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Ecology and Conservation of the Endangered Least Bell's Vireo

by

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Summary

At one time considered common, the least Bell's vireo (Vireo bellii pusillus) was distributed throughout the Central Valley and other low elevation riverine systems in California and Baja California, Mexico, but now has been extirpated from the majority of its breeding range. Habitat loss from agricultural, urban, and commercial developments, flood control and river channelization projects, livestock grazing, and other activities has severely restricted the vireo's range. Limited reproductive success of the vireo as the result of nest parasitism by the brown-headed cowbird (Molothrus ater) in concert with habitat loss has resulted in a decline in the overall vireo population to about 300 breeding pairs.

Extensive suitable riparian habitat for the least Bell's vireo must be secured and protected so that the population can increase and be maintained in perpetuity. Additional information on vireo population ecology, genetics, and biological requirements should be obtained and assessed to maximize reproduction. Demographic data will aid in determining the reproductive rate that is necessary to sustain the subspecies on a perpetual basis. High quality, early successional stage riparian woodland is essential for providing adequate nesting habitat. In areas with active cowbird control programs, vireo productivity apparently has been enhanced. An expansion of such efforts and a long-term commitment to cowbird control and vireo nest monitoring to remove cowbird eggs and young will be essential. Methods to reintroduce vireos into the Central Valley and other areas within the historical range that are presently unoccupied should be evaluated.

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Introduction

The least Bell's vireo (Vireo bellii pusillus) was once widespread and abundant throughout the Central Valley and other low elevation riverine valleys of California. Historically, its breeding range extended from the interior of northern California to northwestern Baja California, Mexico. In the last several decades it is believed to have been extirpated from the Sacramento and San Joaquin valleys and now is primarily distributed in coastal riverine systems in southern California and northwestern Baja California, Mexico.

Because of the depleted population and reduction in remaining habitat, the least Bell's vireo was listed as endangered by the California Fish and Game Commission on 27 June 1980, under the California Endangered Species Act of 1970. On 3 May 1985, the Fish and Wildlife Service proposed listing the least Bell's vireo as endangered and designating critical habitat. It was officially listed as endangered on 2 May 1986. No decision on the critical habitat aspects of the proposal has yet been made.

Description

The first account of the least Bell's vireo, written by J. G. Cooper (1861), was based on two specimens he collected in 1861 along the Mojave River near Manix in San Bernardino County, California. The original description of the least Bell's vireo (Coues 1866) stated,

"The color of the upper parts is a plain dull ashy gray on the head; tinged with grayish olivaceous on the rest of the upper parts. Above grayish ash, becoming more or less ashy olivaceous on the back; not more so on the rump than elsewhere. Below pure white, including under wing coverts; on the breast sometimes a faint suffusion of the lightest possible shade of brownish gray; sides under the wings moderately tinged with sulphur yellow. A narrow short superciliary streak; edges of eyelids, two bands on wings and narrow margins of outer border of wings and tail, dull white; on the latter tinged with olivaceous."

Taxonomy

Four subspecies of the Bell's vireo (A.O.U. 1957) have been recognized. All subspecies are apparently isolated from one another throughout the year (Hamilton 1962). The least Bell's vireo (Vireo bellii pusillus) breeds in California and northwestern Baja California, Mexico, and winters in southern Baja California. Vireo bellii bellii is found in the central United States from Colorado to Tennessee. Vireo bellii medius is distributed in southwestern Texas and eastern Mexico, and Vireo bellii arizonae occurs in Arizona, Utah, Nevada, California (along the Colorado River), and Sonora, Mexico. Although all subspecies are fairly similar in behavior and life history, they are segregated during the nesting season. Virtually all Bell's vireos winter in Mexico. Least Bell's vireos are believed to overwinter in southern Baja California, Mexico (R. Hutto, pers. comm., as cited in RECON [Regional Environmental Consultants] 1988).

Historical Distribution and Present Status

Historically, the least Bell's vireo was an abundant and widespread subspecies extending from interior northern California near Red Bluff (Tehama County) south through the Sacramento–San Joaquin valleys and Sierra Nevada foothills and in the Coast Ranges from Santa Clara County south to near San Fernando, Baja California, Mexico. Populations were also found in the Owens Valley, Death Valley, and at scattered oases and canyons throughout the Mojave Desert. Workers in the late 19th century and even as late as the 1940's invariably described the subspecies as common to abundant and conspicuous (Cooper 1861; Baird et al. 1874; Belding 1878; Fisher 1893; Anthony 1893, 1895; Grinnell and Swarth 1913; Grinnell and Storer 1924; Grinnell et al. 1930; Grinnell and Miller 1944). From these historical accounts it seems that the vireo was present in many numbers within virtually all suitable riparian areas.

Apparently the least Bell's vireo has been eliminated from the Sacramento and San Joaquin valleys, at one time the center of its breeding range (Figure). Presently, the known breeding range is restricted to two localities in the Salinas River Valley (Monterey and San Benito Counties, Roberson, pers. comm.), one locality along the Amargosa River (Inyo County), and to numerous small populations in southern California south of the Tehachapi Mountains (Table 1) and in northwestern Baja California, Mexico.

Widespread loss or degradation of riparian habitats and brood parasitism by the brown-headed cowbird (*Molothrus ater*) have resulted in the rapid reduction in numbers of least Bell's vireos. Beginning in 1910–20, brown-headed cowbirds increased dramatically in numbers (Grinnell and Miller 1944; Gaines 1974, 1977; Laymon 1987). During an intensive survey in 1973, no least Bell's vireos were found in formerly occupied habitat between Red Bluff, Tehama County, and Stockton, San Joaquin County (Gaines 1974). Various intensive surveys of virtually all potential breeding



Figure. Historical and present range of the least Bell's vireo (*Vireo bellii pusillus*).

		Sites ^a		Number of territorial males ^b		
County	1981–85	1986	1987	1981–85	1986	1987
San Benito	1			1		
Monterey	0	1	0	0	3	0
Inyo	0	1	1	0	2	2
San Bernardino	0	2	1	0	2	1
Santa Barbara	3	1	1	26	57	25
Ventura	1	1	1	5	8	1
Los Angeles	3	2	2	7	2	2
Orange	1	0	1	1	1	0
Riverside	8	7	6	29	36	33
San Diego	30	18	19	223	287	373
Total	47	33	32	292	398	440

Table 1. Distribution of territorial least Bell's vireos (Vireo bellii pusillus) by county.

^a Number of breeding localities.

^b Number of known territorial males. Note: If the area was surveyed in 1985 and no vireos were located, the 1985 figure (0) is used; otherwise the latest population figure obtained from 1981 to 1985 is used.

habitat in California have been conducted (Gaines 1977; Goldwasser 1978; Goldwasser et al. 1980; RECON 1986, 1988; Salata 1980, 1981, 1983a, 1983b, 1984, 1986, 1987; Collins et al. 1986; Dames & Moore 1987; Wier and Jones 1987; and unpublished Fish and Wildlife Service data). Least Bell's vireos have been reported from 46 of more than 150 former localities surveyed in the United States from 1977 through 1985. The latest field results from 1987 (RECON 1988) indicated that there were territorial males at 32 locations. Based on this information, the present breeding population status of the least Bell's vireo per county in California indicates that the birds are concentrated in San Diego, Santa Barbara, and Riverside Counties. The birds are rare and greatly localized in geographic range. The recent surveys in 1987 indicated that there are about 440 territorial males and 283 known breeding pairs in the United States (RECON 1988). A substantial proportion (26.7%) of territorial males are believed to be unpaired.

In 1980, Wilbur (1981) found 40 pairs distributed in six locations in Baja California, Mexico. Although he believed more birds were present than his incomplete survey indicated, habitat was nevertheless limited and susceptible to many of the same developmental pressures present in the United States. Of the eight historical Mexican locations, vireos were noted at five sites and one new location was described.

Life History

Reproductive Ecology

Breeding biology seems to be similar in many subspecies of Bell's vireo (Nolan 1960). Males arrive several days ahead of females and appear on the breeding range from mid-March to early April (Barlow 1962; Salata 1984). Male least Bell's vireos establish and defend a territory within which all reproductive activities are conducted, from pair formation to fledgling of young. In the Gibraltar Reservoir area, territory size was usually 0.4 to 1.6 ha (Gray and Greaves 1984). On the Prado Basin–Santa Ana River area, mean territory size was 0.58 ± 0.26 ha and ranged from 0.15 to 1.31 ha (Hays, pers. comm., as cited in RECON 1988). Territories on the Sweetwater River in 1986 averaged 0.76 ± 0.30 ha and ranged from 0.20 to 1.66 ha (RECON 1988).

Studies of banded and colored marked least Bell's vireos indicate that they are quite site tenacious as adults, with males often returning to the territory used the previous year (Salata 1983b). Juveniles are considerably more inclined to disperse. For example, in 1983, 31 of 50 birds banded the preceding year returned to the same nesting vicinity. As most passerine species have a high annual mortality, a reasonable estimate of first-year mortality is 75%, and mortality after that about 50%. If

mortality is similar in vircos, 13 to 25 of these birds would likely return. However, the return rate of 31, being much higher, implies that perhaps all of the birds that survived returned to the previous year's breeding area.

Once the pair bond is established, nest building commences in a few days. It is believed that the female selects the nest site, after which both members of the pair construct the nest—a process that usually takes 4-5 days (Pitelka and Koestner 1942; Barlow 1962).

On the Sweetwater River, the height of nests above the ground averaged 0.93 ± 0.40 m (n = 25). Along the San Diego River nests were placed, on the average, 1.31 ± 0.63 m (n = 24) from the ground. Similar measurements for the San Luis Rey River indicated nest heights of 1.06 ± 0.33 m (n = 16; RECON 1988). The average height of 226 nests recorded by Salata (1984) for the Santa Margarita River was 1.01 m, with a range of 0.25-2.36 m. The nests are usually near the edge of a thicket, providing the advantage of an unobstructed approach to the nest. However, selection of an edge for nest location has the disadvantage of increasing accessibility of predators to the nest and enhances the probability of detection.

Usually a horizontal or downsloping forked branch or horizontal parallel stem supports the nest. The compact nest is a cup-shaped structure composed of leaves, bark, willow catkins, spider webs, and other material. Vireos use forbs, shrubs, and trees for nesting (Gray and Greaves 1984). However, several plant species are used more than expected on the basis of their availability in the habitat. These include the California wild rose (*Rosa californica*) and coast live oak (*Quercus agrifolia*; Gray and Greaves 1984).

The average height of vegetation supporting vireo nests on the Sweetwater River was 3.18 ± 1.82 m (n = 29) and on the San Luis Rey River was 4.14 ± 2.37 m (n = 23). Vegetation was slightly higher on the San Diego River with nest trees being 5.01 ± 2.54 m (n = 21;RECON 1988).

Egg laying begins 1–2 days after nest completion. Three to five eggs are laid with a mean of four (Bent 1950). The mean clutch size was 3.4 of 196 nests examined in 1981–84 by Salata (1984).

Least Bell's vireos may produce two broods of young and occasionally up to four per season, although it is thought that most are capable of successfully raising only one brood (Fromer, pers. comm.). After the young from the first clutch have fledged, the pair may build or finish constructing another nest nearby. While the male cares for the fledglings, the female may attempt to produce and incubate another clutch (Greaves and Gray, pers. comm.).

Incubation requires about 14 days and both adults participate. Young are fed by both parents and fledge in about 10–12 days (Pitelka and Koestner 1942; Nolan 1960; Barlow 1962). Young may remain in the territory and are cared for by the adults perhaps as long as 40 days (Nolan 1960).

Most least Bell's vireos migrate from the breeding area from late July to late September (Salata 1983a, 1983b, 1984), although stragglers have been noted in October and November (McCaskie and Pugh 1965; McCaskie 1969). Occasionally individual birds may overwinter in the United States (McCaskie and Banks 1964; McCaskie 1970; Hays, pers. comm., 1985, 1986).

As shown in Table 2, nesting, hatching, and fledgling success values were consistently lower in studied areas that contain substantial degraded habitats (e.g., San Luis Rey, San Diego, and Sweetwater rivers) than in higher quality riparian woodlands (Santa Margarita and Santa Ynez rivers). The trend to higher productivity in unmodified areas was also reflected in data even when cowbird control and vireo nest monitoring programs were carried out in both the relatively unmodified and degraded habitats.

To examine the effects of land-use patterns, reproductive success of vireos was compared with the habitat type surrounding their territories (RECON 1986). Those selecting areas bordered by coastal sage scrub and grasslands tended to be more successful than those bordered by agricultural and urban areas. Those territories adjoining golf courses, campgrounds, and sand mines had significantly fewer successful pairs than those neighboring chaparral, coastal scrub oak, or grasslands (N = 45, $\chi^2 = 33.4$, df = 1, p < 0.001; RECON 1986).

Annual reproductive success may be defined as the number of fledglings produced per nesting pair (Table 2). Since 1982, reproductive success has varied from a low of 0.25 on the San Luis Rey River in 1984 (Jones 1985), to a high of 3.3 in 1986 at Gibraltar Reservoir–Santa Ynez River (RECON 1988).

Foraging Behavior and Diet

Most of the insect food composing the vireo's diet is obtained from the dense riparian vegetation it uses for nest sites and protection of young. A wide variety of insect types are eaten, including true bugs, beetles, grasshoppers, moths, and particularly caterpillars (Bent 1950). Apparently the least Bell's vireo eats more large insects, such as grasshoppers, than do other subspecies (Chapin 1925; Bent 1950).

Although most foraging – especially during the early to middle portion of the nesting season – occurs in the vicinity of the nest sites, vireos use neighboring plant communities later in the season. Moreover, vireos in the Gibraltar Reservoir area fed on insects found on numerous plant species in several different habitats (Gray and Greaves 1984; Keeney, pers. comm.). Salata (1983b) observed vireos foraging most frequently on willow (*Salix* spp.), usually within the riparian habitats, although he also detected occasional feeding in both oak woodland and adjacent chaparral on the Santa Margarita River. Of 31% of all vireo pairs along the Sweetwater River, one or both members were observed feeding at least once in nonriparian areas adjacent to their territories (Kus and Miner 1987). These birds traveled 3–61 m (average distance, 15.5 m), and 94% of the observations occurred less than 30 m from the edge of the riparian vegetation. Birds using the nonriparian areas tended to occupy the narrowest portions of the riparian habitat (Kus and Miner 1987).

It is apparent that vireos forage extensively in low and high shrub layers. Although foraging occurs throughout all levels of the vegetation profile, it appears concentrated at levels from the ground up to 4 m. In 1981–83, Salata (1983b) found that 69% (n = 131) of foraging observations were within this height range (mean foraging height, 3.7 m; range, 0.1–10.7 m). The mean height of plants (n = 100) used was 6.0 m (range, 0.9–13.7 m). Although both the low and high shrub layers are heavily used as foraging substrate, the low shrub layer is essential for providing nesting habitat. Hence it is crucial for vegetation in the breeding habitat to be continuous or nearly so to the ground.

Methods of obtaining prey include gleaning-picking prey from leaf or bark substrates (93%), hovering-removing prey from vegetation surfaces while fluttering in the air (30%), and hawking-aerial pursuit and capture of a volant prey item (2%; Salata 1983b). These values exceed 100% because more than one behavior may have been associated with each observation.

Habitat Requirements

Habitat needs of the least Bell's vireo during migration and in the wintering areas are unknown. Nor is there available information on the status of the subspecies or its habitat on the wintering grounds. Little is known about migration routes, behavior during migration, or behavior on the wintering grounds.

Usually the least Bell's vireo selects dense vegetation in riparian zones for nesting. Several plant communities are classified as riparian habitats. These include willow-cottonwood forest, oak woodland, shrubby thickets, and dry washes. Of 126 locations of California nests recorded in the literature and in museum records, 71 (56%) were in willows (*Salix* spp.) and 14 (11%) were in wild rose (*Rosa* spp.). The remaining nests were distributed among 20 other species of vines, shrubs, herbs, and trees. Bell's vireos in interior portions of the United States are far less dependent on willows for nest sites, which may reflect plant availability rather than an actual preference (Nice 1929; DuBois 1940; Pitelka and Koestner 1942;

Table 2. Hatching success, nesting success, fledging	ss, nesting succe	ess, fledging rate, an	d reproductive su	iccess ^a of the leas	rate, and reproductive success ^a of the least Bell's vireo (Vireo bellii pusillus).	pusillus).	
Location	Hatching (%)	Number of eggs laid	Nesting success	Fledging rate	Average number of fledglings per nesting pair and per successful pair	Year	Source
Santa Margarita River (Camp Pendleton)	33	247	84	64	2.08/2.78	1982	Salata (1983a)
Santa Margarita River	70	271	63	57	2.85/3.21	1983	Salata (1983b)
Santa Margarita River	57	197	59	59	1.60/2.24	1984	Salata (1984)
					2.70/	1986	RECON (1988)
					2.57/2.90	1987	Salata (1987)
Gibraltar Reservoir	62	238	38	36	1.98/3.27	1980	Gray and Greaves (1984)
Gibraltar Reservoir	56	262	42	35	1.90/2.84	1981	Gray and Greaves (1984)
					3.3/-	1986	RECON (1988)
San Luis Rey	19	32	18	9	0.25/1.0	1984	Jones (1985)
			23	1	1.0/-	1986	RECON (1986)
					1.2/-	1987	RECON (1988)
San Diego River	5	63	5	5	0.17/3.0	1984	Jones (1985)
			38	I	1.81/-	1986	RECON (1986)
					2.50/-	1987	RECON (1988)
Sweetwater River	33	57	22	16	0.50/225	1984	Jones (1985)
			69	I	2.9/-	1986	RECON (1986)
					1.7/-	1987	RECON (1988)
Santa Ana River					1.1/	1986	RECON (1988)
^a Hatching success = Number of eggs that hatch. Nesting success = Percent of nests with eggs that fledge at least one young. Fledging rate = Percent of eggs that produce fledglings. Reproductive success = Number of fledglings produced per breeding pair.	umber of eggs cent of nests w ant of eggs that = Number of f	that hatch. ith eggs that fledge produce fledglings fledglings produced	e at least one you d per breeding p.	ıng. air.			

Mumford 1952; Nolan 1960; Barlow 1962; Wiens 1963, as cited in Wilbur 1980).

In much of the range of the least Bell's vireo, the majority of dense, low-growing vegetation, often willows, is found along water courses. The frequent use of willows seems to be largely a function of their abundance (Wilbur 1980; Goldwasser 1981; Gray and Greaves 1984; Salata 1981, 1983a; RECON 1988). For example, on the Sweetwater River 54% of the nests (15 of 28) were in the most dominant shrub species and 18% (5 of 28) in the second most dominant. On the San Diego River 29% (7 of 24) and 25% (6 of 24) were in the two most common shrub species. On the San Luis Rey River the first and second most dominant shrubs contained 46% (10 of 22) and 27% (6 of 22), respectively, of the nests (RECON 1988).

In territories of least Bell's vireos, willows often dominate the canopy layer, with a mean canopy height of about 8 m (Salata 1983a). Because shrub stem density and foliage density in the 0–4-m zone were greater in areas with nesting least Bell's vireos than in areas without them, Salata (1983a) believed that a dense, shrubby layer near the ground was a critical component in the breeding habitat. Goldwasser's (1981) findings that the most critical structural component is the presence of a dense shrub layer from 0.6 to 3.0 m from the ground corresponds with the work of Salata (1983a) and Gray and Greaves (1984).

As determined from recent field data (RECON 1988) for southern California, vireo nest sites are most frequently located in stands between 5 and 10 years of age. Even though mature trees are present at many of the sites, the average age of willow vegetation in the immediate vicinity of most nests is between 4 and 7 years. When mature riparian woodland is selected, vireos nest in areas with a substantial robust understory of willows as well as other species (Goldwasser 1981). With the available information, it is not possible to say conclusively whether the vireo actually prefers vegetation between 5 and 10 years of age or whether its selection merely reflects the availability of vegetation of this age range in the area. Additional vegetational analyses of areas lacking nesting vireos would aid in answering this question. The ecosystem dynamics of scouring of vegetation by flooding and river meandering rejuvenates the "gallery," otherwise the old-age stands would persist and the tall canopy would continue to shade and reduce the understory. Therefore, it is apparent that riparian plant succession is an important influence in maintaining vireo habitat.

Vireos also may incorporate and even nest in very young riparian habitat. On the Sweetwater River in 1987, vireos nested and foraged in reestablishing riparian growth 1–2 years old (RECON 1988). Use of this young vegetation depends on the characteristics of the site.

A recent field analysis of vireo habitat structure and composition involved measuring habitat variables at sample points along the length of each drainage surveyed (RECON 1986). Although the results indicated substantial variability between the sites, sites occupied by vireos differed significantly from vacant sites in six of the seven characteristics sampled. Significant differences were found in width of the riparian belt, and in percent cover of aquatic vegetation, percent herbaceous cover, shrub cover, tree cover, and tree cover with shrub understory. No significant difference was observed in the length of the riparian belt variable. Birds tended to establish territories in sites with a particular habitat configuration, including small amounts of aquatic and herbaceous cover, large amounts of shrub and tree cover, and a large proportion of tree cover with shrub understory. The investigators (RECON 1986) concluded that their findings supported those of Salata (1981, 1983a, 1983b) and Goldwasser (1981) in that dense shrub cover and a high degree of understory development are the primary nesting habitat requirements.

In addition, factor analysis (a multivariate statistical technique) was performed on the habitat data and produced two factors, which together explained 50.7% of the total variance among all sites (RECON 1986). The percent shrub cover, percent tree cover, and proportion of tree cover with shrub understory variables constituted the first factor and accounted for about 33% of the variance. These variables were strongly and positively intercorrelated. A fourth variable, percent cover of open ground or herbaceous species also was contained in Factor 1, but was negatively correlated with the other three variables. The second factor explained the additional 18% of the variance and consisted of the riparian width and riparian length variables, which were positively correlated and negatively correlated with the percent cover of aquatic and emergent aquatic plant species (RECON 1986).

For each site individual scores on each of the two factors were then computed and the means compared for sites with and without vireos. Sites with vireos scored significantly higher on Factor 1 than those without, and significantly lower on Factor 2 (RECON 1986). Therefore, the findings using this statistical technique agree with the analysis of the individual variables. Apparently vireos select sites with large amounts of shrub and tree cover, a large degree of vertical stratification, and small amounts of aquatic and herbaceous cover.

Factors Affecting Population Levels

In 1944, the least Bell's vireo was regarded as "common, even locally abundant under favorable conditions of habitat," but in the "last fifteen years a noticeable decline has occurred in parts of southern California and in the Sacramento-San Joaquin Valley" (Grinnell and Miller 1944). Unfortunately the reduction in vireo numbers was not curtailed and has been attributed to nest parasitism by the brown-headed cowbird along with rapid and extensive loss and degradation of habitat.

Habitat Modifications

As the human population in California increased, riparian woodlands were initially cleared for agricultural purposes and for firewood. Winter flooding of bottomlands was reduced by constructing dikes and dams. Flood control projects and channelization of rivers further reduced available vireo habitat. The need for agricultural, industrial, and domestic water resulted in extensive dam construction. These activities inundated or removed large amounts of least Bell's vireo breeding habitat. Impounding water upstream and diverting water to canals and cropland lowered water tables downstream so that dense vegetation could not grow or was reduced. Livestock grazing destroyed the choice lower strata of vegetation preferred by the vireos (Overmire 1962). Similar activities have been observed in riparian habitat in Baja California (Short and Crossin 1967).

Historically, the Central Valley may have contained 60-80% of the original vireo population. However, more than 95% of historical riparian habitat in the Central Valley has been lost and the vireo is now extirpated there (Smith 1977). Similar habitat losses have also occurred throughout its remaining stronghold in southern California, and Baja California habitats are presently declining as well.

Because of these widespread habitat losses, remaining breeding birds are segregated into small, disjunct, widely dispersed subpopulations. In 1987, there were 283 breeding pairs of least Bell's vireos in the United States (RECON 1988). The six largest remaining subpopulations, the Sweetwater River (60 breeding pairs), San Diego River (21 breeding pairs), San Luis Rey River (33 breeding pairs), Prado Basin-Santa Ana River (20 breeding pairs), Santa Margarita River (98 breeding pairs), and Santa Ynez River-Gibraltar Reservoir (20 breeding pairs), represent about 89% of the total breeding pairs. Of the overall population of 440 territorial males, these six subpopulations contain 344 (78%). In 1987 a sizable portion (26.7%) of the territorial males appeared to be unpaired. Many of the subpopulations are threatened by a variety of projects associated with the increasing human population throughout the range of the vireo.

Biogeographic and insular ecological theories (Wilcox 1980) suggest that small (i.e., the 28 vireo subpopulations with less than 50 individuals), remnant populations (accounting for about 25–33% of the total population) are more vulnerable to extirpation than larger populations would be. All other factors being equal, if a given local

population is small and relatively isolated, the chances of extirpation are greater. Because of the relatively high mortality of most passerines, localized extirpations are likely even without natural or man-caused disasters to local habitats or the reduced vireo reproductive success attributed to cowbird nest parasitism.

Moreover, no other populations of vireos may be close enough or population recruitment at other breeding areas may be insufficient to repopulate extirpated populations in later years. Also, if local habitats are destroyed (e.g., by severe flooding such as occurred in southern California in 1978 and 1980), there may be no nearby habitat available to which vireos can disperse until destroyed riparian habitat regenerates. In such situations, vireos may be forced into habitats less suitable to their nesting and foraging requirements, resulting in heightened mortality, reduced reproductive success, and declining population numbers.

Cowbird Nest Parasitism

Regarded as a widespread nest parasite, the brown-headed cowbird, rather than constructing its own nest, lays its eggs in the nests of other species. It is often found in close association with livestock, presumably because the grazers flush insects that the cowbirds consume (Salata 1983a). Usually the cowbird lays one or two eggs per nest and may remove (or otherwise destroy) an equal number of the host's own eggs. Using this reproductive strategy, the cowbird is successful for a number of reasons. Eggs of brown-headed cowbirds are larger than those of most host species and usually hatch first because of a shorter incubation period. Because cowbird young are very aggressive and generally larger than the host's young, they have a competitive advantage over the host's young and continue to outcompete them for food and parental care. As the dominant nestlings, the cowbirds secure more than their share of food from the parents. In this scenario, the host's own young do not thrive and often not even one survives to fledge.

Brown-headed cowbirds have been documented using at least 130 bird species as hosts (Friedmann et al. 1977). With the exception of a few winter or vagrant records, brown-headed cowbirds were absent from most least Bell's vireo habitat before 1900, and apparently were very rare in the rest of it. An increase in irrigated agriculture and other anthropogenic factors provided new habitat and triggered an increase in cowbird range and numbers that has been described as "remarkable, in fact unparalleled by any of our native birds" (Willett 1933).

The first reported cowbird eggs in least Bell's vireo nests were discovered in 1907 (Linton 1908). Soon it was difficult to find nests of this species that had not been parasitized (Dawson 1923; Hanna 1928; Rowley 1930; Grinnell and Miller 1944; Goldwasser et al. 1980; Salata 1981). Many birds with a long association with cuckoos (*Cuculus* spp.), cowbirds (*Molothrus* spp.), and other brood parasites are able to recognize eggs of the parasites (O'Connor 1984). Unfortunately, because the least Bell's vireo was exposed to cowbird parasitism rather recently, it has not had the opportunity to adapt to this threat.

Not only is the vireo a relatively poor host because it does not fledge many cowbirds (Friedmann 1963), but parasitized nests are less successful in fledgling the host species than are nonparasitized nests (Laymon 1987). Yet vireo nests seem to be among the easiest to locate and may be favored if present.

Apparently, least Bell's vireos readily accept cowbird eggs. Salata (1983a) reported that during 1982 only 4 of 37 (11%) cowbird eggs were rejected and only 2 of 37 (5%) nests with cowbird eggs were abandoned by least Bell's vireos on Camp Pendleton in San Diego County.

Bell's vireos may be particularly vulnerable to parasitism during the second half of the breeding season (June–July) because by then many riparian birds are beyond the egg-laying stage, thus fewer potential hosts are available to the cowbirds (Salata 1983a). In the first half of the breeding season, cowbirds usually lay one egg per nest, but more than one egg per nest becomes more common during the second half of the vireo's breeding season (Salata 1983a).

Although the cowbird has been blamed for the vireo's decline in California (Tate 1981), cowbird parasitism may be symptomatic of the more crucial problem of habitat loss and degradation (Gray and Greaves 1984). For example, in degraded habitats which usually support only a small number of vireos, cowbirds are often abundant and are responsible for serious reductions in vireo productivity. Land-use patterns surrounding the riparian zone are also important. If only a small amount of cowbird habitat is available or no habitat is present, there should be little or no problem with nest parasitism (Laymon, pers. comm.)

Further, depressed productivity in the larger breeding populations of vireos may limit the opportunities for population dispersal into unoccupied habitats. It may be difficult to augment smaller populations or to expect founding pairs to successfully produce enough young to establish a new local population.

In 1983, an intensive cowbird trapping program was undertaken along the Santa Margarita River during which 244 cowbirds (157 males, 79 females, 8 immatures) were captured. Of the 86 vireo nests, only 9 (10%) indicated evidence of cowbird visitation. In contrast, in 1982 no cowbird trapping was undertaken and at least 44 of 93 nests (47%) were visited by cowbirds. Thus, the successful trapping program is credited with significantly increasing vireo productivity within the study area from 104 fledglings per 100 breeding adults in 1982 to 143 fledglings per 100 breeding adults in 1983 (Salata 1983b). On the Sweetwater River in 1986, extensive cowbird trapping was undertaken with a resulting low parasitism rate of 5% of all nests. Trapping continued in 1987, in which no nests were known to be parasitized (RECON 1988).

Reducing the adverse effects of cowbird nest parasitism was not solely dependent on a trapping program. Nest monitoring to detect cowbird eggs or young was also undertaken in 1986 and 1987 in certain areas. When cowbird eggs were removed, vireo productivity increased because many pairs then were able to successfully fledge vireo young (RECON 1986, 1988). If it is assumed that all nests containing cowbird young would have failed to fledge any vireos, then nest monitoring to remove cowbird eggs or young increased the number of successful nests by about 140% at the San Luis Rey site, 25% at the San Diego River site, and 6% at the Sweetwater River site in 1986 (RECON 1986). Further, on the San Diego River, 32% (6 of 19) of all pairs and 33% (13 of 40) of all nests were parasitized in 1986. Although the number of breeding pairs did not substantially increase from 1986 to 1987, reproductive success rose substantially to 2.5 fledglings per pair. It is believed this increased productivity was largely the result of continued efforts to remove cowbirds in the area (RECON 1988).

Assuming that only cowbird young fledge from a parasitized nest hatching cowbird eggs (Pitelka and Koestner 1942; Mumford 1952), production by least Bell's vireos in the above studies undoubtedly would have been significantly reduced if cowbird eggs and young had not been removed from vireo nests. Laymon (1987) concluded that with a 47% parasitism rate, a vireo population would become extinct in 18 years. Moreover, these results suggest that an active cowbird trapping program in conjunction with monitoring of vireo nests to eliminate cowbird eggs or young is an effective means of enhancing vireo reproductive success and, thereby, increasing population size.

Nest Predation

Unlike many other passerines, least Bell's vireos typically build their nests within 1 m of the ground, increasing the accessibility of the nest to terrestrial predators. Because male vireos may sing while on the nest, they may inadvertently attract the attention of passing predators. With the introduction of house pets, feral cats, and the surrounding of remnant breeding habitats by encroaching urban development, abnormally high predator densities sometimes occur. Fragmented, small habitats pose greater risks of predation than would larger, more natural habitats. Because predators often find nests during an "area concentrated search," the congregating of a population in a limited habitat increases its susceptibility to predation (Anderson and Wiklund 1978).

Signs of predation were noted at 50% of the nests (7 of 14) examined by Goldwasser (1980) in southern California. During 1982, Greaves (pers. comm.) detected evidence of predation in 42 of 102 nests (41%) in Gibraltar Reservoir. Eggs or young disappeared in 25 of 93 nests (27%) in 1982 and 27 of 86 nests (31%) in 1983 (Salata 1983a and 1983b, respectively). In 1984, predation rates for the San Luis Rey, San Diego, and Sweetwater rivers were 45%, 18%, and 22%, respectively (Jones 1985). Predators are believed to include the raccoon (Procyon lotor), Virginia opossum (Didelphis virginiana), coyote (Canis latrans), long-tailed weasel (Mustela frenata), dusky-footed woodrat (Neotoma fuscipes), deer mouse (Peromyscus maniculatus), house mouse (Mus musculus), rat (Rattus rattus), domestic cat (Felis domesticus), gopher snake (Pituophis melanoleucus), and perhaps other species.

Conservation Efforts

Status surveys of the least Bell's vireo in California and Baja California, and preliminary evaluation of local population dynamics and habitat preferences have been funded by the California Department of Fish and Game, California Department of Transportation, U.S. Fish and Wildlife Service, U.S. Forest Service, U.S. Marine Corps, Corps of Engineers, and Santa Barbara Audubon Society. Additional survey work and other studies have been funded by the State of California through the San Diego Association of Governments (RECON 1986, 1988), and private entities such as Home Capital Development Corporation.

A limited amount of cowbird control has been initiated by the U.S. Fish and Wildlife Service through Section 6 of the Endangered Species Act and migratory bird funding, and the California Department of Fish and Game in cooperation with local organizations. Other cowbird trapping has been the result of consultations between the U.S. Fish and Wildlife Service and the Federal Highway Administration (on behalf of the California Department of Transportation), Corps of Engineers, and other Federal agencies. Cowbird control and nest monitoring also have been funded by the U.S. Marine Corps, U.S. Forest Service, and San Diego Association of Governments.

In 1982, the U.S. Fish and Wildlife Service organized the Least Bell's Vireo Working Group, consisting of Federal, State, and local governments and private individuals, to promote interagency cooperation regarding conservation activities for the vireo. This group coordinates banding color schemes and band return results, collates yearly survey data including results of cowbird trapping and nest monitoring, and disseminates information on vireo management.

Management Considerations

Dispersal

On the basis of a limited number of banded vireos along the Santa Margarita River, Salata (1983a, 1983b) believed that vireos are site tenacious, with adults returning to the previous year's nesting area. One-year-old birds returning to initiate breeding for the first time tended to disperse from their natal area and be less site tenacious than the older adults. Obviously more data in this area are needed.

To assess dispersal patterns requires that vircos be individually marked, such as by banding. Field studies within and between the various drainages to observe marked birds will provide data on dispersal distances from natal nests of young birds, movement of territorial males and females from one season to the next, and seasonal movement as the nesting season progresses. The last item refers to possible movement of members of a pair after they finish using a nest and before initiation of a second or later clutch. If birds do not move more than a short distance from the territory used the previous year or the territory where they fledged, then natural recolonization probably will be slow and will rely on restoring nearby habitats.

Under normal circumstances, vireos should reoccupy nearby restored areas given the opportunity. However, whether or not this occurs depends on the tendency of vireos (both adults and young) to return to the vicinity of the territory used the previous year. Some dispersal is anticipated as populations expand. As previously stated, first-year vireos tend to disperse farther than older birds. From the limited data available, it seems that the vagility of juveniles will determine, in large part, whether the population expands naturally to recolonize areas and whether gene flow and genetic variability are enhanced in other subpopulations. Dispersal distance will be instrumental in determining the role of natural expansion in recovery. Should habitat not be available within the average dispersal distance, other means to augment or recolonize areas will be necessary. A better understanding of the factors influencing juvenile and adult dispersal, site tenacity, and recolonization is needed. Because nestlings have been color-banded on several watersheds for the last 2 years, data from these birds may eventually resolve some of these issues.

Population Dynamics

In populations with overlapping generations (such as those of vireos) the rate of increase will depend on fecundity and mortality, which varies depending on the age of the individuals in the population. Rates for age-specific mortality for the least Bell's vireo can be inferred from similar data on other small, migratory passerines. First-year mortality in vireos from natural causes would be expected to approximate 75%, whereas adult survival from year to year is estimated at about 50%. Limited field data on the Santa Margarita River appear to approximate the estimated rates based on returning banded birds; a mortality of 53% in adult birds and 76% between hatching and 1-year of age was calculated (Salata 1983b). Here again, additional field data are required.

As a reproductive strategy, individuals of a species with high mortality may find it advantageous to begin breeding as early as possible (for vireos, this means first-year birds) and produce a maximum number of eggs during the nesting season. Vireos are limited in clutch size to the number of eggs for which the pair can provide adequate care. Hence, increasing the number of eggs may be accomplished by renesting during the season (and by quickly renesting if a nest is lost to predation or abandoned because of cowbird parasitism or other causes). During the 1986 breeding season, unsuccessful pairs were known to initiate renesting as many as 4 times (RECON 1986). It has been postulated that because of time and energy limitations, two broods may be the maximum number that can be successfully fledged (RECON 1986).

Using equations for allometric regression, Calder (1984) summarized the relation between body mass and average adult mortality, maximum life span, life expectancy, and potential natural longevity. Regional Environmental Consultants (1986), using body weight estimates of 8 to 14 g for the least Bell's vireo, predicted life history characteristics. Life history models were

developed by using assumptions on mortality and natality. The proportion of banded birds that returned was assumed to reflect survival (and, hence, indicate mortality). Because some birds may have dispersed to different areas to breed, the actual mortality may have been less. Return rates for the Santa Margarita banded birds were 47% for adults and 24% for juveniles (birds hatched the previous year; Salata 1983b).

Because the mean number of young per clutch is 4, and it seems from the limited available data that at least some pairs may raise two clutches in a given breeding season, the maximum hypothetical natality per breeding pair is estimated at 8 per year. Natality rates have varied from 0 to 3.3 fledglings per breeding pair. The 3.3 was derived from the Santa Margarita River subpopulation in 1986 (RECON 1988) and as such may represent a reasonable figure for populations not under intensive pressure from cowbird parasitism. Those subpopulations under pressure from nest parasitism averaged about 1 fledgling per pair (RECON 1986).

From the above data, a life table was constructed based on the population equation

$$= \sum R^{-x} l_x m_x$$

1

where R is the ratio of individuals in the population at one time to the number of individuals in the previous time unit (population growth), x is the age in years, 1_x is the probability for an individual to survive to age x, and m_x is the number of female young born per individual female at age x. For stable populations R = 1, for decreasing populations R < 1, and for increasing populations R > 1.

Table 3 shows the results of simulations of population growth based on the life table format (RECON 1986). In both instances, it was assumed that adult mortality $q_{X(a)} = 0.531$ and first-year mortality $q_{X(j)} = 0.764$. In

			Variables ^a		
Population size	Reproductive rate	R	r	q <i>x(j)</i>	$q_{x(a)}$
table	2.248	1.000	0.000	0.764	0.531
increasing	2.900	1.154	0.143	0.764	0.531
Increasing	3.000	1.178		0.764	0.531
Increasing	3.500	1.295		0.764	0.531

 Table 3. Life table simulations for populations of least Bell's vireo (Vireo bellii pusillus) with stable and increasing size (RECON 1986).

^a Reproductive rate = Number of female young born per female at age x (birth rate).

R = Population growth (population change).

r = Instantaneous rate of population increase.

 $q_{x(a)} =$ Adult mortality.

 $q_{x(i)} =$ Juvenile mortality.

the top portion of the table, the population is stable as indicated by R = 0, and requires a birth rate of 2.248 offspring per year.

In the second simulation, the population is increasing, as seen by R = 1.154, and requires a birth rate of 2.900. For example, using extrapolation, a population of 300 pairs should reach 2,500 pairs in about 20 years.

Population size changes are affected dramatically by different birth rates, as shown in Table 4. From these simulations, if the birth rate is 0.5 and growth rate is 0.575, it appears that the vireo may be extinct in 10.3 years. A birth rate of 2.5 and growth rate of 1.06 may achieve a population size of 5,000 birds in 48.68 years (RECON 1986). A birth rate averaging 1.9 young fledged per pair was obtained from the Sweetwater, San Diego, and San Luis Rey rivers in 1986 (RECON 1986). If this figure approximates vireo rangewide natality, the model predicts that the population will decrease (R < 1.00) and the vireo may become extinct in less than 100 years. From this preliminary model, it appears that a reproductive rate of at least 2.25 young fledged per pair each year is necessary for the population to slowly begin to expand. Given the current conditions, such a reproductive rate can only be a reasonable expectation if rangewide cowbird trapping and vireo nest monitoring are continued.

Special Considerations Associated With Small Populations

Vireos are susceptible to problems associated with low population numbers because they apparently are site tenacious and because the majority of nesting locations have fewer than five breeding pairs. In essence, without dispersal or immigration, many vireo breeding subpopulations may constitute genetically isolated units. If so, vireos would be subject to the potentially deleterious effects of genetic drift and inbreeding depression. These effects can reduce genetic variability in a population and consequently affect the fitness and survival of inbred individuals.

As the effective population size declines and inbreeding increases, deleterious recessive alleles are more likely to be expressed and may result in a decline in reproductive success (Soule 1980; Frankel and Soule 1981). It is established that inbreeding depression prevents long-term maintenance of small, isolated, closed populations (Conway 1980; Senner 1980; Brussard 1986). Because so many vireo subpopulations are small, it is important to determine how much genetic exchange occurs between these units. If at least one migrant per year enters and breeds in each localized subpopulation, the population essentially is panmictic (a single breeding population or deme) and the effective population size is much larger. Thus, in most instances, the probability of genetic effects due to small population size are usually considered minor compared with other considerations. Banding and color-marking studies or possibly enzyme polymorphism studies (such as electrophoresis) may be used to reveal the extent of genetic exchange and the genetic distinctiveness of the virco populations. Providing for gene flow can be accomplished artificially by exchanging eggs or nestlings, if necessary.

Small populations of vireos are also subject to extirpation from catastrophic events. Such an event could eliminate a major portion of the total population that now is concentrated in San Diego County, such as the four major subpopulations that are found there. To guard against such a loss, the vireo should be managed to encourage an expansion in distribution, such as into

		Time (years) to achieve		
Birth rate	R	Extinction	5,000 birds	
0.5	0.575	10.30		
1.0	0.703	16.15	_	
1.5	0.823	29.19	_	
2.0	0.941	93.79		
2.25	1.000	_	_	
2.5	1.060	_	48.68	
2.9	1.154		20.00	
3.0	1.178	_	17.22	
3.5	1.295		10.88	
4.0	1.414	_	8.12	

Table 4. Effect of birth rate (m_x) on population change (R) and predicted times (generations or years) for a hypothetical population of 300 least Bell's vireos (Vireo bellii pusillus) to become extinct or reach 5,000 birds.

the Central Valley, so that it would be unlikely that any one catastrophic occurrence would result in extinction.

Habitat and Population Maintenance

The draft Least Bell's Vireo Recovery Plan (U.S. Fish and Wildlife Service 1988) states that its goal is to establish and maintain a viable, self-sustaining population by protecting, securing, and managing least Bell's vireo habitat distributed within 13 key management areas (Santa Ynez River, Santa Clara River, Prado Dam-Santa Ana River, Coyote Creek/Northwest Anza-Borrego Desert State Park, Santa Margarita River, San Luis Rey River, Jamul-Dulzura creeks, Sweetwater River/Reservoir, Tijuana River, San Diego River, Santa Ysabel Creek-San Dieguito River, Salinas River, and other historical locations). It is anticipated that about half of the total vireo population will be located within parts of the presently unoccupied historical range.

In Section 9 of the Endangered Species Act of 1973, as amended, "taking" of listed species is prohibited. Within the broad legal definition, "take" is considered to be kill, harm, or harass. Section 10(a) of the Endangered Species Act covers the development of a habitat conservation plan (HCP) and issuance of a permit to take an endangered species incidentally. To obtain such a permit, an applicant must submit a conservation plan that specifies the possible effects of such taking and the actions the applicant will undertake to minimize and mitigate such effects. The Fish and Wildlife Service may issue a Section 10(a) incidental take permit provided that, among other things, the permit application is supported by an HCP whose implementation will ensure the long-term conservation of the species, and that the taking of the species will not appreciably reduce the likelihood of the survival and recovery of the species in the wild. Issuance of such a permit is subject to the requirements of Section 7(a)(2) of the Act as well as Section 102(2)(C) of the National Environmental Policy Act [42 U.S.C. 4332(2)(C)].

The San Diego Association of Governments is coordinating the effort by local governments, State and Federal agencies, private entities, and conservation organizations to prepare a comprehensive species management plan that will consist of one or more habitat conservation plans. Each HCP will be specific for a particular watershed. Funding for this effort originated with the State legislature, which initially appropriated \$150,000 for the project, with both private and public entities providing matching funds. The San Diego Association of Governments used these initial funds to contract with the Regional Environmental Consultants to prepare the comprehensive species management plan and the HCP's. Regional Environmental Consultants program includes collection of biological and land-use data, censusing vireos, monitoring nest parasitism in selected areas, and conducting hydrological analyses. In addition, the effects of aggregate mining and of existing and proposed land uses will be assessed. With this information, RECON is developing HCP's for the San Diego River, San Luis Rey River, and Prado Dam-Santa Ana River. The Sweetwater River HCP is being completed by Westec Services for a private landowner.

Vireo habitat must be protected so that it can be managed and maintained to increase vireo survival and productivity. Management of vireo habitat should include a population monitoring program consisting of routine annual censuses and nest monitoring, as well as an effective cowbird control program. It may also be necessary to control predators to limit predation on eggs and nestlings. Disturbance to habitat from livestock grazing and human activities should be minimized. Monitoring of water and soil for chemical pollution derived from agricultural, commercial, oil field, residential, vector control, or vegetation control sources is necessary so problems can be detected and resolved before there is a threat to the least Bell's vireo, its habitat, or its food resources. Habitat restoration and maintenance will be essential, including removing exotic vegetation and ensuring that the proper riparian successional stage of the habitat is available.

To properly manage vireo populations, additional data are needed on the relation of small patch size to vireo use to determine minimum acceptable size, appropriate size and shape of the habitat for long-term viability, and location of the breeding habitats (including adjacent land uses) in relation to habitat suitability and other preserve design features. Species-specific characteristics such as dispersal and colonization tendencies and population demographics are essential for assessing the population's stability and genetic variability. Perpetual conservation of the vireo dictates that reintroduction into historical range is essential for its recovery. Strategies exploring the available technologies and options for accomplishing this are being examined by the Service.

To successfully manage the population will necessitate additional information on food abundance, availability, and quality; presence and pressure of predators; structure and composition of the vegetation components in the habitat; complexity of the habitat; and human-related uses of the habitat and their effects on habitat quality with respect to the vireo. Several studies are under way that focus on some of these issues.

A number of factors may influence the availability, accessibility, and quality of vireo food resources. Vireo foraging behavior should be quantified to detail foraging exploitation strategies and use patterns in various areas. Habitats of certain configurations, such as wide versus narrow width of the riparian vegetation, may enable more efficient foraging (e.g., parents can provide more food for the young in a given time if flight distances to foraging substrate are reduced). Avian use patterns may be modified under high-density conditions as the population size fluctuates. Under high-density circumstances, certain individuals (likely to be first-year birds) may be relegated to less desirable parts of the area where survival and reproductive success will be lower. Additional information on dietary preferences will aid in assessing the potential for insecticide problems. With these data, it should be possible to design and manage habitat reserves to maximize the vireo population.

Unfortunately, almost no information is available on the condition and management of areas where vireos overwinter. Because substantial losses during migration or winter could more than offset any increases in the postbreeding population accrued from, for example, cowbird control and vireo nest monitoring, data are needed on vireo ecology during the nonnesting season. With information on foraging behavior, roosting sites, habitat selection, predator pressures, and the impacts of human-related activities on wintering and migration areas, recommendations can be developed to reduce any negative effects in these areas.

Creation and maintenance of riparian habitat is essential to managing vireo populations. Methods of maintaining vireo quality habitat should be explored and assessed, such as controlling water flow rate and amount, manual manipulation of the habitat to remove senescent plants or retard succession or modify land elevations, and planting of riparian vegetation (timing, type of vegetation, plant spacing and location, etc.). A number of revegetation programs for relatively small areas are under way as the result of compensation measures required during construction of various projects. Field tests to determine the merits of the various methods should elucidate the most effective strategies for restoring and maintaining prime habitat for vireo use.

Because vireos prefer early successional riparian habitat with a dense understory, a rotational schedule to reset succession will be needed to provide continually suitable habitat. Otherwise, as riparian habitat proceeds through the natural pattern of succession to maturity, the understory becomes too thin for vireo nesting. Additional research may be required to develop a long-term rotation strategy to ensure availability of the appropriate successional stage and to maximize effective management.

Factors influencing the population demographics, including the growth, structure, and population size of the least Bell's vireo, should be examined with the goal of maximizing natality and longevity. Mortality should be reduced as much as possible to allow for an increase in vireo numbers and encourage population expansion through recolonization. With the above information, the population growth models will be refined.

The initial 12 key management areas have been described, but actual boundaries should be demarcated. Habitat measurements can be collected and assessed to estimate the amount of currently available habitat and the maximum amount that could be created and maintained on a long-term basis. Sites for reintroduction (both areas near occupied habitat, and particularly areas from which vireos now are extirpated) must be selected according to standardized criteria. These reintroduction sites will constitute the 13th key management area.

Vireo Productivity

Long-term viability and recovery of a population depends on a host of factors (habitat quality, predation pressure, disturbance, etc.) that influence reproductive success and survivability of young. Preliminary data indicate that about 2.25-2.50 fledglings per breeding pair are needed to maintain or increase the population. These figures are based on reproductive success rates reported by Salata (1983b, 1984) for an increasing population of least Bell's vireo along the Santa Margarita River and population simulation modeling based on a variety of assumptions. As more data become available, the models will be reevaluated and refined. In the meantime, the goal is to obtain a 3.0 mean reproductive rate, as this provides for faster recovery than the 2.25–2.50 rate and offers some buffer if the model's results are inaccurate.

Because nest parasitism by brown-headed cowbirds is a limiting factor for many populations of least Bell's vireos, parasitism must be reduced so that vireo reproductive success is enhanced. Control measures involve the trapping of cowbirds and removal of cowbird eggs and young from vireo nests. Other questions warrant investigation, such as whether parasitism is as much a problem in prime habitat as in degraded habitat. Are larger vireo populations less affected? Such data will aid in determining priorities for cowbird control.

Some information on habitat requirements and use patterns by cowbirds is already available in the literature, but needs to be gathered and evaluated with respect to the particular habitat conditions provided by these riparian systems. For example, cowbirds apparently parasitize more nests in fence rows, in thin strips of vegetation, and along the edges of vegetation types than they do in large blocks of homogeneous habitat (Wiens 1963; Lowther and Johnston 1977; Gochfeld 1978). If this is true, then the thin strips of vegetation (often bordered by agricultural land) in which many least Bell's vireos now breed are especially conducive to cowbird parasitism. The few remaining areas of true riparian "forest" may become increasingly important to the survival of the least Bell's vireo, although there is some question that even the largest of these is expansive enough to seriously limit cowbird activities (Lowther and Johnston 1977). Additional field work will be necessary to fine-tune the habitat use patterns including such information as how far cowbirds fly from their foraging and roosting areas to lay eggs.

More precise information on the response of vireos to nest parasitism is needed. Vireos may abandon parasitized nests, but what other responses do vireos have and how prevalent are they? Does the vireo have any defense against nest parasitism? Is it likely vireos will adapt to cowbird parasitism and learn to cope with it as other species apparently have? Although some data are available on cowbird nest site selection and reproductive strategy, additional data more specific to vireos in these habitats are needed. Is there a way to manipulate vireo habitat to make it less attractive to cowbirds without causing the vireos to abandon it? Perhaps it will be possible to develop a management strategy for discouraging cowbird use of vireo nests.

Nest parasitism seems to be a critical proximate factor limiting vireo population numbers. A long-term commitment to continuing and expanding existing efforts at cowbird control and vireo nest monitoring is essential for increasing the numbers of least Bell's vireos.

Reestablishment of Vireos Within Historical Range

Vireos historically were distributed throughout the San Joaquin and Sacramento valleys as far north as Red Bluff. In fact, although the Central Valley, including the Sierra Nevada foothills, supported the majority of the vireo population, the vireo now is extirpated from this area. Potential sites for reintroduction should be assessed for habitat quality and suitability in these northern and central portions of the historical range. Of critical importance are current threats at the site, methods of reducing or eliminating the threats, the likelihood of vireo success in restored or managed areas, size of the area that could be protected and managed, and the size of the vireo population that may be supported in the area. In selecting sites one must consider how the area can be protected through conservation agreements and the speed with which such agreements can be consummated. Areas that will require extensive and prolonged cowbird trapping or are near a large reservoir of cowbirds may receive lower priority for reestablishment than areas with fewer management problems. Application of pesticides may reduce vireo food resources or available vegetation. Strategies must be in place for controlling or reducing such losses before restoring the habitat or reintroducing vireos. Any needed habitat rehabilitation should be completed before reintroduction. All such areas must be protected, secured, and managed to maximize long-term survival of vireos.

It is possible that some natural expansion into suitable areas (after undertaking appropriate management actions) will occur in the vireo's presently unoccupied historical range in southern California. However, because of the distances involved and the site tenacity of the vireo, it is unlikely that the bird will return naturally into the Central Valley-once the center and an important component of the breeding range. Therefore, the feasibility of various reintroduction methods should be explored. Because of potential problems with species-specific song recognition and species recognition in young vireos raised by non-vireo host parents, as well as other biological problems posed by transferring eggs or nestlings, it may be more feasible and profitable to consider mist-netting juvenile birds and releasing them in parts of the presently unoccupied historical range. An analysis of the various reintroduction strategies is now under way.

Before collecting juveniles (or other vireos) for reintroduction, vireo subpopulations will be evaluated to determine which can support the loss of birds to be used in the release program. If numbers are insufficient, then the possibility of captive propagation will be explored, but this action would be considered only as a last resort.

Monitoring Vireo Status

It is essential that the status of vireo populations be determined annually so that the efficacy of management efforts can be ascertained. Survey results should reflect the total count of breeding pairs based on surveys of all sites, including reintroduction locales, and should use one standardized technique.

Virtually all U.S. least Bell's vireos overwinter in Mexico, and their status there must be monitored. In addition, least Bell's vireos breeding in Baja California must be surveyed annually.

Adequate habitat conditions, availability, and distribution are crucial to the recovery of least Bell's vireos. The monitoring program should include evaluating the habitat status, including the effects of public and private projects and other activities. If monitoring indicates a decline in habitat quality or quantity, remedial measures should be instituted.

Emergency Provisions

Current data indicate that there are about 300 breeding pairs of least Bell's vireos in the United States. Subpopulations vary from 1 to 140 territorial males. With such low numbers, a catastrophic occurrence – especially in any of the six major breeding centers that compose about 89% of the

extant breeding population – could reduce vireo numbers to a level from which they could not recover. If the total population of the least Bell's vireo falls below 150 pairs, emergency tasks must be carried out immediately.

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