

MAINTAINING SITE INTEGRITY FOR BREEDING LEAST BELL'S VIREOS¹

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Abstract: Least Bell's vireos (Vireo bellii pusillus) exhibit a high degree of between-year fidelity to breeding area. Use of many sites in an isolated population in Santa Barbara, California, spans at least 10 years. Males and females show different types and degrees of tenacity to territories, as well as to some nest-sites. More than 60 percent male and nearly 30 percent female returning birds utilized the previous year's territories. While pair bonds remain strong throughout the breeding season for most birds, mate fidelity may be determined by such factors as population size and its sex ratio. Dimorphic behavioral traits such as these which are difficult to ascertain present researchers and managers with profound problems when studying the vireos and designing habitat alteration projects around the species' requirements.

Facing a combination of natural forces that threaten its water supply at Gibraltar Reservoir, the City of Santa Barbara has undertaken several measures designed to alleviate some, if not all, of the problems it has begun reconstruction of the dam's base for earthquake safety, attempted to desilt the reservoir in order to halt its declining capacity, and is developing plans to either raise the dam to increase the reservoir or find alternate sources of water. In 1978, least Bell's vireos were discovered in habitats on alluvium in and adjacent to the reservoir (Gray and Greaves 1980). A detailed banding study of its life history and population dynamics was conducted from 1979-83 (Greaves 1987). Since its listing at the Federal level as an Endangered species in 1986, the city and U.S. Forest Service have continued to monitor the local population with annual censuses. In 1987, a second detailed study of the population was begun in order to assess its size and structure. Return rates of adult and first-year (FY) birds were determined, and nesting activities monitored to find rates of success and brown-headed cowbird (*Molothrus ater*) parasitism. The study will continue through 1996.

Study Area and Methods

The study area is located six miles north of the City of Santa Barbara in the Los Padres National Forest on both city and federal lands along a two-mile section of the Santa Ynez River, including a mile-long sediment-filled

portion at the east end of Gibraltar Reservoir, and a two-mile section of Mono Creek extending northward from its confluence with the reservoir and the Santa Ynez River. In all, more than 240 ha. comprise the study area, composed of riparian and adjacent habitats ranging in width from 50 to more than 400 meters. For detailed descriptions of habitats and vegetation structures, see Gray and Greaves (1984), Greaves and others (1987), and Olson and Gray (1989).

In order to adequately ascertain population size and structure, I conducted a banding project, starting in 1987 and continuing through 1988, using various combinations of U.S. Fish and Wildlife Service aluminum and colored plastic leg bands. A drainage band (red for Santa Ynez River population) is required for each bird that is banded. Census methods followed those outlined earlier (Greaves 1987). Data were collected on the numbers of males and females present, age structure of the population, numbers of nests built, eggs produced, eggs that hatched, young fledged, and known-aged birds returning as potential breeders. Territories were areas with readily discernible and defended boundaries that were, generally, re-used from year to year. Nest sites were smaller locations within a territory, usually a single shrub or clump of weeds or shrubs. Successful nests were those that fledged at least one vireo chick.

I determined factors that affected breeding success, and made recommendations concerning predators, cowbirds, and human activities in the study area. Censuses of other birds were made in order to monitor changes over time in composition of the entire bird community, paying close attention to the numbers and locations of the three other vireo species, warbling (*V. gilvus*), Hutton's (*V. huttoni*), and solitary (*V. solitarius*), that shared the riparian habitats with the least Bell's vireos. Changes in the numbers and locations of these species were noted in order to determine if inter-generic competition might be influencing the apparently declining population of least Bell's vireos as compared to the previous study's estimate of the four species' composition within the bird community.

Results

For the two breeding seasons of this study, the population contained less than half the number of birds

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found in the previous study (Greaves 1987). Numbers of males, females, pairs formed, young vireos produced, and cowbirds in the area were as follows:

	1987	1988
Vireo males present	25	22
Vireo females present	17	14
Vireo pairs formed	19	21
Vireo young produced	63	47
Cowbird males present	7	5
Cowbird females present	6	6
Cowbird eggs or young at/in vireo nests	1	2

In 1988, returning vireos were distributed as follows:

	Returned	# to same territory
1987 vireos		
Males banded (N=22)	12	10
Females banded (N=15)	9	3
Males unbanded (N=3+)	4	3
Females unbanded (N=2 to 4)	2	0
Nestlings/fledglings banded (N=61)	-	-
First-year (FY) males banded	7	0
First-year (FY) females banded	3	0
Nestlings/fledglings unbanded (N=2)	-	-
First-year (FY) males unbanded	(1)	0
First-year (FY) females unbanded	0	-

Ten of 61 banded 1987 fledglings returned to the study area in 1988. Three of these (two males, one female) were from one nest while two other males were from a nest in an adjacent territory along Mono Creek; all five found other birds with which to mate, including at least one other first-year (FY) male. The two males from the second nest above were paired sequentially with the same female, which had been banded as an adult in 1987. Two other FY males remained unpaired throughout 1988. None of the FY birds mated with siblings or their own parents. Their dispersal distances from site of fledging ranged from 0.2 to 1.6 miles.

In 1987, two females were suspected of being sequentially polyandrous (see Greaves, 1987, for discussion). In 1988, at least six females made seven mate changes by the end of June, either during the latter part of first brood feedings or fledging, or immediately after failure of previous nesting attempts. No adult birds were found dead in 1987. However, in 1988, two females were killed at their nests by unknown predators; one male (an FY bird) never re-mated, while the other later was successful in raising a brood with a female that had been previously successful elsewhere in the study area. One male disappeared from a viable nest, and his mate immediately joined an adjacent unpaired male and raised a brood from their first nest.

All 1988 territories were within the boundaries of territories found in 1987, all of which were used one or more times in the previous study (Greaves and

others 1987). One male-initiated nest was begun on the same fork as was used by the same pair in 1987, but abandoned in favor of a site chosen by the female. Another 1988 nest was placed within a meter of a successful 1987 nest by a completely different pair than had nested there in 1987. Many 1988 nests were within five meters of former nests, some dating as far back as 1980.

After noting that one nest had been abandoned subsequent to parasitism in 1988 and another cowbird egg was found, desiccated, beneath a fledged nest, a limited cowbird removal program was undertaken along a quarter-mile section of the Santa Ynez River that was consistently (and, historically) used for mid-day feeding and flocking. Two two-hour periods were required to take seven of the eight cowbirds; the other was shot a mile upstream on the Santa Ynez River in a woodland adjacent to an active least Bell's vireo territory.

In mid-May 1988, five female and three male cowbirds were shot with a 20-gauge shotgun in a part of the study area in which they foraged during mid-day. No further least Bell's vireo nests were found to be affected by cowbirds subsequent to these few removals. Three weeks after the eight cowbirds were shot, a fledged cowbird was seen with a pair of yellow warblers (*Dendroica petechia*) and was also shot. In early July, two cowbird chicks were removed from nests in adjacent blue-gray gnatcatcher (*Polioptila caerulea*) territories, and a female cowbird was observed near one of the two nests. In addition, a cowbird egg had been found in the nest of a pair of common yellowthroats (*Geothlypis trichis*) in 1988; several other species' nests had been found parasitized from 1980-87, including Hutton's vireos, lazuli buntings (*Passerina amoena*), rufous-sided towhees (*Pipilo erythrophthalmus*), and song sparrows (*Melospiza melodia*).

Censuses of other bird species indicated that most species were in lower numbers in 1987 and 1988 than had been found in the previous study. However, in 1988, the number of solitary vireos seemed to increase (from less than a half dozen males in 1987 to 12 males in 1988), and hummingbirds, which were virtually absent during 1987, were abundant throughout 1988, including a tremendous number of Allen's hummingbirds (*Selasphorus Basin*) after mid-June, a species formerly seen only in early spring and late summer in much smaller numbers. Costa's (*Calypste costae*) and Anna's (*C. anna*) hummingbirds predominated, with no verified records in either year of the formerly common black-chinned hummingbird (*Archilochus alexandri*) (Gray and Greaves 1980).

While warbling vireos are widespread throughout the west, their occurrence in sizable populations has not been recorded often: the Gibraltar Reservoir study area contained nearly 100 pairs in the early 1980's (Gray and

Greaves 1980), but was found to have declined as dramatically as the least Bell's vireo had in 1987 and 1988, still out-numbering the latter by a 2:1 ratio. Hutton's vireos breed in a broader ecological area of the west, in more arid regimens, utilizing oak and chaparral woodlands, even when adjacent to riparian areas with sufficient vegetation. In the study area, all four species of vireo were found to use riparian vegetation for feeding, as well as nesting, their foraging and nesting niches separated to some extent by community characteristics, but more often along horizontal boundaries, with warbling vireos using the oak and willow-cottonwood canopies, the solitary and Mutton's using, respectively, interior and exterior edge and understory tree canopies between 4 and 20 feet, with least Bell's vireos nesting generally in weedy situations below 4 feet, in the openings in between thickets, within thickets, and within closed canopied woodlands. All four species foraged in all levels, but generally used the same levels within which they nested for food-gathering and tending fledglings. A more complete discussion of the variety of wildlife in the study area can be found in Gray and Greaves (1980) and Gray and others (1989).

Discussion

It is clear that the rates of return for male and female least Bell's vireos to the same and adjacent territories continue to follow those found in the past (Greaves 1987). While the percentage of females returning from 1987 to 1988 remained about the same (33 percent) as in the past study (31 percent), the percentage of males returning to the same territory (83 percent) in 1988 was far higher than that of males returning to the same territory (63 percent) in the previous study. The primary difference between the size of the study population from 1979-83 (annual mean of 46 males and 40 females) compared to the current population size (annual mean of 23 males and 15 females) may partially account for the difference in male tenacity to sites. With fewer conspecifics nearby and larger areas available for territories, the males may not have been under as much competitive pressure to vacate a territory or shift its center from 1987 to 1988 as they had in the past; females, on the other hand, may change mates or territories from year to year at about the same rate regardless of population size, tenacity based more on success or failure than on affinity to particular sections of the habitat.

Return rates for FY birds was about the same as in the previous study; 18 percent of 1979-82 fledglings, compared to 16 percent of 1987 fledglings, 16 percent being well within the range (11-32 percent) for the previous study. However, the male to female ratio in 1988 FY birds (7:3) was more than double the

total encountered previously (25:23, range 3:4 to 8:5). Individual year samples appear to vary on the order of 2:1. The ratio in 1988 may be within a normally occurring range, since it is not significantly different from the ratio found in 1983 (8:5), a year in which the overall male to female ratio increased to nearly 57:43. Indeed, the smaller population found in 1983 from the previous four seasons, with its greater FY male to female ratio, may have been the first indication in the area that smaller populations would contain a higher percentage of males, such as found in 1987 and 1988.

As a population shrinks, fewer females returning to an area may be one of the first obvious changes: the ratio of males to females in 1983 was slightly less than that found in 1987 (60:40) and 1988 (61:39) but greater than had been previously encountered (51:49 to 54:46 from 1980-82)(Dames and Moore 1987). No data exist as to the male to female ratios for the years 1984-86, so it is difficult to ascertain whether or not the recent ratio is a continuation of a long-term trend or the result of other factors, such as the long drought begun in late 1986 and continued through the 1988 breeding season.

As the study population became imbalanced during the past study period, mate switching by females appeared to increase in frequency. Disturbances at nest sites by predators and cowbirds could account for some normal mate switching behavior, while researchers may account for some of the later increase, roughly paralleling the increase from 1987 when there was relatively little researcher disturbance until adults were banded later in the season to 1988 when there was continued disturbance by researchers. Some evidence exists (Greaves 1987) to partially discount researcher disturbance as the sole cause of increased mate switching. Indeed, if the researcher were a primary cause of disturbance, many tenacious pairs should not have remained together through as many nesting attempts or breeding seasons following handling by the researcher. Cumulatively, however, the effects of predation, cowbirds, researchers, and drought may be sufficient to encourage an increase in the female's natural tendency to switch mates.

If, for instance, other disturbances, such as bulldozer, off highway vehicle, or hiker travel were to occur in an area, these additional pressures could be sufficient to cause areas to be permanently abandoned by females, followed then by the males. Indeed, vast areas within which male least Bell's vireos have been found just outside the study area that appear to contain sufficient habitat for breeding pairs, receive greater amounts of human impacts than the more isolated study area, and do not contain permanent, or consistently occupied territories. Often, only unpaired males are found, which do not remain more than a week in those locations.

The re-use of territories and specific nest sites by a pair of birds from one year to the next appears to be a common strategy among least Bell's vireos (Greaves 1987; Greaves and others 1987). Indeed, such behavior appears to extend to birds occupying adjacent, overlapping territories. In 1988, a pair of vireos built a nest within another unpaired FY male's defended territory. After their nest was predated, a previously successful female joined the unpaired male and they built a nest directly atop the other pair's failed nest, incorporating some of its material. In spite of the availability of nearby habitat for nest sites, the FY male and his new mate chose a site that had been recently used. Unfortunately, it was not an ideal location for a nest, and the female was killed by a predator while still laying eggs in the new nest. Only one other nest had ever been re-used: of 469 nests observed, it was a doubly successful nest for the male that defended it, raising two broods, each with a different female (Greaves 1987). Thus, while failure may preclude the likelihood that a nest or site will be re-used during a given season, often encouraging the birds to move great distances for subsequent nesting attempts, success appears to encourage the re-use, even from year to year, of specific locations, often to the exact fork on the host plant.

Thus, disturbances that cause nest failures may contribute to the tendency of females to switch mates. This would allow the female a greater array of nest site alternatives, but does not seem to increase the likelihood of success for that female or her mate during any given season. Indeed, monogamy proved to be a more reliable strategy during the previous study for increased nest success (Greaves 1987). A greater number of second successful nests arose from second nesting attempts by a monogamous pair than among those arising from sequential matings in the current study population as well.

There is insufficient past or present data from the study area to indicate any predator- or cowbird-related causes for the decline in the least Bell's vireo population. Drought has been mentioned as a likely explanation for the decline of many of the local species. Censuses conducted along the Salinas River in 1987 indicate that drought or adverse local weather conditions may have been the primary factor in depressing most riparian bird species during the 1987 breeding season (Greaves 1988). Simultaneous with the decline of least Bell's vireos in Santa Barbara has been a tremendous increase in the species in other populations in southern California. While it might be convenient to attribute all the decline of birds in the study area to drought, there are several other factors which should be considered, among which is the difference in the manner in which the Santa Barbara and other populations have been managed to ameliorate the effects of cowbirds.

Cowbird trapping programs have been conducted at several of the other southern California sites for at least four breeding seasons, while only in 1988 were adult cowbirds taken out of the habitat in Santa Barbara. The primary control method used in the past in Santa Barbara was the removal of cowbird eggs or chicks from any nests in which they were found. The cumulative effects of parasitism might have led to decreased successful reproduction by birds in nearby areas, as well as in the study area among birds not studied. Populations of most other species could have slowly declined during that period to their current levels. There appears to be no direct evidence on how the cowbird has caused any particular species or community of birds to decline or change over time. Only circumstantial evidence suggests that cowbirds have lowered populations in many southern and central California regions. By inference, the conclusion has been drawn that previously high rates of parasitism, along with the virtually failed reproductive efforts on the parts of least Bell's vireos in several of the populations, may account for the loss of adult vireos from the Santa Barbara area. With no young produced in other localities, it is apparent that the other populations cannot provide dispersers to colonize new, or repopulate older, areas with additional breeders. Conversely, in areas from which cowbirds have been removed in large numbers, many populations appear to be making remarkable recoveries. (Data on file, U.S.F.W.S., Laguna Niguel, California.)

In addition, the problem of population viability needs to be addressed. We currently do not know what constitutes a viable genetic pool among least Bell's vireos. The high rate of return among FY birds to the Santa Barbara study area might indicate the absence of other areas into which they might have dispersed for breeding. Combined with a dearth of breeders filtering into the area from other drainages, the effects could be the inter-breeding of siblings and of parents with their young. So far, there has been no evidence of either occurrence, in both the current as well as the past study at the site. Thus, the high return rate of FY birds might indicate that previous assumptions about return rates for FY birds need to be reconsidered. Other studies and their accompanying conclusions about survival rates among FY birds, such as that conducted by Nolan (1978), were made on small parts of larger populations, the boundaries of which were not as readily apparent as those found along the narrow riparian corridor in the several least Bell's vireo study areas. Four percent of previously fledged prairie warblers (*Dendroica discolor*) returned to breed within his study population, compared to a ratio (based on plumage characteristics) of 2:1 for after-second-year (ASY) to FY males, a ratio comparable to that encountered at Gibraltar Reservoir in 1988 when 14 ASY and 7 FY males were identified.

(Unpubl. data on file, Greaves.) Only with continued monitoring of all least Bell's vireo populations, will it be possible to discover whether a 16 percent survival rate is, as suggested by Nolan, rather high for FY birds in general, or whether, due to the inability of researchers to adequately cover the vast areas in which the warblers bred and ultimately dispersed, one might expect a higher number of young to survive to breeding, as appears to be the case among least Bell's vireos from the Santa Barbara area.

Until there is evidence of large numbers of FY birds from one drainage becoming breeders in other drainages, management objectives for least Bell's vireos should assume a high degree of isolation from each other of the more distant populations, especially where the distance is as great as that between Santa Barbara and its nearer large least Bell's vireo breeding centers nearly 150 miles to the south. Each population should be considered to be its own source of replenishing, future genetic material, and projects tailored to that interpretation of observed behavior. With a return to regular weather patterns, such as existed during the late 1970's and early 1980's, bird populations may re-establish themselves in former numbers. By continuing banding research and cowbird removal programs, we will provide a future data base from which to obtain answers to the questions raised above.

Conclusions and Management Recommendations

It is clear that males and females respond differently to factors in the environment that affect territoriality and site tenacity. Males establish and vigorously defend well-defined areas within the study area, while females move from one area to the next until they find mates whose territories contain the requisite habitat characteristics that they need for breeding. First-year birds constitute a sizable and important part of each population, and may be limited in their options of dispersal sites, preferring to return to their natal area in much higher than previously assumed numbers. Weather-induced changes in population may affect male: female ratios, and alter reproductive results sufficiently to temporarily depress breeding populations in one area while increasing them in other areas less affected by the adverse weather patterns. While there appears to be a correlation between cowbird removal and increases in local populations of least Bell's vireos, no direct evidence has been gathered to indicate that the entire California and Mexican population of least Bell's vireos has declined solely due to cowbird depredations.-

The above factors must be considered by managers when undertaking or mitigating projects that remove

least Bell's vireo breeding habitats. Other objectives that should be considered by researchers and managers immediately include the following:

1. Declare Critical Habitat for those larger populations, where the Department of the Interior has delayed such designations for more than two years from its original mandate.
2. Continue research on dispersal and return rates for at least another five years, using banding studies wherever feasible.
3. Continue cowbird removal programs in all areas where least Bell's vireos breed to ensure that cowbirds do not have major impacts on reproduction of riparian avifauna.
4. Maximize habitat diversity along riparian corridors, creating or increasing buffer zones between natural settings and surrounding altered or degraded areas.
5. Conduct major revegetation programs on all major streams in California, using as guides data collected during studies of riparian systems throughout the southwest, paying close attention, for least Bell's vireos, to such studies as conducted by Olson and Gray (1989).
6. Eliminate all detrimental human activities in flood-plains.
7. Recognize the importance of least Bell's vireo habitats to other riparian obligate and non-obligate species (Gray and others, 1989; Hunter and others 1987; Johnson and others 1987).
8. Recognize the importance of individual birds to the entire state-wide populations of endangered species, such as the least Bell's vireo. We should not wait until a species reaches the critical stage as that of the California condor (*Gymnogyps californianus*) or the extinct state of the dusky seaside sparrow (*Ammodramos maritima nigrescens*) before considering the individual bird expendable.
9. Protect and enhance isolated habitat islands within which apparently unpaired males may be encountered. With the tendency of females to wander between mates, isolated males may be important to tying together the apparently isolated sub-populations of the species. All smaller populations should be considered, therefore, to be dynamic parts of a larger state-wide or regional population, in spite of the current data suggesting that all populations may be reproductively isolated from one another.

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