Wilson Bull., 104(3), 1992, pp. 425–433

WINTER TERRITORIAL BEHAVIOR OF GRAY VIREOS

JOHN M. BATES[1]

ABSTRACT.—I studied a color-marked population of wintering Gray Vireos (*Vireo vicinior*) over two seasons (1985–1986 and 1986–1987) on study sites near Puerto Lobos, Sonora, Mexico. Some individuals had been banded as early as three years previously. Ten of 14 (71%) vireos banded in the winter of 1985–1986 returned to the same territories in the following winter. Territories were defended throughout the winter and averaged 0.9 ha in size. Territorial interactions occurred frequently along boundaries as neighbors trespassed to forage on each others' territories. Most birds appeared to defend individual territories, and both males and females probably held territories. *Received 2 July 1991, accepted 18 Dec. 1991.*

In a review of the literature on avian competition in the nonbreeding season, Greenberg (1986) noted that only a few studies had been carried out on territorial wintering birds over the entire winter season (Schwartz 1964, Myers et al. 1979, Rappole and Warner 1980, Greenberg 1986). Despite the lack of detailed studies, Greenberg suggested that territoriality is common among small insectivorous passerines in winter. Since Greenberg's review there have been several additional studies (Holmes et al. 1989, Ornat and Greenberg 1990), but we still lack basic data on demography and behavior of most insectivorous migrants in the nonbreeding season. Most information about vireos in winter is restricted to geographic distribution and habitat selection (Barlow 1980; but see Tramer and Kemp 1980, Greenberg, in press). The present study addresses aspects of territoriality and foraging behavior for Gray Vireos (*Vireo vicinior*) wintering along the coast of Sonora, Mexico. Data I present here include five seasons of banding data of which two include data on a group of color-banded wintering Gray Vireos.

Gray Vireos breed in open pinyon pine and juniper woodland and in the ecotone between this habitat and several types of lower elevation chaparral habitats from central Texas to California and Baja California and from southern Nevada and Utah to southern Arizona, southwestern Texas, and northern Coahuila, Mexico. Most Gray Vireos winter in the deserts surrounding the Gulf of California (A.O.U. 1983); however, there apparently is an isolated population of unknown size wintering in the Chisos Mountains of Texas (Barlow and Wauer 1971). Gray Vireos arrive on their wintering grounds in mid-September and remain through the end

[1] Dept. of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, Arizona 85721. (Current address: Museum of Natural Science and Dept. of Zoology and Physiology, Louisiana State Univ., Baton Rouge, Louisiana 70803.)

of April. Thus, most of these birds spend seven months of the year in a desert region that receives as little as 100 mm of rainfall annually.

STUDY SITES AND METHODS

The two study sites, Arroyo San Lorenzo (30°17′N, 112°48′W) and Cerro Prieto (30°19′N, 112°48′W) are south and north, respectively, of Puerto Lobos, Sonora, Mexico, on the eastern shore of the Gulf of California. The Puerto Lobos area is part of the Lower Colorado River Valley subdivision of the Sonoran Desert Scrub biome (Turner and Brown 1982), but the arroyos at the study sites share vegetational features with central Gulf Coast flora found farther to the south. These arroyos are dominated by "stem succulents," including two species of elephant tree (*Bursera hindsiana* and *B. microphylla*) and two species of columnar cacti (*Pachycereus pringlei* and *Lophocereus schottii*). Also common in the arroyos are jojoba (*Simmondsia chinensis*), sangre-de-drago (*Jatropha cuneata*), wolfberry (*Lycium* sp.), and ironwood (*Olneya tesota*). The surrounding hillsides are sparsely vegetated, primarily by creosotebush (*Larrea tridentata*) and white brittlebush (*Encelia farinosa*).

The study site at San Lorenzo is a desert arroyo (wash) roughly 2 km long and about 100 m wide that is the main drainage from a group of hills several km east of the coast. A large alluvial fan covered with teddy bear cholla (*Opuntia biglovi*) runs along much of the north edge of the site and steep canyon walls border much of the southern side. Searches conducted both upstream and downstream from the area revealed vireos in densities similar to those on the site. There are several small sparsely vegetated side canyons to the north and south where vireos also maintained territories. The much smaller Cerro Prieto site occupies a shallow drainage that runs along the base of an isolated volcanic hill into coastal dunes 0.5 km from the coast. On this site, all territories were in the main drainage. Although these study sites are about 10 km apart, they have similar vegetation and fauna, and for most aspects of the study, they have been considered together.

Field work was conducted on seventeen three-to-five-day trips to the study areas: four during winter 1985–1986 (first date of trips: 11 January, 27 February, 15 March, 4 April); 12 trips during the winter of 1986–1987 (first date: 5 September, 25 September, 2 October, 25 October, 10 November, 28 November, 11 December, 2 January, 12 January, 27 February, 18 March, 4 April) were during the winter of 1986–1987, and a return trip in 1988 (first date: 2 January).

In the first winter of the study, I tried to capture and mark as many vireos as possible. In contrast, during the 1986–1987 winter, mist netting was done on an irregular basis, usually to catch unbanded birds seen in certain areas and also to provide information on the movements of previously banded birds. All captured vireos were weighed, measured and banded with a unique three-color band combination and a U.S.F.W.S. aluminum band. During the winter of 1986–1987, 25 entire days and 22 half-days (296 h, 11 trips) were spent primarily gathering data on movements and other behaviors of individually marked birds. "Full" days were days when 100% of the daylight hours were spent on the study sites. On half-days, the morning or late afternoon hours were spent on the sites, but not both.

I mapped each study area by establishing one transect through each of the sites with stakes placed every 30 m. Plants and other features could be located relative to one another by pacing their perpendicular distance from the transect with the aid of a compass. Most of the time on the study sites was spent wandering through the sites in search of vireos. Whenever a vireo was encountered, either by sight or by vocalization, I attempted to identify it by color-band combination and follow it for as long as possible. Movements and positions of birds were noted in the field and plotted on study site maps. I determined territorial boundaries of the birds by mapping all movements observed for each bird. From these data,

TABLE 1
NUMBER OF RETURNING MARKED GRAY VIREOS TO TWO STUDY SITES IN SONORA, MEXICO, OVER SIX WINTERS

	Years after initial marking					
	1	2	3	4	5	6
Number marked	39	18	4[a]	4	3	2
Number resighted	18	11	4	3	2	1

[a] Seven birds banded first in the 1985–1986 winter were not followed after the 1987–1988 winter; thus it is not known whether or not they returned for a third winter.

I determined territory size as well. I made special note of areas where there were repeated confrontations between color-banded individuals. I also collected data on foraging, which is presented elsewhere (Bates, in press). Field data were dictated into a cassette recorder and later transcribed into field notebooks.

RESULTS

Banding data—S. M. Russell banded Gray Vireos and other species on the San Lorenzo study site for several days each spring, beginning in March of 1983 and continuing through March 1985. Of 39 Gray Vireos banded by Russell or me (including birds from Cerro Prieto) between March 1983 and the spring of 1987, 18 (46%) were observed or netted the winter following banding, and 11 of those 18 (61%) of marked birds that returned the first winter also returned the second year (Table 1). Because wintering Gray Vireos are difficult to observe or capture, and more than several days are required to detect all individuals at a site, these values are an underestimate of the actual return rate. This can be seen in the return data from the winters in which the sites were intensively studied.

From January through April, 1986, I color banded 14 birds on the two study sites. Ten of these 14 birds (71%) returned in the winter 1986–1987. An additional bird with an aluminum band was seen at the San Lorenzo site in January 1986 where in the 1986–1987 winter I caught and color banded a bird banded previously by Russell. Despite spending only four days on the sites in January 1988, I relocated eight color-banded birds. One of these birds was banded by Russell in March 1983, indicating that the bird was going through at least its sixth winter (Table 1) and had been captured or observed in the same area on the San Lorenzo site in all but one of these winters. Another individual also was banded in March 1983 and was spending its fifth winter on the sites in 1986–1987. Neither bird was found in the 1984–1985 winter, but this probably means they were not mist netted, not that they were not present (Russell pers. comm.).

During the 1986–1987 winter, some individuals were encountered only once or a few times, whereas other birds were seen repeatedly. No birds had arrived when I made the 5 September trip, but eight of 18 birds observed on the sites early in the season were seen on at least five of the 11 other trips. On some trips, an individual was not positively identified by color-band combination, but vocalizations were heard within the bird's territory. No individual bird was detected on all of the 11 trips due to the often secretive behavior of the species during the nonbreeding season and to the apparent departure of some individuals prior to April 2, when the last visit to the sites was made.

Evidence for territoriality—The behavior of wintering Gray Vireos can be defined as territoriality because the vireos actively exclude conspecifics from specific areas throughout the season. This active defense of an area against conspecifics distinguished territories from home ranges (Munger 1984). Neighboring birds were frequently seen in disputes that involved vocalizations and chases. These events occurred in the same areas throughout the winter. Disputes started when one bird was detected trespassing on another's territory. After a chase, one bird would usually give a trill that would be answered by the other. These trills are peculiar to Gray Vireos relative to other vireo species. The vocalization is almost never heard on the breeding grounds (pers. obs.), yet it is the most frequent vocalization on the wintering grounds (Bates 1987). The birds would square off across the same area each time. If the trills were close together along the boundary, one bird would usually move away from the boundary soon after the incident, and often, one or both birds would begin to sing. These types of interactions also occurred where other territories came together, and trilling and occasional singing were heard from two to three birds on adjacent territories throughout the winter. Pairs of trills given by one bird, and then another, and chases such as described above were also heard and seen along other territorial boundaries throughout the study sites, although in many cases flights of the birds and the dense vegetation prevented identification of the individuals involved.

Over the course of the winter, territories generally did not change, and behavior of birds seen outside what was thought to be their territories was different than behavior on the territory (see below). Territories appear to be stable from year-to-year, as all 11 color-banded birds that returned in the winter of 1986–1987 returned to areas that included the sites at which they were captured in the previous winter. This was also true of the eight color-banded individuals seen in January 1988. The two oldest banded birds on the site were seen or netted over at least five winters in the same parts of the San Lorenzo site (Russell, pers. comm.; Bates 1987).

Mean (±SD) territory size for Gray Vireos was 0.9 ± 0.36 ha (N = 9,

range = 0.3–1.4 ha). The distribution of vegetation in the arroyos caused vireo territories to be linearly arranged. Thus, some of the boundaries for each bird abutted unsuitable habitat such as the cholla-dominated fan to the north of the San Lorenzo site.

Movements of marked and unmarked birds.—During the 1986–1987 winter, one vireo netted in early October was not seen again; another was seen in October and November but not afterwards. Three other birds caught in the central portions of the study areas for the first time early in fall 1986 were seen again. One of these birds was seen throughout the winter. It defended a small portion of the main arroyo at San Lorenzo, and apparently expanded its territory to include more of the arroyo as the winter progressed. The other two birds appeared again on the Cerro Prieto study site on well-defined territories of other individuals in late March. In both cases the territory holder was not seen during late March. Considering the time of year and that one of the reappearing birds was singing from an exposed perch, the territorial bird had probably migrated from the study site. These birds may represent first-winter birds, but they may also represent older birds with territories off the study site.

In late September and October, unbanded birds on the sites are to be expected as birds arrive and territories are established. Once territories are re-established, unbanded birds should become less frequent. Only five sightings of unbanded birds on the main study areas were recorded from November to May 1987. These sightings are thought to represent four individuals, perhaps wandering birds seeking unoccupied areas, or trespassing birds from territories off the study sites. No influx of unbanded vireos was observed in the spring.

Evidence for trespassing.—Color-banded individuals were often observed crossing or having crossed into a neighbor's territory. On two occasions, I mist netted trespassing color-banded birds in the middle of territories adjacent to their own. Birds holding territories adjacent to one another would frequently enter each other's territory. When a bird reached the edge of its territory it would often continue foraging silently into the next territory until detected by the territorial holder. One bird penetrated as far as 70 m into a neighbor's territory. This behavior occurred throughout the winter. Trespassing did not seem attributable to ill-defined boundaries. Once a territorial bird detected a neighboring invader, a chase ensued followed by trills by one or both birds and often countersinging across an open area. This was repeated in the same area, with the birds even occupying the same two bushes on several different occasions. I have observed the same behavior in individuals wintering in similar habitat in the Sierra Pinta Mountains of southwestern Arizona 150 km north of Puerto Lobos.

Trespassers were silent and foraged inconspicuously in the densest vegetation available. The only trespassing bird I heard vocalize on a neighbor's territory was a bird in April on the territory of a neighbor that had already migrated. Gray Vireo behaviors such as those exhibited by trespassing neighbors match descriptions of behavior in wintering Hooded Warblers (*Wilsonia citrina*) considered to be nonterritorial or floating individuals (Rappole and Warner 1980). During the entire study, I observed only four individuals that may have been "floaters." My observations of Gray Vireos indicate that most aggressive interactions in the winter, even ones involving long chases, result from the detection of a trespassing neighbor, not a nonterritorial "floater." On two occasions, territory holders disappeared from the sites; however, this resulted not in a floating bird's gaining a territory, but in a neighbor's expanding its territory to include part of the unoccupied area.

DISCUSSION

Our knowledge of migrant birds on their wintering grounds is growing; however, with few exceptions (Myers et al. 1979, Price 1981) studies that have monitored wintering populations across the entire winter period have been limited to members of the Parulidae (Schwartz 1964, Rappole and Warner 1980, Holmes et al. 1989, Ornat and Greenberg 1990). Therefore, my description of Gray Vireo winter territorial behavior is an addition to this body of literature and can be compared to and contrasted with it.

Between-year site fidelity observed in Gray Vireos is similar to that described for Greenish Warblers (*Phylloscopus trochiloides*) in India (Price 1981). The 46% return rate for all banded Gray Vireos the year following banding and the 71% return rate for Gray Vireos banded in 1985–1986 are comparable to the 52% return rate for all Greenish Warblers Price studied, and a 67% return rate for Greenish Warblers returning to undisturbed habitat. Similarly, Nesbit and Medway (1972) reported a 63% return rate for Eastern Great Reed Warblers (*Acrocephalus orientalis*) in Malaysia. The overwinter site fidelity in the vireos is high, similar to that reported for Black-throated Blue Warblers (*Dendroica caerulescens*) wintering in Jamaica (Holmes et al. 1989), but not as high as that reported for American Redstarts (*Setophaga ruticilla*) in the same study.

Differences between Gray Vireos and other species are probably related to the vireos' unusual winter range and strong preference for wintering in coastal desert areas dominated by elephant trees (*Bursera microphylla*; Bates, in press). For Greenish Warblers (Price 1981) and for Northern Waterthrushes (*Seiurus noveboracensis*) in Venezuela (Schwartz 1964), individuals that had wintered farther south began migrating north through

areas with wintering populations before the local wintering individuals had departed. This pattern of movement was not seen in the vireos, perhaps because the birds have a relatively short migration route compared to those of the warblers and waterthrushes. There are very few records of either spring or fall migrant Gray Vireos away from known breeding or wintering localities.

Gray Vireos also defend larger winter territories than have been reported for other species. Price (1981) found Greenish Warbler territories to average only six trees, and Rappole and Warner (1980) reported the average territories of wintering Hooded Warblers and Wood Thrushes (*Hylocichla mustelina*) in tropical forest in Veracruz, Mexico, to be only 0.25 ha, or one-fourth that of the average Gray Vireo winter territory. Gray Vireo winter territories are still smaller than the 2.4 to 8 ha breeding territories reported for the species in central Arizona and Texas (Barlow 1978).

There is evidence that sexual segregation in the winter, as has been reported for some sexually dichromatic parulids (Lynch et al. 1985, Holmes et al. 1989, Ornat and Greenberg 1990), does not occur in monochromatic Gray Vireos. This suggests that vireos are similar to Greenish Warblers (Price 1981), another monochromatic species. Price found both male and female Greenish Warblers sang and held territories. Although I was unable to determine the sex of birds on my study sites, of eight Gray Vireo specimens (Univ. Arizona) collected in March from the same habitat at a site in Sonora, Mexico, 90 km south of Puerto Lobos, four are males and four are females, suggesting no segregation occurs in this portion of the species' winter range. Furthermore, Barlow and Wauer (1971) also reported collecting both males and females wintering in the Chisos Mountains, Texas. Thus, there is no evidence for sexual segregation in the nonbreeding season on a large geographic scale.

It is not known whether there might be behavioral dominance between sexes (or age classes) at a site as has been found in wintering American Redstarts (Holmes et al. 1989). J. C. Barlow (pers. comm.) suggests that only male Gray Vireos respond by singing to playback of recorded songs in winter. If this is true, then most of the individuals that I followed for extended periods of time were males (although no individuals on the study sites responded consistently to playbacks of recorded songs). Two birds that were never heard singing despite being seen regularly throughout the study, may therefore have been females. These birds also had small territories (0.3 and 0.6 ha).

The trespassing behavior of the vireos is similar to that described for "floating" Hooded Warblers wintering in Mexico (Rappole and Warner 1980). These authors cited three reasons indicating that there were a substantial number of nonterritorial individuals, or floaters, on their sites

in southern Mexico (1) These individuals were captured throughout the winter on other birds' territories; (2) These individuals took over territories of occupants given the opportunity; and (3) Movement and other behaviors of these individuals were different from those of territory owners. All three of these traits were exhibited by territory-holding neighbors in my study, suggesting that an individual on another bird's winter territory is not necessarily a floater.

Two hypotheses might explain the high frequency of trespassing that I observed in Gray Vireos. First, trespassing may allow a bird to obtain additional resources at little cost, without depleting the ones that it defends. The other is that trespassing may be a challenge to a neighboring bird, testing whether that neighbor is capable of defending its territory. This may be especially true near the end of the winter, when birds were observed foraging and even singing on adjacent territories recently vacated by birds that had apparently left the study area. Trespassing does not undermine the adaptive nature of territoriality. Although a cost of leaving a territory to trespass is that another bird may forage on the undefended resources (for the vireos this is fruit of *B. microphylla* and insects; Bates, in press) of the trespasser, earlier defense of a territory probably deters some usage of those resources by another individual even without the physical presence of the defender. The trespasser benefits immediately in terms of depleting a resource that it does not defend, and it may also gain information about resources in areas that might become vacant in the future.

ACKNOWLEDGMENTS

Assistance with field work came from a number of people whose help is greatly appreciated, especially that of R. Bowers and R. Bates. The people of Puerto Lobos, Sonora were always friendly and helpful. S. Russell and R. Bates provided advice and encouragement throughout the work, which was shaped by discussions with T. Myers, J. Dunning, R. Greenberg, B. Harney, T. Huels, and K. Rosenberg. The manuscript benefited from the criticism of M. Balph, K. Burns, P. Marra, J. Remsen, B. Winternitz, and R. Zink. Banding supplies were purchased with a grant from the James R. Silliman Memorial Fund.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. 6th edition, A. O. U., Washington, D.C.

BARLOW, J. C. 1978. The effect of habitat attrition on vireo distribution and population density in the northern Chihuahuan desert region—U.S. and Mexico. Pp. 591–596 *in* Trans. symp. biol. resources of the Chihuahuan Desert region—United States and Mexico (R. H. Wauer and D. H. Riskind, eds.). Natl. Park Serv. Trans. and Proc. Series, No. 3.

———. 1980. Patterns in ecological interactions among migrant and resident vireos on the wintering grounds. Pp. 97–107 *in* Migrant birds in the Neotropics: ecology, behavior,

distribution and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Inst. Press, Washington D.C.

——— AND R. H. WAUER. 1971. The Gray Vireo (*Vireo vicinior* Coues; Aves: Vireonidae) wintering in the Big Bend region, west Texas. Can. J. Zool. 49:953–955.

BATES, J. M. Frugivory on *Bursera microphylla* (Burseraceae) by wintering gray vireos (*Vireo vicinior,* Vireonidae) in the coastal deserts of Sonora, Mexico. Southwestern Nat. (in press).

———. 1987. Winter ecology of the Gray Vireo (*Vireo vicinior*) in Sonora, Mexico. M. S. thesis, Univ. Arizona, Tucson, Arizona.

GREENBERG, R. S. 1986. Competition in migrant birds in the nonbreeding season. Pp. 281–307 *in* Current ornithology, Vol. 3 (R. F. Johnston, ed.). Plenum Press, New York, New York.

———. Forest migrants in non-forest habitats on the Yucatán penninsula. *in* Ecology and conservation of Neotropical migrant land birds (J. M. Hagan and B. W. Johnston, eds.). Smithsonian Inst. Press, Washington D. C. (in press).

HOLMES, R. T., T. W. SHERRY, AND L. REITSMA. 1989. Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. Condor 91:545–561.

LYNCH, J. F., E. S. MORTON, AND M. E. VAN DER VOORT. 1985. Habitat selection between wintering sexes of Hooded Warblers (*Wilsonia citrina*). Auk 102:714–721.

MUNGER, J. C. 1984. Home ranges of horned lizards (*Phyrosoma*): circumscribed and exclusive? Oecologia 62:351–360.

MYERS, J. P., P. G. CONNERS, AND F. A. PITELKA. 1979. Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. Auk 96:551–561.

NESBIT, I. C. T. AND L. MEDWAY. 1972. Dispersion, population ecology and migration ecology of the Eastern Great Reed Warbler (*Acrocephalus orientalis*) wintering in Malaysia. Ibis 114:451–494.

ORNAT, A. L. AND R. GREENBERG. 1990. Sexual segregation by habitat in migratory warblers in Quintana Roo, Mexico. Auk 107:539–543.

PRICE, T. 1981. The ecology of the Greenish Warbler (*Phylloscopus trochiloides*) in its winter quarters. Ibis 123:131–144.

RAPPOLE, J. H. AND D. W. WARNER. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pp. 353–393 *in* Migrant birds in the Neotropics: ecology, behavior, distribution and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Inst. Press, Washington D.C.

SCHWARTZ, P. 1964. The Northern Waterthrush in Venezuela. Living Bird 3:187–231.

TRAMER, E. AND T. R. KEMP. 1980. Foraging ecology of migrant and resident warblers and vireos in the highlands of Costa Rica. Pp. 285–297 *in* Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Press, Washington D.C.

TURNER, R. M. AND D. E. BROWN. 1982. Tropical-subtropical desertlands. Pp. 180–222 *in* Biotic communities of the American Southwest—United States and Mexico (D. E. Brown, ed.). Desert Plants 4:1–342.