NEST-SITE TENACITY OF LEAST BELL'S VIREOS

JAMES M. GREAVES, 327 W. Islay Street, Santa Barbara, California 93101

In 1978, the total population of Least Bell's Vireo (*Vireo bellii pusillus*) was estimated at 90 pairs (Goldwasser et al. 1980). With the expected listing of the subspecies as endangered by the California Fish and Game Commission, and interest in listing it at the Federal level, information on the vireo's breeding biology and population dynamics was needed. No such data were available, and studies of the nominate subspecies (*V. b. bellii*) addressed only reproductive rates and nesting substrate with data gathered from small samples over many years (Overmire 1962) or reported sample sizes too small (Mumford 1952; Nolan 1960; Barlow 1962) to be useful for analysis of population dynamics. For five breeding seasons, 1979-1983, I conducted a banding study of a Least Bell's Vireo population at Gibraltar Reservoir, Santa Barbara County, California, in order to assess the population's dynamics. My investigation reveals new information about the vireo's mating system and territoriality that raises serious questions that managers of its breeding habitats must understand and adequately address.

METHODS

I used unique combinations of U.S. Fish and Wildlife Service aluminum bands and colored plastic bands to mark the vireos. Beginning in 1979, I began banding nestlings, and in 1980 I began mist-netting adults. I continued the banding through the 1983 season.

I surveyed the adult population at least once a week in 1979, by walking through the study area and marking the locations of singing adult males, pairs, and nests on aerial photographs and maps. Counts were made by listening for males and searching all habitats in and adjacent to the riparian willow-cottonwood forests in the study area. Habitat descriptions of the study area can be found in Gray and Greaves (1984). Eighty percent of the contiguously occupied habitats constituted the study area.

Data on breeding success by males and females were compared by means of chi-square contingency tables. I compared data by sex and whether the birds were monogamous or polygamous within a season. Successful nests were those that fledged at least one young vireo. Territories were areas with readily discernible and defended boundaries (either stream courses or particular trees or shrubs) that were generally reused from year to year. Nest sites were smaller locations within a territory, usually a single shrub or a clump of weeds or shrubs.

RESULTS

I banded 40 adult males, 42 adult females, and 312 nestlings or fledglings. Forty-eight of the young returned during subsequent years as 25 males and 23 females. From 1980 through 1983, a cumulative total of 185 males and 161 females (yearly mean, 46 and 40, respectively) was found in the study population. Of these, 114 males and 105 females (yearly mean, 29 and 26,

respectively) were banded, and represented 65 individual males and 65 individual females, of which 57 males and 65 females attempted to breed at least once. Actual annual sex ratios from 1980 to 1983, including unbanded birds, were 50.5:49.5 (n = 91), 53.9:46.1 (n = 89), 53.3:46.7 (n = 90), and 56.7:43.3 (n = 76), respectively.

Males and females act differently in regard to nest site fidelity. Of 48 returns by 26 banded males, 63% were to the same territory and 85% were to the same or adjacent territory. Of 29 returns by 19 banded females, only 31% were to the same territory and 59% were to the same or adjacent territory. Forty-one of 50 banded males (82%) and 19 of 44 banded females (43%) remained faithful for the duration of the study to the territory in which I first detected them.

Twenty-two females were sequentially polyandrous, and 12 males were sequentially polygynous. Polyandry consisted of females moving from one territory to another, with polygyny the result of a new female joining a territorially tenacious male after its prior mate(s) had moved elsewhere. In addition, I suspected several instances of simutaneous polyandry and one of simultaneous polygyny.

Forty-two of 57 banded males (74%) and 43 of 65 banded females (66%) successfully raised at least one nestling to fledging. Of birds breeding for a second year (SY), 37 of 51 males (73%) and 41 of 57 females (72%) bred successfully at least once. Of all birds, banded and unbanded, 62 of 98 males (63%) and 65 of 98 females (66%) were successful. At least 57 of 86 monogamous males (66%) and 51 of 78 monogamous females (65%) were successful. The only significant difference was between monogamous and polygamous males at the 90% confidence level, with monogamy the more successful form. None of the other comparisons was significant at that level, and none approached the 70% confidence level.

Most territories remained centered on the same clump of shrubs or small trees throughout the study, but in some the centers shifted while remaining within the boundaries of previous territories. From 1980 through 1982, however, some larger areas containing a few territories became more crowded. One section contained four territories in 1980 and 1981 but had seven territories in 1982. In 1983, only two territories were found in the same area.

From one year to the next, nest sites were generally in the same clump of shrubs, even when different males and females were found on the territory. A few nests were found in the same shrub within a few feet of the nest of the previous season. Only three nests (n = 403) were on the exact fork or immediately above the previous season's fork. Only one nest was used more than once, by a male that was successful in raising two broods, one with each of two different females, both of which were themselves polyandrous.

Females switched mates following either the success or failure of a nest. No switching was observed during the actual care of a clutch or brood. In 1983, a first-year banded female successfully raised a brood of four with one male, then immediately moved to an adjacent, unpaired male who had previously failed with an unbanded female. Another, older banded female raised a brood of four with one male and then moved to an unmated male who had been constructing a nest several territories away prior to the fledging of his prospective mate's first brood. He was then seen feeding at least

one of the two accompanying banded fledglings, while his new mate proceeded to lay eggs in his nest. Such moves as these discounted the interpretation that handling by humans may have affected the behavior of the birds, causing them to move to avoid disturbance.

DISCUSSION

Within-season mate switching by females was sufficiently frequent to suggest that males and females use different strategies to maximize reproductive success. Most passerine species have been presumed to be strictly monogamous (Möller 1986), though some exhibit varying degrees of polygamy (Fitch and Shugart 1984). There have been no other reports of polygamous behavior among the Vireoninae. While an increasing number of articles have described and attempted to explain advantages and causes of polygamy (Orians 1969; Leisler 1985), few examples of polyandry have been documented among passerines. Most examples of polygamy address polygyny in several small passerines (Möller 1986). Graul et al. (1977) attempted to explain possible factors influencing polygyny and polyandry. Verner and Willson (1966) discussed the influences that habitats might have on mating systems, and predicted that polyandry should be a rare occurrence among passerines.

Gowaty (1981), in describing mating strategies other than polygyny, defined sequential polygamy as "mating and parenting which occurs without significant overlap between successive mates," meaning that a female would contribute substantially to the raising of a first brood before attempting another brood with a new mate. This strategy describes the sequence of events that I found at Gibraltar Reservoir.

The apparent availability of unmated males in the study population might be sufficient enticement to nearby females to encourage mate switching, whether the females were successful or not with their first mates. Indeed, Smith et al. (1982) suggested that polygyny was a result of a similar, though opposite, sex bias in Song Sparrows. Most such examples of polygyny, however, are of primary and secondary females simultaneously mating with one male and brooding clutches presumably both fathered by the single male. I found no such simultaneity in the population I studied. In fact, polygamous behavior appeared to be only one of several means that females used to maximize their reproductive success. Many females dwelt in large territories containing an abundant supply of nest sites, allowing the pair to build numerous nests, even though all failed. The avilability of nearby, unpaired males did not seem to distract many repeatedly unsuccessful females from monogamy while, simultaneously, other successful females switched mates immediately after completion of nesting duties in their first territories, often traveling more than a mile to a new territory containing a previously unpaired male.

The data on mate switching and between-year site fidelity together show that males and females have developed different strategies regarding nest site selection and fidelity. Males establish and maintain fixed territories, while females search for one mate among many who possesses a suitable nesting location. Females view the entire area of habitat as one large potential territory from which they may select one or more mates during their lifetimes.

Indeed, only 3 of 26 males retained the same mate from one season to the next.

The strategy of the female, viewing the habitat area as one large potential territory, could result in greater genetic mixing. The male becomes more familiar with his territory and its resources, so he is better able to provide the young with the necessary food while they are in the nest and to lead them to good foraging areas once they have fledged. The female is free either to remain with her young or to move to another male with whom she can start a new brood. Even though many successful broods were followed almost immediately by another attempt with the same mate, the ability to move to another male, whether or not the necessity arises, presents the female with a greater array of opportunities for success than she might have had if she remained strictly monogamous.

A clear understanding of the vireo's relationship with its breeding habitats is important for management of this species. The primary implication for proper management of its breeding habitats is as follows: the males and females obtain a territory differently, with the males being tied much more closely to a certain plot of habitat. Managers should be aware that actions that disturb or alter the vireo's habitats might not affect the more tenacious male but could be sufficient to drive females from the disturbed area. The male Least Bell's Vireos that are scattered on isolated territories throughout southern California may be defending territories that are inadequate to meet a female's needs. The presence of a singing male does not establish the presence of a female or that the habitat is suitable for a breeding pair.

Mistakes of past management of other endangered passerines should be used as lessons in methods to be avoided or altered by managers of the Least Bell's Vireo. Understanding of these errors should be combined with factual data and the proper understanding of these data. With such a synthesis, we can better ensure that the Least Bell's Vireo and its breeding habitats will recover their place as viable members of our natural heritage.

ACKNOWLEDGMENTS

S. Laymon ran statistical tests and helped edit the paper. M. Freel continued Forest Service support begun by P. Schempf. The U.S. Fish and Wildlife Service, through P. Sorensen and S. Wilbur, encouraged and supported research. A. Craig of California Department of Fish and Game helped find funds to continue the research. V. Gray conducted invaluable vegetational data collection and analysis. P. Collins and D. Schroeder offered criticism and advice on methods and analysis of field work. P. Collins and V. Gray provided editorial assistance with manuscripts.

LITERATURE CITED

Barlow, J.C. 1962. Natural history of the Bell Vireo, *Vireo bellii* Audubon. Univ. Kan. Publ. Mus. Nat. Hist. 12(3):241-296.

Fitch, M.A., and Shugart, G.W. 1984. Requirements for a mixed reproductive strategy in avian species. Am. Nat. 124:116-126.

Goldwasser, S., Gaines, D., and Wilbur, S.R. 1980. The Least Bell's Vireo in California: a de facto endangered race. Am. Birds 34:742-745.

Gowaty, P.A. 1981. An extension of the Orians-Verner-Willson model to account for mating systems besides polygyny. Am. Nat. 118:851-859.

Graul, W.D., Derrickson, S.R., and Mock, D.W. 1977. The evolution of avian polyandry. Am. Nat. 111:812-816.

Gray, M.V., and Greaves, J.M. 1984. The riparian forest as habitat for the Least Bell's Vireo (*Vireo bellii pusillus*), in California Riparian Systems: Ecology, Conservation and Reproductive Management (R.E. Warner and K.M. Hendrix, eds.), pp. 605-611. Univ. Calif. Press, Berkeley.

Leisler, B. 1985. Ecological and behavioral prerequisites for the evolution of polygamy in Reed Warblers (*Acrocephalus*). J. Ornithol. 126:357-381.

Moller, A.P. 1986. Mating systems among European passerines: a review. Ibis 128:234-250.

Mumford, R.E. 1952. Bell's Vireo in Indiana. Wilson Bull. 64:224-233.

Nolan, V., Jr. 1960. Breeding behavior of the Bell vireo in southern Indiana. Condor 62:225-244.

Orians, G.H. 1969. Evolution of mating systems in birds and mammals. Am. Nat. 103:589-603.

Overmire, T.G. 1962. Nesting of the Bell vireo in Oklahoma. Condor 64:75.

Smith, J.N.M., Yom-tov, Y., and Moses, R. 1982. Polygyny, male parental care, and sex ratio in Song Sparrows: an experimental study. Auk 99:555-564.

Verner, J., and Willson, M.F. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology 47:143-147.