



Cooperative National Park Resources Studies Unit

ARIZONA

STATUS AND NESTING HABITAT REQUIREMENTS
OF BELL'S VIREO ALONG THE COLORADO RIVER IN
GRAND CANYON NATIONAL PARK, ARIZONA:
A PRELIMINARY REPORT

Bryan T. Brown and R. Roy Johnson

University of Arizona
Tucson, Arizona 85721

Western Region
National Park Service
Department of the Interior
San Francisco, Ca. 94102

COOPERATIVE NATIONAL PARK RESOURCES STUDIES UNIT

University of Arizona/Tucson - National Park Service

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ABSTRACT

The status, distribution, and habitat requirements of Bell's Vireo (Vireo bellii) along the Colorado River corridor in Grand Canyon National Park were identified during field work in the spring of 1982. Habitat requirements were determined at 0.1 acre (0.04 ha) circles centered at nests and in adjacent random control areas. Bell's Vireo is a common summer resident along the river below National Canyon, and is a rare breeder upriver to Mile 43. Mean nest height (N = 40) is 118 cm, with 80% of nests occurring in the introduced shrub, salt cedar (Tamarix chinensis). Significantly higher foliage volume, numbers of salt cedar shrubs, and total shrub stem counts occur in vireo nesting habitat compared to adjacent control areas. Vireo nests tend to be placed on tiny limbs of smaller shrubs that are located within 5 m of an open edge. Parasitism by Brown-headed Cowbirds (Molothrus ater) was noted in 5% of 1982 active nests (N = 22). The ecological mechanism behind the preference shown by vireos for salt cedar is unclear. Recommendations to management and plans for future research are outlined.

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INTRODUCTION

Bell's Vireo (Vireo bellii) is a small insectivore whose breeding range extends across the southern United States and northern Mexico from Indiana and Texas to California. In Arizona, Bell's Vireo reaches the northern limit of its lowland breeding range in the Grand Canyon region and along the Virgin River. The species has recently expanded its range upriver to Mile 43 (Brown et al. in prep). Formerly it bred along the Colorado River in Grand Canyon only as far upstream as Whitmore Wash (River Mile 188; River Miles measured downstream from Lees Ferry, River Mile 0). This range expansion seems to be related to vegetation changes along the Colorado River as a result of Glen Canyon Dam.

In the arid Southwest, Bell's Vireo exhibits a marked preference for dense riparian vegetation in which to breed (Bent 1950). This riparian dependence has, in part, been responsible for a decline in vireo numbers in Arizona and California as much riparian habitat has been lost to urbanization, phreatophyte control, agriculture, and water storage projects. An equally important factor causing the decline in some areas is brood parasitism by Brown-headed Cowbirds (Molothrus ater). Cowbird nest parasitism reduces vireo nesting success, an impact which has been documented by Goldwasser (1978) and Goldwasser et al. (1980). In California, vireo numbers have been so reduced that the subspecies there is now on the state endangered list. Bell's Vireo appears to be doing well in Arrizona, although it has sometimes been locally eliminated (Phillips et al. 1964, Rea 1977, Rosenberg et al. 1982). The Colorado River in Grand Canyon represents the best documented instance of recent Bell's Vireo range expansion and associated increase in numbers in the Southwest. This portion of the Colorado River, to our knowledge, is the only major segment of a southwestern river where riparian vegetation has actually increased in contrast to the general loss and degradation of riparian habitat throughout the Southwest (Johnson et al. 1977, Johnson 1978).

The Least Bell's Vireo (V. b. pusillus) in California has received much scientific attention due to its endangered status (Goldwasser 1978, 1981; Goldwasser et al. 1980; Salata 1980, 1981; Gray and Greaves in press). There, Bell's Vireo preferentially nests in dense riparian areas characterized by a willow (Salix spp.) dominated understory. Generally, cowbird parasitism is high, nesting success is low, and large tracts of apparently suitable habitat are unoccupied (Goldwasser et al. 1980).

In Arizona, Bell's Vireo (V. b. arizonae) research has been scanty, limited primarily to the extensively-modified Lower Colorado River (California side) (Barlow/^{et al.}1970, Edwards 1980, Serena in press). Here, vireos prefer dense stands of willow (Salix goodingii) and honey mesquite (Prosopis glandulosa), while apparently selecting against salt cedar (Tamarix chinensis) and arrowweed (Tessaria sericea). Cowbird parasitism is high, nesting success low, and areas of apparently suitable habitat are unoccupied (Serena in press).

This study was undertaken in response to the need to document Bell's Vireo nesting habitat requirements in Arizona; to determine the present range and density of vireos in the Grand Canyon region; and to identify the present rate of cowbird parasitism. The purpose of this study is to report on Bell's Vireo breeding ecology and nesting habitat requirements along the Colorado River corridor in Grand Canyon National Park for the 1982 nesting season. Individual objectives are:

1. Determine the present range and density of nesting vireos.
2. Document nesting habitat requirements.
3. Identify the present rate of cowbird parasitism.

This is part of a proposed three-year study to determine the nesting habitat requirements of the entire obligate riparian breeding bird community along the Colorado River and the effects of the operation of Glen Canyon Dam on the

riparian avifauna of the Grand Canyon. The information generated by this study will identify the extent to which Bell's Vireo and other obligate riparian birds have adapted to the new habitat created by Glen Canyon Dam and how future activities of the dam might influence their habitat and status in the region.

STUDY AREA

The area encompassed by this study includes only that portion of the Colorado River corridor in Grand Canyon National Park which is at or below the pre-1963 high-water flood zone. This extends from Lees Ferry (River Mile 0) to the mouth of Diamond Creek (River Mile 225). This does not include those tributaries or side canyons which are away from the zone of influence of the river. The elevational range of the study area is from 3000 ft (950 m) at Lees Ferry to 1300 ft (395 m) at Diamond Creek.

Prior to 1963, floods in excess of 300,000 cubic feet/second (cfs) (Dolan et al. 1974) effectively scoured the riverbanks of virtually all but annual vegetation. The only perennial riparian vegetation occurring in this regime existed as small, narrow, disjunct stands of honey mesquite (Prosopis glandulosa), catclaw acacia (Acacia greggii), and Apache-plume (Fallugia paradoxa) at the pre-dam high-water line. Relict areas of this vegetation type persist today along the river.

Glen Canyon Dam, located on the Colorado River 15 miles (24 km) upstream of Lees Ferry (farthest upstream point of Grand Canyon National Park), was completed in 1963, reducing peak river flows to approximately 30,000 cfs. The elimination of flooding allowed a dense and extensive riparian scrubland and occasional woodland to develop in the pre-dam flood zone (Carothers and Johnson 1975, Turner and Karpiscak 1980). The present vegetation is composed largely of introduced shrub salt cedar (Tamarix chinensis) as well as native shrubs including arrowweed (Tessaria sericea), coyote and Gooding's willow (Salix exigua,

S. goodingii), desert broom and seep willow (Baccharis spp.), and honey mesquite. These shrubs form a dense, closed canopy scrubland of low stature (usually less than 25 ft/8 m) which occurs in a complex mosaic pattern of intertwined monotypic stands up to 1000 ft (300 m) in width. Homogenously-mixed stands are rare. The corridor of riparian habitat, however, is interrupted in places by sheer canyon walls.

The adjacent upland vegetation, composed of elements of both Mohave and Sonoran desertscrub (Brown, Lowe, and Pase 1980; Warren et al. 1982) contrasts with the relatively lush riparian zone. Principal species of this arid, warm desert upland vegetation include: white bursage (Ambrosia dumosa), ocotillo (Fouquieria splendens), snakeweed (Gutierrezia sarothrae), creosote-bush (Larrea tridentata), Lycium spp., and brittlebush (Encilia farinosa). Upland vegetation occurs on steep talus slopes that extend almost to the river's edge, or on adjacent cliff ledges.

METHODS

Relative population density estimates were obtained after the methods of Bull (1981). Singing males were counted and their locations noted during three 18-day, oar-powered raft trips between April 15 and June 27, 1982. Counts were made between 0700 and 1600 hours, after which time male vocal activity virtually ceased.

Nests were located either by following individual birds through their territory or by coordinated, systematic searches involving up to six investigators. The latter ensured a random sample of nests in all habitat types. Upon finding a nest, circles of 0.1 acre (0.04 ha) were centered at the nest and at an adjacent, randomly-selected control site and the habitat measured after the method of James and Shugart (1970) and James (1971). An exception to this

method was in the recording of shrub stem counts. Shrub stems encountered in two armlength transects across the circle were recorded as the number of stems per individual plant of a given species, as opposed to just a total count for shrub stems. This results in information on the relative contribution of each species to the total shrub stem density, as well as indicating the relative proportion of each shrub species at the nest site.

Additional data collected included: height, diameter-breast-high (dbh), and species of nest substrate plant; height and dbh of the four adjacent plants; nest height above ground; diameter of nest substrate limb(s); presence of cowbird parasitism; date and location; evidence of predation; number and/or age of eggs and young; width of riparian zone at nest; distance from nest to water; distance from nest to nearest open edge; and length of open edge in the paired habitat circles.

Relative foliage volume (foliage density) was measured after the method of Maurer and Whitmore (1981). Here, the presence or absence of vegetation (live or dead material) is recorded in successive 0.5 m intervals (or horizontal layers) from 0 to 3 m in height at 20 dimensionless points in the 0.1 acre paired circles. The 20 points are arranged along the four compass directions going out from the center of the circle, five equidistant points per direction, resulting in a random sample of foliage volume. Results are expressed as the estimated percent of volume per horizontal layer (0 to 0.5 m, 0.5 to 1 m, etc.).

Control habitat circles (0.1 acre) were centered at random at distances of 20 to 35 m from the nest in one of the four compass directions. It was important that control circles be adjacent to the nest, or nearly so, and also that they be within the riparian zone. Randomly-selected compass directions that would have placed the control circles outside of the riparian zone into water or upland vegetation were eliminated from the selection process. However,

control circles occasionally located entirely or partly in grassy openings or camping areas within the riparian zone were considered valid.

Paired (nest and control) habitat circles were compared for the following parameters: foliage volume, relative proportion of shrub species and stems/species, length of edge in circle, ground and canopy cover, and maximum canopy height. These comparisons were made by analysis of variance.

Canopy is defined as overstory vegetation above 8 m. An open edge is a vertical structural break between a dense vegetation type and an open area and/or open vegetation type.

RESULTS AND DISCUSSION

Relative Abundance and Distribution

Bell's Vireo males are conspicuously vocal (Bent 1950), the function of their song being to maintain their territorial system (Barlow 1962). Thus, in a linear and relatively narrow study area, the most efficient census method is to count spontaneous singing males and use this as an index of relative abundance. The resulting index must be viewed as a minimum population estimate, as several factors may preclude a totally accurate count of singing males. These include: the noise of rapids, passing motorboats, and wind, which can prevent the observer from hearing the song; inclement weather, which may prevent the male from singing; and normal variation in the rate of vocalization, which would allow the observer to float past a male while it is in a short non-singing interval. In addition, male Red-eyed Vireos fall silent for several days immediately following pair formation (Lawrence 1953), and the same may be true for Bell's Vireo.

A total of 135 singing male Bell's Vireos were counted during the April 1982 census (Table 1), a figure which should be taken as the minimum number of male vireos along the river corridor. As each male theoretically represents a

Table 1. Locations of singing male Bell's Vireos along the Colorado River in Grand Canyon National Park, Spring 1982. Singing males were counted and the location of each was recorded during three 18-day oar-powered raft research trips; each location represents one singing male unless noted otherwise.

15 April to 2 May 1982	10 May to 27 May	10 June to 27 June
<u>Lees Ferry to Phantom Ranch</u>		
	54.5R	43.0L
	55.2L	55.2R
71.1L - (3)	71.1L - (3+)	71.1L - (1)
		72.1L
<u>Phantom Ranch to Havasu Creek</u>		
		142.0 [±] L
<u>Havasu Creek to National Canyon</u>		
166.0R	166.0(L or R?)	166.0R
166.1R		
166.2R		
<u>National Canyon to Fern Glen</u>		
167.3R		
167.7L	167.8R	
167.8L	167.8L	167.8L
167.9R	167.9R	
<u>Fern Glen to Mohawk Canyon</u>		
168.6L		
169.0R	169.0R	168.9L
169.1R	169.0L	169.1L
169.4L	169.05R	169.2R
169.5R		169.3R
170.1L		170.0L
170.2L	170.4L	170.6L
170.8L	170.8R	170.65L
170.9R	170.85R	
171.2R	170.9R	
<u>Mohawk Canyon to Cove Canyon</u>		
171.7R		171.5 to 172.0 (5)
172.3L		172.0L
172.8R	172.8R	172.1L
172.8L	172.8L	172.8L

Table 1. Continued.

15 April to 2 May 1982	10 May to 27 May	10 June to 27 June
<u>Mohawk Canyon to Cove Canyon (continued)</u>		
173.0L	173.1L	173.1L
173.0R	173.1R	
174.0R	173.9L	
174.1R		174.1R
174.1L		
<u>Cove Canyon to Lava Falls</u>		
175.5R	176.4R	175.8R
176.5 ⁺ R	176.5R	177.6L
176.6 ⁺ R	177.2L	177.7R
178.5L	177.3L	178.1R
178.5R	177.3R	178.2L
178.6R	177.4L	178.4R
178.65R	178.5R	178.5L
178.8L	178.7R	178.7R
178.9R	179.0R	178.9R
178.9L	178.9R - 179.0R - (3)	178.9L
179.0R		179.1L
179.0L		179.2L
179.2R		179.3L
<u>Lava Falls to 194-Mile Canyon</u>		
181.8L	182.0R	181.5L
181.8R	183.1R	182.5L
184.3L	183.1L	182.6L
184.4L	183.2L	183.3L
184.1L	186.7L	184.0L
185.2R	186.8R	186.7L
185.8R	187.6R	186.8L
185.9R	187.65R	187.6R
186.1L	187.7R	
186.7R	188.0R - (3+)	188.0R - (4)
186.9L	191.2R	
187.6R	191.3L	
187.7R	191.35 (R or L?)	
187.75R	191.4R	
187.8R	191.9L	191.9L
187.8L	192.4L	
187.9L	192.4R	
192.1L	192.5R	
192.1-192.5 - (4)	192.7L	
192.5R	193.1R	

Table 1. Continued.

15 April to 2 May 1982	10 May to 27 May	10 June to 27 June
<u>Lava Falls to 194-Mile Canyon (continued)</u>		
192.6L	193.4R	
193.2R	193.6L	
193.6L	194.2L	
194.3L	194.3L	
194.8L	194.6L	
<u>194-Mile Canyon to Parashont Canyon</u>		
196.0R	195.2L	
197.1R	196.6R	
197.15R	196.9R	196.8R
197.15L	197.0L	196.9R
197.1L	197.1R	197.1R
197.2L	197.15R	197.15R
197.3R		197.3L
197.35R		
197.4R	197.4L	
197.8R	197.5R	197.5R
197.85R	197.5L	197.55R
197.8L		
198.1R	198.1R	
198.1L		198.1L
198.15R		
198.2R		
198.2L	198.45R	
198.3L	198.5R	
<u>Parashont Canyon to Granite Park</u>		
198.35L	198.9L	
199.3L	198.8R	
199.5R	199.7L	
200.0L		
200.05L	200.1L	
200.2L	200.1R	
200.25L		
200.3L	200.3L	
200.5R	200.3R	
200.6L	200.7L	
200.9L	200.8L	
201.3L	201.0L	
203.3L	201.05L	
203.4L	201.05R	
203.8R	201.6L	
203.9L	201.7L	202.5L

Table 1. Continued.

15 April to 2 May 1982	10 May to 27 May	10 June to 27 June
<u>Parashont Canyon to Granite Park (continued)</u>		
204.1R	202.6R	202.7L
204.15R	202.8R	
204.1L	202.9L	
204.2R	203.0R	
204.4L	203.0L	
204.6R	203.1L	203.2R
204.9R	203.8L	203.4L
204.9L	204.0R	203.5L
205.0R	204.05R	203.5R
205.1L	204.0L	203.8L
205.2L	204.2R	203.9L
205.25L	204.4R	203.95L
205.3L	205.0R	203.95R
207.6L	205.0L	204.0L
207.9L		204.4R
		204.7L
208.0L		204.7R
208.5L-208.8L - (6)	208.5L-208.8L - (2+)	208.7L
208.7R	208.7R	208.7R
<u>Granite Park to Diamond Creek</u>		
	210.2L	
	211.2L	211.2L
212.9R	213.3L	212.9R
213.3L	225.6L	
215.1L		
224.5R		
224.7R		
224.9R		
225.4R		
225.5L		

L = river left, facing downstream
R = river right, facing downstream

pair (females do not sing), an equivalent number of pairs should be present. Counts in May and June revealed fewer singing males (107 and 76 respectively), an occurrence which is related to the higher temperatures experienced in those months, and hence a reluctance on the part of the males to maintain song frequency (Nice 1929, Barlow 1962). In addition, a natural decrease in territorial activity through time and the fact that males sing less after the young leave the nest account for the lower vocalization rate later in the season (Nice 1929). April appears to be the optimum census time for an accurate vireo population estimate.

An identical census of singing male vireos along the river corridor by oar-powered boat in April of 1976 revealed a total of 67 males (S. W. Carothers unpubl. data). The 135 singing males censused in April 1982 represent a doubling in numbers over the 1976 population level. This would indicate that vireo numbers have increased as a possible result of (1) continued expansion of vireos in the available habitat, an attempt to maximize vireo density per unit of habitat, or, (2) the continued development of the habitat itself since 1976 could have provided additional suitable areas into which the vireos have since expanded.

Vireo distribution is also indicated in Table 1. Vireos are rare above River Mile 166, with nesting above that point confirmed only at Miles 42.9L, 71.0L, and 71.1L (Table 2). Large tracts of apparently suitable habitat exist between River Miles 41 and 56, areas which are generally lacking in vireos. It may be that the upriver rate of vireo colonization and range expansion, which is apparently still taking place, has not yet succeeded in populating all favorable habitat, although this may happen in the future. Below National Canyon vireos are common, reaching their highest recorded density (seven singing males per linear mile of riverbank) in the well-developed habitat between River Mile 197.0 and Parashont Canyon (River Mile 198.4).

Table 2. Bell's Vireo known nest locations along the Colorado River in Grand Canyon National Park, 1982 nesting season.

Nests active during 1982 breeding season (N = 22)	Old nests found during 1982 breeding season that were 1 or more years old (N = 18)
42.9L - active #20	167.9R - old #19
71.0L - active #8	167.9R - old #3
71.1L - active #7	167.9R - old #4
167.8L - active #9	178.7R - old #6
167.9R - active #10	178.8R - old #5
178.7R - active #12	187.6R - old #7
178.9R - active #11	187.7R - old #8
187.5R - active #14	187.7R - old #9
187.6R - active #13	191.9L - old #16
198.5R - active #15	191.9L - old #17
204.0R - active #16	191.9L - old #18
204.4R - active #21	198.4R - old #10
208.5L - active #4	198.4R - old #11
208.7L - active #1	204.0R - old #12
208.7L - active #2	208.6L - old #2
208.7L - active #3	208.7L - old #1
208.7R - active #5	211.2L - old #13
211.2L - active #17	211.2L - old #14
211.2L - active #18	
211.2L - active #22	
213.3L - active #6	
225.6L - active #19	

Nesting Habitat Requirements

Nest substrate: Only three shrub species were chosen as nest substrates (Table 3). The majority of the total nests (80%) were placed in the introduced shrub salt cedar. Although salt cedar is a dominant component of the majority of territories sampled, native shrubs as potential nest sites are not lacking (pers. obs.). There appears to be some structural component of salt cedar which the vireos find attractive. Salt cedar has been present in Grand Canyon riparian systems since approximately 1930, although it has only achieved dominance along the river since the mid-1960's (Turner and Karpiscak 1980). The disproportionate use of salt cedar as a nesting substrate, and the adaptive significance of that use, were unexpected. Bell's Vireo research which identified nest substrate choice has occurred in areas where salt cedar does not occur (Goldwasser 1981, Salata 1981, Gray and Greaves in press). The studies of Edwards (1980) and Serena (in press) in Arizona do not identify nest substrate choice.

A small number of the total nests (7%) were found in honey mesquite. Although all habitat types were searched for nests in the approximate proportion of their overall occurrence, the sample may have been biased against nests in mesquite due to the dense, impenetrable, and thorny nature of mesquite stands. In several cases where it was possible to determine the exact boundaries of a vireo territory in which appeared dense stands of both salt cedar and mesquite, the nest was invariably located in salt cedar.

Habitat parameters at and around the nest: The mean and range of selected habitat parameters at the nest site are presented in Table 4. The results indicate a wide range of acceptance for most variables, with several exceptions: relatively small shrubs were generally chosen as nest substrate plants; nests were usually located close to an open edge, or break, in the vegetation structure; nests were always located on small limbs; and most nests were located less than

Table 3. Woody vegetation used as nest substrate plant for Bell's Vireo nests along the Colorado River in Grand Canyon National Park.

Species	1982 active nests only (N = 22)		Pre-1982 old nests only (N = 18)		Total (N = 40)	
	No. nests	%	No. nests	%	No. nests	%
Salt cedar	19	86	13	72	32	80
Arrowweed	1	5	4	22	5	13
Honey mesquite	2	9	1	6	3	7
Total	22	100	18	100	40	100

Table 4. Habitat parameters at and around Bell's Vireo nests along the Colorado River corridor in Grand Canyon.¹

Parameter	Sample size	Mean	Std. error of mean	Range
dbh of nest substrate plant (cm)	38	2.8	0.44	0-12
height of nest substrate plant (cm)	38	2.8	0.22	1-6
nest height above ground (cm)	38	118	7.10	51-295
distance of nest from trunk (cm)	35	40	7.05	0-145
diameter of nest placement limb(s)(mm)	36	4.2	0.24	1-10
distance to water from nest (m)	38	18	4.79	3-150
width riparian zone at nest (m)	38	50	11.16	8-300
distance to nearest open edge from nest (m)	38	5	0.51	1-13

¹Data for 22 active nests from 1982 breeding season and 16 old (pre-1982) nests (N = 38). Analysis of variance between 1982 season nests and pre-1982 nests indicated that there was no significant difference between the two groups for each of the above parameters.

1.2 m in height. The latter agrees with Goldwasser's (1981) California study in which the majority of the nests were found to be below 1.6 m in height, with a range of 0.2 to 3.6 m. Gray and Greaves (in press) refer to the proximity of nests to thicket edges, stating that nests are usually within 1 m of an open edge.

Comparison of nesting habitat to control habitat: No significant difference was found between nesting and control areas for the length of edge present, ground and canopy cover, and maximum canopy height (Table 5). The length of open edge in a given area, a potential indicator of increased diversity and productivity, was considered to be a variable that might influence nest site selection, but this was not the case. Ground and canopy cover were sparse in virtually all areas. The riparian vegetation along the river is so dense in most cases that annuals are deprived of sunlight, while the presence of an actual canopy (overstory vegetation above 8 m in height) was limited to only a few areas of older Gooding's willow and salt cedar. This is similar to the findings of Goldwasser (1981) and Gray and Greaves (in press).

A significantly greater volume of foliage occurs in nesting areas as compared to adjacent control areas (Table 6). This difference holds true for all of the height classes. The foliage volume difference exhibited above 3 m, however, may simply be an artifact of the particular growth form of salt cedar, which in the Grand Canyon typically exhibits dense foliage (living and dead plant material) from 0 to 5 m in height. Goldwasser (1981) noted that the presence of a dense understory (i.e., shrub layer) below 3 m to be the most important aspect of nesting habitat for Least Bell's Vireo in California. Gray and Greaves (in press), however, indicated that the Least Bell's Vireo does not seek out unusually dense stands of vegetation for nest placement. Results of our study do indicate that the total shrub stem count per acre is significantly greater in nest habitat

Table 5. Comparison of habitat parameters in Bell's vireo nesting habitat to control habitat.¹

Parameter	Habitat	Mean	Std. Dev. of mean	Range	N	Difference in nest/adjacent habitat
length of edge (m/0.04 ha)	nest	24	3.18	0-65	35	not significant
	control	30	3.80	0-64	29	
ground cover, in percent	nest	14	2.48	0-44	34	not significant
	control	12	1.69	0-35	34	
canopy cover, in percent	nest	0.44	0.25	0-5	34	not significant
	control	0.15	0.15	0-5	34	
maximum canopy height (m)	nest	5.3	0.19	4-7	29	not significant
	control	5.0	0.35	2-11	25	

¹Data for both 1982 season nests and old (pre-1982) nests. Analysis of variance between 1982 and pre-1982 nests indicated that there was no significant difference between the two groups for each of the above parameters, allowing their combination for an increased sample size.

Table 6. Comparison of foliage volume in Bell's Vireo nest habitat to control habitat.¹

Height classes	Habitat	Mean	Std. error of mean (%)	Range (%)	Differences in nest/ adjacent habitat
0-0.5 m	nest	74	3.15	30-100	significant, P < .01
	control	60	2.78	25-80	
0.5-1 m	nest	63	2.77	25-95	significant, P < .001
	control	46	2.96	15-80	
1-1.5 m	nest	60	2.62	15-88	significant, P < .001
	control	42	3.71	0-85	
1.5-2 m	nest	65	3.01	5-94	significant, P < .001
	control	38	3.53	0-85	
2-2.5 m	nest	56	2.96	10-100	significant, P < .001
	control	28	3.61	0-70	
2.5-3 m	nest	48	3.22	5-80	significant, P < .001
	control	22	3.73	0-65	
greater than 3 m	nest	45	4.30	5-85	significant, P < .001
	control	19	3.50	0-65	

¹Data for both 1982 season nests and old (pre-1982) nests (total N = 34). Analysis of variance between 1982 and pre-1982 nests indicated that there was no significant difference between the two groups for each of the above parameters, allowing their combination for an increased sample size.

compared to adjacent control habitat (Table 6), a finding shared with Goldwasser (1981).

The occurrence of various major riparian shrubs in nesting and control habitat is indicated in Table 7. Both the numbers of individuals and the number of shrub stems for all native shrubs showed no significant difference between nest and control areas, indicating that vireos do not seek out any native plant specifically for nesting purposes. Of particular interest is the significantly higher number of salt cedar individuals and shrub stems in nesting habitat. Though caution must be taken in interpreting this difference, it does appear as if the presence of dense stands of salt cedar are sought out and preferred over native shrubs. The exact mechanism causing this preference can only be surmised. Possibly vireos simply prefer the dense structural composition of salt cedar, which in addition to offering an abundance of horizontal twigs required for nesting attachment would provide a concealed nest site. Another possibility is that numerous clumps of leaf litter and debris located on limbs in salt cedar stands, clumps that superficially resemble nests, may provide an effective camouflage screen against which a vireo nest would not be prominent.

Salt Cedar as a Component of Bell's Vireo Habitat

The prominent role played by salt cedar in Bell's Vireo habitat along the Colorado River in Grand Canyon is an adaptation that requires further investigation. While it is apparent that vireos are using salt cedar to a greater extent than native shrubs for both nest sites and territory composition, the nature of this relationship is unclear. It is not possible to state that salt cedar provides preferred habitat unless it can be demonstrated that its use results in greater nesting success than native plants. It may be that an expanding vireo population has been literally forced into using salt cedar, which actually may not be preferred at all. Likewise, the greater proportion of salt cedar along the river

Table 7. Comparison of the occurrence of major riparian shrubs in Bell's Vireo nest habitat vs. control habitat, arranged in decreasing order of abundance.¹

Species	Parameter	Habitat	Mean	Std. error of mean	Range	Difference between nest/adjacent habitat
<u>Tamarix chinensis</u> (salt cedar)	No.	nest	70	7.88	0-177	significant, P < .001
	plants	control	26	4.55	0-136	
	No. stems	nest	532	50.45	0-1201	significant, P < .001
	per 0.1 acre	control	217	31.07	0-759	
<u>Tessaria sericea</u> (arrowweed)	No.	nest	73	13.85	0-313	not significant
	plants	control	62	10.00	0-182	
	No. stems	nest	209	33.19	0-593	not significant
	per 0.1 acre	control	209	37.52	0-704	
<u>Baccharis sarathroides/sergiloides</u> (desert broom)	No.	nest	15	2.97	0-62	not significant
	plants	control	21	4.33	0-79	
	No. stems	nest	123	26.03	0-649	not significant
	per 0.1 acre	control	150	28.93	0-526	
<u>Baccharis emoryi/glutinosa</u> (seep willow)	No.	nest	1	0.73	0-22	not significant
	plants	control	2	1.83	0-61	
	No. stems	nest	26	14.10	0-400	not significant
	per 0.1 acre	control	16	10.18	0-295	
<u>Salix exigua</u> (coyote willow)	No.	nest	1	0.39	0-10	not significant
	plants	control	1	0.27	0-6	
	No. stems	nest	2	1.15	0-30	not significant
	per 0.1 acre	control	2	1.01	0-29	
<u>Prosopis glandulosa</u> (honey mesquite)	No.	nest	1	0.32	0-10	not significant
	plants	control	1	0.30	0-9	
	No. stems	nest	20	14.99	0-508	not significant
	per 0.1 acre	control	28	14.03	0-328	
All species total shrub stem count	Total shrub count per acre ²	nest	8730	545	3550-12750	significant, P < .001
	control	6330	696	40-11950		

¹ Analysis of variance between 1982 and pre-1982 nests indicated that there was no significant difference between the two groups for each of the above parameters, allowing their combination for an increased sample size (N = 34). Woody plant species that were recorded in nest plots but whose mean occurrence was less than one individual per plot include: Salix goodingii, Acacia greggii, Haplopappus acradenius, Haplopappus spp., Chilopsis linearis, Larrea divaricata, Lycium spp.

² For this parameter, only 1982 nests compared (N = 20).

may simply determine its greater use, although this seems unlikely. This question could be partially answered by establishing the extent to which salt cedar is used as a foraging substrate, as well as its capability of providing sufficient insects to support nestlings and adults alike (as measured by nesting success).

Previous investigators, while in some instances identifying salt cedar as useful on some level to vireos, have implied that salt cedar is less valuable than native shrubs. Serena (in press) found that vireos apparently discriminated against both salt cedar and arrowweed for nesting purposes. She suggested that the sticky, salty exudate which is found on salt cedar may be objectionable to small birds in general; she also identified its salty foliage as an inferior food resource. In addition, she recommended removal of salt cedar and revegetation with native shrubs as a means of providing new optimal vireo nesting habitat. Along the Colorado River, salt cedar has been documented to exhibit a smaller insect biomass, and hence fewer avian insectivores, compared to the mean insect/insectivore biomass for all riparian communities combined (Cohan et al. 1978). Stevens (1976), however, found insect densities on blooming salt cedar to increase 600% over non-blooming plants, although neither was as high as the insect density on native plants. Anderson et al. (1977) likewise demonstrated that salt cedar generally was less useful to birds than native riparian communities. Bell's Vireo apparently used salt cedar when it was supplemented by willows during the breeding season along the lower Colorado River, but did not use it later in the summer (Cohan et al. 1977). Edwards (1980) reports that vireos may breed in areas where salt cedar occurs in combination with dense honey mesquite. Salt cedar dominated habitats are also apparently used for breeding in New Mexico and Texas, where Bell's Vireo is one of the most common breeding birds along the Rio Grande floodplain (Barlow 1977,

Wauer 1977, Serena in press). The use of large, pure stands of salt cedar is not reported in the literature. Our findings are consistent with the negative implication. Even if it is true that monotypic stands of salt cedar are less valuable to vireos, the incorporation of linear monotypic areas of salt cedar into a larger mosaic of native and non-native vegetation, such as occurs along the river in Grand Canyon, may prove useful as an added level of habitat diversity.

Brown-headed Cowbird Nest Parasitism

Only one nest of 22 (5%) active nests discovered in the 1982 breeding season contained a cowbird egg, with no young cowbirds observed. There was no evidence of vireo nest abandonment due to cowbird parasitism. Likewise, no ejected cowbird eggs were seen beneath vireo nests as reported in other areas with heavy cowbird parasitism (Goldwasser 1978, Serena in press).

The recent range expansion of cowbirds and their impact on vireo nesting success is outlined by Goldwasser (1978), Goldwasser et al. (1980), and Serena (in press). Over 50% of all nests found by Goldwasser (1978) and Serena (in press) were parasitized, while 7 to 17% of all nests found by Gray and Greaves (fide Serena in press) failed due to cowbird parasitism (exact percentage actually parasitized is unavailable).

The low incidence of vireo nest parasitism by cowbirds in Grand Canyon may be due to the relatively fewer numbers of cowbirds there, as compared to areas in California or Arizona where vireos have been eliminated (S. Goldwasser pers. comm.). In 1976, nine pairs of cowbirds were found between River Mile 0 and 225 (Carothers and Aitchison 1976). It may also be that cowbirds, as relative newcomers to the region, have not yet had time to develop a proper behavioral search-image for vireo nests (or any other nest) located in salt cedar in contrast to native plants (S. W. Carothers pers. comm.).

CONCLUSIONS AND RECOMMENDATIONS

Bell's Vireo has adapted well to current environmental conditions along the Colorado River in Grand Canyon National Park. The present population appears to be at a healthy level, having apparently doubled since 1976, and may still be expanding its range upriver. The introduced shrub salt cedar is a major component of preferred vireo habitat (dense riparian scrubland), and is likewise used heavily as a nest substrate. Cowbird parasitism on vireo nests is low, which may have played a role in allowing the initial vireo range expansion to occur.

The following critical points are made to management:

1. Salt cedar appears to be a valuable component of vireo habitat, and possibly that of other riparian species, and future salt cedar control or eradication efforts should be carefully examined.
2. Extreme high water releases from Glen Canyon Dam during the breeding season, especially when combined with spring floods down the Little Colorado or Paria Rivers, have the potential for flooding low-lying vireo (or other species') nests, which are located largely below 1.2 m in height. The potential for direct impacts of this sort on vireo nesting should be investigated.
3. Future censusing of vireo populations should be conducted during late April when male singing is at its peak.

ANTICIPATED FUTURE RESEARCH

Future work will focus on obtaining an adequate sample size of nests and nesting habitat for each species of the obligate riparian bird community along the Colorado River in Grand Canyon. This will be accomplished during the spring of 1983 and 1984. Analysis of the data within and among species will indicate

overall community organization based on structural habitat requirements, identifying key habitat components for each species or group of species.

This information will, in turn, show both the short- and long-term effects of Glen Canyon Dam on the obligate riparian bird community, when combined with data being generated elsewhere, in several ways. (1) The beneficial effects to birds of the creation of new habitat by Glen Canyon Dam will be documented. In effect, this will demonstrate the rate and extent of colonization of man-made habitat by birds. (2) Those important avian habitat requirements that might be lost or further modified due to erosion, sedimentation, or other changes resulting from current and proposed water release characteristics of Glen Canyon Dam will be identified. (3) By discovering the mean nest height placement for each species in the community, a model can be constructed of the impact of future water releases from the dam on nesting birds along the river. Creation of the model itself is dependent on the establishment of bench marks (by the Bureau of Reclamation or National Park Service) along the river at high-density breeding areas, in order to correlate water levels to nest placement.

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