. A few species, the Blue Grosbeak in particular, do not arrive at some breeding locations until as late as June. They are one of the few species observed in undiminished numbers in July. Breeding bird abundance in July declined precipitously.

The distribution of breeders in the canyon varies greatly by species. Some species are more upland associated, or can use very small patches of habitat for breeding. These species, including the Lucy's Warbler, Blue-gray Gnatcatcher, and Ash-throated Flycatcher, bred in every reach surveyed. They were the only riparian species we found in many stretches of the sparsely vegetated Upper Granite Gorge (reach 6). Some species appear to be tied to very specific habitats. The Common Yellowthroat, for example, only breeds where there is a patch of emergent vegetation (esp. *Phragmites* and *Typha* spp.) for placing its nest. Most of the obligate riparian species in the canyon were only found in more well vegetated reaches, especially reaches 4 and 10, though many were also found in reaches 1, 5, and 7. In addition to habitat characteristics, biogeographic factors were also important. Those species most closely associated with the Sonoran desert were only found in reach 10. These include the Gambel's Quail, Ladder-backed Woodpecker, Brown-crested Flycatcher, Phainopepla, and Verdin. The presence of these lower Sonoran species gave reach 10 the highest breeding bird diversity of any in the canyon.

ANNOTATED SPECIES ACCOUNTS

The following is a list, in taxonomic order, of all the bird species observed during fieldwork on the Grand Canyon Avian Community Monitoring project, conducted between May 1993 and June 1995, between Lee's Ferry and Diamond Creek. Unless otherwise noted, these include observations made on the Avian Community Monitoring project along the Colorado River and its riparian habitats between Lee's Ferry and Diamond Creek. Observations are from walk-through and point count surveys (Surveys), banding operations (Banding), and general observations as recorded in field notes (Incidental).

Because this project focused on birds of Colorado River riparian habitats, groups not frequenting these habitats are not well represented in these discussions. Waterfowl, raptors, aerial foragers such as swifts and swallows, and more upland-associated species are not well covered in these accounts. Most of our observations on waterfowl were made downstream of Lee's Ferry. For a discussion of wintering Bald Eagles, see Sogge et al. (1995).

Commonly cited references in this section are abbreviated as follows: Phillips et al. (1964), PMM; Monson and Phillips (1981), MP; Brown et al. (1987), BCJ; and Rosenberg et al. (1991), ROHA. Locations of study sites and incidental sightings are given in river miles (RM) below Lee's Ferry (Stevens 1983), followed by R (right bank) or L (left bank). Status and abundance follow the definitions from Brown et al. (1987). Those species we confirmed breeding in the riparian habitat of the Colorado River are marked with a double asterisk (**) before the name.

Loons and Grebes

Common Loon (*Gavia immer*): Rare transient.

Incidental: One in basic plumage; first at RM 72, several more times before last sighting at Phantom Ranch, 19 May 1995.

Pacific Loon (*Gavia pacifica*): Casual transient.

Incidental: One at Lee's Ferry, 7 and 18 January, 12 March 1994.

Western Grebe (*Aechmophorus occidentalis*): Uncommon transient.

Incidental: One above Granite Rapid, 18 April 1995; one at RM 165, 20 May 1995.

Eared Grebe (*Podiceps nigricollis*): Rare transient.

Incidental: One between Lee's Ferry and RM 10, 13 April 1994; one just above Crystal Rapid, 18 April 1995.

Pied-billed Grebe (*Podilymbus podiceps*): Uncommon transient.

Incidental: Present at Lee's Ferry, 13 March 1994; one at Lee's Ferry, 13 April 1995.

Cormorants

Double-crested Cormorant (*Phalacrocorax auritus*): Uncommon winter and summer resident.
Incidental: One between Lee's Ferry and Buck Farm Canyon, 14 February 1993; present at RM 123, 19 April 1995; two adults at RM 199.5, 10 June 1994; one at RM 214.0, 24 June 1994; one in second-year plumage at RM 10, 14 June 1995.

Hérons and Egrets

Great Blue Heron (*Ardea herodias*): Common visitor, all seasons.

Surveys: Eight in January, March, April, May, June, and July. Most commonly in reaches 1, 2, 4.

Incidental: "... one every mile or so ..." between Phantom Ranch and RM 114, 12 February 1995 (DF field notes); present at RM 1.0R, 12 July 1994; one at RM 1.6R, 2 June 1994.

Notes: Earliest on 20 January 1994 below Lee's Ferry, latest around RM 190, 22 September 1994. Observations of a breeding colony below Diamond Creek (Theresa Yates, river boatman) were not confirmed on this project.

Great Egret (*Casmerodius albus*): Rare transient.

Incidental: Three seen at RM 194, 30 January 1994.

Snowy Egret (*Egretta thula*): Uncommon transient.

Survey: One at RM 214.0L, 26 April 1995.

Incidental: One at RM 72, 17 April 1995; one above Phantom Ranch and one at RM 108, 18 April 1995; six at RM 122.8, 20 April 1994; one in Reach 1, 7 May 1994; present at RM 1.0R, 12 September 1994; one around RM 190, 22 September 1994.

Cattle Egret (*Bubulcus ibis*): Casual visitor.

Incidental: One above Granite Rapid, 18 April 1995.

Notes: One of two records for the canyon, this species will undoubtedly be increasing in coming years.

Green-backed Heron (*Butorides striatus*): Rare summer visitor.

Surveys: one at RM 204.5R, 27 April 1994; one at RM 1.6R, 7 May 1994.

Black-crowned Night-heron (*Nycticorax nycticorax*): Uncommon summer resident.

Surveys: One sub-adult at RM 5.2R, 14 April 1995.

Incidental: One sub-adult at RM 168.8, 14 May 1994; two sub-adults at Lee's Ferry, 1 June 1994.

White-faced Ibis (*Plegadis chihi*): Uncommon transient.

Incidental: One seen at Cardenas Marsh, 17 April 1995; one at RM 198.0R, 22 April 1995; three at RM 167, 21 July 1994.

Ducks, Geese, and Swans

Canada Goose (*Branta canadensis*): Fairly common winter visitor.

Surveys: 17 at RM 1.6R, 20 January 1994; one at RM 1.6R, 13 April 1994.

Incidental: Thrity five between Nankoweap Creek and Phantom Ranch, 22 January 1994; 10-15 at RM 171.0R, 26 January 1994; 20-25 in two flocks below Nankoweap Creek, 11 February 1995.

**** Mallard** (*Anas platyrhynchos*): Uncommon summer and winter resident.

Surveys: Numerous, mostly from Reach 4: three males in January, 26 (23 males) in February, four in March (two pairs), five in May, and three in June. Reach 1: two in April, one in June.

Incidental: 30 flying by Between RM 5.2 and RM 46.7, 16 February 1995. Female flushed from grassy uplands (probably off a nest) at RM 48.5L, 17 April 1994. Female incubating ten eggs at Lee's Ferry, 1 June 1994. Brood of seven ducklings and one of one duckling at RM 43 and RM 46.7, 15 May 1995; a brood of nine, only days old, at eddy below RM 49.1R, 16 May 1995.

Notes: This was the only species of duck we found breeding in the canyon, broods most often being seen in April, May, and June between South Canyon and Nankoweap Creek. Though most common in winter and summer, some were seen in every month of the year.

Green-winged Teal (*Anas crecca*): Uncommon winter visitor.

Incidental: Two at Lee's Ferry, 18 January 1994; 20 between RM 54 and RM 88, 22 January 1994; 35 between Lee's Ferry and RM 54, 19 February 1994; in "medium numbers" (DF field notes) between Phantom Ranch and RM 114, 12 February 1995; 10-15 at RM 5.6, 12 March 1995; 20 flying upstream between RM 5.2 and RM 46.7, 16 March 1995; five at Kwagunt Marsh (above rapid, river-right), 18 May 1995; present between RM 97 and RM 123, 12 May 1994; 17 at RM 31, 14 September 1994; seven at RM 55, 17 September 1994; three between RM 128 and RM 167, 20 September 1994; and seven with Blue-winged Teal around RM 190, 22 September 1994.

Notes: The presence of this species in the Upper Granite Gorge below Phantom Ranch in February is significant. Because this reach contains few large eddies or other suitable habitat, these birds were probably moving through, suggesting that northern migration begins as early as February. In fact, this species is one of the earliest migrants among waterfowl, with migration in the Central Flyway beginning in February (Kortright 1967, p. 201).

Northern Pintail (*Anas acuta*): Uncommon winter visitor.

Surveys: ten at RM 1.6R, 9 February 1995.

Incidental: 21 between Lee's Ferry and RM 54, 19 February 1994; 20 attacked by a Peregrine Falcon in Furnace Flats (no casualties), 17 September 1994.

Blue-winged Teal (*Anas discors*): Fairly common winter visitor.

Incidental: Two at RM 66, 17 April 1994; approximately 90 at RM 70, 11 May 1994; 21 between RM 123 and RM 167, 19 September 1994; six between RM 176 and RM 171, 20 September 1994; 18 around RM 190, 22 September 1994.

Cinnamon Teal (*Anas cyanoptera*): Uncommon transient.

Incidental: Six between Lee's Ferry and RM 54, 19 February 1994; eight between RM 54 and RM 88, 23 February 1993; three between RM 10 and RM 46, 13 April 1994; five at RM 55, 17 April 1994; present between RM 97 and 123, 12 May 1994; pair at RM 107, 18 April 1995; present at RM 1.6R, 15 May 1995.

Northern Shoveler (*Anas clypeata*): Rare transient.

Incidental: One between Lee's Ferry and RM 54, 19 February 1994; two between Lee's Ferry and RM 47, 19 April 1994; present between RM 5 and RM 46.7, 14 April 1995; 21 between RM 86 and RM 123, 19 September 1994.

Gadwall (*Anas strepera*): Common winter resident.

Incidental: Seen between Lee's Ferry and RM 40, 14 February 1993; 73 at Lee's Ferry, 19 February 1994; third-most common species at Lee's Ferry, 9 February 1995.

American Wigeon (*Anas americana*): Common winter resident.

Incidental: four between RM 52 and RM 88, 22 January 1994; 47 between Lee's Ferry and RM 40, 14 February 1993; 76 between Lee's Ferry and RM 52, 19 February 1994; second-most common species at Lee's Ferry, 9 February 1995; ten between RM 5.2 and RM 46.7, 16 March 1995; one between RM 88 and RM 123, 19 September 1994.

Wood Duck (*Aix sponsa*): Casual transient.

Incidental: one female above South Canyon, 15 May 1995.

Canvasback (*Aythya valisineria*): Rare transient.

Incidental: "Occasionally seen" at Lee's Ferry.

Redhead (*Aythya americana*): Common winter resident.

Incidental: Twenty between Lee's Ferry and RM 52, 19 February 1994; two males and one female at RM 1.4, 12 May 1995; one at Lee's Ferry, 4 June 1993.

Ring-necked Duck (*Aythya collaris*): Uncommon winter visitor.

Incidental: One hundred twenty between Lee's Ferry and RM 52, 19 February 1994; two between RM 52 and RM 88, 23 February 1993; a pair in eddy at RM 171.1R, 22 September 1994.

Lesser Scaup (*Aythya affinis*): Common transient.

Incidental: Five between RM 52 and RM 88, 22 January 1994; four between RM 52 and RM 88, 23 February 1993; a few between RM 1.0 and 46.7, 20 January 1994; one taken by Peregrine Falcon at RM 60, 20 March 1995.

Surf Scoter (*Melanitta perspicillata*): Casual winter resident.

Incidental: One at Lee's Ferry, 18 January 1994, 11 April 1994, and 21 July 1992.

Common Goldeneye (*Bucephala clangula*): Common winter resident.

Surveys: 13 in January 1994, 17 in February 1995, and nine April 1995.

Incidental: Though most common in Reach 1, also seen in reaches 4, 5, and 10. Approximately 80% of all ducks seen between RM 5.6 and 46.7, 20 January 1994 (DF field notes); three between RM 52 and RM 88, 22 January 1994; 650 between RM 1.0 and RM 40, 14 February 1993; 97 between RM 40 and RM 52, 15 February 1993; 76 between RM 52 and RM 88, 23 February 1993; the most numerous species at Lee's Ferry, 9 February 1995; 20 at RM 8 and 30 below Soap Creek Rapid, 9 February 1995; less than one hundred below Nankoweap Creek, 11 February 1995; "numerous" between RM 5.6 and 46.7, 16 March 1994; 163 between RM 5.0 and 46.7, 16 March 1995; 45 between RM 5.2 and 46.7, 13 April 1995.

Bufflehead (*Bucephala albeola*): Fairly common winter resident.

Surveys: Three at RM 1.0R 13 March 1994; one at RM 1.6R, 16 March 1994; two at RM 74.4L, 18 April 1995;

Incidental: "Several" on 20 January 1994 between RM 1.0 and RM 46.7, 8 between RM 52 and RM 88, 22 January 1994; five at RM 7.0, 9 February 1995; 190 between Lee's Ferry and RM 52, 19 February 1994; "numerous" between RM 1.0 and 46.7, 16 March 1994 (DF field notes); five between RM 10.0 and RM 46.7, 13 April 1994.

Ruddy Duck (*Oxyura jamaicensis*): Rare transient.

Incidental: Five at Lee's Ferry, 18 January 1994; present at Lee's Ferry, 12 March 1994.

Common Merganser (*Mergus merganser*): Fairly common winter and uncommon summer resident.

Surveys: Three at RM 49.2L, 11 February 1995.

Incidental: One between RM 1.0 and 46.7, 20 January 1994; 17 between RM 52 and RM 88, 22 January 1994; seven between RM 1.0 and RM 40, 14 February 1993; 23 between Lee's Ferry and RM 52, 19 February 1994; three between RM 52 and RM 88, 23 February 1993; six between RM 10.0 and RM 46.7, 13 April 1994; two at RM 52, 17 April 1994; two at RM 87, 13 April 1994; one at RM 5.1, 13 May 1993; present between RM 1.0 and RM 46.7, 14 July 1994; one at RM 30, 14 September 1994.

Hooded Merganser (*Lophodytes cucullatus*): Rare winter visitor.

Incidental: Two males at Lee's Ferry, 17 January 1994; two males and three females at Lee's Ferry, 14 February 1993; four females just above Lee's Ferry, 13 March 1994.

New World Vultures

Turkey Vulture (*Cathartes aura*): Common transient.

Surveys: One at 174.2L, 14 May 1994; two at RM 174.7, 20 April 1995; and three at 174.4, 21 May 1995.

Incidental: First spring migrants in 1994 were six birds at RM 198.0, 30 March; first spring migrants in 1995 were two birds, also at RM 198.0, 23 March. Numerous groups, including one flock of 13 birds moving north at RM 224, 23-29 March 1995; one between RM 171 and RM 198, 22 September 1994.

Kites, Eagles, Hawks and Falcons

Bald Eagle (*Haliaeetus leucocephalus*): Uncommon winter resident.

Surveys: one adult at RM 50.0R, 11 February 1995.

Incidental: One adult at RM 17, and two to five more adults between RM 17 and RM 46.7, 20 January 1994; two below RM 52, 22 January 1994; two adults between RM 1.0 and 46.7, 16 March 1994; one adult and one juvenile at RM 6R, one adult and one juvenile above Redwall Cavern, one adult and one "osprey" plumage, one mile below Redwall Cavern, and two adults on a pinnacle at RM 34R, 9 February 1995; two adults at Nankoweap Creek, 11 February 1995.

Osprey (*Pandion haliaetus*): Rare transient.

Incidental: One at Lee's Ferry, 14 April 1994 and 15 May 1995; one above Crystal Rapid, 18 April 1995; one at RM 74.4, 18 September 1994; one at RM 196, 24 September 1994; one at RM 204, 25 September 1994.

Northern Harrier (*Circus cyaneus*): Rare transient.

Incidental: One at Lee's Ferry, 6 January 1995; one second-year bird or female over uplands at RM 1.0, 18 January 1994; one juvenile at RM 218, 27 July 1995.

Northern Goshawk (*Accipiter gentilis*): Rare transient.

Incidental: One at RM 52, 17 April 1994.

Sharp-shinned Hawk (*Accipiter striatus*): Uncommon winter resident.

Surveys: one at RM 46.7R, 17 March 1995; one sub-adult at RM 198.0R, 30 March 1994; one sub-adult at RM 205.8R, 28 September 1994.

Incidental: One adult and one sub-adult at Lee's Ferry, 6 January 1995; one around RM 15, 20 January 1994; one at Nankoweap Creek, 16-22 February 1993; one above Sheer-wall Rapid, 16 March 1994; one at RM 198.0R, 24 March 1995; one at RM 50, 17 September 1994; one sub-adult at RM 198.0, 23 September 1994; one at RM 204, 28 September 1994.

Cooper's Hawk (*Accipiter cooperii*): Rare transient.

Surveys: One at RM 204.5R, 27 September 1994.

Incidental: One sub-adult bird at RM 198.0R, 23 September 1994. "Accipiters generally numerous" along the river from RM 198 to 205, 26 September 1994 (DF field notes); one at RM 1.0R, 12-13 August 1994; one around mist nets at RM 1.0R, 13 October 1994.

**** Red-tailed Hawk** (*Buteo jamaicensis*): Common permanent resident.

Surveys: three in March, one in April, two in May and two in July (all years combined)

Incidental: One around RM 80 eating a rock squirrel, 19 September 1994; one being mobbed by a pair of Peregrine Falcons around RM 125, 21 March 1995; one high above river at RM 46.7, 17 March 1995.

Golden Eagle (*Aquila chrysaetos*): Uncommon summer and winter resident.

Incidental: One high above the river at RM 74, 10 February 1995; one high above river at RM

46.7, 17 March 1995; one between Lee's Ferry and RM 5.6, 13 April 1994; one near Cardenas Marsh, 17 April 1994; one sub-adult flushed from among dense riparian vegetation in Spring Canyon, 26 June 1995.

American Kestrel (*Falco sparverius*): Uncommon transient.

Surveys: One at 174.7R, 20 April 1995; one at RM 50.0R, 18 July 1994; one at RM 200.4R, 25 September 1994.

Incidental: One at Lee's Ferry, 6 January 1995; one at Nankowep Creek, 16-22 February 1993; three between RM 1.0 and 46.7, 16 March 1994; one between RM 10 and RM 46.7, 13 April 1994; one at RM 49.2L, 10 July 1993; one at RM 74.4, 18 September 1994; one between RM 88 and RM 123, 19 September 1994; one between RM 198 and RM 204, 25 September 1994.

**** Peregrine Falcon** (*Falco peregrinus*): Uncommon summer and winter resident.

Surveys: total of 12 -- one in February, five in March, four in May, and two in June.

Incidental: Observations were too numerous to list. We observed more Peregrines in March (three), and September, especially in reaches 1, 4, and 5. We found evidence of breeding at RM 46.7R (a pair with a first-year bird, 15 July 1994) and at RM 125.5 (a pair dive on a Red-tailed Hawk above river, obviously territorial).

Notes: We had numerous opportunities to watch Peregrines hunting. We observed a pair, one carrying prey, possibly a teal, at RM 13, 16 March 1995; one killed a Lesser Scaup at RM 60, but lost it in the rapid, 20 March 1995; one killed a female teal, possibly Green-winged, at RM 209, then lost it in the rapid, 1 April 1994; a pair were diving on White-throated Swifts and bats at RM 204.5R, 18 May 1994; a female captured a Brewer's Sparrow below RM 1.0R, 13 September 1994; one stooped on a flock of Northern Pintail in Furnace Flats, 17 September 1994.

Prairie Falcon (*Falco mexicanus*): Rare transient.

Incidental: One above river just below Lava Falls, 9 June 1994.

Gallinaceous Birds

**** Wild Turkey** (*Meleagris gallopavo*): Rare permanent resident.

Surveys: one at RM 49.1R, 17 April 1995; one at RM 50.0R, 5 June 1994; one at RM 46.7R, 15 July 1994.

Incidental: We observed this species many times, always in Reach four, Lower Marble Canyon. We observed tracks at RM 46.7R, 22 January 1994; tracks in wet sand at RM 49.1R, 17 April 1995; four (one male, three females!) at RM 52L, 17 April 1994; two birds at 46.7L flew across the river, 8 May 1994; a bird at 49.2L, 10 May 1994; one at RM 50.0R flew across river, 5 June 1994; one female at RM 47, 9 June 1993; two at RM 50.0R, 17 September 1994. Most important, Dave DeRoissers, NPS river ranger, showed us Wild Turkey egg shells at RM 51.0L, 5 June 1994.

Notes: MP (p.30) has one record from "... the bottom of the Grand Canyon, 9 Aug. 1970." BCJ (p.177) does not consider this species a permanent resident along the river, though it does state, "... a few are even reported from along the river." These birds are seen fairly frequently by river

guides, and probably represents a self-sustaining, resident population. They probably originated from reintroductions on the Kaibab Plateau (PMM, p.30)

Gambel's Quail (*Callipepla gambelii*): Rare permanent resident.

Surveys: three at RM 198.0R, 30 January 1994; at RM 208.7R in 1994, we observed one in May, three in June, and 13 in July.

Notes: The status of this species in the region is unclear. Statewide, it is "Abundant resident in all areas where mesquite occurs, including the Grand Canyon . . ." (MP, p. 28). In the Grand Canyon, BCJ (p. 178) consider them "common and localized", but only up to around RM 249. Apparently, they were once fairly abundant in Havasu Canyon and some probably remain (ibid.).

Coots and Rails

Virginia Rail (*Rallus limicola*): Uncommon transient.

Incidental: One at Lee's Ferry, 5 May 1994; remains of one found on beach at RM 1.0R, 20 June 1995; one at RM 59L, 17 September 1994.

Sora (*Sora porzana*): Rare transient.

Surveys: One at RM 202.5R, 27 April 1994, in a patch of arrowweed; one in marsh 6.5 miles above Lee's Ferry, 3 June 1993.

Notes: There are very few records for the Sora in the Grand Canyon (BCJ, p. 180).

American Coot (*Fulica americana*): Fairly common winter and summer resident.

Surveys: One at RM 1.0R, 12 April 1995.

Incidental: Seven at Lee's Ferry, 7 January 1994; two at Lee's Ferry, 18 January 1994; several at Lee's Ferry, 9 February 1995; one at Lee's Ferry, 14 April 1995.

Shorebirds

Black-necked Stilt (*Himantopus mexicanus*): Uncommon transient.

Incidental: One at RM 1.4, 13 April 1994.

Killdeer (*Charadrius vociferus*): Common summer resident and uncommon winter visitor.

Surveys: One at RM 1.6R, 9 February 1995; one at RM 1.0R, 15 March 1994; four on 16 March 1995 -- two at RM 2.0L, one at RM 5.1L, and one at RM 5.2R; one at RM 108R, 22 March 1993; on RM 213.6L, 28 March 1995; one at RM 1.6R, 12 April 1995; two at RM 1.0R, 13 April 1994; two at RM 2.0L, 15 May 1995.

Incidental: One between RM 54 and RM 88, 22 January, 1994; one between Lee's Ferry and RM 10, 13 April 1994; one at Lee's Ferry 14 April 1995.

**** Spotted Sandpiper** (*Actitis macularia*): Common summer resident.

Surveys: We observed 23 -- one in March (Reach 1), 14 in May (reaches 1, 5, 7, and 10), two in June (reaches 1 and 7), three in July (reaches 1, 4, and 5), and three in September (reaches 1, 4, and 10).

Incidental: One below Nankoweap Creek, 22 January, 1994; 18 in flocks of two to five between RM 5.0 and 46.7, 15 May 1995; present at RM 1.0R, 12 July 1994; eight between Lee's Ferry and RM 46.7, 14 September 1994.

Notes: An adult with two chicks at RM 1.6R, 12 July 1994 was our only breeding record.

Lesser Yellowlegs (*Tringa flavipes*): Uncommon transient.

Incidental: One at RM 204.5R, 25 April 1995.

Common Snipe (*Gallinago gallinago*): Rare transient.

Incidental: One under the dock at Lee's Ferry, 19 January 1994; one at Lee's Ferry, 6 January 1995; one at RM 122.8L, 23 March 1994.

Gulls

Ring-billed Gull (*Larus delawarensis*): Uncommon transient.

Surveys: one at RM 171.1R, 14 May 1994.

Incidental: Three above Little Colorado River, 21 March 1994; eight at RM 70, 18 March 1995; a flock of 20 at Lee's Ferry, 14 April 1995; six at RM 46.7R, 14 April 1994; 44 at RM 46.7R, 15 April 1994; small flock between RM 97 and RM 123, 12 May 1994; three sub-adults at RM 1.4, 12 May 1995; one sub-adult at the mouth of Nankoweap Creek, 18 May 1995.

California Gull (*Larus californicus*): Rare transient.

Incidental: Present below RM 204.5, 28 March 1995; one with group of Ring-billed Gulls between RM 97 and RM 123, 12 May 1994.

Pigeons and Doves

Rock Dove (*Columba livia*): Uncommon transient.

Incidental: One accompanying a female Great-tailed Grackle at Lee's Ferry, 18 January; again 13 March 1994; again 12 April 1994.

**** Mourning Dove** (*Zenaida macroura*): Common summer resident.

Surveys: 75 Mourning Doves on 65 Surveys: 25 in May, 29 in June, seven in July, and six in September. We observed 27 in 1993, 27 in 1994, and 21 in 1995. We found them most often in Reach 1 (n = 33), then 10 (n = 23), then 4 (n = 10), then 7 (n = 5), then 5 (n = 3).

Incidental: Too numerous to list. They were seen from 17 April to 21 September.

Notes: PMM (p. 42) gives dates in northern Arizona "... mostly from the middle of April to the middle of September ..." corresponding well with our data. We found four active nests between 18 May and 6 July, in reaches 1, 7, and 10.

Roadrunners

Greater Roadrunner (*Geococcyx californianus*): Uncommon permanent resident.

Incidental: One at RM 1.0R, April 1993; individuals around Lee's Ferry on 8 May 1994, 30 May 1994, 11 July 1994, and 12 October 1994; one at RM 216, June 1993; one at RM 185, 18 June 1993.

Notes: The furthest upstream record in BCJ (p. 192) is at Nankoweap Creek, suggesting that this species has recently expanded its range in the canyon to Lee's Ferry.

Owls

Great Horned Owl (*Bubo virginianus*): Uncommon permanent resident.

Incidental: One calling at the mouth of Mohawk Canyon, RM 171.5L, 28 January 1994; one at RM 46.7R, 19 March 1994; one calling at RM 46.7R, 14 March 1995; one at RM 46.7R, 15 April 1994; one just downstream from the Navajo Bridge, 15 April and again 15 May 1995; one at RM 5.2R 13 May 1995; one at RM 46.7R, June 1993; one between RM 171.0 and RM 198.0, 22 September 1994.

Spotted Owl (*Strix occidentalis*): Rare permanent resident.

Incidental: One was heard calling at narrowest section of Spring Canyon, several miles from the river, 24 April and again 24 June 1995. This is a very rare record for the canyon.

Goatsuckers

Common Poorwill (*Phalaenoptilus nuttallii*): Uncommon summer resident.

Incidental: remains of one bird at RM 206R, 20 May 1994; one flushed one from a dry wash above RM 224L, 28 March 1995; one between RM 1.0R and RM 46.7R, 15 May 1995; one heard at RM 47, 8 June 1993 and near RM 47 R, 15 April 1995.

Swifts

Vaux's Swift (*Chaetura vauxi*): Uncommon transient.

Surveys: two at RM 1.0R, 14 September.

Incidental: Five at RM 122.8L, 19 September 1994.

White-throated Swift (*Aeronautes saxatalis*): Common summer resident.

Surveys: 152 on 12 surveys between 17 March and 17 September. We counted three flocks in March, four in May, and four in September. Most commonly observed in Reach 4 (n = 11) but also frequently in Reach 1 (n = 1).

Notes: We observed Peregrines preying on this species at RM 204.5 and RM 46.7.

Hummingbirds

**** Black-chinned Hummingbird (*Archilochus alexandri*):** Common summer resident.

Surveys: 284 on 264 surveys -- 51 in March, 90 in April, 80 in May, 46 in June, and 15 in July. We found them breeding in 27% of sites surveyed in 1993 (n = 33), 73% of sites in 1994 (n = 48), and 71% of sites in 1995 (n = 52). Note, however, that because surveys in 1993 did not begin until May, many early breeders may have been missed. We found this species in every reach that we surveyed. Earliest dates were 19 March 1995 and 20 March 1994, both at RM 46.7R. Our latest date was 7 September 1993 at RM 171.0R. They were not seen on the September 1994 trip, which arrived at RM 171.0R on 21 September.

Notes: Though this species ranked sixth in abundance among the riparian breeding birds found on walking surveys, we found more Black-chinned nests than any other (n = 14), except the Bell's Vireo. This apparent contradiction is due to several factors. First, they occur in extremely high abundance as a riparian nesting species (BCJ, p. 200) and the female quickly returns to its nest after being disturbed, making nests easy to locate. Second, because they do not sing loudly to advertise their territorial boundaries, detection probability on surveys is low relative to other common breeders, therefore general surveys tend to underestimate their numbers. Though our sample of nests was small, we found interesting differences from Brown (1992) regarding nest site location and nest substrate. Though they found no nests in OHWZ vegetation, three of the 13 nests we found (23%) were in hackberry trees in the OHWZ. Also, they found 94% of all nests in tamarisk, we found only five (38%) in tamarisk. However, our low counts in tamarisk probably has more to do with differences in nest-finding methods because we did not do systematic nest searches.

**** Costa's Hummingbird (*Calypte costae*):** Fairly common breeder.

Surveys: Thirty four birds -- one in February, 15 in March, 16 in April, and two in May. Our earliest date was at RM 206.5L, 17 February 1995, and our latest was 22 May 1995 at RM 197.6L.

Incidental: Male displaying and singing at Bass Camp, RM 108R, 22 March 1994 and again, 19 April 1994; male at RM 171.0R, 27 March 1994; male singing at ledges below Lava Falls, 28 March 1994; one heard at RM 198.0R, 29 March 1994; a male seen at RM 46.7R, 17 March 1995; one heard at RM 217L, 28 March 1995; one heard at RM 224L, 26 April 1995. One was observed displaying at banding station at RM 204.5R, 25-27 March 1995 and again 24-26 April 1995.

Notes: This is an interesting species, "... the dry desert hummingbird *par excellence* ..." and is among the first spring migrants; 17 February not being exceptionally early (PMM, p. 62). It is a Sonoran desert species and almost all our survey records are from the lower canyon (31-or 91% from reaches 10 and 11). By late May, they have all left the canyon (BCJ, p. 201), apparently for the coast of California and Baja (PMM, p. 62).

Broad-tailed Hummingbird (*Selasphorus platycercus*): Uncommon transient.

Incidental: Heard male at RM 204.5 27 April 1994.

Rufous Hummingbird (*Selasphorus rufus*): Rare fall transient.

Incidental: One at RM 49.0, 17 July 1994; one adult male at RM 1.0R, 26 July 1994; two

fighting at RM 1.0R, 11 August 1994.

Kingfishers

Belted Kingfisher (*Ceryle alcyon*): Fairly common transient.

Surveys: One at RM 204.5R, 24 April 1995.

Incidental: Female at RM 90, 19 March 1995; present between RM 1.0 and RM 46.7, 14 April 1995; several between RM 120 and 167, 19 April 1995; three (one male, two females) around RM 131.3, 20 April 1994; one at RM 119.0, 12 July 1993; four between Lee's Ferry and RM 46.7, 14 September 1994; numerous (all males) along river above Phantom Ranch, 19 September 1994; five or six more seen between RM 122.8 and RM 167.0, 20 September 1994.

Notes: Though they appeared more abundant in reaches with little vegetation like the Upper Granite Gorge and the Muav Gorge, this may be due simply to their greater visibility.

Woodpeckers

Red-naped Sapsucker (*Sphyrapicus varius nuchalis*): Uncommon transient.

Surveys: One at RM 46.7R, 22 January; one at RM 198.0R, 30 January 1994; one at RM 1.0R, 12 April 1994; one at RM 168.8 R, 22 July 1994; one at RM 174.2L, 22 September 1994; two at RM 198.0R, 23-25 September 1994; one at RM 200.5R, 25 September 1994; one at RM 202.5R, 25 September 1994; one at RM 213.6L and RM 214.0L, 28 September 1994.

Banding: Two at RM 198.0R, 31 January 1994 and 24 September 1994.

Incidental: One at RM 46.7R, 22 January 1994; one visiting tamarisk sap wells at RM 171.0R, 27 January 1994; a male at Bass Camp, RM 108R, 19 April 1994; one around RM 87L in tamarisks, 18 September 1994; and a male seen foraging in tamarisks at RM 171.0R, 21 September 1994.

Notes: This was the most common woodpecker we observed in the canyon, and the only one frequently seen on winter surveys (both in January 1994 and February 1995). The Red-shafted Flicker was observed in both years, but only in 1995 on surveys. Though not common (a total of four winter records), this is an interesting species for several reasons. According to PMM, the winter range is difficult to identify because transients pass through the state as late as November, and as early as January. Thus birds we saw may have been early migrants. However, they are recognised as uncommon winter residents along the river corridor (BCJ, p.207). Second, Red-naped Sapsuckers in the canyon make extensive use of the exotic tamarisk for drilling their sap wells. Because the river corridor is very close to the edge of winter range for this species, the relatively recent development of dense stands of tamarisk may have facilitated northern extension of the winter range of the Red-naped Sapsucker. However, most of our survey records are from Reach 10 (13 of 15 or 87%), where we also found sap wells in mesquite, a species present before the dam.

Ladder-backed Woodpecker (*Picoides scalaris*): Uncommon permanent resident.

Surveys: One at RM 198.0R, 15 May 1994; one at RM 204.1R, 24 June 1995; one at 198.0R, 23 July 1994; one at RM 204.5R, 26 July 1994; one at RM 204.5R, 26 September 1994.

Incidental: One at RM 198.0R, 23 July 1994, and heard one at RM 200.5R, 25 July 1994.

Notes: BCJ (p. 207) consider it a rare permanent resident of the western part of the canyon. Our observations suggest that its occurrence in Colorado River riparian habitat is seasonal, during the hottest months. During other months it probably resides in adjacent upland Sonoran desert-scrub, where it can nest in plants as small as yucca stalks (PMM, p. 75). However, breeding on the lower Colorado occurs predominantly in riparian habitats, from February through June. Juveniles disperse from the lower Colorado in late June and July (ROHA, p. 225), suggesting that the birds we saw could represent post-breeding dispersal from possibly distant populations.

Northern (Red-shafted) Flicker (*Colaptes auratus cafer*): Uncommon winter visitor.

Surveys: We found it on six surveys, one in February and five in September.

Banding: One at RM 46.7R, 16 September 1994.

Incidental: One at 171.0L, 27-28 January 1994; one at RM 198.0R, 30 January 1994.

Tyrant Flycatchers

Olive-sided Flycatcher (*Contopus borealis*): Rare transient.

Incidental: One at RM 204.5R, 19 May 1994.

Western Wood-pewee (*Contopus sordidulus*): Fairly common transient.

Surveys: One at RM 49.1R, 10 May 1994; one at 204.5R, 19 May 1994; one at RM 49.1R, 17 May 1995; one at 204.1, 25 May 1995; one at 204.5R, 25 May 1995; one at 5.1L, 7 June 1993; one at 5.2R, 7 June 1993; one at 125.5R, 19 June 1995; one at RM 1.0R, 13 September 1994.

Banding: One at RM 1.0R, 13 September 1994; one at RM 198.0R, 17 May 1994; and two at RM 204.5R, one 9 May 1994 and one 25 May 1995.

Incidental: Two at RM 1.0R, 31 May 1994; one at RM 1.0R, 14 May 1995; one at Lee's Ferry, 9 June 1995; one at RM 1.0R, 24 September 1994.

A note on the following species of the genus *Empidonax*: These species are very difficult to properly identify in the field, their songs being the only good diagnostic character in most cases. Unfortunately, they rarely sing during migration and only the Willow Flycatcher breeds in the canyon. Thus our banding results provide the best records for some species in the canyon, because diagnostic characters include measurements of wing and bill which can only be made in the hand. The Gray Flycatcher is one exception because it is the only empidonax that flicks its tail down rather than up when perched, and the Western Flycatcher is another, possessing a large, teardrop shaped eye ring.

**** Willow Flycatcher** (*Empidonax traillii*): Rare summer resident.

Surveys: Two at RM 1.0R, 2 June 1994; one at RM 1.6R, 2 June 1994; one at RM 46.7R, 10 July.

Banding: Two at RM 1.0R, one on 12 August and one on 13 October 1994; two at RM 46.7R, one on 10 June and one on 9 July 1994 (one of these later nested at RM 51, 1995); two at RM 198.0R, one on 26 April 1994 and one on 23 April 1995; one at RM 204.5R, 27 May 1995.

Incidental: One singing at Cardenas Marsh, 11 May 1994; one singing at RM 204.5R, 19 May

1994; two singing at RM 1.0R, 2 June 1994; one singing at RM 46.7R, 9 July 1993; one at RM 1.0R, 12 August 1994.

Note: For more information on this species in the Grand Canyon see Sogge et al. (1995).

Hammond's Flycatcher (*Empidonax hammondi*): Uncommon transient.

Banding: One at RM 198.0R, 27 April 1994.

Notes: This is an important record because this species's status in the region is not well known. Only three confirmed records exist for the canyon (BCJ, p. 210).

Dusky Flycatcher (*Empidonax oberholseri*): Uncommon transient.

Banding: one at RM 1.0R, 12 May 1995; two at RM 46.7R, one on 8 May 1994 and one on 17 May 1995; one at RM 198.0R, 16 May 1994; two at RM 204.5R, one on 19 May 1994 and one on 25 May 1995.

Notes: These records are important; the only two previous records in the canyon are both from September (BCJ, p. 210).

Gray Flycatcher (*Empidonax wrightii*): Uncommon transient.

Surveys: Two at RM 204.5R, 27 April 1994; one at RM 208.7R, 27 April 1995; one at 1.0R, 7 May 1995; one at 46.0L, 16 May 1995.

Banding: One at RM 46.7R, 17 May 1995; two at RM 198.0R, 26-27 April 1994; one at RM 198.0R, 21 April 1995; two at RM 204.5R, 24 April 1995.

Notes: Previously, there was only one record from the river in the canyon (BCJ, p. 211).

Western Flycatcher (*Empidonax difficilis*): Uncommon transient.

Surveys: One at RM 49.1R, 10 May 1994.

Banding: one at RM 1.0R, 13 September 1994; two at RM 204.5, 19-20 May 1994.

** **Black Phoebe** (*Sayornis nigricans*): Common summer and uncommon winter resident.

Surveys: Thirty birds from March through July. All March records from Reach 10, other months included reaches 1, 4, 5, 7, and 10.

Incidental: Too numerous to list. Earliest date, below RM 214, 17 February 1995; latest 16 July 1994 at RM 174.4R.

Notes: Though considered an uncommon and localized breeder in the Grand Canyon (MP, p.101), it is a more common breeding species than suggested by our data. This is because we focused on riparian vegetation to which the Black Phoebe is not tied in the canyon. For example we found several old nests in the Muav Gorge. Though considered an uncommon winter resident along the river (BCJ, p. 212), we did not observe this species at all in January 1994.

We found eight Black Phoebe nests during the project. In addition, we saw three active nests while floating by RM 190, 24 April 1994. A nest under construction below flood level at RM 110L, 21 March 1995, was the earliest we saw. The preferred nest site of this species is under a ledge over water (PMM, p. 83), which makes this species especially vulnerable to nest inundation due to fluctuating river flows in the canyon. We found several interesting nests. One, attached to a lava boulder at RM 209R, 27 April 1994, was approximately 0.4 meters above the river. It contained one live nestling about half way to fledging. Two dead nestlings were

suspended from the rim by their feet, entangled in the mud of the nest. Upon revisiting it on 20 May, we found that a second nest had been built on top of the old one with the head of one dead nestling sticking out in between. At RM 214.0L, we found a bird nesting under an overhang over dry land, something this species rarely does. Nesting was seen in this location in 1994 and 1995. We did not notice the tendency for this species to nest only around tributary mouths in the canyon (BCJ, p. 212). However, it was more common in the lower reaches (one in Reach 1, two in reach 4, two in reach 5, three in reach 7, 22 in reach 10), possibly due to the availability of fine sediments for nest building.

**** Say's Phoebe (*Sayornis saya*):** Common summer and uncommon winter resident.

Surveys: 159 birds: two in January, 13 in February, 44 in March, 27 in April, 26 in May, 24 in June, 19 in July, and 4 in September. Occurred in all reaches surveyed.

Notes: This is another species which is not tied to riparian habitat in the canyon, so our surveys may underestimate their numbers around our study sites. We found several nests: a pair was seen building a nest at RM 171.0R, 27 March 1994. The nest on ledge of cliff, 7 meters above top of 40 meter talus slope. We later found at least two eggs, 23 April, but the nest appeared abandoned. We found an active nest 10 cm above 1983 flood line with two very young nestlings and one egg, 28 March 1995.

This was the only flycatcher we found wintering in the canyon. This species is listed by MP (p. 102) as "wintering sparingly north to the Navajo Indian Reservation and inside the Grand Canyon." In January 1994 we only found two birds during surveys (RM 1.6 and RM 168), but we found them "numerous below RM 110" (DF field notes). In February 1995, surveys detected 12 individuals at 10 sites, all below RM 125. From field notes, we began seeing them below Nankoweap Creek (RM 52), 11 February. BCJ (p. 212) state that, "This species winters uncommonly along the river, with some birds moving to higher elevations in early February"; our observations support this.

PMM (p. 84) put the beginning of spring migration in early March. From our observations, either migration begins somewhat earlier in the canyon, or birds wintering lower in the canyon begin moving upstream in February. Higher counts in March may represent a wave of migrants moving through the canyon. On the lower Colorado River, numbers decline markedly in late April (ROHA, p. 234), later than expected if migrants in March are coming from the lower Colorado.

Vermillion Flycatcher (*Pyrocephalus rubinus*): Rare summer visitor.

Incidental: Adult female at Parashant Wash, 22 July 1994.

**** Ash-throated Flycatcher (*Myiarchus cinerascens*):** Common summer resident.

Surveys: We counted 235 birds on Surveys: 14 in April, 58 in May, 92 in June, and 71 in July. All April records are from Reach 10. In May, June, and July, they were found in all reaches surveyed.

Banding: 51 birds: two in April, 12 in May, 18 in June, and 19 in July. Twenty-eight in breeding condition (bearing an enlarged cloacal protruberance or brood patch): two in April, seven in May, 13 in June, and six in July.

Notes: This was the seventh most abundant riparian breeder in the canyon. We considered them to be breeders in 16 of 33 sites (48%) surveyed in 1993, in 32 of 48 sites (66%) in 1994, and in

31 of 52 sites (60%) in 1995. Only one nest found -- in broken-topped hackberry snag at RM 197.6L. First noticed active, 22 May 1995, possibly in nest-building stage. Revisited, 22 June, adults feeding young.

Ash-throated Flycatchers were more common in Reach 10 than other reaches (breeding at 20 of 22 sites). They began showing up at new places in July, possibly representing post-breeding dispersal upstream in the canyon. In July, they showed up for the first time in at nine sites (four in Reach 1, three in Reach 4, and two in Reach 5).

**** Brown-crested Flycatcher (*Myiarchus tyrannulus*):** Rare, localized summer resident.

Surveys: Counted 28 birds: six in May, 11 in June and 11 in July. Twenty-one of these records are from RM 198.0R, the rest within one river-mile of this site.

Banding: Seven were banded, three with brood patch. All are from RM 198.0R.

Incidental: One heard calling at RM 196.5R was the furthest upstream.

Notes: This is a very localized population. Just downstream at 199.5R, none were ever detected. The banding records are very important because this species is difficult to tell from the smaller Ash-throated without morphometric data taken while banding (though the voice is distinctive). Previous to this, this species' status in the canyon was unsure. BCJ (p. 213) state, "... there are no specimens or photographs to help establish the status of this bird in the region." Now its status as a breeder, though very localized, is well established.

This is a very interesting species in the state. The closest breeding records are from Beaver Dam Wash in the northwest corner of the state (MP, p. 100). On the lower Colorado, their status has changed fairly dramatically in this century. It was not found there until 1921, the first nest at Needles was found in 1949, and it has since moved into the Kern Valley in California (ROHA, p.239). We should continue to pay close attention to this species in the canyon to observe changes in this small populations, possibly paralleling the expansion of the Bell's Vireo (Brown et al. 1983).

Cassin's Kingbird (*Tyrannus vociferans*): Uncommon transient.

Surveys: One at RM 174.7R, 20 April 1995; two at RM 5.1L and RM 5.2R, 15 May 1995 (probably the same bird); one, also at RM 5.1L, 7 June 1993.

Incidental: One at RM 46.7R, 15 July 1994.

Western Kingbird (*Tyrannus verticalis*): Rare summer resident.

Surveys: One at RM 5.1L and RM 5.2R on 2 June and 14 July 1994; one at RM 74.4R, 18 July 1994.

Incidental: One seen in cottonwoods at Deer Creek, 20 April 1994; one at RM 198.0R, 22 April 1995; one seen at RM 204.5R, 13 June 1994.

Notes: It seems likely that the birds from RM 5.1L and 5.2R represent mis-identification of the Cassin's Kingbirds seen here in 1993 and 1995.

Swallows

A note on swallows and swifts: Our riparian surveys were not focused on aerial foragers in general and probably seriously under-counted all swallows and swifts. Though these counts are not a well standardized method for estimating abundance, they provide a relative index of abundance in different reaches of the canyon and give some ideas of arrival and departure dates. One interesting pattern pointed out by several boatmen is the tendency for swallows to concentrate at the lower end of rapids in some reaches of the river, presumably due to concentrations of flying insects there.

Tree Swallow (*Tachycineta bicolor*): Fairly common transient.

Incidental: Numerous at mouth of Little Colorado River and below, 17 April 1995; numerous below Lava Falls, 20 April 1995; a few around Lee's Ferry, 14 May 1995.

Violet-green Swallow (*Tachycineta thalassina*): Common summer resident.

Surveys: We counted 336 Violet-green Swallows on 75 surveys -- four in March, 18 in April, 64 in May, 103 in June, 117 in July, and 30 in September. Earliest date, 28 March 1995 at RM 208.7R; latest date, 14 September 1994 at RM 1.0R. Found in every reach surveyed, but most abundant in the upper reaches of the canyon. We counted 123 in Reach 1, 151 in Reach 4, seven in Reach 5, six in Reach 7 and four in Reach 10 (all spring migrants in March).

Incidental: More than 300 at Lee's Ferry, 14 April 1995; large concentrations around RM 32 and 38, 7 May 1994; numerous at Lee's Ferry, 10 July 1994.

Northern Rough-winged Swallow (*Stelgidopteryx serripennis*): Fairly common transient.

Surveys: One at RM 1.0R, 6 May 1994.

Incidental: Present at RM 171.0R, 27 March 1994; >5 at Lee's Ferry, 14 April 1995; below RM 209, 27 April 1994; numerous around Lee's Ferry, 14 May 1995; one at RM 210, 20 July 1993; three at RM 1.0R, 14 September 1994; two between RM 47 and RM 72, 17 September 1994.

Bank Swallow (*Riparia riparia*): Uncommon transient.

Incidental: Present below RM 209, 27 April 1994; present at Lee's Ferry, 14 May 1995.

**** Cliff Swallow (*Hirundo pyrrhonota*):** Common transient.

Incidental: Present below RM 209, 27 April 1994; five at Lee's Ferry, 14 April 1995; numerous at mouth of Little Colorado River and below, 17 April 1995; numerous below Lava Falls, 20 April 1995; two between Lee's Ferry and RM 46.7, 14 September 1994.

Notes: One nest-building at RM 2.0 R, 14 June 1995; an old nest at RM 3.5R, 9 February 1995. Observations of nest-building are interesting since the last documented nesting of this species was in 1975 (BCJ, p. 217).

Barn Swallow (*Hirundo rustica*): Fairly common transient.

Incidental: One at Lee's Ferry, 14 April 1994; present below RM 209, 27 April 1994.

Crows and Jays

Scrub Jay (*Aphelocoma caerulescens*): Uncommon winter visitor.

Surveys: One at RM 125.5R, 13 February 1995; one at RM 198.0R, 26 April 1994; one at RM 204.5R, 27 April 1994; one at RM 174.4R, 22 July 1994.

Incidental: One being scolded by Blue-gray Gnatcatchers at RM 198.0R, 25 April 1994.

Pinyon Jay (*Gymnorhinus cyanocephalus*): Uncommon winter visitor.

Incidental: A flock of around 50 at RM 119.6L, 13 February 1995; present at RM 1.0R, 12 April 1994.

American Crow (*Corvus brachyrhynchos*): Casual transient.

Incidental: Two at RM 46.7R, 17 March 1995; 13 at RM 46.7R, 16 April 1995.

**** Common Raven** (*Corvus corax*): Common permanent resident.

Surveys: Eighty birds on surveys -- three in January, nine in February, 14 in March, 14 in April, nine in May, 12 in June, eight in July, and 11 in September.

Incidental: A pair followed surveyors at RM 47, 23 January 1994; one took fledgling Black-throated Sparrow at RM 120, 20 July 1994; a pair building a nest in cliff, possibly 150 meters above the river at RM 198.0R, 31 March 1994; two nestlings visible, 15 May 1994. Next year, a pair was building a new nest at same location, 24 March 1995.

Notes: Unlike ravens elsewhere in the canyon, ravens at RM 198.0R never visited camp. Several interesting questions arise from watching this behavior. What is the effect on the ravens' reproductive success and population density from subsidies provided by rafters? What are the ecological effects of subsidizing the populations of this powerful and opportunistic predator?

Chickadees and Titmice

Mountain Chickadee (*Parus gambeli*): Uncommon winter visitor.

Surveys: One at RM 1.0R, 19 January 1994; one at RM 50.0R, 23 January 1994; one at RM 119.5R, 25 January 1994; one at RM 74.4R, 21 March 1994.

Banding: Two at RM 1.0R, 19 January 1994; one at RM 46.7R, 21 January 1994.

Notes: BCJ (p.223) consider this species a rare transient to the river in spring and fall only, so our records expand on this a little.

**** Verdin** (*Auriparus flaviceps*): Rare and local permanent resident.

Banding: One hatch-year bird at RM 204.5R, 26 July 1994.

Incidental: A used nest, possibly from 1993 but in good condition, in a graythorn bush toward upland side of RM 204.5R, 13 June 1994. Another used nest nearby, on 26 May 1995.

Notes: These are very important records as they are the first breeding records above the head of Lake Mead, where the Verdin's status was previously uncertain (BCJ, p. 224). Occasional sightings of this species have been made as far upstream as Havasu Creek (ibid.). The observation of nests in 1994 and 1995 suggest that there may be a small resident population at Spring Canyon. State-wide, the Verdin is considered a common resident of Sonoran Desert-

scrub, "... except the bottom of the Grand Canyon ..." (MP, p. 122). ROHA (p. 253) suggest that populations are limited by the severity of winter weather, so this species is undoubtedly near the edge of its geographic range in the lower canyon. The nearest breeding records are from the Virgin River (MP, p. 122). More field work will undoubtedly turn up other breeding records in the lower reaches of the Grand Canyon.

**** Bushtit (*Psaltriparus minimus*):** Fairly common winter visitor.

Surveys: Twenty-nine were counted on seven surveys -- flocks at RM 5.1, 5.2 and 46.7, 20-22 January 1994; a pair at RM 1.6R, 16 March 1995; two at Lee's Ferry, 28 August 1993; three at RM 204.5R, 26 September 1994.

Banding: Fifty-seven were banded -- 11 at RM 1.0R, 18 January 1994; 16 at RM 46.7R, 21 January 1994; two at RM 1.0R, 15 November 1994; 28 at RM 1.0R, 9-11 January 1995.

Incidental: A flock was seen at RM 5.6R, 9 February 1995; present at Lee's Ferry, 20 June 1995; flock of ten at RM 204.5R, 27 September 1994; pair building a nest in a tamarisk at Lee's Ferry behind the Park Service trailer, 14 March 1995. Apparently, it was successful (Grahame 1995).

Notes: This was the fourth most abundant species on the January 1994 trip. It seems that this species is common in the upper reaches of the canyon during January, and February and rare elsewhere. This is probably a more abundant species wintering in the upper canyon but because it is a flocking species with wide ranging habits, it was not frequently seen on our surveys. According to BCJ (p.224), this is one of the most abundant birds using the Colorado's riparian habitat during the winter, and we found no evidence to contradict this.

Wrens

Rock Wren (*Salpinctes obsoletus*): Common permanent resident.

Surveys: We counted 164 -- three in January, ten in February, 38 in March, 34 in April, 21 in May, 30 in June, 16 in July, and 12 in September.

Banding: Only two were banded, one at RM 46.7R, 8 July 1993; one at RM 198.0R, 23 September 1994.

Notes: Seasonal differences may well have much to do with detectability differences. This very vocal species is much more easily detected in the breeding season when males are almost constantly singing from every cliff in the canyon. One interesting pattern observed also affects detection probability. Seasonal use of riparian habitat went from 0 in the winter to over 50% of all observations in July. Despite these complicating factors, seasonal trends from our surveys appear to contradict previous observations, "... winter populations density of the rock wrens is somewhat higher than it is during the summer breeding season." (BCJ, p. 228).

Canyon Wren (*Catherpes mexicanus*): Common permanent resident.

Surveys: We counted 248 -- seven in January, 12 in February, 29 in March, 27 in April, 27 in May, 69 in June, 47 in July, and 26 in September.

Banding: One at RM 46.7R, 8 July 1993; one at RM 50.0L, 18 July 1994; one at RM 1.0R, 28 August 1993; one at RM 1.0R, 12 September 1994.

Notes: Like the Rock Wren, this species prefers rocky upland habitat and is highly vocal during

the breeding season. It also makes higher seasonal use of riparian habitat during the summer: from 16% of February observations to 51% of July observations in riparian habitat. This is why the few birds banded were captured in July, August, and September. Unlike the Rock Wren, this is a much more sedentary species (ROHA, p. 258; BCJ, p. 229).

**** Bewick's Wren (*Thryomanes bewickii*):** Common summer and fairly common winter resident.

Surveys: We counted 408 individuals on 359 surveys -- eight in January, nine in February, 60 in March, 55 in April, 73 in May, 104 in June, 54 in July, and 40 in September. They were most abundant in reach 4, then reach 10, then reach 1, then reach 5. One was found in reach 6, and four in reach 7.

Banding: We banded 89 Bewick's Wrens on the project: two in January, two in March, eight in April, 18 in May, 26 in June, 23 in July, and 10 in September. The increase in abundance in May through July is from annual reproduction: 13 hatch-year birds were banded in May, 13 in June, and 20 in July.

Notes: This was the fifth-most abundant riparian breeding species from survey data. They were breeders at 53 of 133 sites (40%) surveyed. Like the other wrens, detectability changes enormously during the breeding season, so we probably undercounted this species in fall and winter. This species is definitely a winter resident of riparian habitat in the canyon. From banding data it is not clear whether wintering individuals stay for the breeding season or migrate out and are replaced by individuals wintering elsewhere in Arizona (BCJ, p. 229). Of 14 banded individuals that were seen in more than one season, only two, a male and a female, were clearly residents. The female was caught at RM 1.0R in July and August 1993, March, April, June, and September 1994, and January and March 1995. The male was caught at RM 46.7R in June 1993, January, April, and June 1994, and June 1995. Six were seen only in the breeding season of at least two years, so appear to winter elsewhere. Finally, one was only seen in January and September 1994 so could be a winter resident. The pattern for the other four was too unclear to interpret.

MP (p. 127) recorded this species "wintering commonly in that part of its breeding range that lies south and west of the Mogollon Plateau . . . and among dense weeds and brush of the Lower Sonoran Zone west to the Colorado River." Seasonal changes in abundance from our survey data suggest that birds move into the canyon in March and stay for the summer. Winter counts were seven in January 1994 and nine in February 1995, compared with 21 in March 1994, 21 in April 1994, 16 in March 1995, and 10 in April 1995. The males start singing in March, at which time the detection probably of this loud singer increases considerably. It is likely that quiet individuals present in January and February would be missed.

House Wren (*Troglodytes aedon*): Uncommon transient.

Surveys: One at RM 76.5L, 18 April 1995; one at RM 1.0R, 14 May 1995; one at RM 50.0R, 17 May 1995; one at RM 171.0R, 22 July 1994; one at RM 168.8R, 21 September 1994.

Banding: One at RM 1.0R, 14 May 1995; one at RM 171.0R, 22 April 1994; one at RM 198.0R, 31 March 1994; one at RM 198.0R, 27 April 1994.

Incidental: One at RM 198.0R, 21 April 1995.

Winter Wren (*Troglodytes troglodytes*): Rare transient and winter visitor.

Surveys: One at RM 46.7R, 22 January 1994; one at RM 46.7R, 17 March 1995.

Marsh Wren (*Cistothorus palustris*): Fairly common transient.

Surveys: We observed 19 on surveys -- five in March, seven in April, one in May, and six in September.

Banding: Twenty-three were banded: 16 at RM 1.0R, one at RM 46.7R, three at RM 198.0R, and three at RM 204.5R. There were four in March, 11 in April, two in May, four in September, and two in October.

Incidental: One at Crystal Creek in phragmites and cattails, 19 April 1994.

Notes: Earliest date was 13 March 1994 at RM 1.0R, latest date was 13 October at RM 1.0R.

Dippers

American Dipper (*Cinclus mexicanus*): Uncommon permanent resident.

Incidental: One across from the mouth of the Paria River, one at Boulder Narrows, one at RM 27, one around RM 30, and one at South Canyon, all 9 February 1995; five between RM 1.0R and RM 42. 14 February 1993; one between RM 42 and RM 47, 15 February 1993.

Kinglets, Gnatcatchers, and Thrushes

Golden-crowned Kinglet (*Regulus satrapa*): Rare winter visitor.

Incidental: One at RM 1.0R, 13-14 December 1994; one at RM 1.0R, 9 January 1995.

Ruby-crowned Kinglet (*Regulus calendula*): Common winter resident.

Surveys: We counted 163 on 152 surveys -- 19 in January, 42 in February, 28 in March, 26 in April, and three in May. This was both the most abundant and most widely distributed winter species observed. We found it in all reaches surveyed on January and February trips and on 61% of all winter surveys (n = 81).

Banding: We banded 66 birds -- 39 at RM 1.0R, eight at RM 46.7R, four at RM 171.0R, 12 at RM 198.0R, and three at RM 204.5R. There were 17 in January, one in February, seven in March, 23 in April, two in May, one in September, six in October, six in November, and three in December.

Notes: PMM (p.135) consider this species common from October to April in lower sonoran riparian habitats in Arizona, but rare north of the Mogollon Plateau. On the lower Colorado River Laurenzi et al. (1982) found that abundance of kinglets in riparian vegetation was highest in late fall and early winter and declined to the lowest winter numbers in February. Fewer still were present in March, and almost all were gone by April. Winter abundance was negatively correlated with the severity of winter weather.

Its occurrence in the canyon is in the northern-most extension of this habitat in Arizona, where it may benefit from the tamarisk there. This species is one of the only foliage-gleaning insectivores wintering in the canyon (Laurenzi et al. 1982, Erlich et al. 1988) foraging extensively on the exotic tamarisk.

The phenology of spring migration is complex. In reaches 1 and 4 they were fairly abundant through April, while in reach 10 they were virtually gone by April. In the upper

reaches, there were two separate peaks of abundance in 1994 survey data, from nine individuals in January, to three in March, 16 in April, and three in May. The banding data follows the same pattern. In 1995, the pattern was more of a steady decline, with no kinglets seen in May. This could suggest two waves of migration, possibly of birds moving upstream.

Of 66 kinglets banded in the canyon in 1994 and 1995, 42 (66%) were males. The highest capture rate was in January 1994, when 12 of 18 birds captured were males. The only months when more females were captured were October 1994 (two males, four females), and April 1995 (four males, seven females). It is likely that more males than females winter in the canyon, and the pattern of differential migration is due to males in the canyon leaving in March and the females further south or downstream coming through in April.

**** Blue-gray Gnatcatcher (*Polioptila caerulea*):** Common summer resident.

Surveys: We counted 442 individuals on 382 surveys. We observed 11 in March (all in reach 10), 107 in April, 149 in May, 135 in June, 35 in July, and five in September. They were found in all reaches surveyed.

Banding: We banded 41 birds, including 13 hatch-year birds -- eight at RM 1.0R, four at RM 46.7R, nine at RM 171.0R, 13 at RM 198.0R, and seven at RM 204.5R.

Notes: This was the fourth-most abundant riparian breeder on our surveys. They were breeders at 76 of 133 sites surveyed (57%) between 1993 and 1995. They were most abundant in reach 10 and then 4. This species is more upland associated than many other riparian breeders and this, coupled with their relatively quiet song, made detection difficult. Earliest date was 23 March at RM 46.7R and latest was 27 September at RM 204.5R.

One surprising fact noted through color-banding and spot-mapping was the large breeding territories held by this species. Only one male was banded at RM 46.7R and he was observed wandering over the entire area of this, our second-largest site. On the other hand, at RM 198.0R we found two simultaneously active nests at the downstream end of the site and there were probably at least three pairs breeding there.

We found 14 nests: seven in tamarisk, three in acacia, and four in mesquite. Three mesquite nests were built inside dead mistletoe growth. The fourth nest was 4 m up in the broken top of a mesquite snag, about a half-mile up Spring Canyon Wash. This species was parasitized by cowbirds. We found one feeding a cowbird nestling at RM 46.7R, one feeding a cowbird fledgling at RM 49.2L, and a pair chasing a pair of adult cowbirds away from their nest at RM 1.0R. This nest was later abandoned.

Western Bluebird (*Sialia mexicana*): Uncommon winter resident.

Surveys: Fifteen at RM 198.0R, 20 January 1994; four at RM 198.0R, 31 January 1994; four at RM 198.0R, 16 February 1995; six at RM 204.5R, 17 February 1995; one at RM 204.5R < 25 March 1995.

Notes: We found large flocks feeding on mistletoe berries, and these were our only study sites with considerable mistletoe. Where mistletoe occurs in the lower canyon, this species may be more common than our surveys indicate. According to MP (p.141), they "winter . . . irregularly on the desert where mistletoe occurs" and BCJ (p. 233) consider them "uncommon in early spring along the river". Most were seen in 1994, 19 birds at RM 198.0R.

Mountain Bluebird (*Sialia montanus*): Rare winter visitor.

Incidental: A flock of 15 between Lee's Ferry and RM 52, 19 February 1994.

Townsend's Solitaire (*Myadestes townsendi*): Fairly common winter resident.

Surveys: Twenty birds on 10 surveys -- four in February, 14 in March, and two in April. All were found in reach 10.

Incidental: present at RM 140, 20 March 1995.

Notes: Like their relatives, the Western Bluebird, they often occurred in flocks, feeding off mistletoe berries, but were also seen eating Lyceum berries at RM 171.0R. Unlike the bluebirds, they actively defended good food sources, keeping bluebirds and Phainopeplas away.

Hermit Thrush (*Catharus guttatus*): Rare transient and winter visitor.

Surveys: One at RM 198.0R, 16 February 1995; one at RM 122.8L, 19 April 1995; one at RM 205.8R, 20 May 1994.

Banding: One at RM 1.0R on 15 November 1995; two at RM 198.0R, on 31 January 1994 and 23 March 1995.

Notes: The records from November and January are especially important, because there is only one previous winter record (BCJ, p. 234). This is also an excellent example of the value of mist-netting as a survey technique. The presence of many secretive migrant and wintering birds such as the Hermit Thrush, would have probably gone unnoticed otherwise.

American Robin (*Turdus migratorius*): Fairly common transient.

Surveys: Sixteen on surveys -- seven in February, two in March, four in April, and three in May.

Banding: One at RM 198.0R in March 1994.

Incidental: One at RM 198.0R, 24 March 1995; five at RM 1.0R, 12 October 1994.

Notes: Their presence in the lower canyon in February but not January suggests that February is the beginning of migration for this short-distance migrant in the canyon. However, they are recognised as uncommon wintering birds in the canyon (BCJ, p. 236), so we may have observed wintering birds in 1995.

Mockingbirds and Thrashers

Northern Mockingbird (*Mimus polyglottus*): Uncommon summer resident.

Surveys: Eleven -- two in April, four in May, two in June, and three in July. Nine of these were in reach 10.

Banding: Five at RM 198.0R, one at RM 204.5R, and three at RM 1.0R; eight in breeding condition (five males with cloacal protruberance, three females with brood patches between April and July).

Incidental: One at RM 168.8R, 21 April 1994; one at RM 171.0R, 20 April 1995; a pair at RM 204.5R, 18 May 1994; one at RM 122.8L, 8 June 1994; one at RM 55, 10 July 1993.

Notes: Though no nests were found, this is strong evidence that they are breeding in the canyon. Also, in 1994, a pair were seen in both May and June at RM 204.5R, so they could have bred there. This is interesting since their status along the river was previously unclear (BCJ, p. 236).

Crissal Thrasher (*Toxostoma crissale*): Rare summer resident or visitor.

Surveys: One at RM 198.0R, 17 February 1995; one at RM 173.1R, 22 July 1994.

Incidental: One at RM 204.5R, 13 June 1994; one singing at RM 204.5R, 26 July 1994.

Notes: This is a secretive species of riparian thickets and there are few records from the Grand Canyon (BCJ, p. 237). There are several September records from the Little Colorado River and South Rim (PMM, p. 124), suggesting that these were migrants from a breeding population in northeastern Arizona. The status of this rare bird on the river remains unclear.

Pipits and Wagtails

American Pipit (*Anthus rubescens*): Uncommon transient.

Surveys: One at RM 74.4R, 12 February 1995.

Incidental: One at RM 30, 13 April 1994; approximately 150 hawking insects over the river at RM 1.0R, 12 October 1994; one at RM 6 on 14 April 1995.

Waxwings

Cedar Waxwing (*Bombycilla cedrorum*): Rare transient.

Surveys: One at RM 171.0R, 20 April 1995.

Incidental: One up Spring Canyon, 23 June 1995; two at RM 198.0R, 22 May 1995.

Silky Flycatchers

**** Phainopepla** (*Phainopepla nitens*): Uncommon summer resident.

Surveys: Eighteen birds -- one in February, two in March, five in April, eight in May, and two in June; all at RM 204.1R and 204.5R.

Incidental: Several up Diamond Creek, 31 January 1994; "fairly abundant" along river at RM 224, 28 April 1994 (DF field notes); male at RM 46.0L, 16 May 1995; adults feeding fully fledged young at RM 209L, 1 April 1994; one seen at Lee's Ferry, 31 May 1994; one at RM 198.0R, 15 July 1993..

Notes: One nest was found in a mesquite at RM 204.5R, 26 May 1995. Adults were feeding young at this time. The male fed one nestling a mistletoe berry.

Shrikes

Loggerhead Shrike (*Lanius ludovicianus*): Uncommon summer visitor.

Surveys: Two at RM 198.0R, 23 July 1994; one at RM 206.5L, 28 September 1994; one at RM 214.0L, 28 September 1994.

Banding: One at RM 198.0R, 12 June 1994; one at RM 198.0R, 23 July 1994.

Incidental: Several around RM 198.0, 24 July 1994; one at RM 97.4R, 19 September 1994; one at RM 204.5R, 27 September 1994.

Vireos

**** Bell's Vireo (*Vireo bellii*):** Common summer resident.

Surveys: We counted 541 on 441 Surveys: 44 in March, 100 in May, 162 in June, and 57 in July. Of these, only four were outside of reach 10, all in reach four.

Banding: 120 birds -- one in March, eight in April, 33 in May, 62 in June, 13 in July, and 3 in September; 67 hatch-year birds -- 12 in May, 43 in June, and 12 in July. This was also one of two species for which color-banding gave us an idea of movements. One was seen at RM 204.5R with a color-band from RM 198.0R, (date please?).

Incidental: Several others in reach 4 during travel and outside study sites -- several males singing below Nankoweap Creek, 17 April 1995; male singing above Nankoweap Creek, 10 May 1994; male singing at RM 50.0L, 17 April 1995; male singing at RM 48.5R (furthest upstream in Reach 4 on this project), 15 May 1995; one at Lee's Ferry, 9 June and 20 June 1995 was the furthest upstream on this project. Earliest date, 25 March 1995 at RM 198.0R; latest just above Havasu Creek, 20 September 1994.

Notes: This was the second-most common breeder on our surveys, only surpassed in numbers by the Lucy's Warbler. Bell's Vireos bred at 55 of 133 (41%) sites surveyed between 1993 and 1995. They bred in all but two sites below RM 170. Hence, where they do occur in the canyon, they occur in higher number than the most abundant species, the Lucy's Warbler.

We found 21 nests of this species, more than any other species. Nest substrates included tamarisk (57%), mesquite (29%), coyote willow (5%), seep willow (5%), and arrowweed (5%). The earliest nest was under construction at RM 198.0R on 25 March 1995.

Despite this species' well known status as a host of the Brown-headed Cowbird (PMM, p. 143), we never found cowbird eggs, nestlings, or fledglings with the Bell's Vireo. This species has a low parasitism rate compared to other species in the canyon (Brown 1994). This may be due to the cowbird's low numbers in the lower reaches of the canyon where the vireo is most common and all nests were found on this project. It is possible that higher cowbird parasitism rates above Nankoweap Creek have hindered the upstream range expansion of the Bell's Vireo in the canyon (see Brown et al. 1983).

Gray Vireo (*Vireo vicinior*): Rare transient.

Surveys: One at RM 206.5L, 26 April 1995.

Banding: One at RM 1.0R on 12 May 1995.

Solitary Vireo (*Vireo solitarius*): Uncommon transient.

Banding: One at RM 1.0R, 5 May 1994; one at RM 198.0R, 31 March 1994; one at RM 198.0R, 23 September 1994; one at RM 204.5R on 24 April 1995.

Incidental: One at RM 46.7R, 16 September 1994; one at RM 88, 19 September 1994.

Warbling Vireo (*Vireo gilvus*): Uncommon transient.

Banding: Two at RM 204.5R, 19-20 May 1994; two at RM 1.0R, 11-13 September 1994; one at RM 198.0R 25 September 1994; one at RM 204.5R, 27 September 1994.

Wood Warblers

Orange-crowned Warbler (*Vermivora celata*): Fairly common transient.

Surveys: Fifteen -- two in May and 13 in September.

Banding: Nineteen -- ten at RM 1.0R, four at RM 46.7R, four at RM 198.0R, and one at RM 204.5R. Seven were banded in May, five in September, and seven in October.

Incidental: One at RM 198.0R, 22 April 1995; one at RM 209.0, May 1993.

Nashville Warbler (*Vermivora ruficapilla*): Rare transient.

Surveys: One at RM 198.0R, 24 September 1994.

Banding: One hatch-year bird at RM 198.0R, 24 September 1994; same bird seen on the survey.

Notes: This is one of two records of this species along the river corridor (BCJ, p. 244).

Virginia's Warbler (*Vermivora virginiae*): Uncommon transient.

Banding: Two at RM 1.0R, 5-6 May 1994; two at RM 46.7R, 8 May 1994; two at RM 1.0R, 12-13 May 1995; one at RM 46.7R, 18 May 1995; one at RM 1.0R, 11 August 1994.

Notes: These are interesting records; "It is almost unknown as a transient below the rims, with only a few spring sightings from the river." (BCJ, p. 245).

**** Lucy's Warbler** (*Vermivora luciae*): Common summer resident.

Surveys: 1,779 on 1,190 Surveys: 199 in March, 332 in April, 491 in May, 657 in June, 99 in July, and one in September. We found them in every reach surveyed. Earliest date, 17 March at RM 46.7R; latest date, 2 September 1993 at RM 49.1R.

Banding: 315 birds -- 13 in March, 20 in April, 85 in May, 151 in June, and 46 in July. There were 46 hatch-year birds in May, 77 in June, and 36 in July.

Notes: This was by far the most common and widespread riparian breeding species in the canyon. They bred at 113 of 133 (85%) sites surveyed between 1993 and 1995.

Despite their great abundance, we only found nine nests, due to this species extreme shyness around its nest. For this reason, the easiest time to find them is when they're making many trips to feed nestlings (which are often noisy). In fact, all the nests we found were in this stage. The earliest nest was found 21 April at RM 198.0R, when nestlings were already being fed. The latest nest fledged young at RM 46.7R on 17 June. Though well known as the "mesquite warbler" (Bent 1953, p. 129), in the canyon it has adapted to the exotic tamarisk (BCJ, p. 245). Nest substrate was tamarisk for four nests, mesquite for two nests, cavities in cliffs for two, and acacia for one. The "cavities" this species used in tamarisk were provided by hollowing out dense clods of dead tamarisk needles piled up on branches or adhering to the trunk of tamarisk trees.

Contrary to BCJ (p. 245), we did not find this species limited to "... sizeable tracts of suitable riparian habitat . . .", but found males singing even in the sparsely vegetated Upper Granite Gorge, often in small clumps of one or two acacias isolated on barren cliff-faces above the river. Whether these birds were reproducing or even attracting mates, however, remains to be seen.

Though this species was the most abundant we found in the canyon, it should be a candidate for long-term population monitoring. It could be a species of future concern for

managers for several reasons. It has a relatively small geographic range, occurring only in the southwestern U.S. and northern Sonora, Mexico. It is a habitat specialist of heavily impacted riparian habitat, and is further specialized by its close association with mesquite. It is on the edge of its range in the canyon, a place where the future of riparian mesquite habitat is in question under current dam management (Anderson and Ruffner 1988). Whether it can sustain its numbers while nesting and foraging in a new riparian plant community remains to be seen.

**** Yellow Warbler (*Dendroica petechia*):** Fairly common summer resident.

Surveys: 229 on 218 surveys -- 17 in April, 109 in May, 61 in June, 20 in July, and 22 in September.

Banding: 118 birds -- three in April, 85 in May, three in June, 8 in July, 13 in August, and six in September.

Notes: This was the eighth-most abundant breeding species. They bred at 43 (32%) of 133 sites surveyed between 1993 and 1995. All these sites were in reaches 1, 4, and 10.

The high counts in late April and May are undoubtedly due to migrants passing through the canyon during this month. For example, during April 1994, we counted five males singing at RM 168.8R, but only two in May and June. Banding data sheds further light on this subject. Only four of 48 females banded had brood patches, and only 16 of 44 males banded had a cloacal protuberance. At all banding sites, we counted 16 breeding pairs on surveys from 1993 to 1995. Hence, more than half of the birds banded were probably passing through.

We found five nests of this species, one in May and four in June. All were in tall tamarisks, as stated in BCJ (p. 245).

Yellow-rumped Warbler (*Dendroica coronata*): Fairly common winter resident.

Surveys: 40 birds -- two in January, four in February, 13 in March, nine in April, five in May, and seven in September. They were found in reaches 1, 4, and 10.

Banding: Nine birds -- one in March, two in April, four in May, one in November, and one in December.

Incidental: Two at RM 47.0R, 15 September 1994; one at Lee's Ferry, 6 January 1995; two between RM 1.0R and RM 40, 14 February 1993.

Notes: This is the only warbler we found wintering in the canyon, and it was not very abundant (two in January 1994 and four in February 1995). Across the continent this species winters further north than all other *Dendroica* warblers. In Arizona, it is a common winter bird of the Lower Sonoran Zone and sycamore riparian habitats around the state. The western, Audubon's form predominates (PMM, p. 151).

PMM (p. 152) consider the Myrtle form uncommon in winter and spring migration, and BJC (p. 247) consider it accidental in the canyon during migration, with only four observed, in April and May. However, of the four birds we found in February 1995, one was a male Myrtle race, and another Myrtle was seen in March 1995. Based on this small sample of sightings, the Myrtle race may be more common than previously thought. However, it should be noted that these birds were identified by the white throat patch of the male Myrtle, a characteristic not recognised by PMM (p. 152).

Black-throated Blue Warbler (*Dendroica caerulescens*): Accidental.

Banding: One female at RM 1.0R, 12 October 1994.

Notes: This is one of two records for the canyon (BCJ, p. 246). Only 46 records exist for the entire state, mostly from the fall (MP, p. 160).

Black-throated Gray Warbler (*Dendroica nigrescens*): Rare transient.

Incidental: One male at RM 46.7R, 9 May 1994.

Northern Waterthrush (*Seiurus noveboracensis*): Two were banded: one at RM 198.0R, 27 April 1994 and one at RM 1.0R, May 1995.

Notes: This species is considered an irregular transient by BCJ (p. 249), but may be more common and overlooked due to its secretive habits.

Blackpoll Warbler (*Dendroica striata*): Accidental.

Banding: A hatch-year bird at RM 204.5R, 26 September 1994.

Notes: This is a new record for the canyon. In the state, it is considered a sparse visitor with few records (MP, p. 165).

MacGillivray's Warbler (*Oporornis tolmiei*): Uncommon transient.

Surveys: One at RM 204.5R, 27 April 1994; one at Lee's Ferry, 28 August 1993; one at RM 5.2R, 30 August 1993; one at RM 1.0R, 13 September 1994; one at RM 198.0R, 23 September 1994.

Banding: Twenty-two were banded: 17 in May, and five in September. Eight were at RM 1.0R, two at RM 46.7R, four at RM 198.0R, and 8 at RM 204.5R.

Incidental: One at RM 47.0R, 15 September 1994; and several on Bright Angel Creek above Phantom Ranch, 19 September 1994.

Wilson's Warbler (*Wilsonia pusilla*): Common transient.

Surveys: Eight birds -- four in May and four in September.

Banding: Forty-five birds -- 33 in May, one in June, and 11 in September. There were 14 at RM 1.0R, eight at RM 46.7R, one at RM 171.0R, five at RM 198.0R, and 17 at RM 204.5R.

Incidental: One at Deer Creek, 20 April 1994; several at Lee's Ferry, 6 May 1994.

**** Common Yellowthroat** (*Geothlypis trichas*): Common summer resident.

Surveys: Eighty-four birds -- one in March, nine in April, 40 in May, 34 in June, 12 in July, and eight in September. Earliest date, 25 March 1995 at RM 204.5R; latest date, 24 September 1994 at RM 198.0R.

Banding: Forty-five birds -- one in March, five in April, 22 in May, 9 in June, 3 in July, and 5 in September. Nine were hatch-year birds.

Incidental: male singing up Crystal Creek in phragmites and cattails, 19 April 1994; male singing up Bright Angel Creek, 18 April 1995.

Notes: This was the 11th-most abundant breeding species. We found them breeding at 25 (19%) of 133 sites surveyed between 1993 and 1995. Like the Yellow Warbler, we probably counted some migrants in May, judging from high counts on surveys and from banding in that month.

We found five nests: two in phragmites and cattail, two in seep willows, and one in a clump of tall grass (*Andropogon* sp.). The two in phragmites and cattail were parasitized by Brown-headed Cowbirds, and one nest was consequently abandoned. One nest would have been

inundated by 20,000 cfs while another was on the border of the inundation zone.

This is one of the species directly affected by dam operation, through possible nest inundation. Equally important, it has probably benefitted more from interim flows than any other riparian breeding species through habitat alterations associated with low flows. This is because yellowthroats prefer to nest in emergent vegetation, which has increased under interim flows. Marshes have decreased in area during this time but increased in number along the river (Mike Kearsley, pers. comm.). Common Yellowthroats seem willing to nest in the smallest patch of cattails and phragmites (e.g., two pairs nesting at RM 46.7R in two patches of emergent vegetation amounting to less than 50 m²). This fact may also help explain why these species are so frequently parasitized by the Brown-headed Cowbird (two of five nests we found). Concealing a nest in such a small patch of vegetation makes it considerably easier for a cowbird, a predator, or even a nest-searcher to find.

**** Yellow-breasted Chat (*Icteria virens*):** Common summer resident.

Surveys: We counted 149 birds on 132 surveys. We found two in April, 53 in May, 78 in June, 15 in July, and one in September. The earliest date for this species was 26 April 1994 at RM 198.0R, and the latest was 18 September 1994 at RM 74.4R.

Banding: Sixty-two chats -- three in April, 27 in May, 19 in June, nine in July, two in August, and two in September. Birds in August and September were all hatch-year.

Notes: This was the ninth-most abundant breeding species on our surveys. They were breeders at 39 (29%) of 133 sites surveyed between 1993 and 1995. We found three nests: two in tamarisk and one in seep willow. The one in the seep willow, at RM 1.0R, was destroyed while active when the bush was removed by a beaver. It then re-nested successfully in a tamarisk, the nestlings were banded and one was recaptured there, 12 October 1994.

This is another bird which is affected by interim flows through habitat changes. This species seems to prefer dense vegetation with a good proportion of coyote willow and seep willow (BCJ, p. 252). These two plant species have developed healthy stands close to the river where flows no longer flood shorelines as deeply as before interim flows, thus increasing chat habitat.

Tanagers

Western Tanager (*Piranga ludoviciana*): Uncommon transient.

Surveys: One at RM 47.5L and one at RM 50.0R, 17 May 1995; one at RM 158.8L, 18 May 1993; one at RM 204.5R, 18 May 1994; one at RM 46.7R, 16 July 1994; one at RM 213.6L 27 July 1994.

Banding: We banded twelve: eight in May (all at RM 204.5R), two in July, and two in September. Incidental: "Numerous" at RM 204.5R, 18 May 1994 (DF field notes); present at RM 1.0R, 12 July 1994; one male and one female at RM 204.5R, 26 July 1994; three at RM 213.6L, 27 July 1994; three at RM 47.0R, 15 September 1994; a male at RM 1.0R, 14 May 1995.

**** Summer Tanager (*Piranga rubra*):** Rare summer resident.

Surveys: Twenty-two birds -- nine in May, five in June, four in July, and four in September.

Only two of these observations were outside of reach 10, in reach 4.

Banding: Two (a pair), 10-11 June 1994; a hatch-year bird, 19 July 1993; one adult female and one hatch-year bird, 25 July 1995. All were banded at RM 198.0R

Incidental: A male singing at RM 46.7R, 16 May 1995; adult and second-year males at RM 46.7R, 15 June 1995; adult male singing at RM 50.0L, 10 May 1994; male at RM 50.0L, 5 June 1994; pair at Phantom Ranch, 6 June and again 19 July 1994; pair in cottonwoods at Deer Creek, 13 May 1994; male singing at RM 198.0R, 15 May 1994; pair at RM 197.6L, 10 June 1994, the female carrying nesting material; one at RM 198.0L, 23 July 1994; male at RM 197.0L, 24 July 1994; a banded male at RM 198.3R, 24 July 1994, and again at RM 198.0L, 23 September 1994; male at RM 204.5R, 18 May 1994; one at RM 204.5R, 26 September 1994.

Notes: Clearly, the pair banded at RM 198.0R are breeding, probably successfully considering two hatch-year birds were banded there. Though we found several males singing in reach 4 during every year of the project, we saw no females or other evidence of breeding. Perhaps this will change. This species has expanded its range upstream in the past 30 years (BCJ, p. 252), and as the riparian vegetation changes, we can expect to see some continued changes in distribution in the canyon. This a species of concern in the West, where it only breeds in riparian habitat. Changes in breeding range in the canyon are therefore of regional importance.

Grosbeaks and Allies

Black-headed Grosbeak (*Pheucticus melanocephalus*): Uncommon transient.

Surveys: One at RM 46.7R, 14 May 1993; one at RM 50.0R, 15 May 1993; one at RM 171.0R, 14 May 1994; one at RM 198.0R 15 May 1994; two at RM 1.0R, 7 June 1993; one at RM 198.0R, 11 September 1993.

Banding: One at RM 1.0R, 12 May 1995; one at RM 204.5R, 19 May 1994; one at RM 1.0R, 13 July 1994.

Incidental: A male singing at RM 198.0R, 15 May 1994; several at RM 204.5R, 18 May 1994.

**** Blue Grosbeak** (*Guiraca caerulea*): Uncommon summer resident.

Surveys: Fifty-seven birds on 53 surveys -- 15 in May, 12 in June, 28 in July, and one in September. We found them in reaches 1, 4, 5, and 10.

Banding: One at RM 1.0R, 13 May 1995; one at RM 1.0R, 1 June 1994; one at RM 46.7R, 7 July 1994; one at RM 1.0R, 12 July 1994.

Incidental: Pair at RM 46.7R, 9 May 1994; pair up Spring Canyon, 19 May 1994; one female at RM 1.0R, 30 May 1994, and a pair there the next day; one singing around RM 203.5R, 26 July 1994; one below Nankoweap Creek, 17 September 1994.

Notes: This species was the 14th-most abundant riparian breeder in the canyon. They bred at 26 (19%) of 133 sites surveyed between 1993 and 1995. This was one of the last breeding species to arrive on the breeding grounds. The earliest date was 9 May 1994 at RM 46.7R and the latest was 17 September 1994 at RM 47.5L. We found four nests: one on 20 May being incubated, two in June, and one in July. All were on the edge of a tamarisk patch in a tamarisk. The nest found 17 July at RM 47.5L contained two cowbird eggs.

**** Indigo Bunting (*Passerina cyanea*):** Rare summer resident.

Surveys: A male singing at RM 46.7R on 18 May 1995; two at RM 204.5R, 26 May 1995; one banded male at RM 204.5R, 24 June 1995.

Banding: Two second-year males at RM 204.5R, one 27 May 1995, the other 26 June 1995.

Incidental: One at RM 46.7R, 15 June 1995.

Notes: There were obviously two males here in June because an observer (DF) saw the banded bird two days before the other was banded. One of the males at RM 204.5R was later seen paired with a female Lazuli Bunting. This is the only breeding record for this species on our project, though it has been observed breeding in the canyon before (BCJ, p. 255). That this bird paired with a Lazuli Bunting is not very surprising. Since this species has expanded its range west, numerous hybrid Indigo X Lazuli crosses have been observed (Erlich et al. 1988, p. 558).

**** Lazuli Bunting (*Passerina amoena*):** Fairly common summer resident.

Surveys: Twenty-one birds on 18 surveys -- one in April, nine in May, six in June and five in September. We considered this species a breeder at one site in 1993, and two in 1995, counting the female paired with the Indigo Bunting mentioned above.

Banding: One at RM 1.0R, 13 April 1995; one at RM 1.0R, 13 May 1995; one hatch-year bird at RM 171.0R, 6 September 1993.

Incidental: Male singing on Deer Creek trail, 20 April 1994; several at Lee's Ferry, 6 May 1994; male singing in cottonwoods at Deer Creek, 13 May 1994; six hatch-year birds at Lonely Dell Ranch, 13 September 1994; two hatch-year birds at RM 76.0L on 18 September 1994. Juveniles were generally abundant in September.

Notes: The earliest date was 13 April, a male banded at RM 1.0R and the latest was 17 September 1994, a hatch-year bird seen at RM 49.1R. We did not find this species to be common along the river between Lee's Ferry and Diamond Creek (BCJ, p. 254).

Sparrows and Towhees

Green-tailed Towhee (*Pipilo chlorurus*): Uncommon transient.

Surveys: Two birds at RM 46.7R -- one on 15 September 1994, one on 17 September 1994; one at RM 49.1R, 17 September 1994.

Banding: Three birds at RM 1.0R -- one on 12 April 1994, one on 11 April 1995, one on 12 May 1995.

Notes: The earliest date was 11 April 1995 and the latest was 17 September 1994 at RM 49.1R. All the birds we saw were migrants, but one interesting sighting from the canyon could have represented breeding birds. These were several reported from Saddle Canyon, 10 or 11 June 1994, by Rob Marshall (USFWS, Phoenix).

Spotted Towhee (*Pipilo erythrophthalmus*): Uncommon transient.

Surveys: One at RM 46.7R, 20 March 1994; one at RM 198.0R, 30 March 1994; one at RM 46.7R, 16 May 1995.

Banding: One at RM 198.0R, 17 July 1993.

Incidental: Two at RM 198.0, 24 March 1995.

Canyon Towhee (*Pipilo fuscus*): Rare visitor.

Surveys: One at RM 74.4R, 12 February 1995; one at RM 208.7R, 17 February 1995.

Notes: The status of this species in the canyon is poorly known with few records (BCJ, p. 256), so these are important.

**** Rufous-crowned Sparrow** (*Aimophila ruficeps*): Uncommon permanent resident.

Surveys: Twenty-one birds -- one in January, two in February, eight in March, three in May, six in June, and one in September.

Banding: one at RM 171.0R, 27 January 1994; one at RM 46.7R, 14 April 1994; one at RM 198.0R, 21 June 1995; one at RM 46.7R, 9 July 1993; one at RM 50.0L, 18 July 1994; two at RM 198.0R, 24 September 1994.

Incidental: One singing after survey at RM 46.7R, 19 March 1994.

Notes: This species made only occasional use of the riparian habitat, so it is more abundant than appears here. A pair feeding a fledgling at RM46.0L, 15 June 1995, was the only evidence of breeding in one of our study sites. We agree with BCJ (p. 257) that they are more common along the river above Phantom Ranch than below. We observed only six of the 21 in reaches below Phantom Ranch.

Chipping Sparrow (*Spizella passerina*): Uncommon transient.

Surveys: One at RM 5.6R, 13 April 1994; two at RM 1.6R, 13 April 1995; one at RM 122.8L, 19 April 1995; two at RM 204.5R, 26 September 1994.

Banding: Two at RM 1.0R, one on 11 April 1994 and one on 13 April 1995.

Incidental: "Several" at RM 76.0L, 18 September 1994 (DF field notes).

Brewer's Sparrow (*Spizella breweri*): Uncommon transient.

Surveys: Thirteen on nine surveys, all in September. Five were at RM 198.0R, five at RM 1.0R.

Banding: Ten were banded -- five at RM 1.0R and five at RM 198.0R. One was banded on 13 August, all the rest were banded in September.

Incidental: Two at RM 1.0R, 11 April 1994; two at Lee's Ferry, 14 April 1994; one at RM 204.5R, 26 April 1995; present at the mouth of Nankowep Creek, 10 May 1994; one at RM 47.0R, 15 September 1994; and several on Bright Angel Creek above Phantom Ranch, 19 September 1994.

Black-chinned Sparrow (*Spizella atrogularis*): Rare transient.

Surveys: One male singing at RM 206.5L, 26 March 1995.

Lark Sparrow (*Chondestes grammacus*): Uncommon summer visitor.

Surveys: One at RM 204.5R, 18 May 1994.

Banding: One at RM 46.7R on 16 July 1994.

Incidental: One at RM 209, 27 April 1994; one across from Lava Chuar, 19 July 1994; one at RM 46.7R, 14 September 1994; one between RM 46.7R and RM 73, 17 September 1994; one at RM 198.0R, 24 September 1994.

**** Black-throated Sparrow** (*Amphispiza bilineata*): Common summer resident.

Surveys: Fifty-eight on surveys -- six in March, 13 in April, 12 in May, 14 in June, and 13 in

July. They were found in all reaches surveyed but were most common in reaches 5, 7, 8, and 10.
Banding: One at RM 198.0R, 21 June 1995; two at RM 46.7R, 15-17 July 1994; one at RM 198.0R, 18 July 1993; one at RM 198.0R, 23 July 1994; one at RM 204.5R, 27 July 1994.

Incidental: Present at the mouth of Nankoweap Creek, 20 March 1994; a pair at the same place, 17 April 1994 and 10 May 1994; three drinking from the river at Phantom Ranch, 19 May 1995; fledgling at RM 120 eaten by raven, 20 July 1994.

Notes: The earliest date was 20 March 1994 at RM 74.4R and the latest was 27 July 1994 at RM 206.5L. This species was much more associated with the uplands (30 of 51 observations in upland habitat) so was not included when defining the breeding community of our study sites. Like the wrens, it appeared to favor riparian habitats during late June and July.

Sage Sparrow (*Amphispiza belli*): Rare transient.

Surveys: One at RM 214.0L, 28 September 1994.

Banding: One at RM 1.0R on 15 November 1994.

Vesper Sparrow (*Pooecetes gramineus*): Rare transient.

Incidental: One at RM 209L, 1 April 1994.

Savannah Sparrow (*Passerculus sandwichensis*): Rare transient.

Incidental: One at mouth of Nankoweap Creek, 19 March 1995; three at Lee's Ferry, 14 April 1995.

**** Song Sparrow** (*Melospiza melodia*): Fairly common summer and winter resident.

Surveys: Sixty-one birds on 53 surveys -- one in January, 12 in February, 13 in March, eight in April, 15 in May, nine in June, and three in September.

Banding: Twenty-nine birds -- two in January, one in February, five in March, one in April, two in May, one in June, one in July, nine in September, two in October, and five in November.

Incidental: One at RM 46.7R, 15 June 1995.

Notes: This was the 13th most abundant riparian breeder, though our counts may be inflated with migrants and wintering birds. We only found this species breeding in 1995, at five sites (compare with number 14, the Blue Grosbeak, which bred at seven sites in 1995). Three of these sites were new in 1995, all around RM 198.0.

Except for three birds, high numbers in May can be attributed to hatch-year birds, rather than migration. Previous to this project, there was only one confirmed breeding record for this species in the canyon (BCJ, p. 262). We can add three more. We observed adults feeding recently fledged young (tails < 20 mm) at RM 198.2L, 21 June 1995, and banded three hatch-year birds: two at RM 204.5R, 27 May 1995 and one at RM 198.0R, 22 June 1995.

Winter differences between 1994 and 1995 are an interesting example of observer variability. In January 1994, two individuals were found at RM 198.0R. In February 1995, we counted 12 at eight sites ranging from RM 5.1 to 204.5. We found them in reaches 1, 4, and 10. It is possible that differences between January 1994 and February 1995 were largely due to observer variability. Outside of the breeding season this species is not very vocal and skulks in thick brush, making it difficult to see. In 1995, we were assisted in surveying by two excellent and experienced ornithologists who easily identified them by their chip note. Eight of 12 detections in February 1995 were from chip notes heard by these individuals. Hence I am

reluctant to say much about the biological importance of differences between January and February counts.

Swamp Sparrow (*Melospiza georgiana*): Casual visitor.

Incidental: One at Lee's Ferry, 14 April 1995.

Notes: There is only one previous record from the canyon, one collected along the river in 1974 (BCJ, p. 262).

Lincoln's Sparrow (*Melospiza lincolni*): Fairly common transient.

Surveys: Twenty-eight birds -- one in February, ten in March, six in April, two in May, and nine in September.

Banding: Twenty-nine birds -- six in March, ten in April, one in May, 11 in September, and one in November.

Notes: The bird seen in February was at RM 206.5L. Whether it wintered there in the canyon or had begun migrating north already is unknown. BCJ (p. 262) consider it possible that some birds winter in the canyon.

Golden-crowned Sparrow (*Zonotrichia atricapilla*): Casual winter visitor.

Banding: One hatch-year bird at RM 204.5R, 27 September 1994.

Notes: This is one of few records for the canyon.

White-crowned Sparrow (*Zonotrichia leucophrys*): Common winter visitor.

Surveys: We counted 108 on 60 Surveys: 14 in February, 12 in March, 19 in April, 23 in May, and 38 in September.

Incidental: Six at Lee's Ferry, 6 January 1995; 17 at Lee's Ferry, 18 January 1994; several in first basic plumage at the mouth of Nankoweap Creek, 20 March 1994; 25-30 at Lee's Ferry, 12 April 1994; two in first basic plumage at RM 47.0R, 14 September 1994.

Notes: In the hand, we can easily recognize two races in the canyon, *Z. l. gambelii* (Nuttall), with white lores, and *Z. l. oriantha* (Oberholser) with dark lores. Twelve *Z. l. oriantha* were banded, all in May at RM 1.0R. PMM (p. 207) identifies this race as transient in the state, only found in May and September. This race breeds high in the Sierras and Rocky Mountains (Nat. Geo., 2nd edition, p. 404, how do you cite this book?). We banded 49 of the other race, *Z. l. Gambelii*: two in January, one in February, three in March, ten in April, eight in May, 12 in September, four in October, four in November, and five in December. Most (75%) were banded at RM 1.0R. This race is the abundant wintering race in Arizona (PMM, p. 207), also wintering in the canyon. These are earlier migrants and go farther to breed, into Alaska and far northern Canada.

Dark-eyed Junco (*Junco hyemalis*): Common winter resident.

Surveys: 122 on 50 Surveys: 20 in January, 49 in February, 46 in March, and seven in April. The Oregon race was most common.

Banding: Fifty-five banded (including 53 Oregon race) -- 12 in January, three in February, 12 in March, two in April, one in October, eight in November, and 17 in December. These were: 49 from RM 1.0R, two from RM 46.7R, and four from RM 198.0R.

Notes: This was the second most common wintering species. It is not an exclusively riparian species like the Ruby-crowned Kinglet, but winters in all habitats in the Grand Canyon, and

wander widely throughout the day (BCJ, p. 264). Because of this, riparian surveys of relatively short duration (typically 15-60 minutes) are not very good for monitoring this species. Dark-eyed Juncos were detected on 8% of January 1994 surveys (n = 38) and 32% of February 1995 surveys (n = 43). This makes it appear to be a fairly rare species, despite its obvious high winter abundance (ibid.). Mist-netting may have provided a better survey method because nets were run for up to five hours. The longer survey period made it more likely that a flock visiting the site sometime during the day would be observed (caught).

From these data it seems clear that these birds prefer the upper reaches of the canyon, where they're found during the cooler months. Of 55 birds banded, 49 were banded at RM 1.0R, 29 in December and January. However, differences were evident between years. From survey data, they were much more numerous in February 1995 (50 individuals at 14 sites) than January 1994 (20 individuals at 3 sites). In January 1994, Dark-eyed Juncos were not seen below RM 175. In February 1995, we found them distributed throughout the canyon, but were still most common in the upper reaches (11 in reach 1, 12 in reach 4, five in reach 5, six in reach 7, and 15 in reach 10). The upper canyon may well represent the lower elevational limit of this species in average years. Also, the upper canyon lies in closer proximity to forests of the north rim where these birds commonly winter. In Arizona, the various races of the Dark-eyed Junco winter commonly throughout the Transition zone and less commonly in the Upper Sonoran zone (MP, p. 197). In wet years they may also be found in Lower Sonoran habitats, presumably tracking grass seed abundance (Dunning and Brown 1982). The greater numbers and wider distribution seen in late 1994 and 1995 is likely due to birds wintering lower into the desert in 1995, tracking a good seed crop from 1994. However, we have no mist net data from the upper canyon during fall and early winter 1993. Hence, differences between years could be also explained by the northern migration of birds wintering further south in the state and coming through the canyon.

Blackbirds and Orioles

Red-winged Blackbird (*Agelaius phoeniceus*): Fairly common transient.

Surveys: One male at RM 49.2L, 17 May 1995.

Banding: One at RM 198.0R, 22 April 1995.

Incidental: Eleven at Lee's Ferry, 14 April 1995; four females at Lee's Ferry, 6 May 1994; twenty between RM 204.5R and RM 224, 28 September 1994; 14 females foraging in mesquites near Parashant Camp on 22 April 1995.

Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*): Uncommon transient.

Surveys: One female at RM 5.1L, 14 September 1994.

Brewer's Blackbird (*Euphagus cyanocephalus*): Fairly common transient.

Surveys: Sixteen at RM 200.5R, 25 September 1994; 13 at RM 206.5L, 28 September 1994.

Incidental: One at RM 50.0R, 17 September 1994.

Western Meadowlark (*Sturnella neglecta*): Uncommon transient.

Incidental: One at RM 198.0R, 24 September 1994.

**** Great-tailed Grackle (*Quiscalus mexicanus*):** Uncommon summer resident.

Surveys: Eighty-nine birds on 41 surveys -- Most of these, 75 on 34 surveys, were found at Lee's Ferry in 1993, the only year they nested during this study.

Banding: One female, captured in a makeshift drop trap, at RM 204.5R, 18 May 1994. This bird was accompanied by two males.

Incidental: One female at the mouth of Nankoweap Creek, 10 May 1994; present at Lee's Ferry, 13 May 1995; two males at Lee's Ferry, 1 June 1994; and one female with a Rock Dove at Lee's Ferry, 18 January, 13 March, and 12 April 1994.

Notes: This is an especially interesting species, having expanded its geographic range north during this century (first Arizona records from 1930's; PMM, p. 172). It was never seen in the canyon before 1974 (BCJ, p. 267). The Great-tailed Grackle is also a fairly powerful predator, taking eggs and nestlings of other birds (Erlich et al. 1988, p. 620). For example, a male and female were observed at RM 75, June 1993, drowning a fledgling Ash-throated Flycatcher, then carrying it off. Increasing populations of Great-tailed Grackles may exert a new force on the riparian breeding bird community of the canyon. Why a colony bred at Lee's Ferry in 1993, but not during the rest of the project remains a mystery.

**** Brown-headed Cowbird (*Molothrus ater*):** Fairly common summer resident.

Surveys: Twenty-eight birds on 26 surveys -- ten in May, 14 in June, and four in July. We observed 13 in reach 1, 12 in reach 4, and only three in reach 10.

Banding: Two males at RM 1.0R, 30 May 1994; one female at RM 198.0R, 19 June 1993 (recaptured at RM 198.0R, 19 May 1994).

Incidental: Several at Lee's Ferry, 6 May 1994; present at the mouth of Nankoweap Creek, 10 May 1994; two males and one female at RM 1.0R, 30 May 1994; and "abundant at Cardenas Marsh" (DF field notes), 18 May 1995. One male banded at RM 1.0R was seen at the bridge crossing the Paria River.

Notes: Cowbirds are relatively late arrivals to the canyon; earliest date 12 May 1995 and latest was 20 July 1993. We observed several cases of brood parasitism by this species. We found: two cowbird eggs (of five total) in Common Yellowthroat nest at RM 46.7R, 4 June 1994; two eggs in a Blue Grosbeak nest at RM 47.5L, 17 July 1994; a Common Yellowthroat nest at RM 198.0R, 23 July 1994 contained one broken yellowthroat egg and one cowbird egg. This nest was abandoned. We found a cowbird nestling in a Blue-gray Gnatcatcher nest at RM 46.7R, 15 June 1995 and saw a Blue-gray Gnatcatcher feeding a fledgling cowbird at RM 49.2L, 17 June 1995.

The distribution of cowbirds in the canyon is interesting because, despite greater diversity and abundance of breeding birds in reach 10 (especially the Bell's Vireo, a well documented host species), we found them most often in reaches 1 and 4. This may be because reaches 1 and 4 are closer to livestock on the Navajo Reservation, the BLM lands of the Arizona Strip, and livestock facilities and bird feeders on the South Rim, places where the cowbirds prefer to forage. The Bell's Vireo, so common in the lower canyon, has been especially hard hit by cowbird parasitism in southern California (Erlich et al. 1988, p. 623). Whether or not the rarity of Bell's Vireos above Nankoweap Creek is due to brood parasitism there remains to be seen, but PMM (p. 172) state that cowbirds have been found to limit the geographic range of both Bell's Vireos and Yellow Warblers.

This species is of great importance for the dynamics of riparian breeding birds in the

canyon as well as throughout the state. This species was rare in northern Arizona before the widespread abundance of livestock in the region (PPM, p. 173; BCJ, p. 268). In addition to the effects cowbirds have on species already mentioned above, the small breeding population of the Southwest Willow Flycatcher is subject to high rates of brood parasitism (Sogge et al. 1995).

**** Hooded Oriole (*Icterus cucullatus*):** Uncommon summer resident.

Surveys: Seventeen birds on Surveys: five in April, five in May, three in June, and four in July.

Incidental: Pair at RM 168.8R, 21 April 1994; an old nest collected at RM 168.8R in January 1994; male at RM 198.0R, 24 March 1995; pair at RM 204.5R, 25 April 1995; male at Cardenas Marsh, 18 May 1995; male singing at Cardenas Marsh, 6 June 1994; pair at RM 204.5R, 14 June 1994; pair at RM 214.0L, 15 June 1994; and a pair nesting at RM 214.0L, 26 June 1995.

Notes: We considered them breeders at 7 (5%) of 133 sites, all in Reach 10, surveyed between 1993 and 1995. Our earliest date was 21 April 1994 at RM 167.6R and our latest date was 22 July 1994 at RM 168.8R. This species has recently entered the canyon as a breeding species (BCJ, p. 268), as the geographic range expanded further north through California (Erich et al. 1988, p. 264).

**** Northern Oriole (*Icterus galbula bullockii*):** Uncommon summer resident.

Surveys: We counted 13 on Surveys: five in May, five in July, and three in September.

Banding: One at RM 204.5R, 18 May 1994; one at RM 204.5R, 25 May 1995; one at RM 1.0R, 12 June 1995; one at RM 198.0R, 19 July 1993; two at RM 198.0R, 23 July 1994; one at RM 198.0R, 9 September 1993.

Incidental: One at RM 168.8R, 14 May 1994; one second-year male at RM 171.0R, 21 May 1995; one second-year male at Lee's Ferry, 1 June 1994; one at RM 1.0R and 1.6R, 12 July 1994; one at Cardenas Marsh, 11 July 1993; "fairly numerous" around RM 198.0R, especially females and hatch-year birds, 23 July 1994 (DF field notes); several at RM 213.6L, 27 July 1994; four at RM 1.0R, 11 August 1994.

Notes: Our earliest date was 17 May 1995 at RM 50.0R, and the latest was 11 September 1994 at RM 198.0R. The pair at RM 204.5R were our only breeders, the rest being migrants.

Scott's Oriole (*Icterus parisorum*): Rare transient.

Incidental: One adult male at RM 205.6R, 27 July 1994.

Finches

**** House Finch (*Carpodacus mexicanus*):** Common summer resident.

Surveys: 507 on 352 Surveys: seven in February, 62 in March, 62 in April, 13 in May, 163 in June, 76 in July, 26 in September. They were found in every reach surveyed except reach 6.

Banding: We banded 18: one in April, four in May, two in June, and 11 in July.

Notes: This was the third-most abundant breeding species from survey data. House Finches made only limited use of riparian vegetation, while ranging widely across the uplands. This is probably why we banded relatively few. Also for this reason, our riparian surveys probably did not do a good job of counting House Finches in the canyon. Our earliest date was 6 February 1995 at RM 1.6R and our latest was 26 September 1994 at RM 204.5R. However, records exist from every

month along the river (BCJ, p. 271). On 20 March 1995, we found them exceptionally numerous in the wake of the fire up Deer Creek, probably in response to the dense growth of weeds and grasses. We only found two nests, at RM 46.7R on 15 June 1995. These nests were both active within 20 m of each other.

**** Lesser Goldfinch (*Carduelis psaltria*):** Fairly common summer resident.

Surveys: 125 birds on 78 surveys -- 26 in March, 59 in April, 33 in May, four in June, and three in September.

Banding: Two at RM 198.0R, 22 April 1995; one at RM 198.0R, 27 April 1994; one at RM 204.5R, 27 May 1995.

Notes: Our earliest date was 23 March 1995 at RM 197.6L and our latest was 28 September 1994 at RM 208.7R. Despite this, there are records along the river from every month (BCJ, p. 272). We found a female on four eggs in desert broom at the ledges lunch spot, river left below Lava Falls, 14 May 1994. We heard young birds begging food and we greatly disturbed the adults with our presence, but never found the nest in tamarisk at RM 204.5R, 25 April 1995. Like the House Finch, we found them exceptionally numerous after the fire up Deer Creek.

American Goldfinch (*Carduelis tristis*): Rare transient.

Incidental: One male in breeding plumage at the bottom of Deer Creek trail, 20 April 1994.

Old World Weaver Finches

House Sparrow (*Passer domesticus*): Rare transient.

Incidental: A pair at RM 171.1R, 24 April 1994; one at RM 46.7R, 14 April 1994; one at RM 171.0R, June 1993.

Notes: Just prior to the April observations, the weather had been stormy, so these individuals had probably been blown into the canyon. Needless to say, they were happy to see us and spent much time around our camp.

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General Appendices

- General Appendix 1. Listing and location of avian community monitoring study sites in Grand Canyon National Park, 1993-95.
- General Appendix 2. List of bird species observed in riparian habitats during avian monitoring surveys in the Grand Canyon, 1993-95, and their status.
- General Appendix 3. Key to standard 4-letter bird codes, per the American Ornithologists' Union convention.

General Appendix 1. Listing and location of avian community monitoring study sites in Grand Canyon National Park, 1993-95. Direct impact study sites are named in brackets. Photograph number refers to the aerial photograph/negative number on which the patch may be seen (based on U.S. Bureau of Reclamation GCES photographs taken 5-29-95). Unless otherwise noted, UTM's were gathered from a point at each patch with Garmin hand-held GPS units and differentially corrected to ± 10 m estimated horizontal accuracy.

River Mile	Aerial Photograph Negative Number	UTM X	UTM Y
1.0 R [Paria]	11-8	446151	4078815
1.6 R	11-10	445643	4078236
2.0 L	11-10	445247	4078043
3.7 L	12-10	444089	4075305
5.1 L	12-14	443564	4073900
5.2 R	12-16	443243	4073660
5.6 R	12-16	442821	4073325
46.0 L	36-10	420656	4025948
46.7 R [Saddle]	37-1	420037	4025506
47.5 L	37-4	420610	4024523
48.5 L	37-6	420905	4024148
49.1 R	37-9	421529	4023259
49.2 L	37-9	421764	4023087
50.0 R	37-14	422682	4021505
73.9 R	50-5	420577	3991654
74.1 R	50-6	420185	3991553
74.3 R	50-6	419919	3991549
74.4 R	50-8	419672	3991167
74.4 L	50-8	419717	3991486
75.9 R	51-8	418468	3989321
76.0 L	51-8	418322	3989192
76.5 L	52-3	417909	3989064
95.7 L	60-8	389857	3996287
95.9 L	60-8	389752	3996433
97.4 R	62-3	388816	3999060
97.4 L	62-3	388707	3999019
97.5 L	62-3	388613	3999123
97.6 L	62-3	388483	3999217
110.0 R ²	67-4	377058	4011521
112.0 R ²	68-4	374083	4011465
117.5 R	71-5	369335	4008293
119.5 R	72-5	368564	4011022
119.6 L	72-5	368247	4011123
122.8 L	73-13	363760	4011928

River Mile	Aerial Photograph Negative Number	UTM X	UTM Y
125.5 R	75-7	364012	4015582
131.3 R	78-3	369568	4022539
167.0 R	96-2	329128	4013663
167.2 L	96-2	328873	4013584
167.6 R	96-4	328180	4013826
168.5 L	97-6	326805	4012909
168.8 R	97-6	326619	4012825
171.0 R [Stairway]	98-9	323963	4011871
171.1 R	98-9	323833	4011799
172.2 L	99-1	322233	4011250
173.1 R	99-5	320659	4011754
174.2 L	99-8	319606	4012064
174.4 R	100-3	319085	4012119
174.5 R	100-3	318956	4012072
174.7 R	100-5	318290	4011745
197.3 L	113-5	292050	3997262 ¹
197.6 L	113-5	291886	3997267
198.0 R [Parashant]	114-2	291448	3997252
198.2 L ²	114-2	291512	3997109
198.3 R	114-2	291120	3996962
199.5 R	114-6	290684	3995807
200.0 L	114-8	290517	3994434
200.4 R	115-2	290140	3994014
200.5 R	115-2	290036	3993850
202.5 R	115-10	288072	3991594
204.1 R	116-8	288176	3989015
204.5 R [Spring]	116-10	288197	3988204
205.8 R	117-4	289092	3986389
206.5 L	117-7	289057	3985398
206.6 R	117-7	288980	3985094
208.7 R	119-2	290622	3983579
213.6 L	123-3	289849	3976256
214.0 L	123-6	290265	3975733
214.2 L ²	123-6	290421	3975253
224.0 L ²	127-8	287561	3961944
224.1 R ²	127-8	287521	3961964

1 = interpolated from points adjacent to patch

2 = coordinates taken from USGS topo map digital raster graphic (DRG)

General Appendix 2. List of bird species observed in riparian habitats during avian monitoring surveys in the Grand Canyon, 1993-95, and their status (B = breeding, M = migrant, W = wintering, R = year-round resident, V = visitor, may breed in uplands). Status from Brown et al. (1987).

Species	Status	Species	Status
Green-backed Heron (<i>Butorides striatus</i>)	V	Ruby-crowned Kinglet (<i>Regulus calendula</i>)	W
Black-crowned Night-heron (<i>Nycticorax nycticorax</i>)	B,W	Blue-gray Gnatcatcher (<i>Poliopitila caerulea</i>)	B,M,V
Great Blue Heron (<i>Ardea herodias</i>)	V	Western Bluebird (<i>Sialia mexicana</i>)	W
Snowy Egret (<i>Egretta thula</i>)	M	Townsend's Solitaire (<i>Myadestes townsendi</i>)	M
Canada Goose (<i>Branta canadensis</i>)	W,M	Hermit Thrush (<i>Catharus guttatus</i>)	W
Mallard (<i>Anas platyrhynchos</i>)	B,M,W	American Robin (<i>Turdus migratorius</i>)	M
Northern Pintail (<i>Anas acuta</i>)	M,W	Loggerhead Shrike (<i>Lanius ludovicianus</i>)	M,V
American Wigeon (<i>Anas americana</i>)	M,W	Northern Mockingbird (<i>Mimus polyglottus</i>)	B
Common Goldeneye (<i>Bucephala clangula</i>)	M,W	Crissal Thrasher (<i>Toxostoma crissale</i>)	B?
Bufflehead (<i>Bucephala albeola</i>)	M,W	American Pipit (<i>Anthus rubescens</i>)	M
Common Merganser (<i>Mergus merganser</i>)	M,W	Cedar Waxwing (<i>Bombycilla cedrorum</i>)	M,W
Sora (<i>Porzana carolina</i>)	M	Phainopepla (<i>Phainopepla nitens</i>)	B,M
American Coot (<i>Fulica americana</i>)	B,M,W	Bell's Vireo (<i>Vireo bellii</i>)	B
Killdeer (<i>Charadrius vociferus</i>)	M	Gray Vireo (<i>Vireo vicinior</i>)	M
Spotted Sandpiper (<i>Actitis macularia</i>)	B,M	Orange-crowned Warbler (<i>Vermivora celata</i>)	M
Ring-billed Gull (<i>Larus delawarensis</i>)	M	Lucy's Warbler (<i>Vermivora luciae</i>)	B
Turkey Vulture (<i>Cathartes aura</i>)	M,V	Yellow-rumped Warbler (<i>Dendroica coronata</i>)	M,W
Sharp-shinned Hawk (<i>Accipiter striatus</i>)	M,W	Yellow Warbler (<i>Dendroica petechia</i>)	B,M
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	M,V	MacGillivray's Warbler (<i>Oporornis tolmiei</i>)	M
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	M,W	Wilson's Warbler (<i>Wilsonia pusilla</i>)	M
American Kestrel (<i>Falco sparverius</i>)	B,R	Common Yellowthroat (<i>Geothlypis trichas</i>)	B,M
Peregrine Falcon (<i>Falco peregrinus</i>)	M,V	Yellow-breasted Chat (<i>Icteria virens</i>)	B,M
Gambel's Quail (<i>Callipepla gambelii</i>)	V	Black-headed Grosbeak	
Wild Turkey (<i>Meleagris gallopavo</i>)	B,R	(<i>Pheucticus melanocephalus</i>)	M
Mourning Dove (<i>Zenaida macroura</i>)	B,M	Blue Grosbeak (<i>Guiraca caerulea</i>)	B
White-throated Swift (<i>Aeronautes saxatalis</i>)	V	Indigo Bunting (<i>Passerina cyanea</i>)	B,M
Costa's Hummingbird (<i>Calypte costae</i>)	B	Lazuli Bunting (<i>Passerina amoena</i>)	B,M
Black-chinned Hummingbird		Green-tailed Towhee (<i>Pipilo chlorurus</i>)	M
(<i>Archilochus alexandri</i>)	B,V	Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	M
Belted Kingfisher (<i>Ceryle alcyon</i>)	M	Brown Towhee (<i>Pipilo fuscus</i>)	W,B?
Northern Flicker (<i>Colaptes auratus</i>)	M,W	Song Sparrow (<i>Melospiza melodia</i>)	W,M,B?
Red-naped Sapsucker		Lark Sparrow (<i>Chondestes grammacus</i>)	M
(<i>Sphyrapicus nuchalis</i>)	M,W	Black-throated Sparrow (<i>Amphispiza bilineata</i>)	V
Ladder-backed Woodpecker		Rufous-crowned Sparrow (<i>Aimophila ruficeps</i>)	B,V
(<i>Picoides scalaris</i>)	R,V	Chipping Sparrow (<i>Spizella passerina</i>)	W,M
Western Kingbird (<i>Tyrannus verticalis</i>)	M,B?	Black-chinned Sparrow (<i>Spizella atrogularis</i>)	M,V
Cassin's Kingbird (<i>Tyrannus vociferans</i>)	M	Dark-eyed Junco (<i>Junco hyemalis</i>)	W,M
Brown-crested Flycatcher		White-crowned Sparrow	
(<i>Myiarchus tyrannulus</i>)	B	(<i>Zonotrichia leucophrys</i>)	W
Ash-throated Flycatcher		Lincoln's Sparrow (<i>Melospiza lincolni</i>)	M
(<i>Myiarchus cinerascens</i>)	B,V	Brown-headed Cowbird (<i>Molothrus ater</i>)	B
Olive-sided Flycatcher (<i>Contopus borealis</i>)	M	Great-tailed Grackle (<i>Quiscalus mexicanus</i>)	B,M
Western Wood-pewee (<i>Contopus sordidulus</i>)	M	Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	M,W
Black Phoebe (<i>Sayornis nigricans</i>)	B,M	Scott's Oriole (<i>Icterus parisorum</i>)	V
Say's Phoebe (<i>Sayornis saya</i>)	B,R	Northern Oriole (<i>Icterus galbula</i>)	B,M
Gray Flycatcher (<i>Empidonax wrightii</i>)	M	Hooded Oriole (<i>Icterus cucullatus</i>)	B,M
Willow Flycatcher (<i>Empidonax traillii</i>)	B,M	Western Tanager (<i>Piranga ludoviciana</i>)	M
Western Flycatcher (<i>Empidonax difficilis</i>)	M	Summer Tanager (<i>Piranga rubra</i>)	B
Violet-green Swallow (<i>Tachycineta thalassina</i>)	B,V	American Goldfinch (<i>Carduelis tristis</i>)	M
Northern Rough-winged Swallow		Lesser Goldfinch (<i>Carduelis psaltria</i>)	B,V
(<i>Stelgidopteryx serripennis</i>)	M	House Finch (<i>Carpodacus mexicanus</i>)	B,V
Scrub Jay (<i>Aphelocoma coerulescens</i>)	M,W,V	House Sparrow (<i>Passer domesticus</i>)	M?
American Crow (<i>Corvus brachyrhynchos</i>)	V		
Common Raven (<i>Corvus corax</i>)	B,V		
Mountain Chickadee (<i>Parus gambeli</i>)	W		
Bushtit (<i>Psaltriparus minimus</i>)	W		
Bewick's Wren (<i>Thryomanes bewickii</i>)	B,R		
Marsh Wren (<i>Cistothorus palustris</i>)	M		
Canyon Wren (<i>Catherpes mexicanus</i>)	R,V		
Rock Wren (<i>Salpinctes obsoletus</i>)	R,V		
House Wren (<i>Troglodytes aedon</i>)	M		

General Appendix 3. Key to standard 4-letter bird codes. Codes and common names are standardized per the American Ornithologists' Union (1983 and subsequent revisions) convention.

AMCO	American Coot	LUWA	Lucy's Warbler
AMCR	American Crow	LZBU	Lazuli Bunting
AMKE	American Kestrel	MALL	Mallard
AMRO	American Robin	MAWR	Marsh Wren
AMWI	American Widgeon	MGWA	MacGillivray's Warbler
ATFL	Ash-throated Flycatcher	MOCH	Mountain Chickadee
BAEA	Bald Eagle	MODO	Mourning Dove
BCFL	Brown-crested Flycatcher	NAWA	Nashville Warbler
BCHU	Black-chinned Hummingbird	NOFL	Northern Flicker
BCNH	Black-crowned Night Heron	NOMO	Northern Mockingbird
BCSP	Black-chinned Sparrow	NOOR	Northern Oriole
BEKI	Belted Kingfisher	NOPI	Northern Pintail
BEVI	Bell's Vireo	NRWS	Northern Rough-winged Swallow
BEWR	Bewick's Wren	OCWA	Orange-crowned Warbler
BGGN	Blue-gray Gnatcatcher	OSFL	Olive-sided Flycatcher
BHCO	Brown-headed Cowbird	PEFA	Peregrine Falcon
BHGR	Black-headed Grosbeak	PHAI	Phainopepla
BLGR	Blue Grosbeak	RBGU	Ring-billed Gull
BLPH	Black Phoebe	RCKI	Ruby-crowned Kinglet
BRBL	Brewer's Blackbird	RCSP	Rufous-crowned Sparrow
BRSP	Brewer's Sparrow	RNSA	Red-naped Sapsucker
BRTO	Brown Towhee	ROWR	Rock Wren
BTSP	Black-throated Sparrow	RSTO	Rufous-sided Towhee
BUFF	Bufflehead	RTHA	Red-tailed Hawk
BUSH	Bushtit	RUFU	Rufous Hummingbird
CAGO	Canada Goose	RWBL	Red-winged Blackbird
CAKI	Cassin's Kingbird	SAPH	Say's Phoebe
CEWA	Cedar Waxwing	SCJA	Scrub Jay
CHSP	Chipping Sparrow	SNEG	Snowy Egret
CNWR	Canyon Wren	SORA	Sora
COGO	Common Goldeneye	SOSP	Song Sparrow
COHA	Cooper's Hawk	SPSA	Spotted Sandpiper
COHU	Costa's Hummingbird	SSHA	Sharp-shinned Hawk
COME	Common Merganser	SUTA	Summer Tanager
CORA	Common Raven	TOSO	Townsend's Solitaire
COYE	Common Yellowthroat	TUVU	Turkey Vulture
CRTH	Crissal Thrasher	VASW	Vaux's Swift
DEJU	Dark-eyed Junco	VGSW	Violet-green Swallow
GADW	Gadwall	WAVI	Warbling Vireo
GAQU	Gambel's Quail	WCSP	White-crowned Sparrow
GBHE	Great-blue Heron	WEBL	Western Bluebird
GRFL	Gray Flycatcher	WEFL	Western (Cordilleran?) Flycatcher
GRHE	Green Heron	WEKI	Western Kingbird
GRVI	Gray Vireo	WETA	Western Tanager
GTGR	Great-tailed Grackle	WFIB	White-faced Ibis
GTTO	Green-tailed Towhee	WIFL	Willow Flycatcher
HAWO	Hairy Woodpecker	WITU	Wild Turkey
HETH	Hermit Thrush	WIWA	Wilson's Warbler
HOFI	House Finch	WTSW	White-throated Swift
HOOR	Hooded Oriole	WWPE	Western Wood-pewee
HOSP	House Sparrow	YBCH	Yellow-breasted Chat
HOWR	House Wren	YEWA	Yellow Warbler
INBU	Indigo Bunting	YRWA	Yellow-rumper Warbler
KILL	Killdeer		
LASP	Lark Sparrow		
LBWO	Ladder-backed Woodpecker		
LEGO	Lesser Goldfinch		
LISP	Lincoln Sparrow		
LOSH	Loggerhead Shrike		



Aerial Photographs of Study Sites

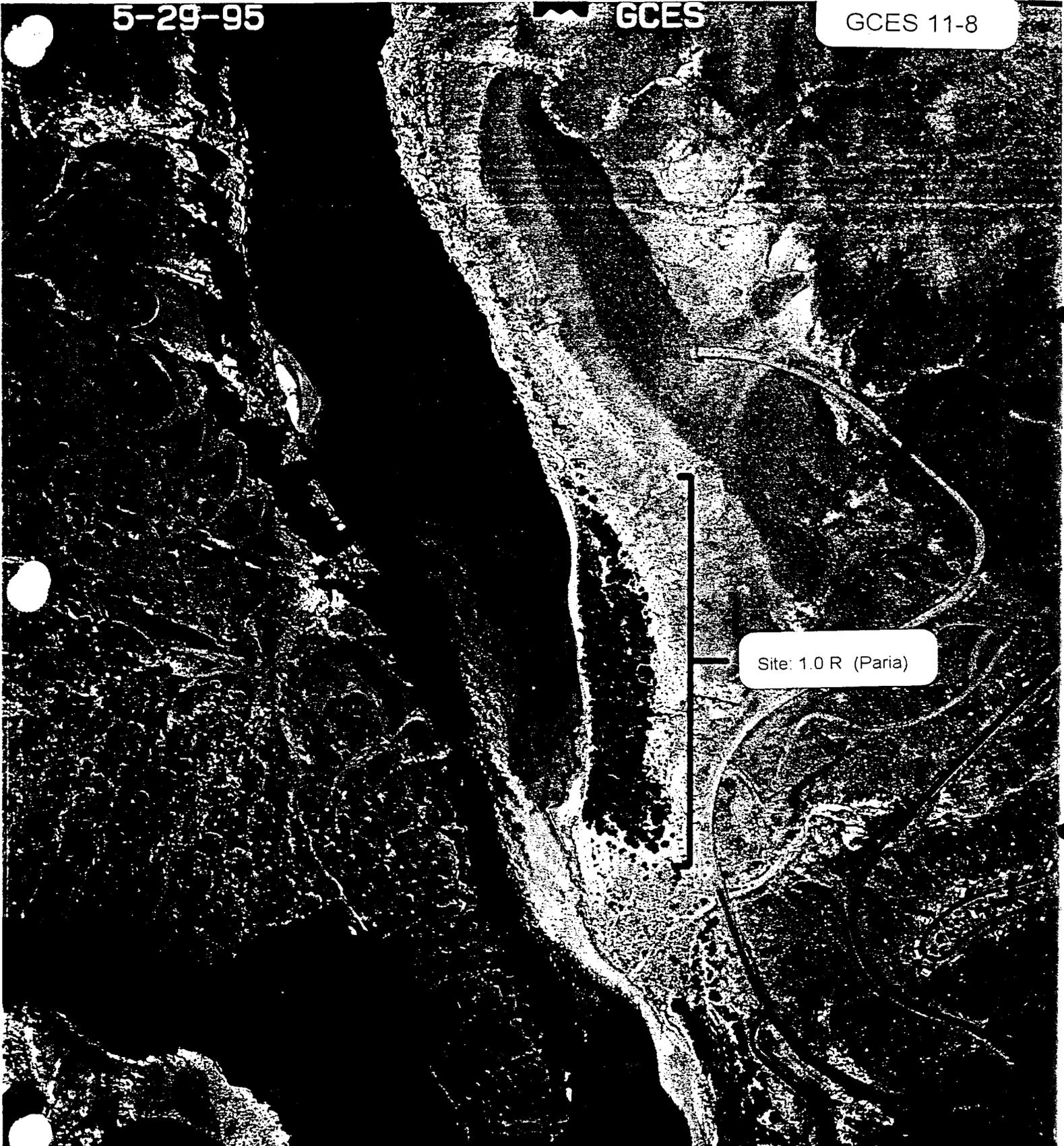
Following are aerial photographs of all riparian bird community survey and banding sites along the Colorado River in the Grand Canyon, 1993 - 1995. Photographs are from U.S. Bureau of Reclamation GCES photo series, taken 5-29-95. Scale is 1:2400. River flow is from page bottom to page top. Each photograph includes the GCES series negative number. Study sites are named and labeled according to their location in river miles (RM). River mile designations follow Stevens (1983). The upper and lower boundaries of each study site are bracketed by the bold red lines, which also specify the beginning and end points for walking and floating surveys.

5-29-95

GCES

GCES 11-8

Site: 1.0 R (Paria)



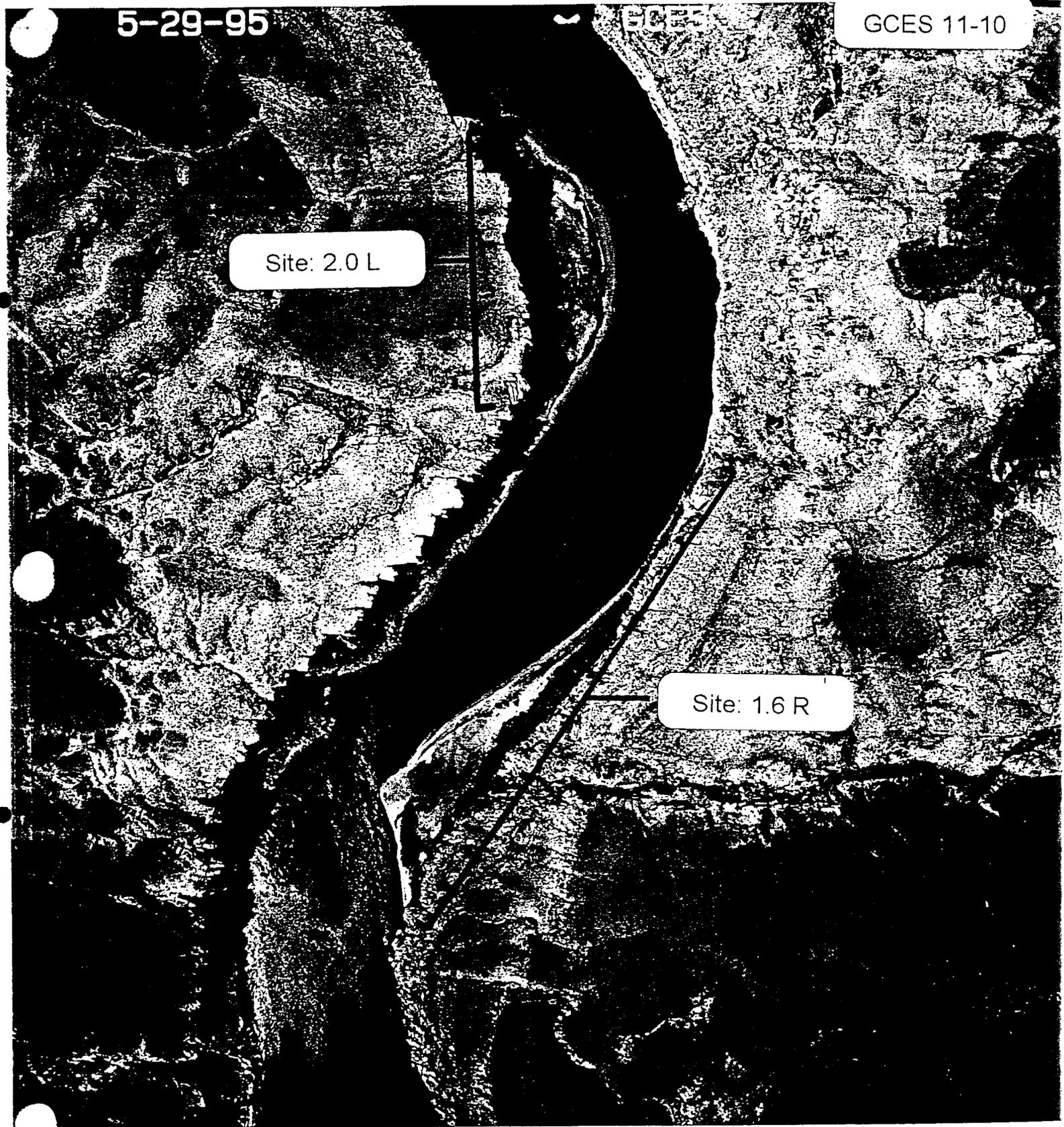
5-29-95

GCES

GCES 11-10

Site: 2.0 L

Site: 1.6 R

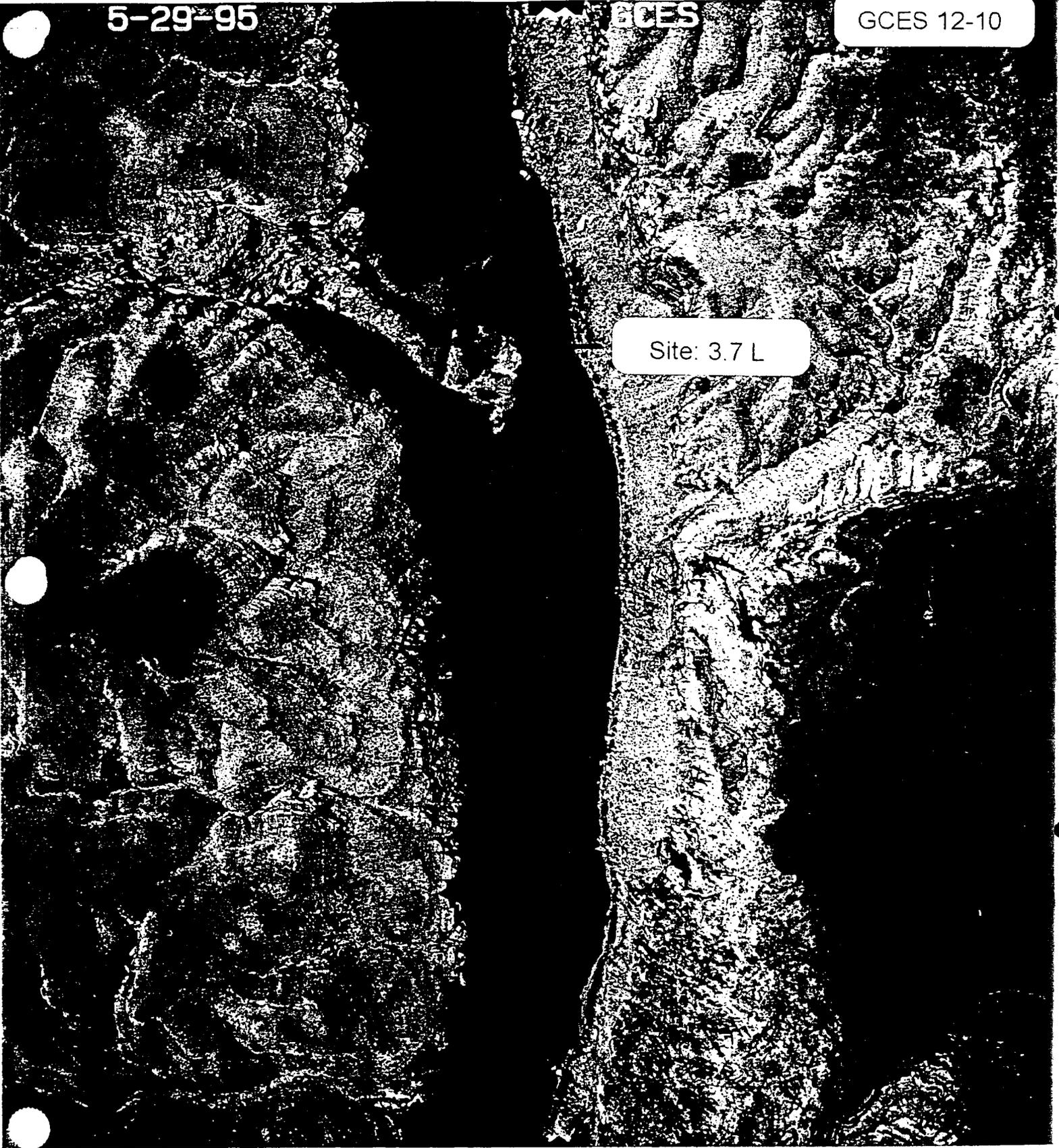


5-29-95

GCES

GCES 12-10

Site: 3.7 L

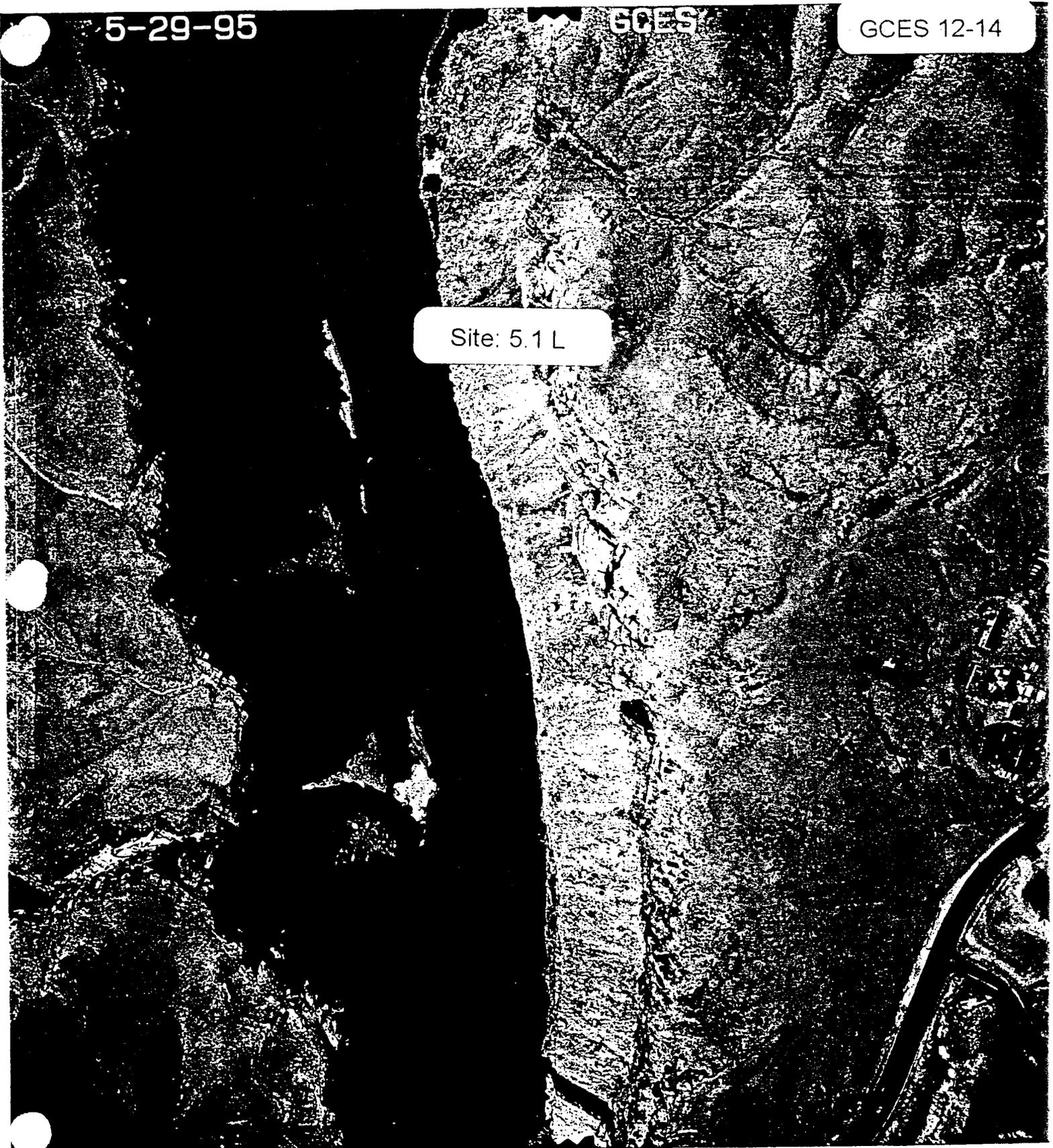


5-29-95

GCES

GCES 12-14

Site: 5.1 L



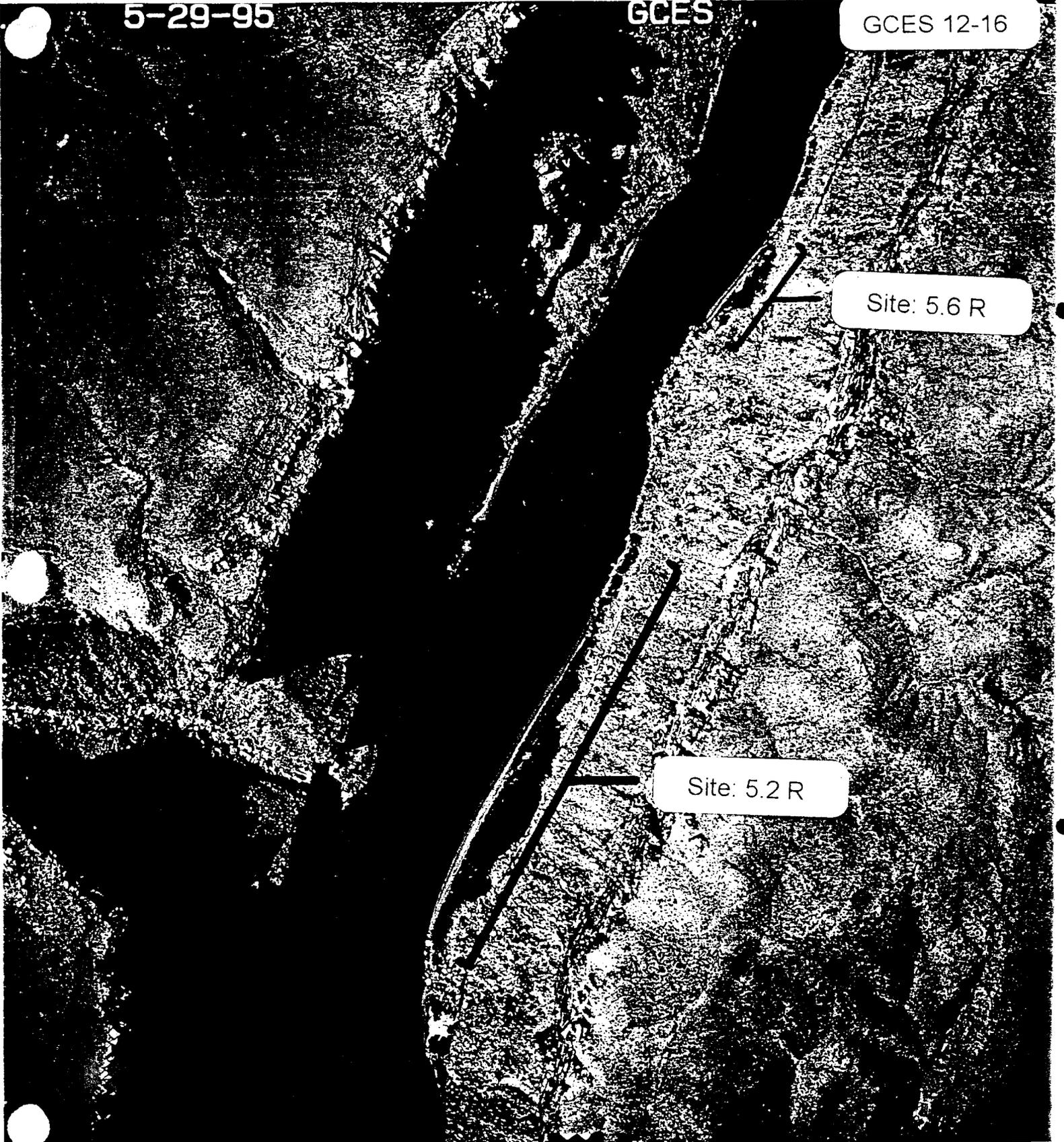
5-29-95

GCES

GCES 12-16

Site: 5.6 R

Site: 5.2 R



5-29-95

GCES

GCES 36-10

Site: 46.0 L



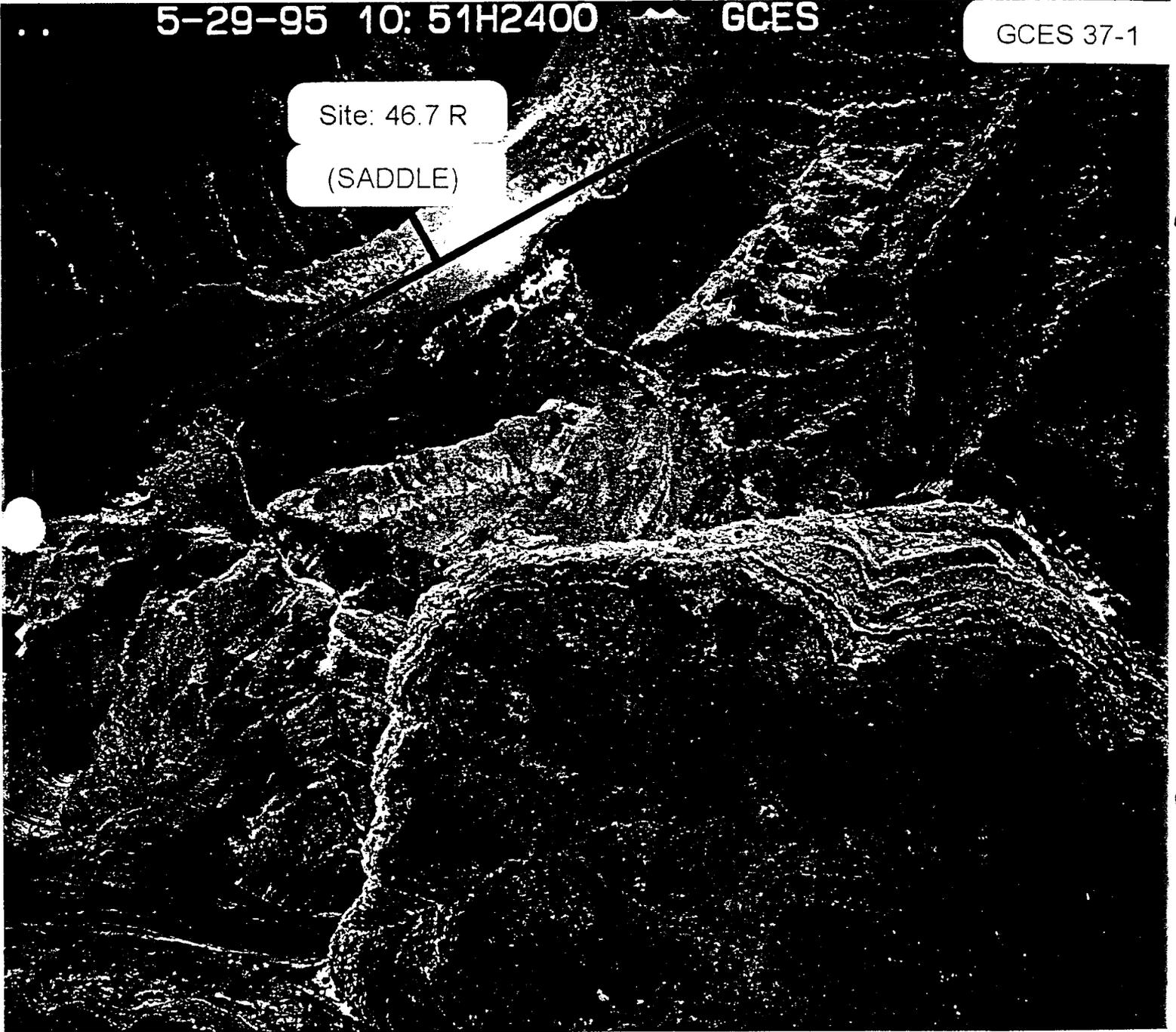
5-29-95 10:51H2400

GCES

GCES 37-1

Site: 46.7 R

(SADDLE)

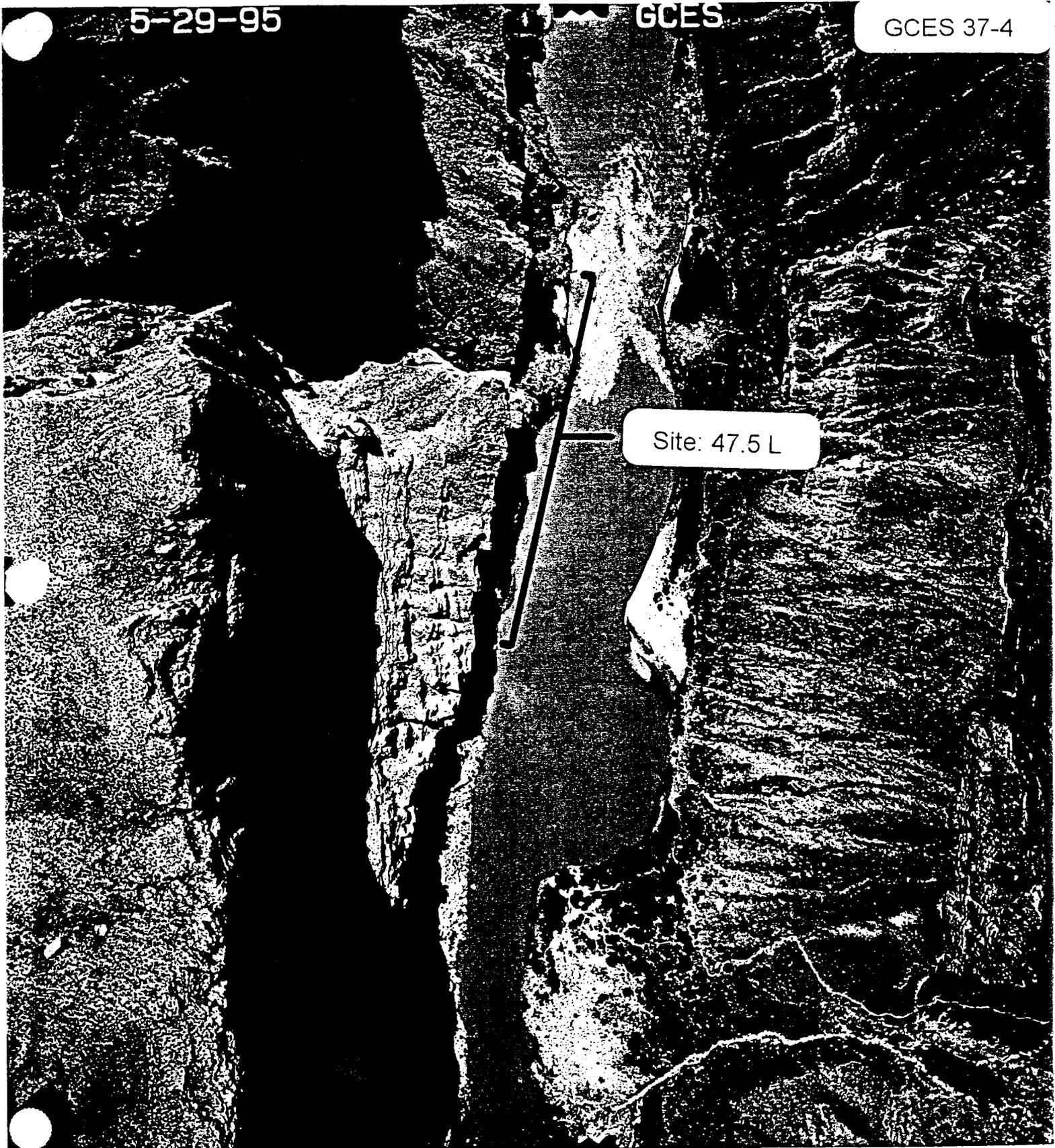


5-29-95

GCES

GCES 37-4

Site: 47.5 L

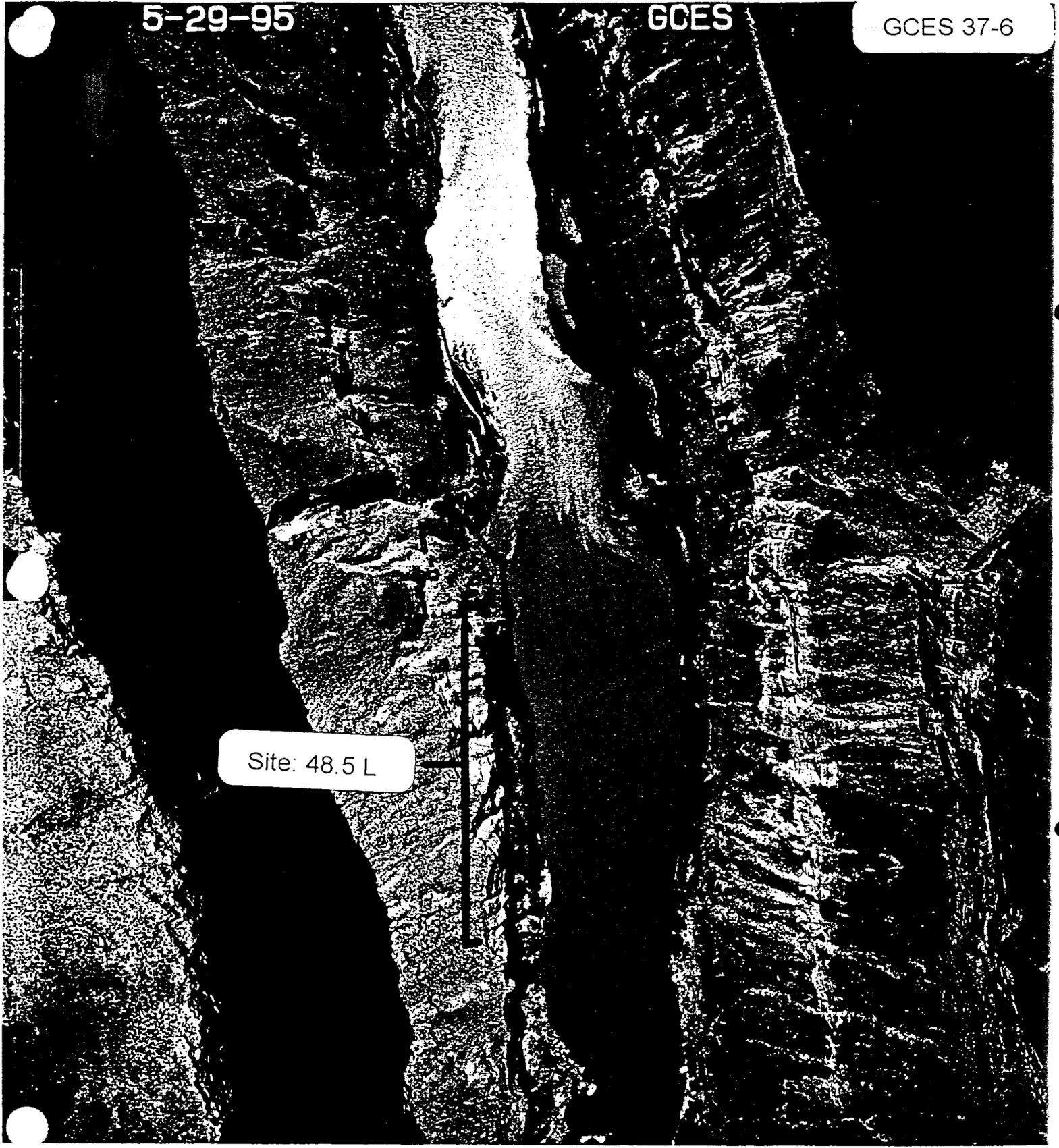


5-29-95

GCES

GCES 37-6

Site: 48.5 L



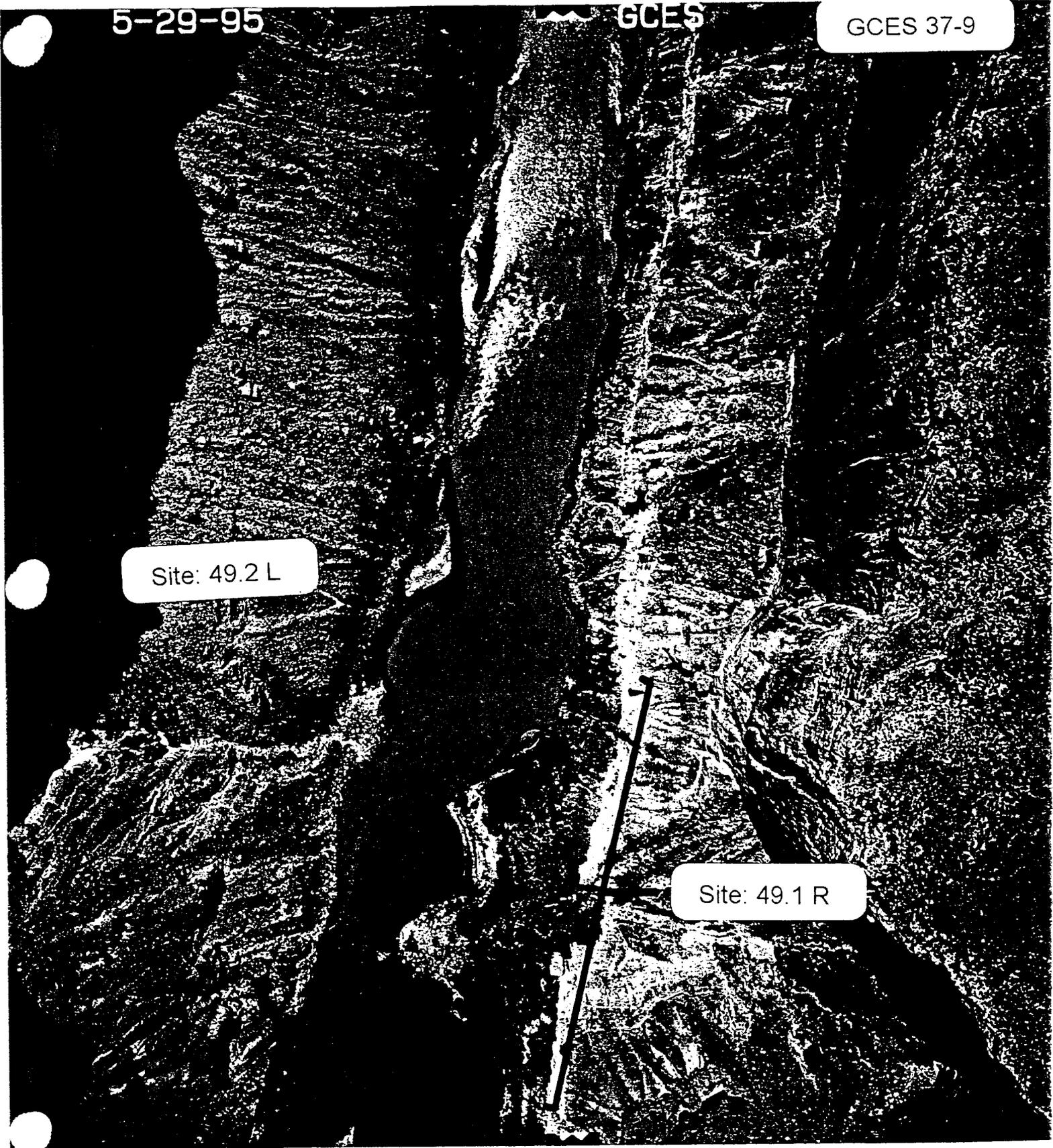
5-29-95

GCES

GCES 37-9

Site: 49.2 L

Site: 49.1 R

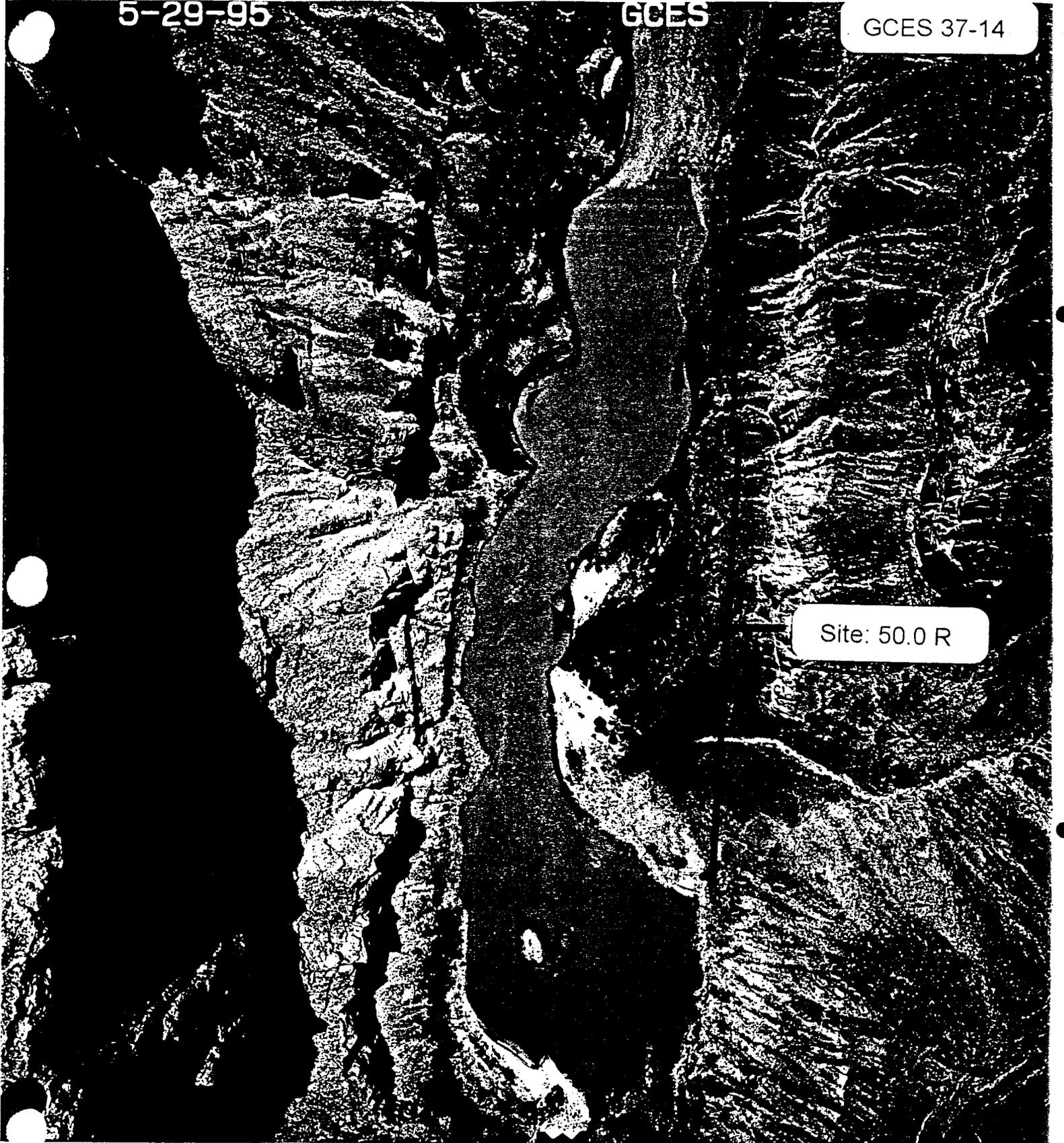


5-29-95

GCES

GCES 37-14

Site: 50.0 R

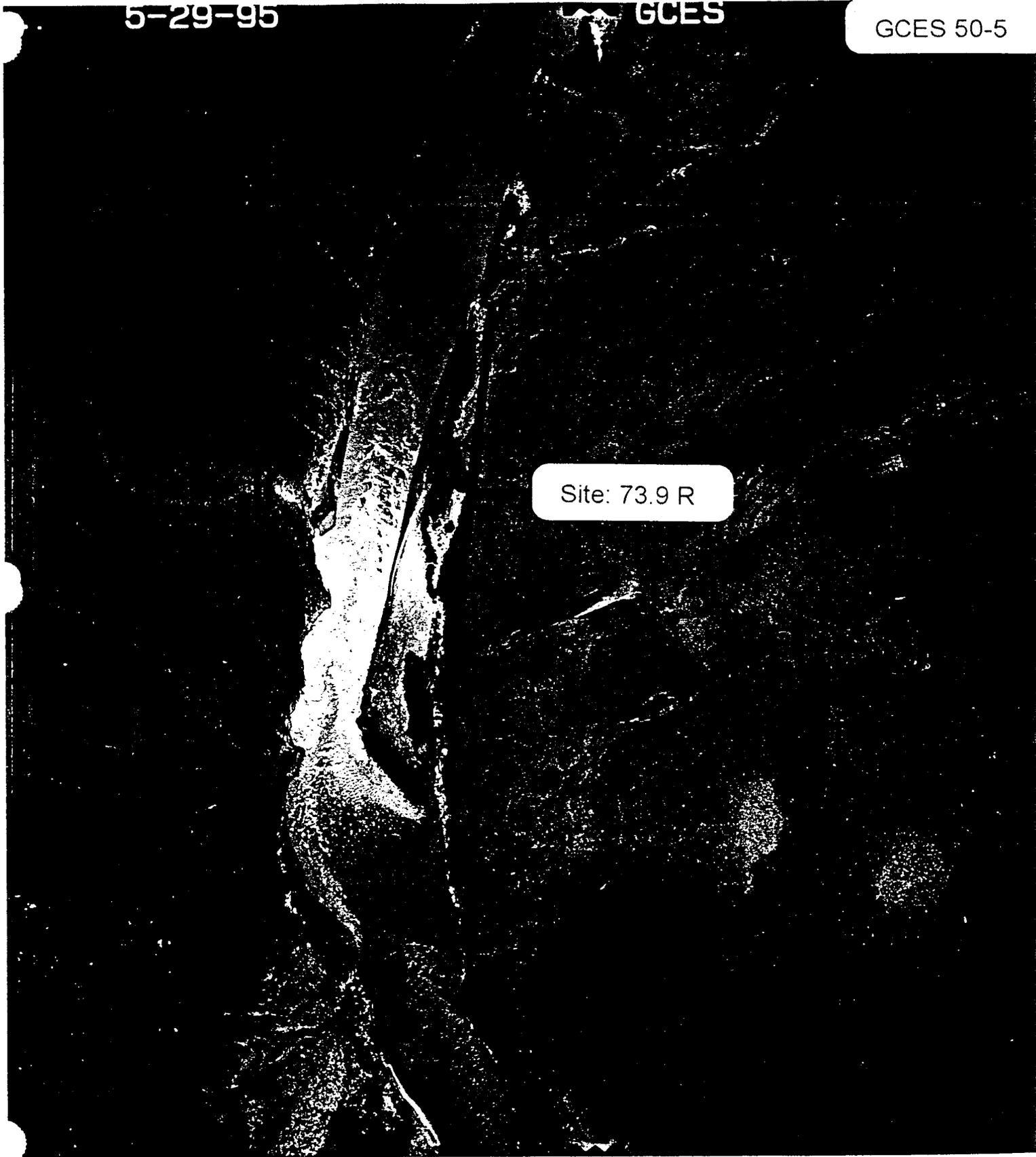


5-29-95

GCES

GCES 50-5

Site: 73.9 R



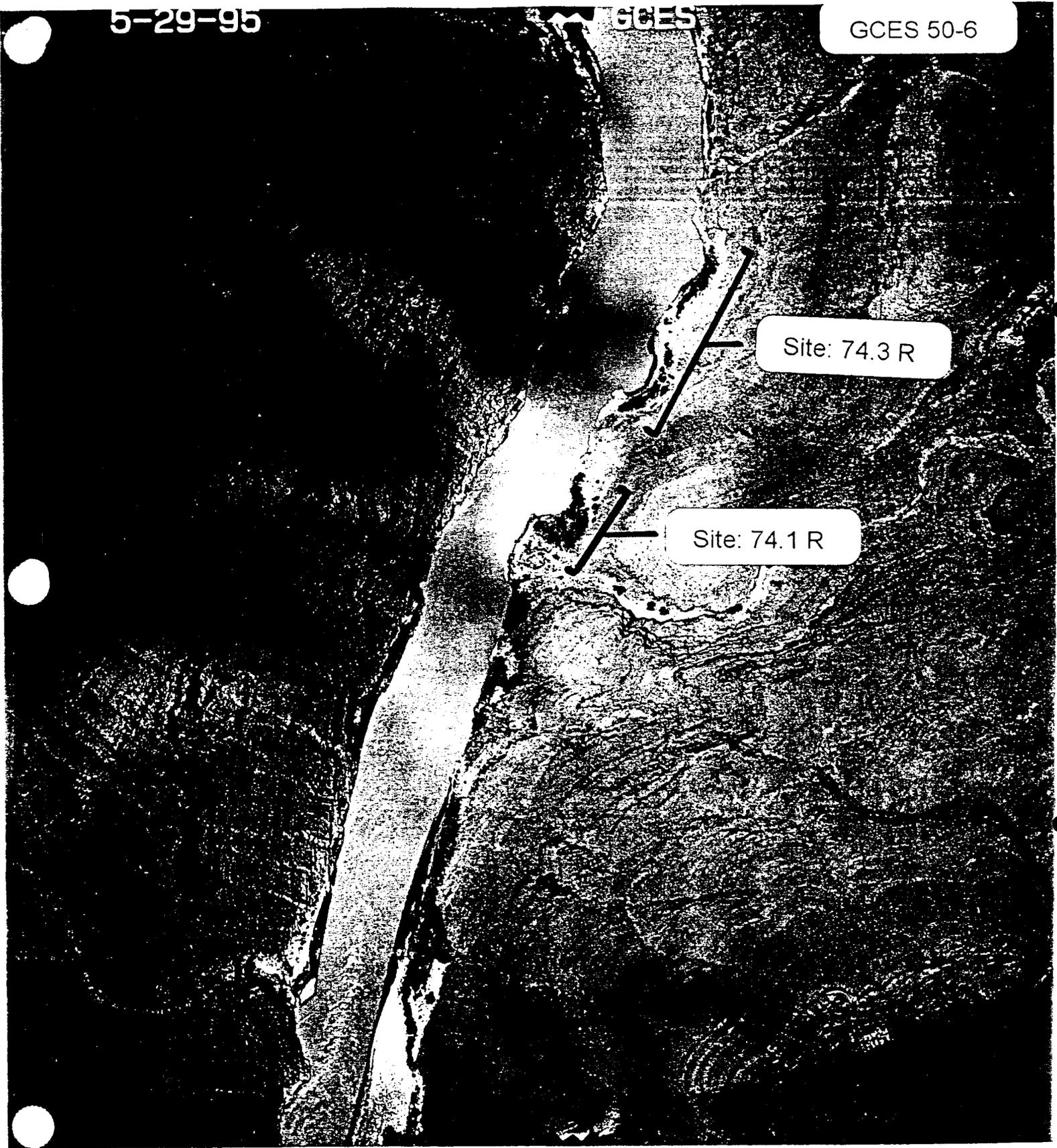
5-29-95

GCES

GCES 50-6

Site: 74.3 R

Site: 74.1 R



5-29-95 TT: 43R2400 GCES

GCES 50-8

Site: 74.4 R

Site: 74.4 L

E I 153 72

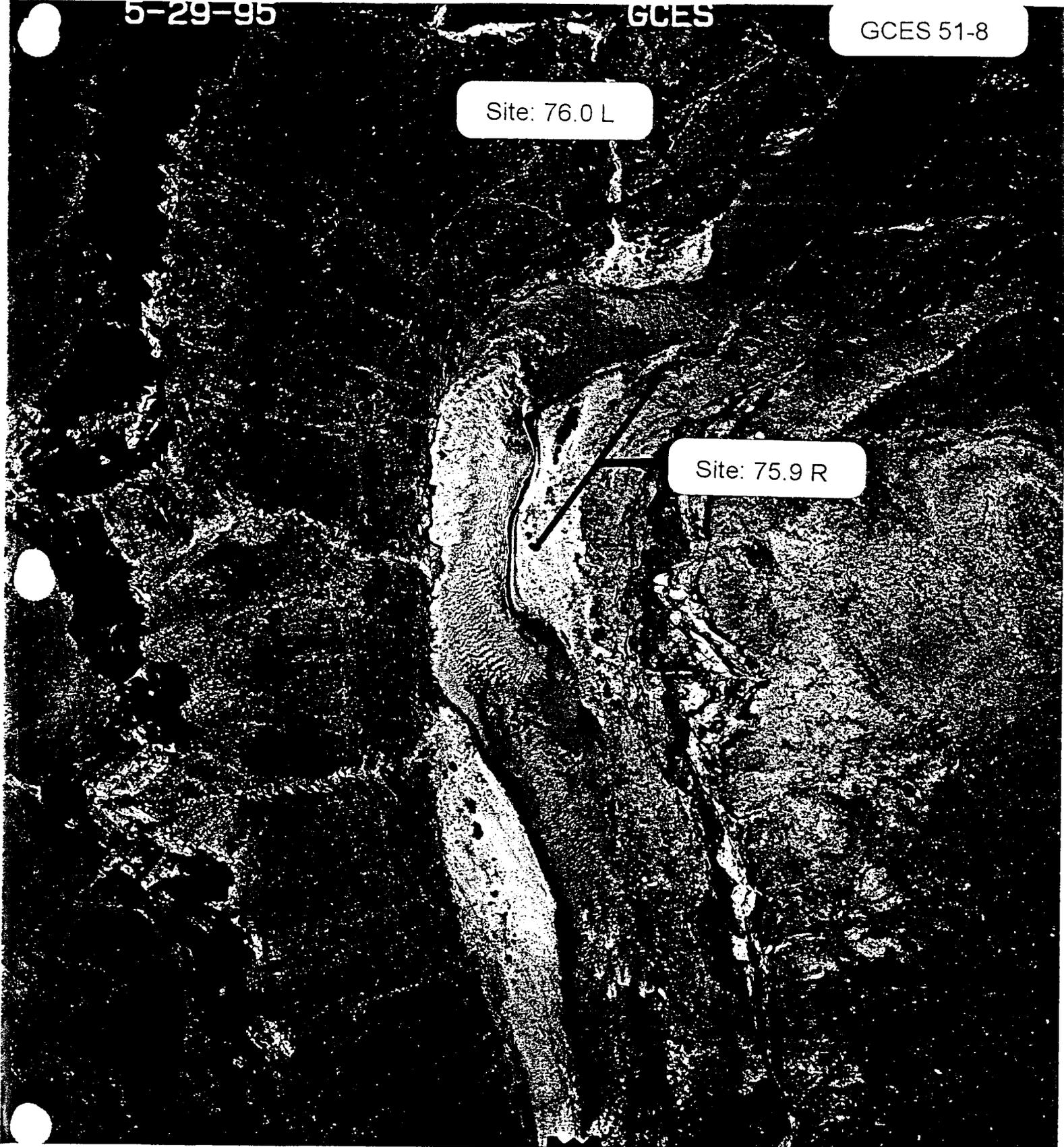
5-29-95

GCES

GCES 51-8

Site: 76.0 L

Site: 75.9 R

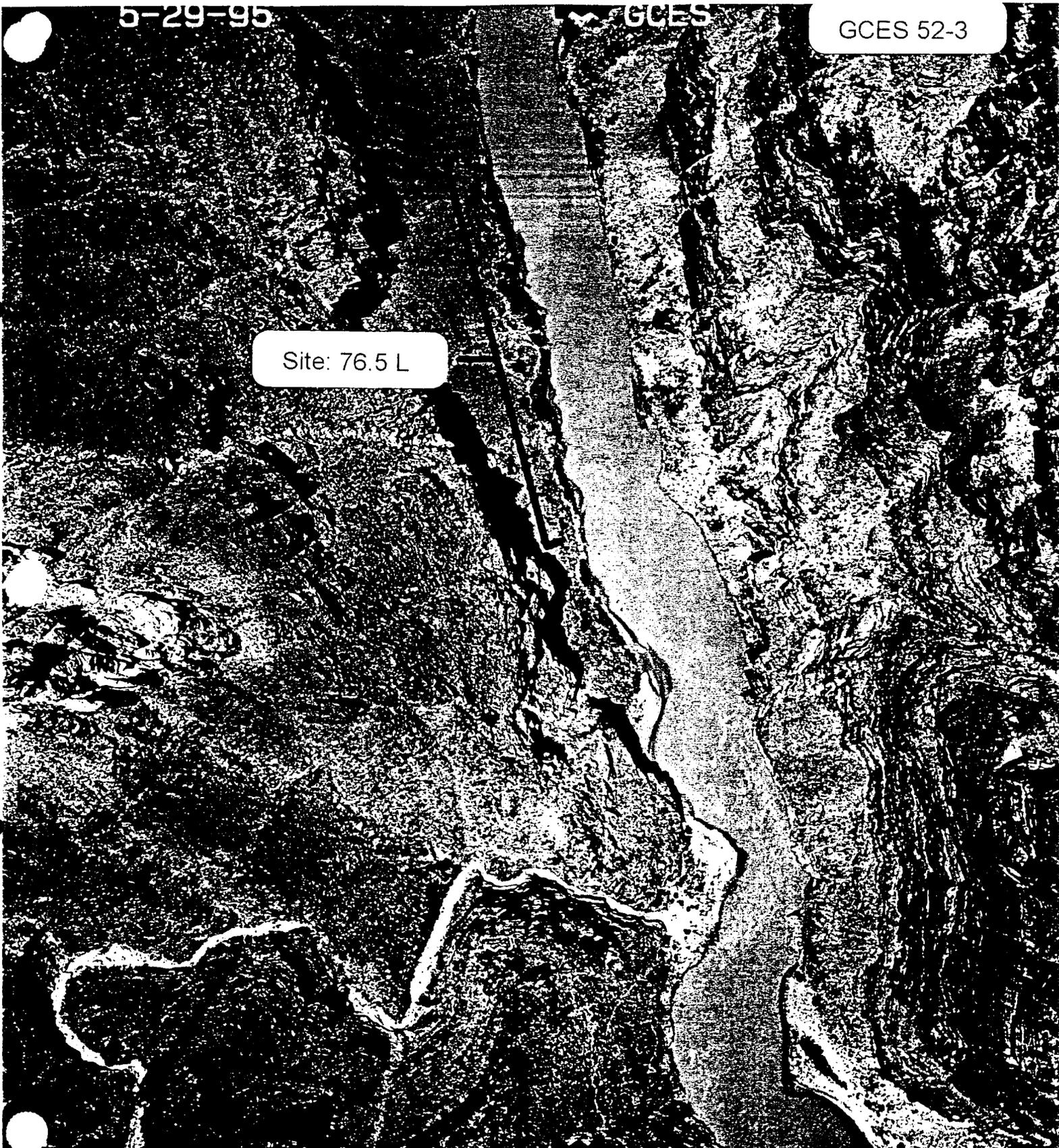


5-29-95

GCES

GCES 52-3

Site: 76.5 L



5-29-95

GCES

GCES 60-8

Site: 95.9 L

Site: 95.7 L

5-29-95

GCES

GCES 67-4

Site: 100.0 R



5-29-95

GCES

GCES 68-4

Site: 112.0 R

5-29-95

GCES

GCES 62-3

Site: 97.6 L

Site: 97.5 L

Site: 97.4 L

Site: 97.4 R

5-29-95

GCES

GCES 71-5

Site: 117.5 R



5-29-95

GCES

GCES 72-5

Site: 119.6 L

Site: 119.5 R

5-29-95 14: 18H2400

GCES

GCES 73-13

Site: 122.8 L

E.L. 153-72

5-29-95

GCES

GCES 75-7

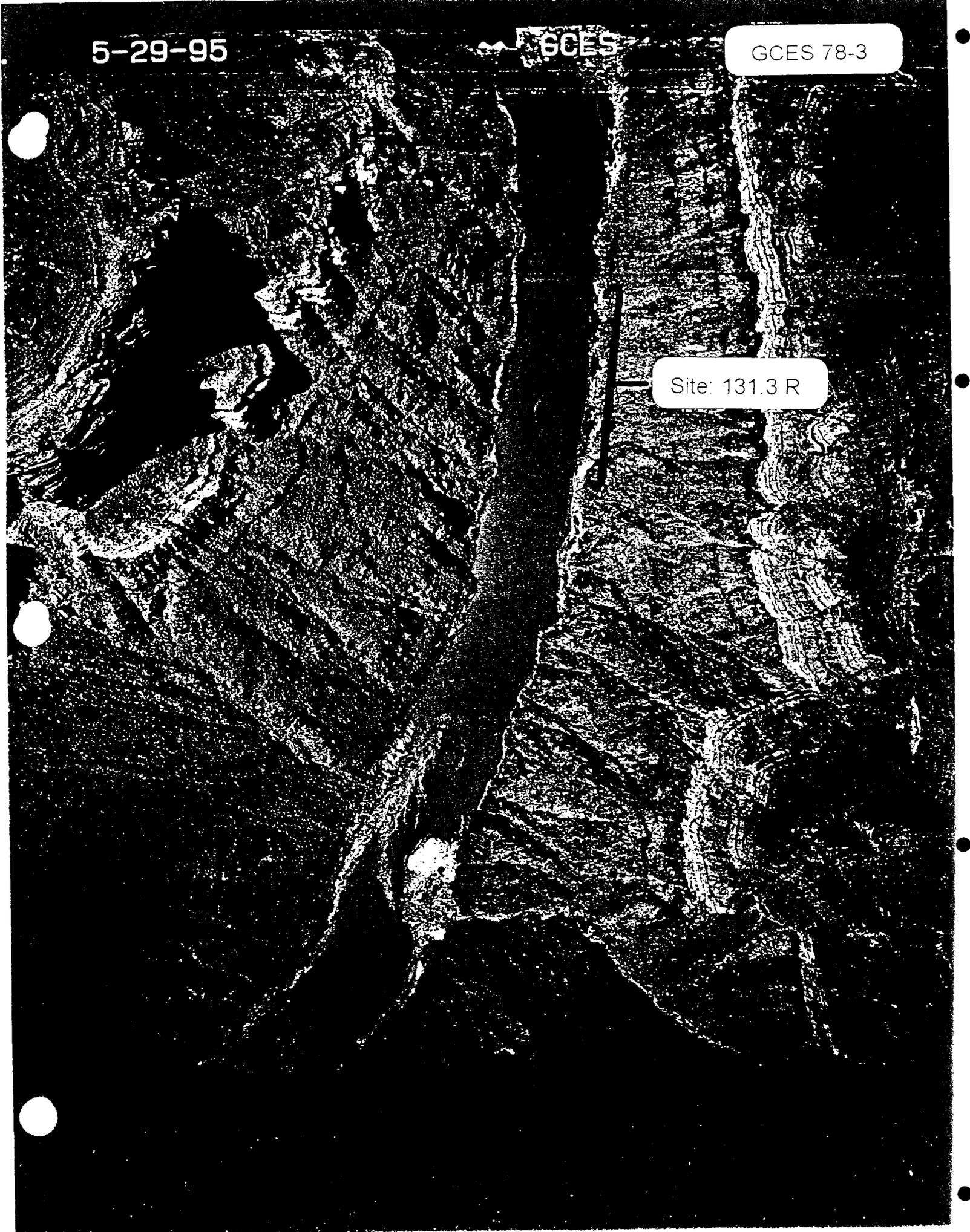
Site: 125.5 R

5-29-95

GCES

GCES 78-3

Site: 131.3 R



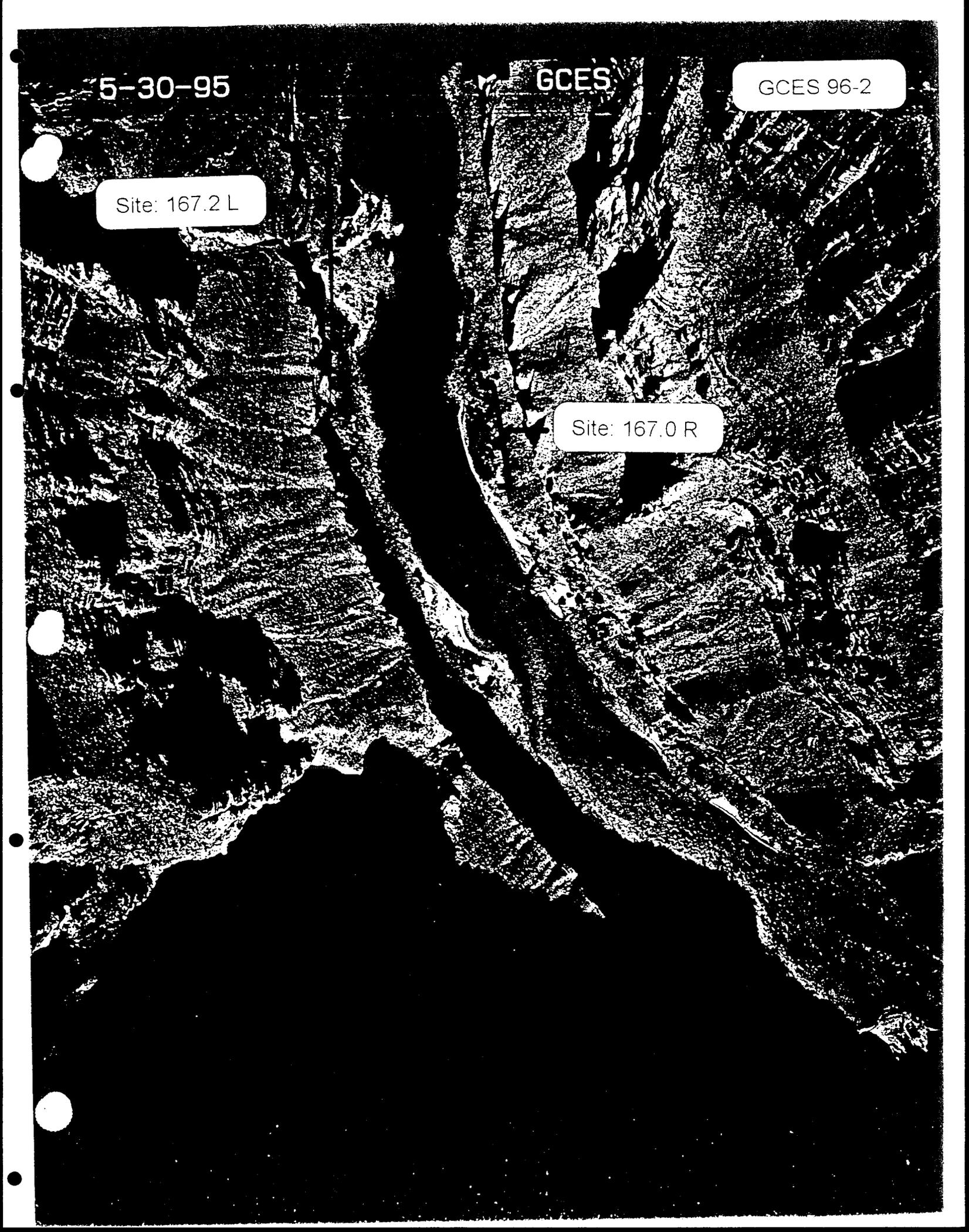
5-30-95

GCES

GCES 96-2

Site: 167.2 L

Site: 167.0 R

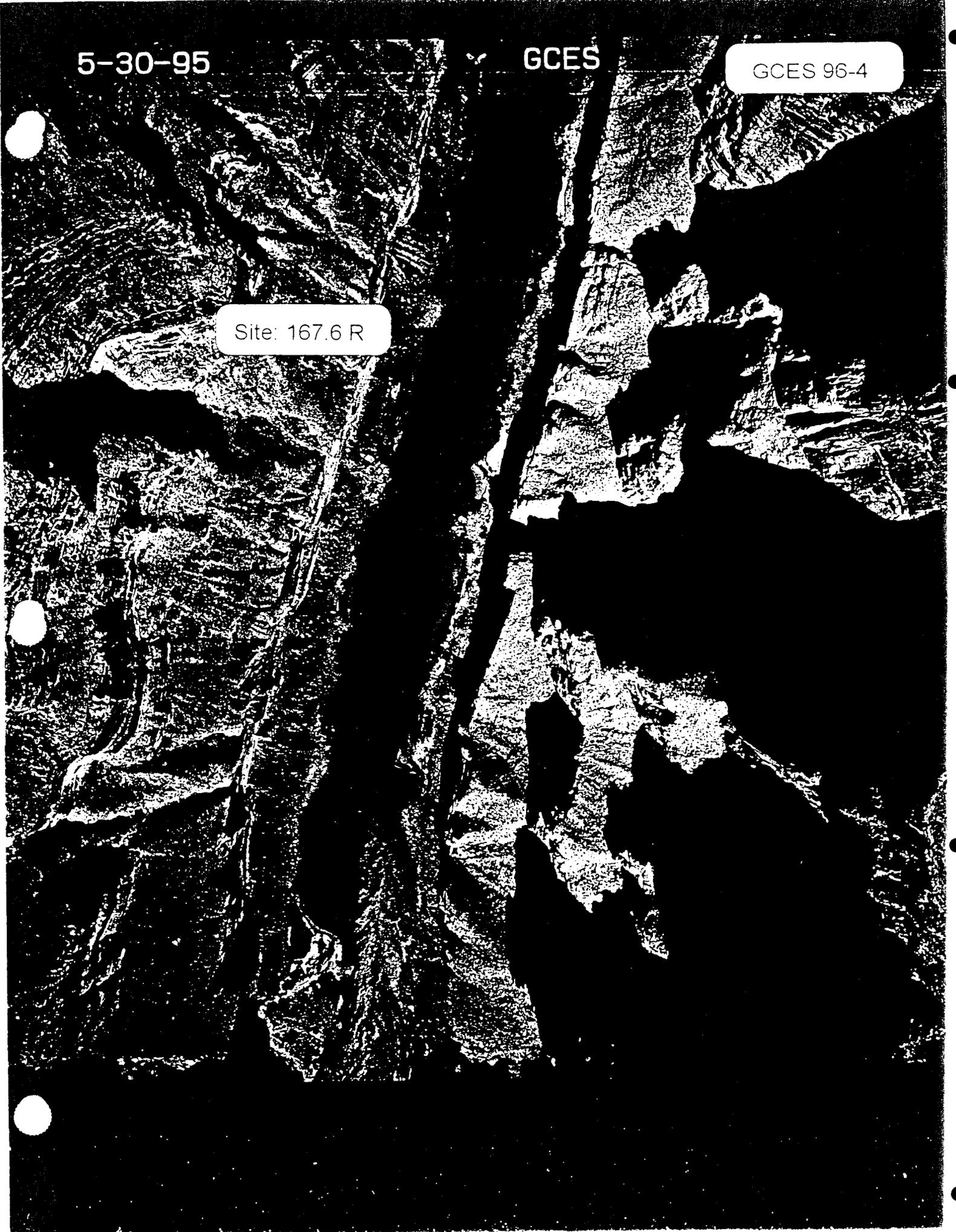


5-30-95

GCES

GCES 96-4

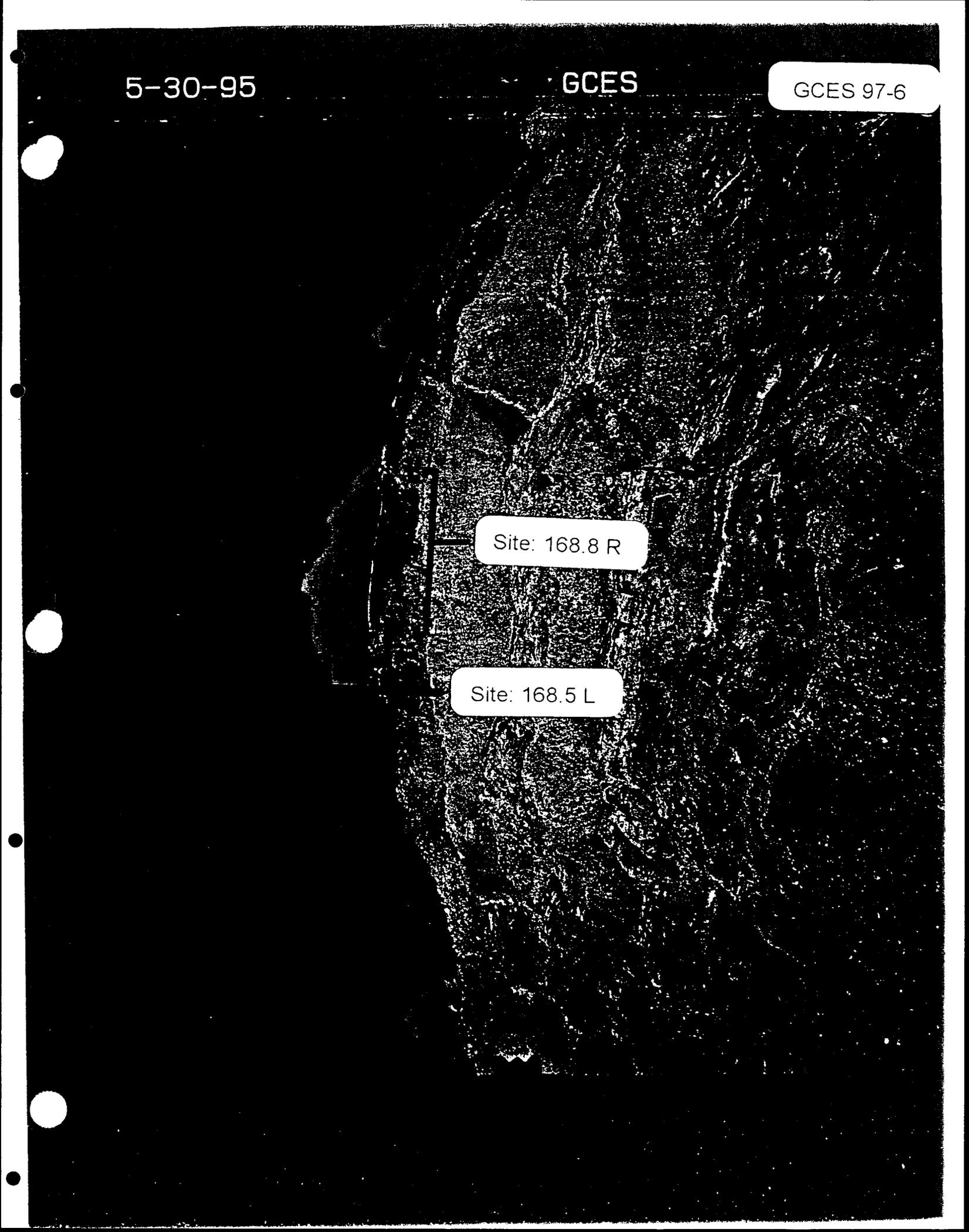
Site: 167.6 R



5-30-95

GCES

GCES 97-6



Site: 168.8 R

An aerial photograph showing a dense forest. Two specific locations are marked with white labels and lines pointing to them. The labels are 'Site: 168.8 R' and 'Site: 168.5 L'. The forest appears to be a mix of different tree types, with some areas showing more open ground or different vegetation patterns.

Site: 168.5 L

5-30-95

GCES

GCES 98-9

Site: 171.1 R

Site: 171.0 R
(STAIRWAY)

5-30-95 9:45 H2400 GCES

GCES 99-1

Site: 172.2 L

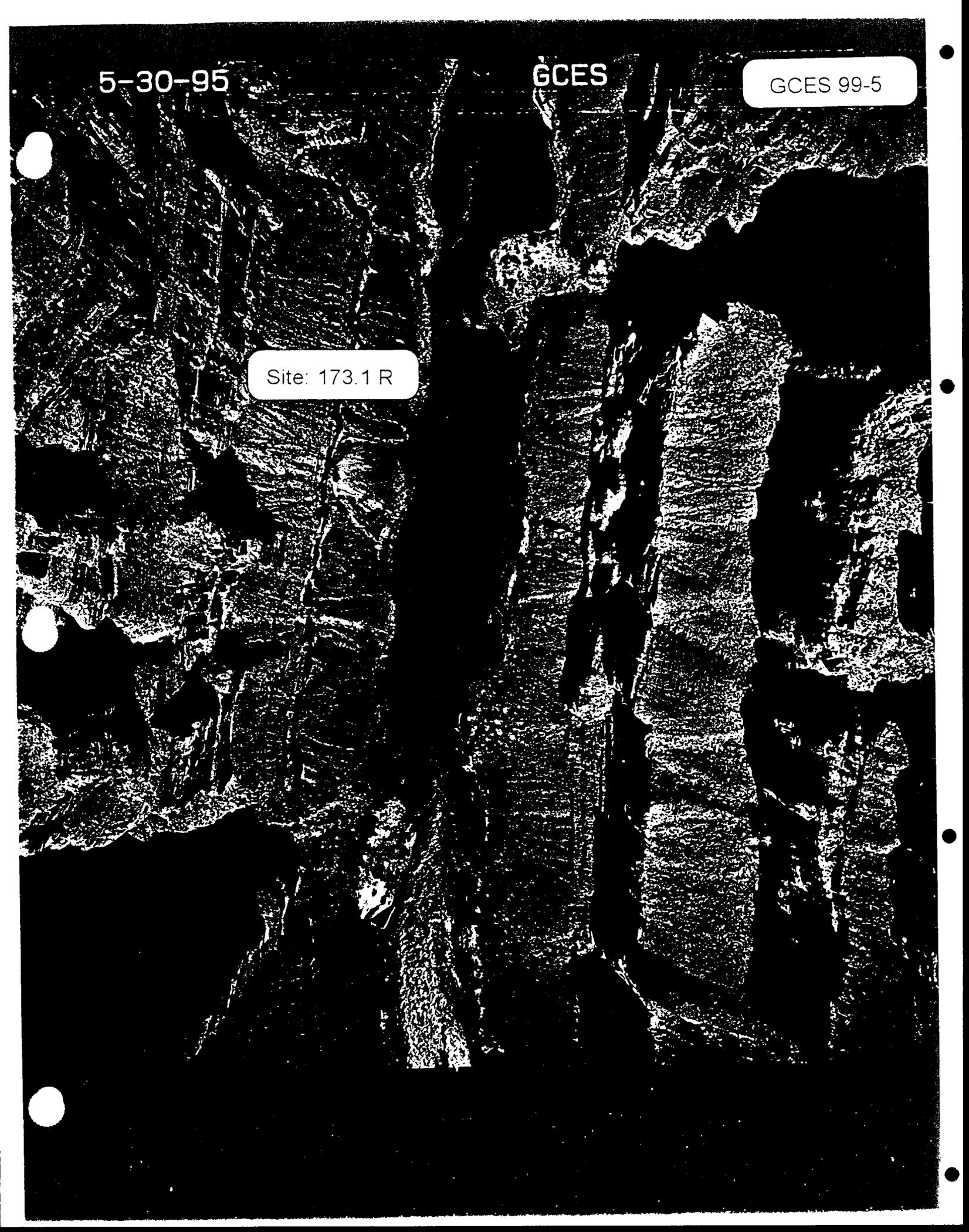
F.L. 153.72

5-30-95

GCES

GCES 99-5

Site: 173.1 R



5-30-95

GCES

GCES 99-8

Site: 174.2 L



5-30-95

REF.
GCES

GCES 100-3

Site: 174.5 R

Site: 174.4 R

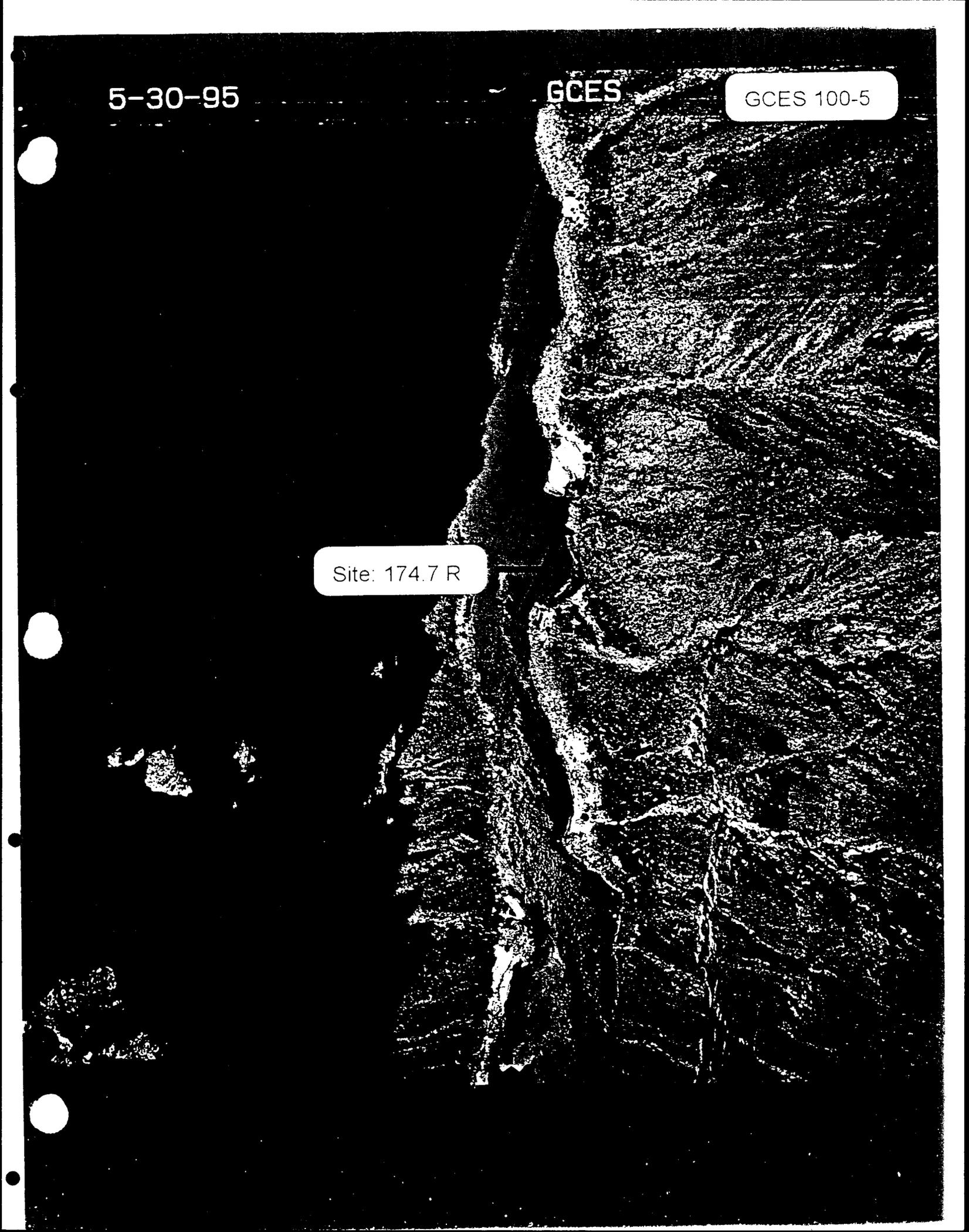


5-30-95

GCES

GCES 100-5

Site: 174.7 R



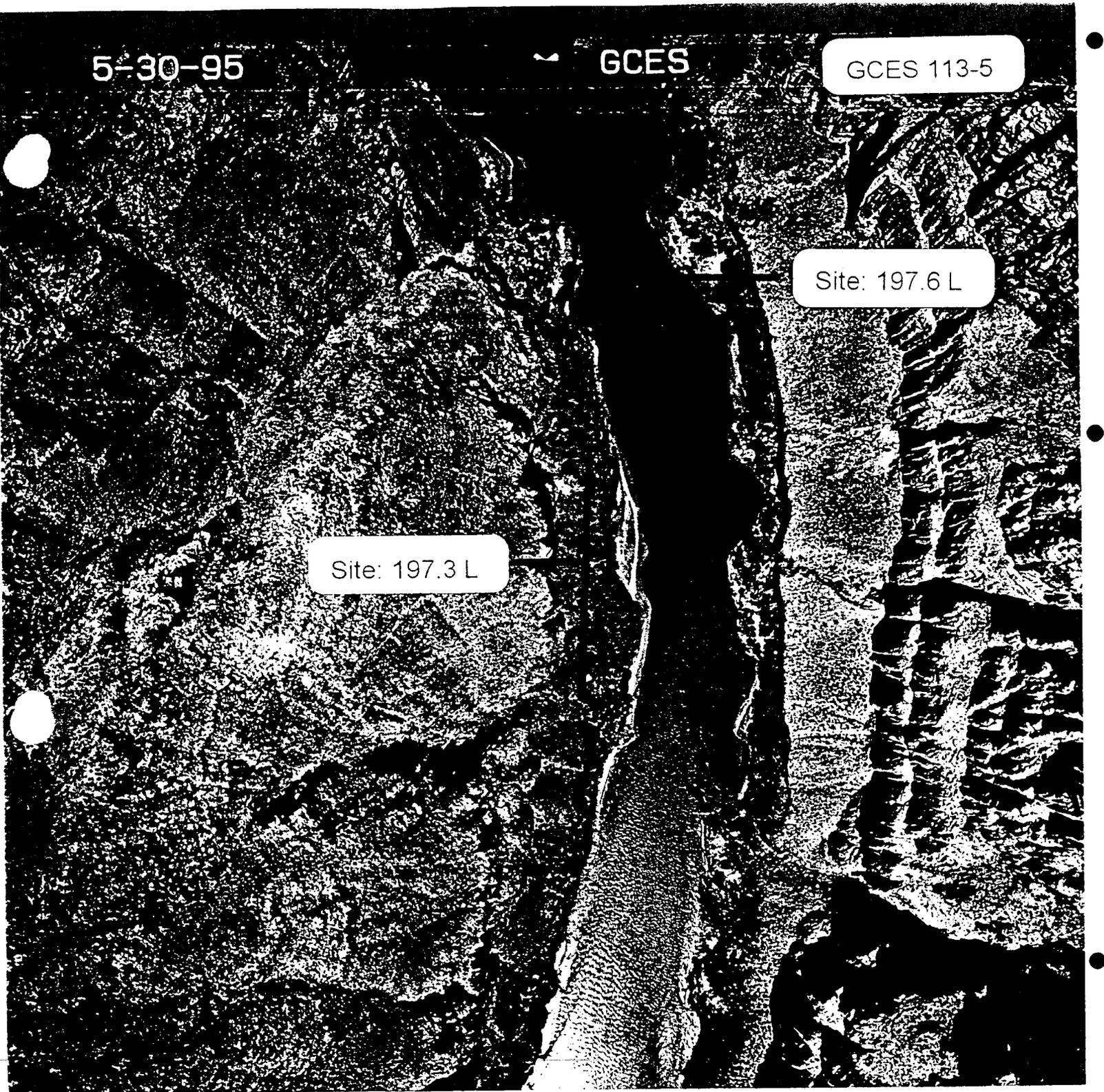
5-30-95

GCES

GCES 113-5

Site: 197.6 L

Site: 197.3 L



5-30-95

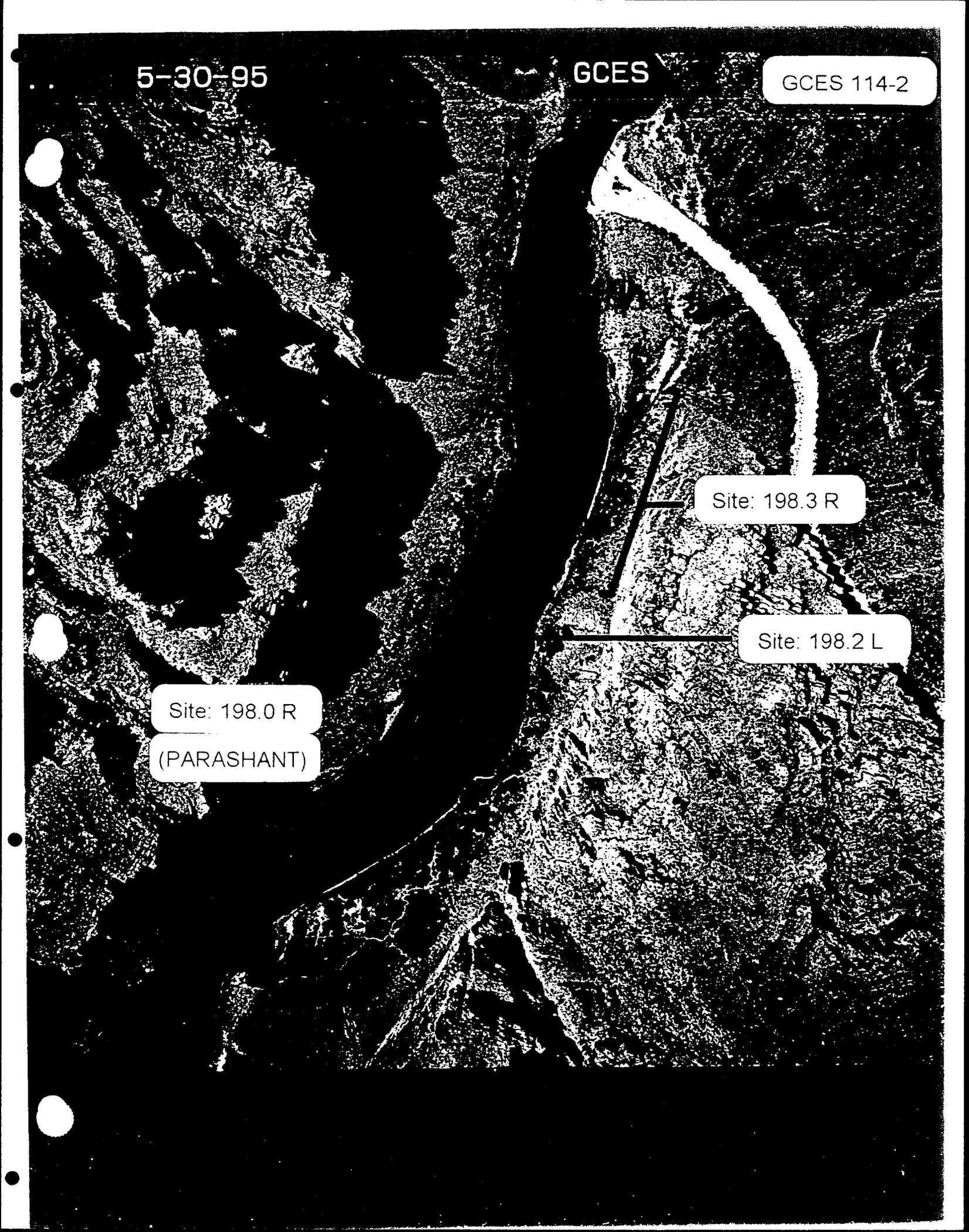
GCES

GCES 114-2

Site: 198.0 R
(PARASHANT)

Site: 198.3 R

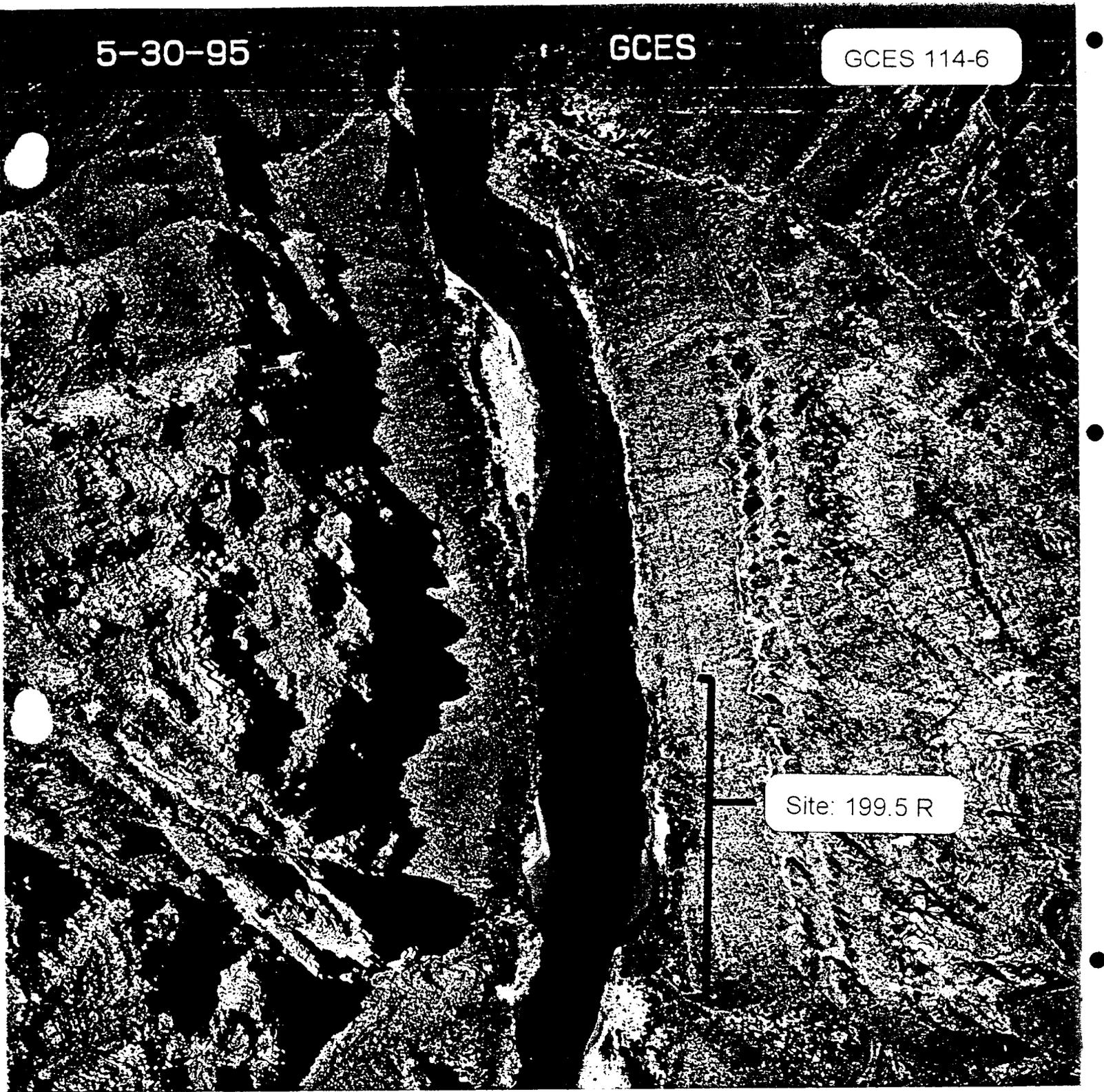
Site: 198.2 L



5-30-95

GCES

GCES 114-6



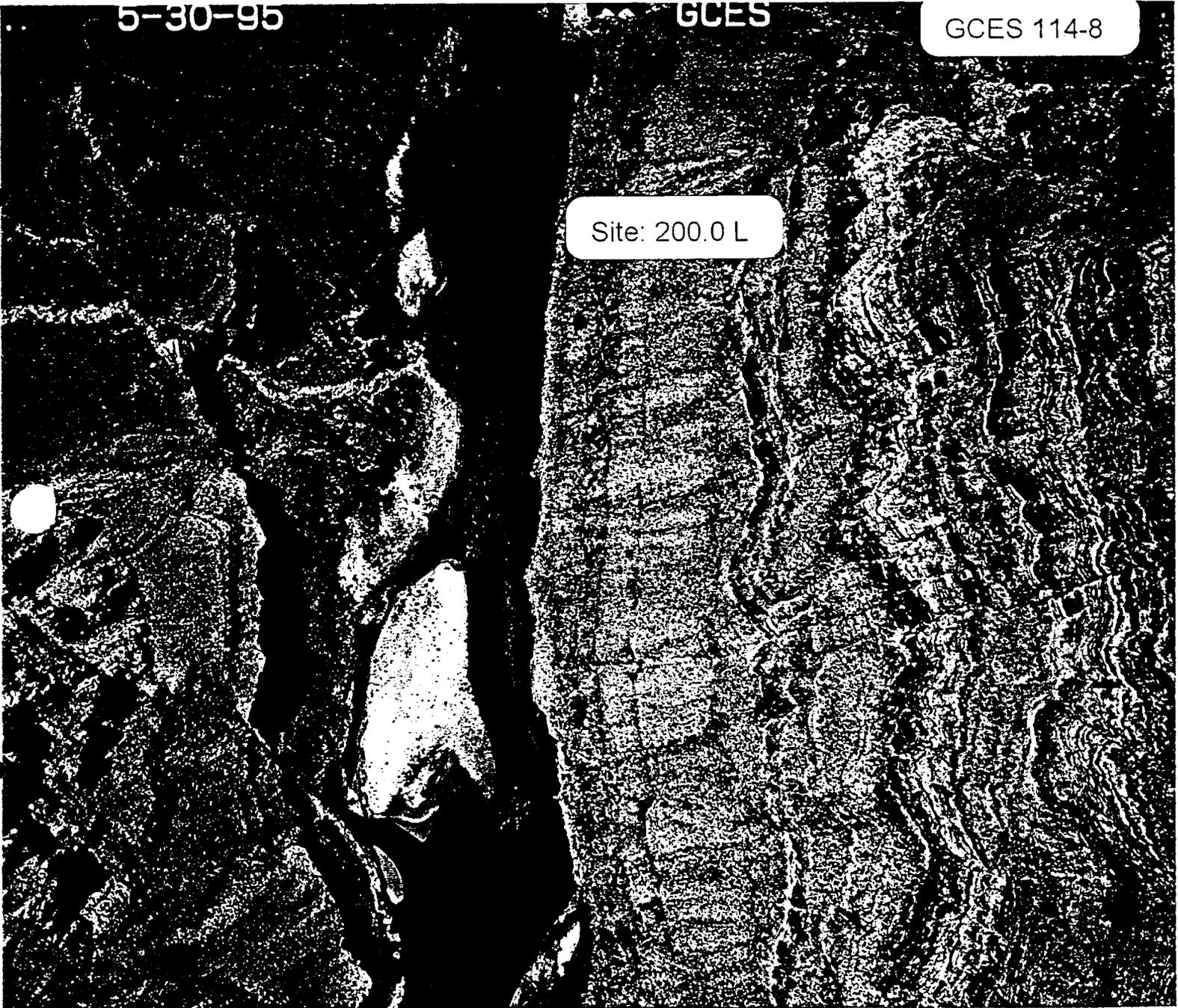
Site: 199.5 R

5-30-95

GCES

GCES 114-8

Site: 200.0 L



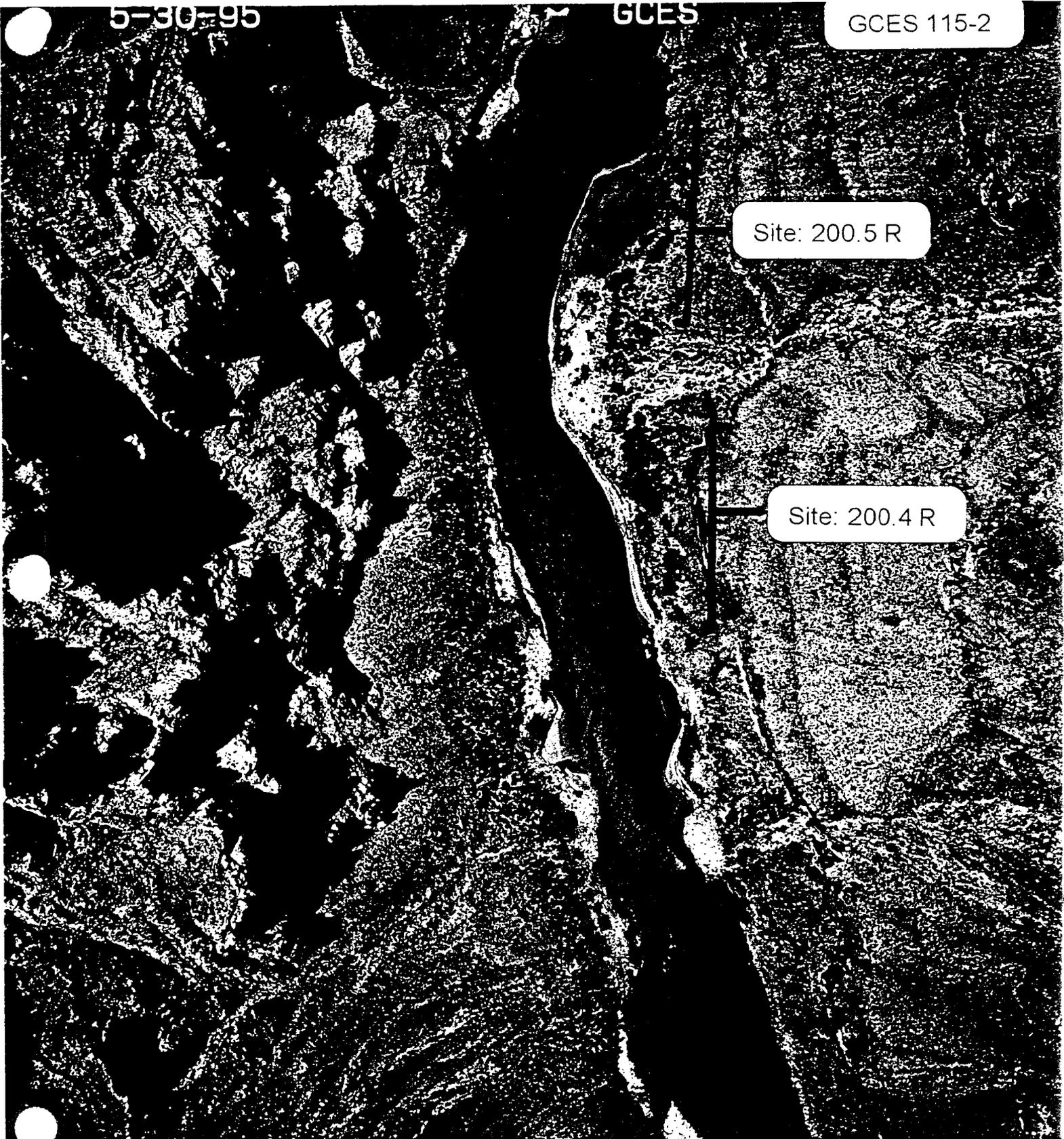
5-30-95

GCES

GCES 115-2

Site: 200.5 R

Site: 200.4 R

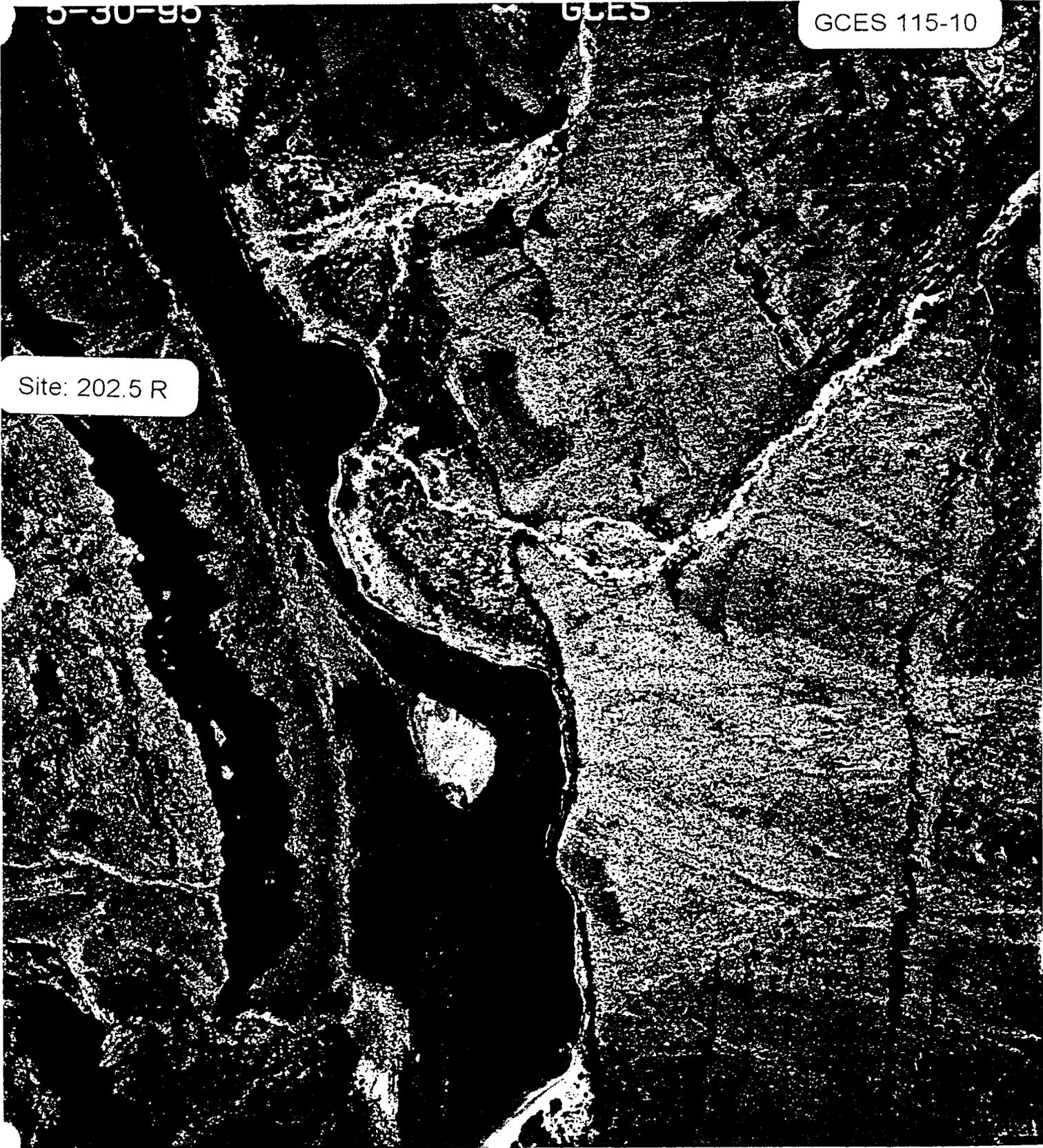


5-30-95

GCES

GCES 115-10

Site: 202.5 R

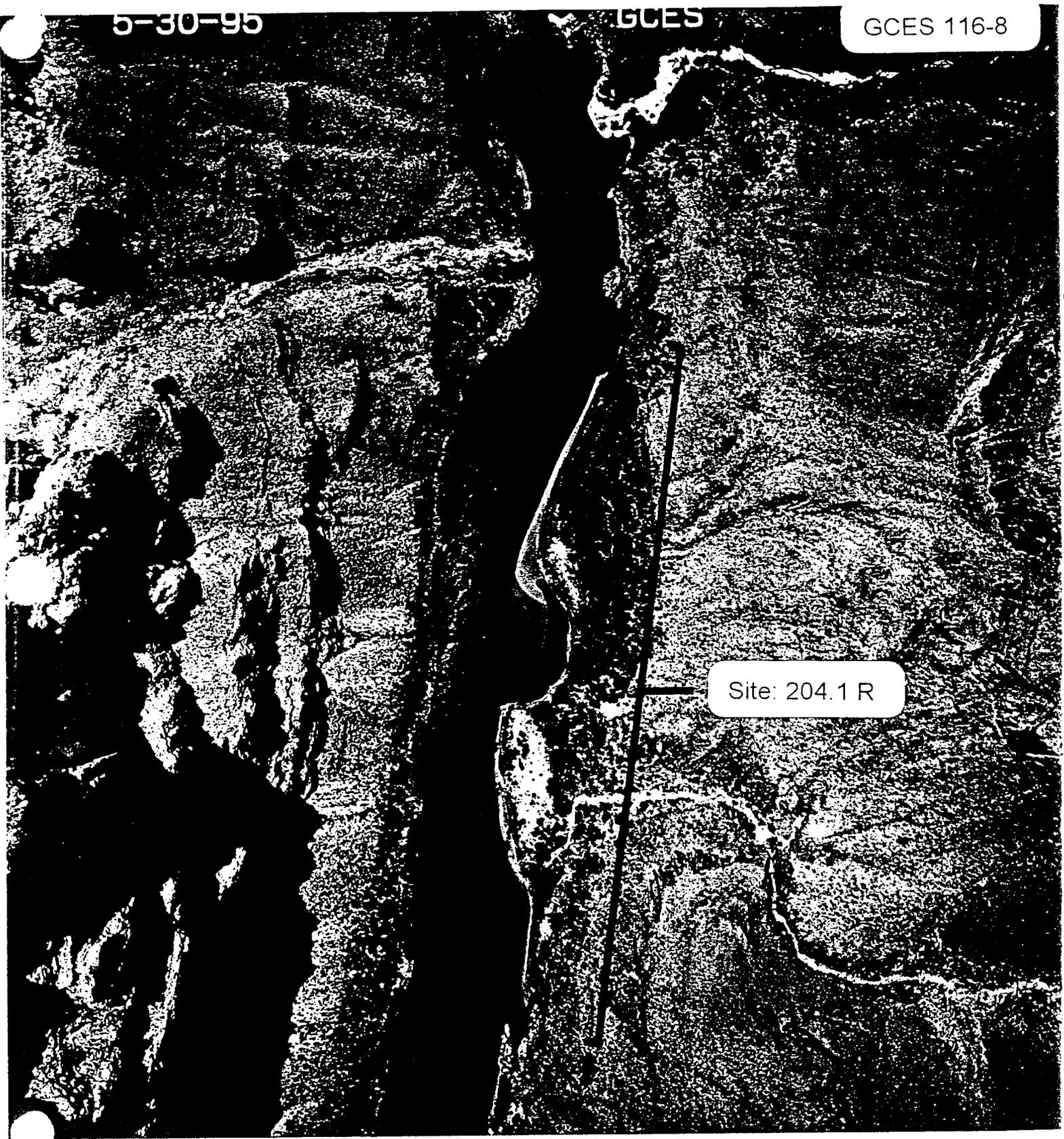


5-30-95

GCES

GCES 116-8

Site: 204.1 R



5-30-95

GCES

GCES 116-10

Site: 204.5 R

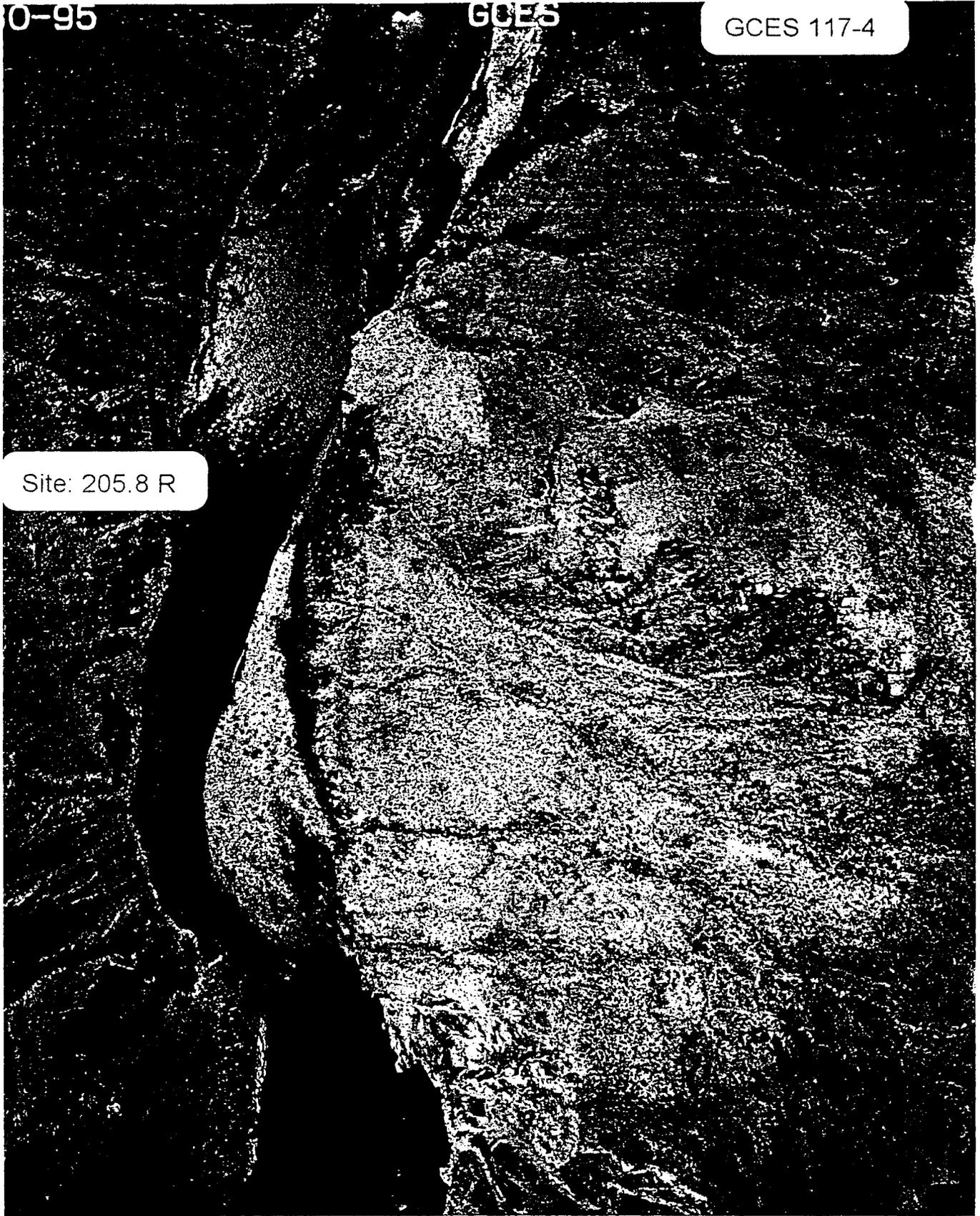
(SPRING)

0-95

GCES

GCES 117-4

Site: 205.8 R



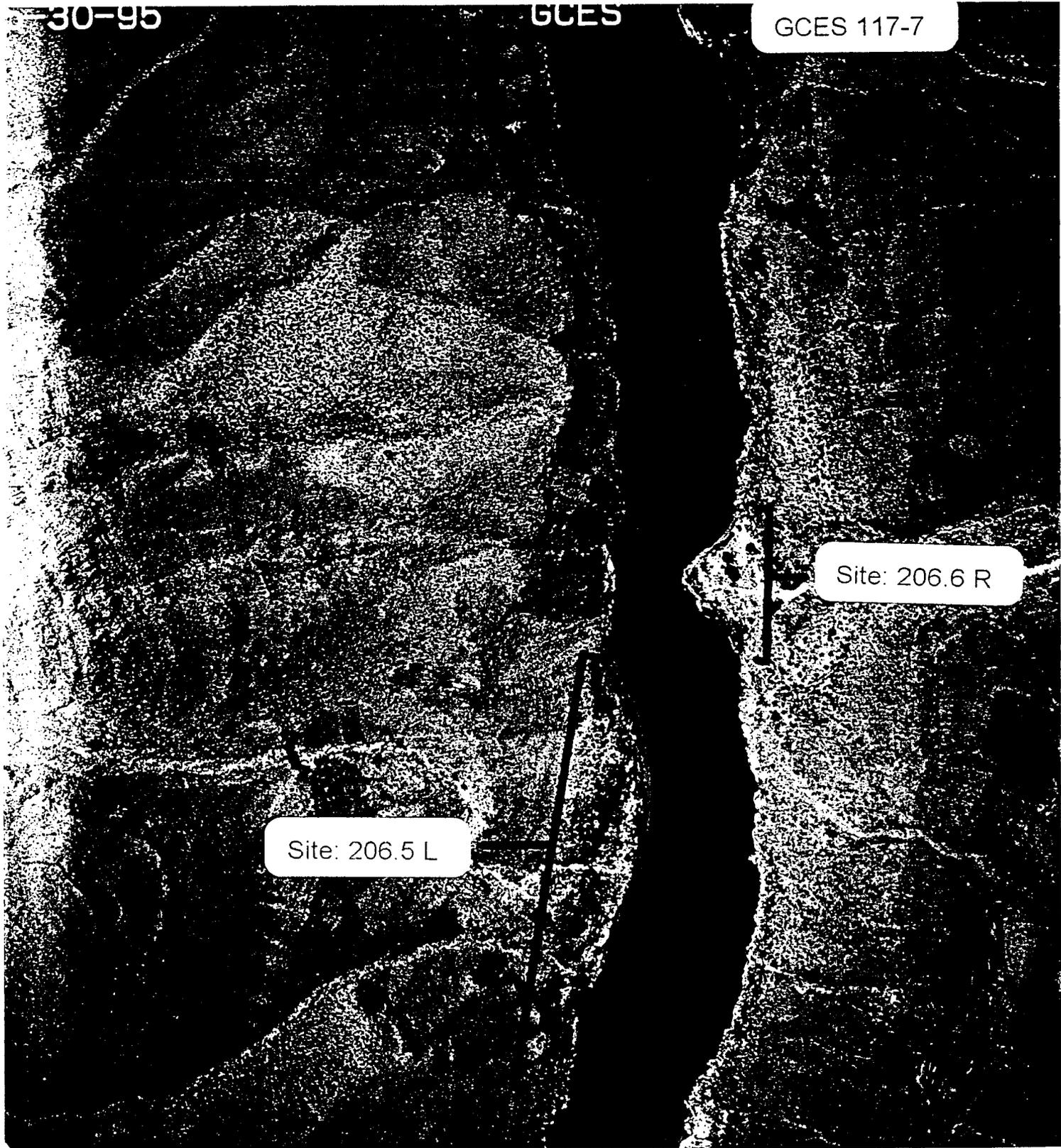
30-95

GCES

GCES 117-7

Site: 206.5 L

Site: 206.6 R

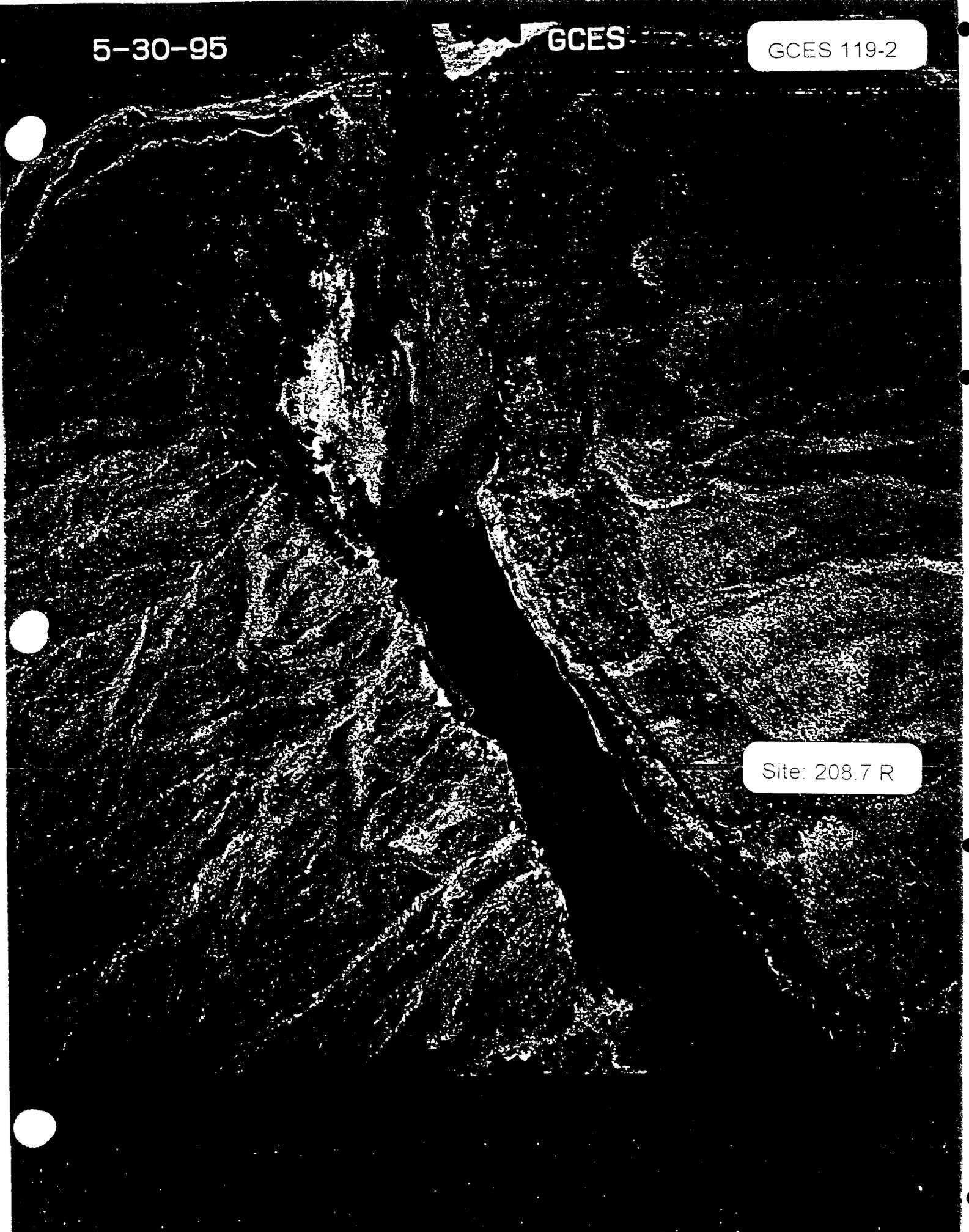


5-30-95

GCES

GCES 119-2

Site: 208.7 R

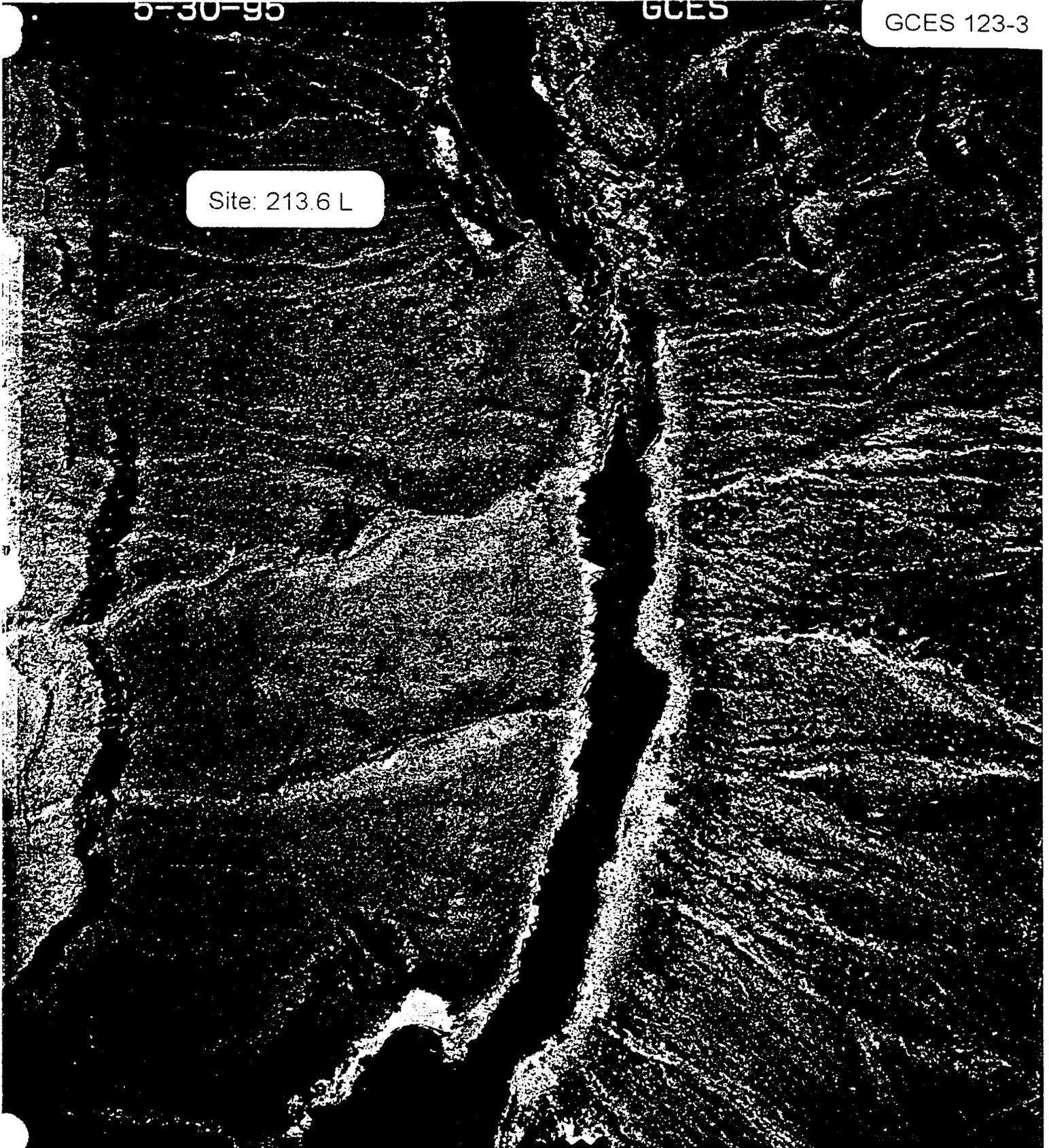


5-30-95

GCES

GCES 123-3

Site: 213.6 L



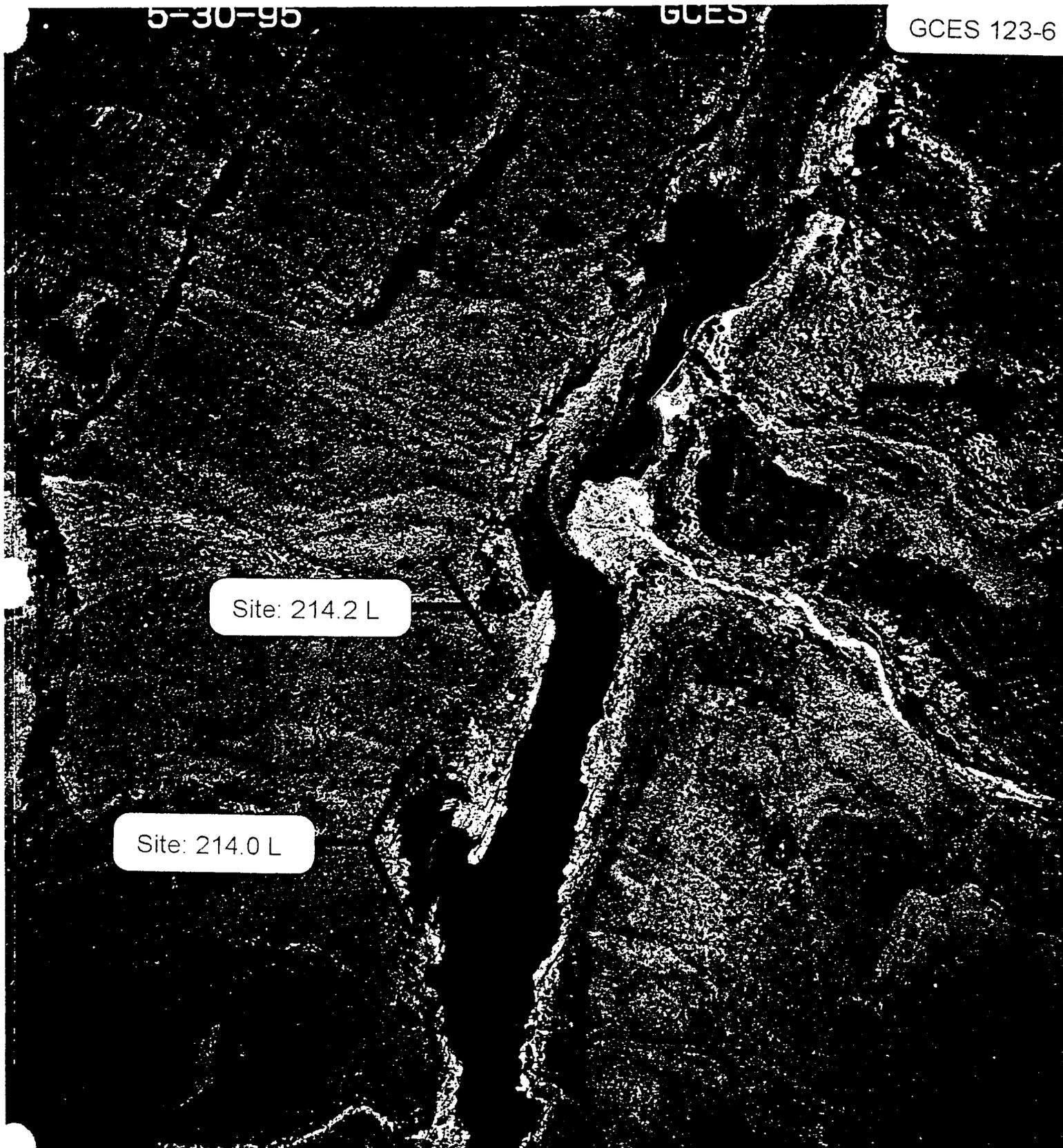
5-30-95

GCES 7

GCES 123-6

Site: 214.2 L

Site: 214.0 L



5-30-95

GCES

GCES 127-8

Site: 224.0 L

Site: 224.1 R

