
Use of Restored Riparian Habitat by the Endangered Least Bell's Vireo (*Vireo bellii pusillus*)

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Abstract

A primary objective of riparian restoration in California is the creation of habitat for endangered species. Four restoration sites in San Diego County were monitored between 1989 and 1993 and evaluated for their suitability as nesting habitat for *Vireo bellii pusillus* (Least Bell's Vireo), a state and federally endangered obligate riparian breeder. Vegetation structure at each site was quantified annually and compared to a model of canopy architecture derived from Least Bell's Vireo territories in natural habitat. Vireo use of restored habitat was documented through systematic surveys and nest monitoring. By 1993, only one site in its entirety met the habitat suitability criteria of the model, but portions of each site during all years did so. Differences between sites in the time required to develop suitable habitat—well-developed layered vegetation from the ground to under 8m in height—were attributable largely to variation in annual rainfall. Vireos visited restoration sites to forage as early as the first growing season, but they did not establish territories or nest there until at least part of the site supported suitable habitat as determined from the model. Placement of territories and nests coincided with patches of dense vegetation characteristic of natural nesting areas. Occupation of restored sites was accelerated by the presence of adjacent mature riparian habitat, which afforded birds nest sites and/or foraging habitat lacking in the planted vegetation. Vireos nesting in restored habitat achieved success comparable to that of vireos nesting in surrounding natural habitat, and there was

no evidence that productivity was reduced in created areas. These findings indicate that creating nesting habitat for this target species is feasible and suggest that the critical components of vireo nesting habitat have been captured in both the design and quantitative assessment of restoration sites.

Introduction

Riparian habitat in the southwestern United States has undergone serious declines during the last several decades, prompting efforts to create and restore woodlands throughout their historical distribution (Anderson & Ohmart 1982, 1985). One of the primary objectives of riparian restoration in southern California is to provide suitable habitat for endangered species. Although riparian habitat in this arid region is unparalleled in the diversity and abundance of wildlife it supports, thus warranting protection on this basis alone, it is the presence of endangered species that provides the legal impetus for mitigating habitat losses through restoration.

Most of the riparian restoration in San Diego County has been driven by the requirement to mitigate for the loss of habitat supporting *Vireo bellii pusillus* (Least Bell's Vireo), a state and federally endangered migratory songbird. This obligate riparian breeder was once abundant throughout California but declined in the face of widespread habitat destruction and parasitism by *Molothrus ater* (Brown-headed Cowbird). By 1986 the state population numbered just 300 pairs, roughly 80% of which occurred in San Diego County (U.S. Fish and Wildlife Service 1988; Regional Environmental Consultants 1989).

Considerable advances have occurred over the last ten years in the technical aspects of the design and implementation of restoration sites (Baird 1989; Baird & Rieger 1989; Hendricks & Rieger 1989). But successful habitat restoration involves considerably more than the establishment of native vegetation in a natural setting and requires consideration of several perspectives. Biologically, the goal of restoration is to create self-sustaining ecosystems functionally equivalent to those being replaced (Jordan et al. 1987). Legally, the stated objective of a restoration project may be more narrowly defined—for example, to create habitat capable of supporting a particular target species. Regulatory agencies are faced with the challenge of determining when the restoration has been successful in achieving its goal, as well as with identifying specific success criteria and methods for the quantitative measurement and evaluation of site performance. Implementing parties desire to achieve compliance with mitigation requirements through means that are not only economically efficient but

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quick, particularly when project construction is dependent on successful "up-front" habitat replacement.

Sufficient time has now passed to allow evaluation of current restoration practices in light of these various considerations. I summarize five years of monitoring data collected at four restoration sites ranging in size from 3 to 18 ha and in age from three to five years. Each of these sites was established prior to development that resulted in the loss of Least Bell's Vireo habitat, and the presence of nesting vireos was identified as the criterion for successful mitigation. I describe quantitatively the development of riparian vegetation at each site and evaluate its suitability as nesting habitat by comparing it to a habitat-based model derived from measurements of vireo territories in natural riparian habitat. I then detail vireo use of restored sites, linking it to vegetation structure, and I consider the power of the model in identifying suitable nesting habitat. Finally, I compare the reproductive success and productivity of vireos nesting in restored and natural habitats.

Study Areas

Three restoration sites along the San Luis Rey River and one on the San Diego River in San Diego County, California, were monitored between 1989 and 1993. The Oceanside and Bonsall sites, named after the municipalities in which they are located, are each 3-ha sites planted in early 1989 by the California Department of Transportation as partial mitigation for highway construction activities along the San Luis Rey River. The Bonsall site was constructed adjacent to mature cottonwood-willow habitat bordering the river, whereas the Oceanside site was isolated from existing riparian vegetation by approximately 100 m until 1991, when a small clump of *Salix* sp. (willow) developed outside the fence enclosing the planted site. Both sites were planted with a combination of 1-, 5-, and 15-gallon container nursery stock as well as transplanted trees, and they were seeded with several annuals (Baird 1989; Baird & Rieger 1989). Species were selected to mimic natural vireo habitat (Hendricks & Rieger 1989) and included a mix of *Salix lasiolepis* (arroyo willow), *S. gooddingii* (black willow), *S. hindsiana* (sandbar willow), *S. laevigata* (red willow), *Baccharis glutinosa* (mulefat), *Populus fremontii* (Fremont's cottonwood), and *Platanus racemosa* (sycamore). The third San Luis Rey River site, near Whelan Lake, is a 4-ha site planted by the U.S. Army Corps of Engineers in 1989 with cuttings and transplanted mature willows. Establishment of this site was a condition for removal of native vegetation within the vicinity of a flood-control project, and the restoration site was comparatively isolated from mature habitat during most of the study period.

The Mission Trails site borders the San Diego River

within a regional park of the same name. Established by the California Department of Transportation in 1990, the site supports 18 ha of riparian vegetation planted in the manner developed for the Bonsall and Oceanside sites. The restored habitat spans mature habitat along the river and is treated here as two sites, north (13 ha) and south (5 ha).

Methods

Vegetation Measurement

Data describing vegetation structure were collected annually at each restoration site, commencing with the first year (growing season) after planting at the Mission Trails sites, the second year after planting at the Oceanside site, and the third year after planting at the Bonsall and Whelan sites. Sampling was conducted during August and September after breeding activity of birds at the sites had ended.

Vegetation was measured at points marked with permanent stakes along transects arrayed to provide uniform coverage of planted vegetation at each site. Between 13 and 28 points per hectare were sampled across sites. Foliage volume at 1 m height intervals was estimated by the "stacked cube" method, developed specifically to characterize canopy architecture in structurally diverse riparian habitat. Field workers recorded percent cover of vegetation, by species, within $2 \times 2 \times 1$ m sampling volumes "stacked" vertically high between the ground and the top of the canopy above the point. Four 2 m lengths of PVC pipe were placed on the ground to define the quadrat boundaries, and connectible lengths of PVC, marked at 1-m intervals, were used to determine height within the canopy. Percent cover was scored in the field by a modified Daubenmire (1959) scale, with cover classes <1, 1-10, 11-25, 26-50, 51-75, 76-90, and >90%. For analysis, cover codes were converted to class midpoints, which were then used to quantify vegetation structure at each sampling point, blocks of selected adjacent points, and each site as a whole.

Bird Surveys

Data on the occurrence of vireos at the restoration sites were drawn from comprehensive bird surveys conducted regularly since site inception at all but the Whelan sites (Kus 1989c). Between 1989 and 1991, surveys were conducted weekly during the breeding season (April-July) and biweekly during the rest of the year. A year-round biweekly schedule of surveys was adopted at the Bonsall and Oceanside sites in 1992.

Observers followed established routes designed to provide coverage of the entire site and recorded the age, sex, behavior, and location of every vireo detected.

Vireo Nesting Activity and Territory Delineation

Nesting activity of vireos using the restoration sites was monitored as part of a larger long-term study of vireos throughout the San Luis Rey and San Diego drainages (Kus 1989a, 1989b, 1991a, 1991b, 1991c, 1991d, 1992a, 1992b, 1993a, 1993b, 1994). Surveys were initiated in mid-March each year to determine the number, location, and breeding status (paired or unpaired) of singing males. Surveys were concentrated on a 32-km stretch of the San Luis Rey River and a 5-km stretch of the San Diego River. Once pairs were located, they were observed for evidence of nesting. Nests were located and monitored throughout the period that they were active to determine clutch size, hatching success, and fledgling success. Territories were visited through early August, and an attempt was made to determine the number and fate of all nests produced by each pair.

Territories were depicted on aerial photographs (scale, 1" = 50' (for Mission Trails) and 1" = 500' (for San Luis Rey) of each study site by plotting and connecting the locations of boundary disputes between neighboring males and each male's outermost singing perches.

Vireo Habitat Suitability Model

A model quantifying vegetation structure of vireo nesting habitat was developed with data from 10 territories in mature habitat along the San Diego River and 11 territories along the Sweetwater River in southern San Diego County (Miner 1989; Newman 1993). At the time the data were collected (1987), these drainages supported two of the densest populations of vireos in California, suggesting a high degree of habitat suitability. They also included sites studied by Hendricks and Rieger (1989) to develop restoration-site planting designs.

Between 24 and 32 points per territory were sampled by the stacked cube method described earlier (Miner 1989; Newman 1993). Average cover at 1-m height intervals was then calculated for each territory. Because the San Diego and Sweetwater territories did not differ significantly, they were combined, and cover at each height was averaged over the 21 territories.

The model was developed as a tool for evaluating whether sites unoccupied by vireos supported habitat suitable for nesting; that is, did the site fall within the range of habitat structure found within the vireo nesting territories? The criteria established for making this determination required that average cover at each height in the site under consideration fall within two standard deviations of the corresponding averages for known vireo nesting habitat, a range representing the 95% confidence interval of each mean (Snedecor & Cochran 1976).

Sites failing to meet these criteria were considered unsuitable as nest sites for vireos.

Results

Vegetation Structure of Vireo Nesting Habitat

Nesting vireos use a subset of available riparian habitat characterized by a well-developed and layered canopy extending from the ground to heights as high as 15 m (Fig. 1). Typically, foliage density is highest within 1–2 m of the ground, the range within which vireos place their nests, and tapers off with increasing canopy height.

Development of Vegetation at the Restoration Sites

Although survival of planted vegetation was generally high, the three San Luis Rey sites exhibited little increase in foliage cover during the first four years of growth, 1989–1992 (Fig. 1). In fact, foliage volume declined at the lower canopy heights as establishing plants dropped leaves and died back. Planted trees and shrubs grew slightly in height but did not develop sufficient lateral growth to create the dense understory characteristic of vireo nesting habitat. A similar pattern was observed over the first two years of growth at the Mission Trails sites. In 1993, however, vegetation structure at all of the sites changed dramatically in the wake of record-breaking winter rainfall and persistent flooding in San Diego County. Average foliage cover doubled at the Oceanside site over the previous year and increased by 45–70% at the other sites.

By 1993, only one site met the model-derived criteria defining nesting habitat suitability, although other sites came close (Fig. 1). The Oceanside site, after five years of growth, supported a riparian stand with the density and vertical stratification typical of vireo nesting territories. The other 5-year-old sites, Whelan and Bonsall, also supported tall, dense vegetation but did not meet the cover criteria at all canopy heights as did the Oceanside site. The vegetation at Whelan differed from vireo nesting habitat in the slight lack of cover within 1 m of the ground, whereas the woodland at Bonsall lacked sufficient cover in the mid-canopy range.

The Mission Trails sites, in their third growing season by 1993, supported riparian habitat with tall canopies and dense foliage at some but not all canopy heights. Relative to the model, vegetation at the south site lacked density at heights below 5 m, whereas that at the north site was relatively sparse between 3 and 5 m, and marginally so at 0–1 m.

Although most sites in their entirety did not meet the model's suitability criteria, portions of all sites in each year did so. Vegetation development was not homogeneous within sites, and it was evident early on that foli-

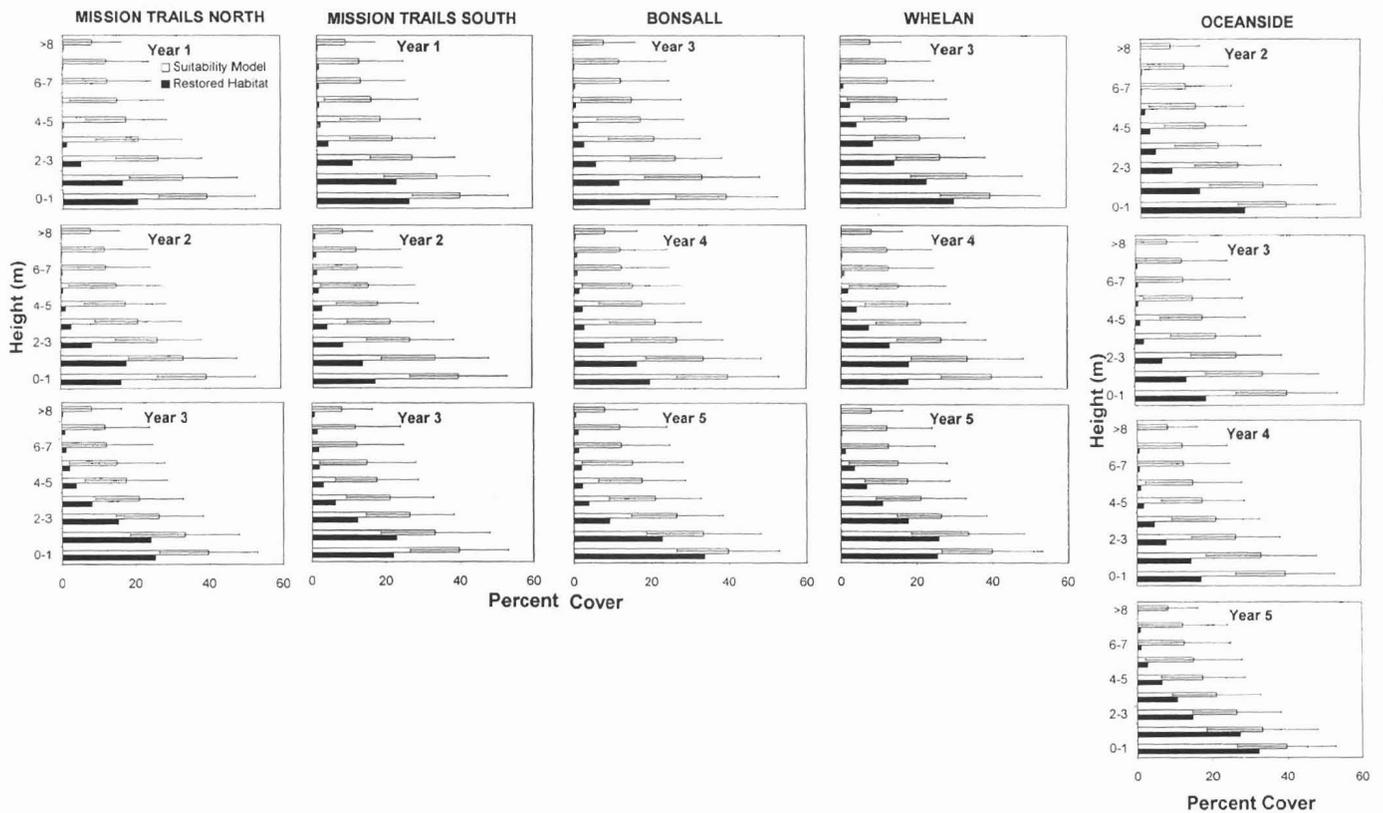


Figure 1. Development of foliage cover at riparian restoration sites relative to habitat suitability model. Model represents means \pm 2 SD; bars bracket range of cover defined as suitable nesting habitat.

age structure was patchy with regard to canopy density and height. Dense patches, identified for analysis by inspection of the cover data, were tested for conformance with the model by evaluating blocks of contiguous sampling points along transects. Points were sequentially added or deleted until the limits of the block meeting the habitat suitability criteria were determined. The blocks were then mapped for each site and year and were assessed with regard to use by vireos, providing an additional and more conservative test of the habitat suitability model (Fig. 2). In some cases, patches were in conformance with the model at all but one or two height classes. Typically, these were patches that were suitably dense but had failed to attain the canopy height characterizing vireo nesting habitat or, conversely, were suitably tall but lacked sufficient understory. These patches meeting some but not all cover criteria were mapped in a manner distinguishing them from patches meeting all criteria, and their use by vireos was evaluated (Fig. 2).

Use of Restoration Sites by Least Bell's Vireos

Vireo use of the restoration sites was classified into four types: (1) foraging by adults and/or fledglings outside

their nesting territories; (2) incorporation of restored habitat into a territory centered in adjacent mature habitat, with nesting confined to the mature habitat; (3) incorporation of restored habitat into a territory centered in adjacent mature habitat, including placement of nests in the planted vegetation; and (4) establishment of a territory entirely within the restored habitat. The degree of habitat suitability required to support each use was expected to increase from type 1 to type 4.

Use of restored habitat for foraging was the earliest type of use observed at the sites, commencing during the first year of growth at the Oceanside, Bonsall, and Mission Trails sites and occurring each year subsequent to that (Table 1). Fledglings from nearby territories, usually accompanied by a parent, were the most common visitors to the restoration sites; migrants in passage also occasionally appeared at the sites for a few days.

Vireos did not establish territories in restored habitat, either partially or entirely, until at least part of the site met the criteria of nesting habitat suitability. Colonization of the Oceanside site did not occur until the site was 4 years old, whereupon an unpaired male occupying existing habitat adjacent to the site incorporated part of the restored habitat into his territory. The following year, by which time the entire site was judged suitable for vireos,

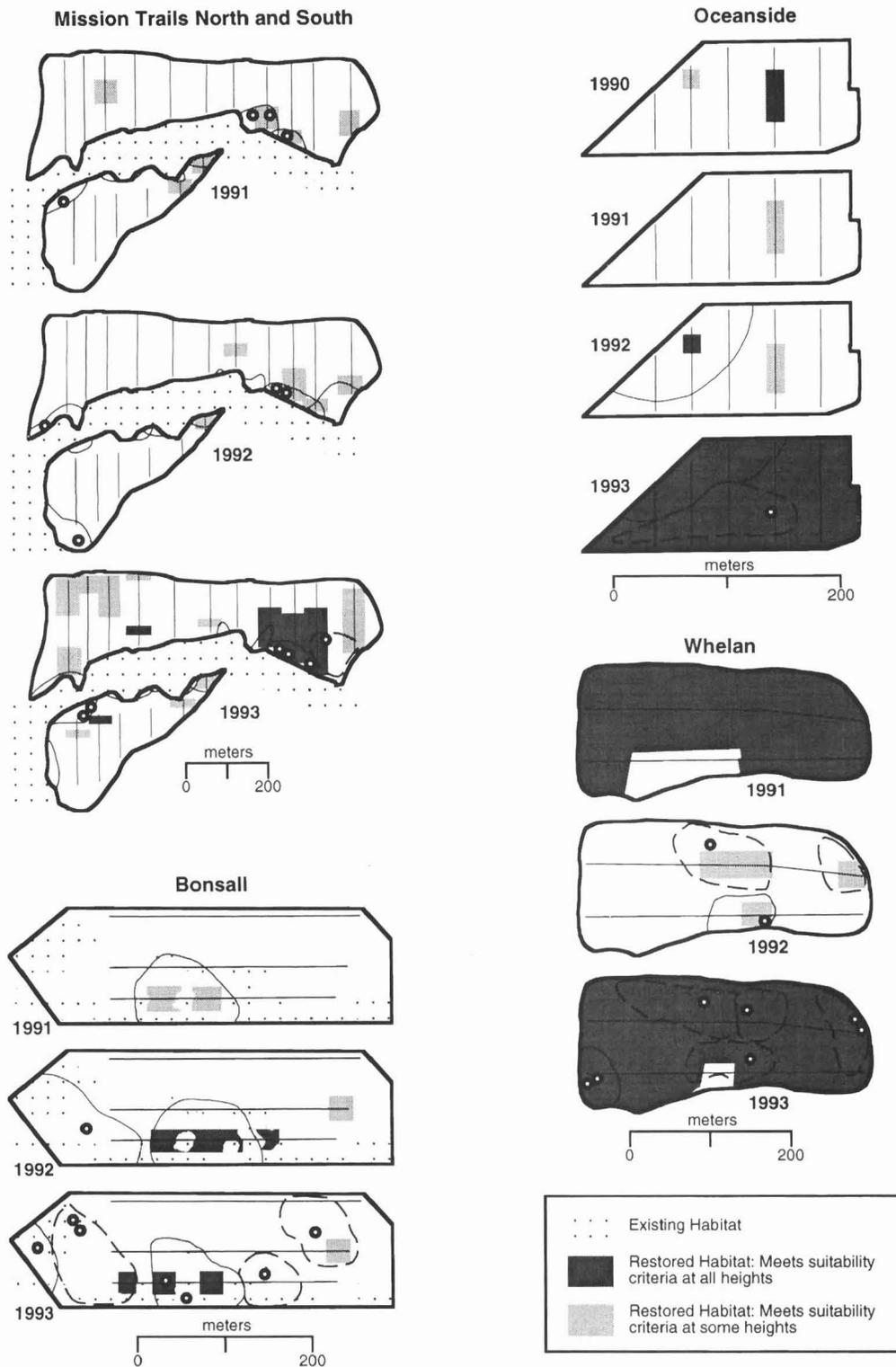


Figure 2. Location of Least Bell's Vireo territories relative to suitable habitat availability at restoration sites. Solid line reflects territory extending into adjacent mature habitat; portion of territory outside restoration site not shown. Broken line reflects territory entirely within restoration site. Circles denote nests. Lines traversing site are vegetation transects. Mapped blocks do not identify the actual patch boundaries, just the portion intersecting a vegetation transect.

a pair occupied this same territory, while a second pair established a territory and nested entirely within the restored habitat. Similarly, vireos did not establish territories at Whelan until four years after planting.

In contrast, colonization of the Bonsall and Mission

Trails sites occurred much earlier, during the second year at the former and the first year at the latter. Moreover, vireos used these young sites as nesting habitat, placing nests in planted vegetation. In all cases, however, vireos occupied territories centered in the exten-

sive mature habitat bordering each of these sites, and nest sites were within a few meters of the edge of this mature habitat. It was not until the fifth year at the Bonsall site and the third year at the north Mission Trails site that vireos established territories strictly within the boundaries of the planted vegetation.

The use of individual restoration sites by territorial vireos was closely linked to the distribution of patches of structurally suitable nesting habitat (Fig. 2). All of the initial colonizers of the Whelan site in 1992 centered territories on patches of tall, dense vegetation. The following year, when nearly the entire site was considered suitable vireo habitat, these patches continued to serve not only as territory cores but nest sites as well. Similarly, the two patches of suitable or near-suitable habitat present from the second year on at the Oceanside site were incorporated into territories when the site was eventually colonized. As at Whelan, one of these patches encompassed the location of the only vireo nest constructed within the site as of 1993.

Until 1993, all vireo territories at the Bonsall and Mission Trails sites occurred along the margins fringed by natural habitat; nevertheless, they too coincided with the patches of well-developed planted vegetation identified along sampling transects (Fig. 2). Both of the territories established in the interior of the Bonsall and Mission Trails sites in 1993 were centered on patches, and, although not depicted in Figure 2, the patches of high-quality habitat in the northeast section of the north Mission Trails site were colonized by a nesting pair in 1994 (B. E. Kus, unpublished data).

Reproductive Success of Vireos Nesting in Restored Habitat

Vireos nesting at restoration sites successfully fledged young during each year they were present (Table 2). Comparing vireos using restored sites to pairs nesting in natural habitat produced no evidence that vireos were less productive in restored vegetation, at least along the San Luis Rey River. Although sample sizes

for the early years are small, vireos nesting at the Oceanside, Bonsall, and Whelan sites consistently fledged as many young per nest and per pair as did birds in nearby mature habitat. The pattern at the San Diego River is less clear and is complicated by the exceptionally high pair productivity documented in 1993 for pairs nesting in natural habitat in the study region (Kus 1994). Although the four vireo pairs nesting at the Mission Trails site that year performed less well by comparison, they achieved a level of productivity higher than that observed for either group during the previous two years.

Discussion

All of the restoration sites monitored in this study eventually supported nesting Least Bell's Vireos, providing the first evidence that it is possible to create suitable nesting habitat for this endangered species. Sites differed in the length of time required to reach this goal, however, making it possible to identify factors influencing vireo use of restored habitat. Some of these factors, such as proximity to existing vireo habitat, are subject to human control; others, such as annual rainfall, are not. Predicting with any great precision the time needed for a particular site to be colonized by vireos is therefore not possible, but the range in characteristics of the sites monitored here and the climatic background against which they were studied suggest that, in the coastal lowlands of southern California, 3–5 years is sufficient to develop habitat with the features that allow nesting vireos to be supported entirely within restored sites.

What factors influence vireo use and colonization of restored habitat? Foraging, the earliest and most extensive form of vireo use observed, occurred well before sites met the model's criteria for habitat structure, indicating that this use can occur independently of the presence of suitable nesting habitat and is thus by itself not a good indicator of habitat quality. Williams (1993), in a study monitoring terrestrial arthropods at the Ocean-

Table 1. Habitat suitability and use of restored sites by Least Bell's Vireo.

Site	Year 1			Year 2			Year 3			Year 4			Year 5		
	Habitat Suitability		Vireo Use	Habitat Suitability		Vireo Use	Habitat Suitability		Vireo Use	Habitat Suitability		Vireo Use	Habitat Suitability		Vireo Use
	All	Part		All	Part		All	Part		All	Part		All	Part	
OC	—	—	F	No	Yes	F	No	Yes	F	No	Yes	F, 1T	Yes	F, 1T, 1T _e	
BO	—	—	F	—	—	F, 1T _n	No	Yes	F, 1T _n	No	Yes	F, 2T _n	No	Yes	F, 2T, 2T _n , 1T _e
WH	—	—	None	—	—	None	No	Yes	None	No	Yes	F, 1T _n , 2T _e	No	Yes	F, 5T _e
MTS	No	Yes	F, 3T, 2T _n	No	Yes	F, 4T, 1T _n	No	Yes	F, 4T, 1T _n	No	Yes	F, 4T, 1T _n			
MTN	No	Yes	F, 2T _n	No	Yes	F, 2T, 2T _n	No	Yes	F, 1T, 3T _n , 1T _e						

Sites: OC, Oceanside; BO, Bonsall; WH, Whelan; MTS, Mission Trails south; MTN, Mission Trails north. Habitat suitability reflects whether all or part of the site was judged suitable for nesting vireos. Vireo use: F, foraging outside territory; T, territory encompassing restored vegetation; T_n, nesting in restored vegetation; T_e, territory entirely within restored vegetation.

Table 2. Reproductive success of Least Bell's Vireos in restored and natural habitats.

Drainage	Parameter	Year							
		1990		1991		1992		1993	
		Restored	Natural	Restored	Natural	Restored	Natural	Restored	Natural
San Luis Rey	No. of pairs	1	33	1	41	4	68	9	76
	No. of nests	2	51	1	71	7	123	11	117
	Nest success (%)	50	47	100	51	57	46	82	40
	No. of fledglings/nest	2.0	1.3	4.0	1.4	1.9	1.3	2.5	1.0
	No. of fledglings/pair	4.0	2.0	4.0	2.4	3.3	2.3	3.0	1.6
San Diego	No. of pairs			4	23	3	21	4	24
	No. of nests			5	40	4	45	6	55
	Nest success (%)			20	43	75	36	50	62
	No. of fledglings/nest			0.4	1.1	1.5	1.0	1.5	2.1
	No. of fledglings/pair			0.5	1.9	2.0	2.2	2.3	4.8

Sources: Kus 1989a, 1989b, 1991a, 1991b, 1991c, 1991d, 1992a, 1992b, 1993a, 1993b, 1994.

side restoration site, documented the presence of likely vireo prey as early as year 1, and by year 2 found no significant difference in the abundance of large prey between the restored site and a nearby natural reference site. Use of young restoration sites by foraging vireos confirms the availability of prey and may be determined largely by the proximity of vireo territories to restoration sites.

Establishment of territories within restored habitat depended on a combination of two factors, the structure of planted vegetation and the site's proximity to natural habitat. The presence of existing habitat along the margins of planted sites reduced the time required for vireo colonization to occur relative to sites lacking an extensive fringe of mature habitat. Presumably this was because vireos using "hybrid" territories were not reliant on planted vegetation to meet all of their habitat requirements, as were birds occupying territories entirely within restoration sites. But the placement of territories spanning restoration site borders was not independent of the structure of planted vegetation. Vireo territories along the margins of the Bonsall and Mission Trails sites coincided with patches of well-developed vegetation, suggesting that expansion of a territory beyond the limits of natural habitat required the availability of structurally suitable planted vegetation nearby. This is supported by the observation that vireos nesting along the San Diego River incorporated restored areas into their territories only when they included patches of suitable habitat; otherwise territories were confined to the natural habitat.

The best and strongest evidence that restoration has achieved its objective is the presence of successfully nesting vireos supported entirely by restored vegetation. This use is clearly influenced by vegetation structure. The model presented here provided a good reference with which to evaluate habitat suitability at the restored sites, and vireo use of sites was consistent with

the habitat-quality determinations based on the model. These findings indicate that the model captured critical components of vireo nesting habitat structure, specifically the need for dense cover within the nest height zone (0–2 m) and the presence of a dense and layered canopy wherein vireos concentrate foraging (Miner 1989). The success with which the model identified the existence of these conditions makes it useful as a standard against which to evaluate, and potentially correct, restoration site performance when Least Bell's Vireos are the target species.

Why did some restoration sites develop rapidly while others progressed slowly? Not surprisingly for a flood-adapted ecosystem, the answer probably lies in the response of vegetation at all sites to the high rainfall prior to the 1993 growing season, breaking a 5-year period of drought. Extensive flooding occurred along both the San Luis Rey and San Diego drainages, recharging soil nutrients and water and ultimately promoting a surge of vegetation growth in the spring. As a result of favorable growing conditions, the Mission Trails sites developed in three years a woodland that took the San Luis Rey River sites five years to achieve. Unpredictability in the timing and amount of annual rainfall characterizes the southern California climate, adding to the uncertainty with which restoration site performance can be predicted and generalized.

Further evidence of the limiting effect of water availability on vegetation development comes from the north Mission Trails sites, where virtually all of the patches of dense habitat occur along small natural drainage channels traversing the site, or within the portion of the site subject to regular flooding from the adjacent river.

Continued research and monitoring will be necessary to further refine our understanding of the factors influencing vegetation development and use of restored riparian habitat by vireos, and to guide modification of

restoration practices as appropriate. The results of this study, however, indicate that restoration holds great promise as a means of reversing the century-long trend of riparian habitat loss in this state, and it has the potential to figure prominently in the recovery of this habitat's endangered inhabitants.

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