

## BANDING RETURNS, ARRIVAL PATTERN, AND SITE-FIDELITY OF WHITE-EYED VIREOS

S. L. HOPP,<sup>1,4</sup> A. KIRBY,<sup>2</sup> and C. A. BOONE<sup>3</sup>

**ABSTRACT.**—We present nine years of return data for individually color-banded White-eyed Vireos and describe patterns of arrival and territory use. Of all opportunities for annual return, 48.3% of males and 50% of females were resighted. Most males arrived between 17 and 30 April, with a median arrival date of 24 April, while most females arrived between 21 April and 1 May with a median arrival date of 26 April; males arrived significantly earlier than females. Older males arrived significantly earlier than younger, as has been reported for several other species. The arrival dates for individual males were consistent across years; an individual's arrival date in one year reliably predicted its arrival date in the next year. Thus, the timing of arrival co-varied with three factors: sex, age, and individual. Nearly all males remained faithful to previous territories, although some shifted so that the new territory overlapped the old. Aspects of our data and those of others suggest our return rates are likely a low estimate of survivorship for the species; the actual survival rate is probably higher. Received 3 May 1998, accepted 23 Sept. 1998.

Recent studies have strongly indicated that populations of many species of migratory birds in North America are declining. This recognition has invigorated research efforts aimed at documenting various aspects of population dynamics among different species and determining the factors underlying these declines (Terborgh 1980, Lovejoy and Oren 1981, Hagan and Johnston 1992, DeGraaf and Rappole 1995, Rappole 1995, Sauer et al. 1996). These studies are useful in establishing current population status for various species, for monitoring relationships between population status and ecological and demographic factors, and for identifying future research and conservation goals. Several approaches have been employed, including point counts of breeding populations, mist-netting of birds at migration stopovers, breeding bird surveys (BBS), and studies of banded populations of birds on both wintering and breeding grounds (Askins et al. 1990, Payne and Payne 1990, Bibby et al. 1992).

Among the groups of birds in decline are migratory species in the family Vireonidae (Robbins et al. 1989). Two species of vireo are federally endangered in the United States: the Black-capped Vireo (*Vireo atricapillus*) found in Texas and Oklahoma (Grzybowski et

al. 1986, USFWS 1991), and a race of Bell's Vireo in California, the Least Bell's Vireo (*V. bellii pusillus*; USFWS 1986, Franzreb 1989). Several other species of vireos have declined in numbers, as determined by the USGS Breeding Bird Survey (BBS; Robbins et al. 1989, Sauer and Droege 1992). A number of studies have addressed different aspects of population dynamics in various vireo species including migration patterns (Remsen et al. 1996, Woodrey and Chandler 1997, Woodrey and Moore 1997), population structure (Grzybowski 1991), aspects of breeding (Graber et al. 1985, Grzybowski et al. 1994, Marvil and Cruz 1989, Barber and Martin 1997), and wintering ecology (Greenberg 1992; Greenberg et al. 1993, 1995). Studies of these types are important for gauging long-term changes in migratory vireo populations and the factors that affect them (Holmes et al. 1989; Lynch 1989, 1992).

One of these Nearctic migrant species is the White-eyed Vireo (*Vireo griseus*), a small passerine that occupies secondary deciduous habitat, thickets, and forest-edge in the eastern United States. Its winter range extends across the southern US from Texas to South Carolina, south through the West Indies, and along the eastern coast of Mexico (Barlow 1980, Hopp et al. 1995). The northern subspecies, *V. g. noveboracensis*, is fully migratory. The southeastern subspecies, *V. g. griseus*, has been reported to migrate (Barlow 1980). However, Bradley (1981) reported that a population near Gainesville, Florida was sedentary,

<sup>1</sup> Dept. of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, AZ 85721.

<sup>2</sup> P.O. Box 193, Independence, OR 97351.

<sup>3</sup> Museum of the Middle Appalachians, 123 Palmer Ave., Saltville, VA, 24370.

<sup>4</sup> Corresponding author; E-mail: SHOPP@u.arizona.edu

with individuals remaining through the winter. The remaining subspecies, *V. g. micrus*, *V. g. bermudianus*, *V. g. maynardi*, and *V. g. perquisitor*, are apparently nonmigratory (Barlow 1980, Hopp et al. 1995). Analyses of the data from the BBS suggest that White-eyed Vireos have been declining in parts of their breeding range (Robbins et al. 1989, Sauer and Droege 1992). Efforts to document these declines and determine factors that influence population structure and territory use are important for monitoring long-term changes in vireo populations.

In the present study we report on returns of banded White-eyed Vireos for nine years in southwestern Virginia. Banded White-eyed Vireos have been reported to show site fidelity in their breeding range (Hopp et al. 1995) and on winter territories (Rappole and Warner 1980). We used this fidelity to territories to directly measure return rates of banded individuals. In addition we report on the pattern of arrival in the spring and outline the use of territories by individuals during the breeding season.

## METHODS

Most birds were banded on two study sites in Washington and Smyth counties in southwestern Virginia. The two sites, each about 35 ha and located 600–800 m above sea level comprised tracts of secondary deciduous growth, typically favored by this species (Conner et al. 1983, Graber et al. 1985, Hopp et al. 1995). Both areas contained 12–16 contiguous White-eyed Vireo territories. Other birds were banded in the same counties at smaller tracts of 3–12 ha, each with 1–6 territories; 2 of these smaller areas were within 5 km of the main study area in Washington County. For all of these study areas the habitat type was mixed, with approximately 60–80% of the areas constituting suitable habitat for the vireos. We attempted to locate and band birds at all smaller appropriate tracts within about 15 km of the site in Washington County. The principal habitat types in this region are deciduous forest or open pastureland; the presence of habitat appropriate for White-eyed Vireos is limited and typically exists in small areas supporting only a few individuals. All but one male in our study shared at least one territorial boundary with another male; most birds shared boundaries with several other males.

We captured most birds soon after their arrival in late April or early May. Males were easily taken in mist nets as they approached tape playbacks of conspecific song. Our attempts to capture females by intercepting approaches to nests clearly disrupted nesting activities, so we discontinued those attempts. On a few occasions females were captured with males, if they

followed them into nets during playbacks. All birds were banded under permit with a unique configuration of USFWS aluminum and plastic color bands.

We began checking for arrivals in known territories and neighboring suitable habitat in the first week of April. Monitoring consisted of listening for singing males in known territories for at least 15 minutes; often we used recorded song to attract males. When detected, males were followed to determine whether they were banded, and to identify the color(s) and configuration for banded individuals. Study areas were checked daily until mid-May; unoccupied territories were then checked at least twice weekly until mid-June. We also checked several other known populations of birds within 15 km of the study areas to potentially detect dispersed birds. We were able to assess returns without recapture by identifying the color-band configurations. Because the males of this species are vocally prolific, it was easy to locate newly arrived males. The arrival dates used in this analysis are restricted to subjects for which we spent at least 15 minutes in the area on the day prior to their first detection, i.e., we were confident they were not present on the previous day. Determining arrival dates for females was more difficult because they are behaviorally cryptic, and because they sometimes changed locations after a day or two. Most reliably, finding males allowed us to locate females. Whenever a male was located, we observed him long enough to determine whether a female was also present. In most cases, changes in the males' behavior was indicative of pairing status; unpaired males usually sang at high rates from high, exposed perches, while paired males typically spent more time in lower areas and sang at lower rates (Hopp et al. 1995). Because newly paired males stay close to females it was relatively easy to assess pairing status. Because females were mostly unbanded, determining whether a particular female was a new arrival or had moved from a neighboring male's territory was not possible. Arrival dates for females could be unambiguously determined by assessing the total number of females on the entire study site, with changes between successive days indicating new arrivals. Arrival dates for females used in this analysis are only those we could definitively determine to be new arrivals.

We considered an individual's territory to be the total area the bird was observed to occupy throughout the course of a season without outside influence either by other birds or by the researchers. Site fidelity was then defined as use of an area that overlapped a territory from the previous year by at least 50%. Approximately two-thirds of the males also served as focal subjects for studies of vocal communication, and hence provided more complete data on territory use.

We also examined the encounter records for White-eyed Vireos from the Bird Banding Laboratory (BBL) through 1996. These records include encounters within the same 10' block (prior to 1958) and document individuals encountered outside the original 10' block where they were banded. These records potentially provide information about the dispersal of both hatch-

TABLE 1. Returns of male White-eyed Vireos known to be at least one year old when banded.

Banding year	Number banded	Returns in years following banding					
		One	Two	Three	Four	Five	Six
1985	8	3	2	2	1	0	—
1986	4	3	2	1	1	1	0
1987	11	7	4	1	1	1	0
1988	11	5	3	0	—	—	—
1989	14	10	1	1	0	—	—
1990	13	8	6	0	—	—	—
1991	13	4	1	0	—	—	—
Total	74	40	19	5	3	2	0
Percent <sup>a</sup>		54	26	7	4	3	0

<sup>a</sup> Calculations based on percent returns relative to banding year.

ing year (HY) and adult (after hatching year; AHY) birds. To assure that we were assessing dispersal rather than migratory movements, we considered only birds with both banding and encounter dates between 16 May and 16 September inclusive. These dates are well within the average spring arrival and fall departure dates for this species throughout most of its range (see appendix 1 in Hopp et al. 1995).

## RESULTS

**Returns of banded birds.**—During the breeding seasons of 1985–1991, we banded 74 adult male birds used in this analysis. We also banded 5 females and 42 nestlings/fledglings, most of which were known to have survived until they were capable of sustained flight. Returns of males for each year from 1986–1994 individually and combined are given in Table 1. The percentage returns are based on combined data from nine years, computing the number that return relative to the banding year. Because these subjects were all banded as adults (AHY), these percentages give an indication of survivorship in the successive years following banding. The two individuals surviving five seasons after banding were thus at least six years old. Our oldest bird (not included in this analysis) arrived as an AHY bird in 1990 and was still alive in the summer of 1998, making him at least 9 years old.

Calculating the probability of return given that a bird was alive in the previous year, 40 of 74 (54.1%) returned the year following banding, 19 of 40 (47.5%) returned the second year, 5 of 19 (26.3%) returned the third year, 3 of 5 (60.0%) returned the fourth, 2 of 3 (66.7%) returned the fifth year, and none of 2

## Distributions of Arrival Dates

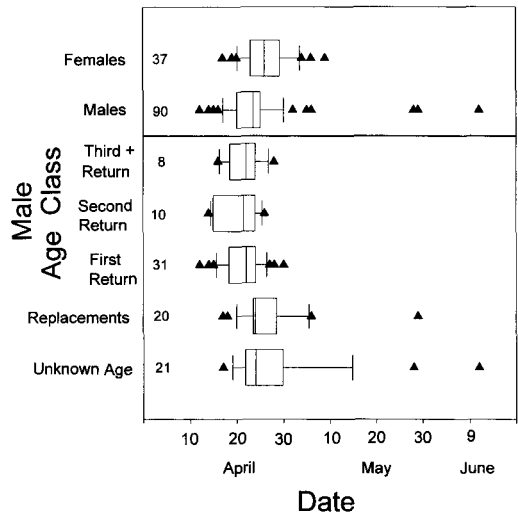


FIG. 1. Box plot of arrival dates for all females and males. Males are further divided into various age classes (see text for explanations). For each plot the total box encompasses the second and third quartiles for each distribution, with the central vertical line showing the median arrival date. Horizontal lines show the 10–90% range of dates, and triangles indicate individual arrival dates in the outlying 10% ranges.

returned the sixth year following banding. Over the nine year period, there were 143 opportunities for return and 69 documented returns. Thus the percentage of male White-eyed Vireos returning in any year, given the bird was known to be alive the previous year, was 48.3%. Of the five females banded, three returned in the year following banding and one individual returned in the second and third years following banding. Of the ten opportunities for female returns, five (50.0%) were resighted. We did not recover any of the birds banded as nestlings or fledglings.

**Male arrival pattern.**—We obtained 90 arrival dates from 63 individuals. The combined dates ranged from 12 April to 11 June with a median arrival date of 23 April (Fig. 1). Most birds arrived during the two weeks between 16 April and 30 April (75 of 90: 83.3 %). There were six arrival dates prior to 16 April, with three of these from the same banded individual in successive years. Eight arrival dates were after 30 April, five of these in early May (2 May, and two each on 5 May and 6 May) and three were well outside the distri-

bution of other arrivals—28, 29 May and 11 June. These three extremely late unbanded individuals likely represent relocations rather than arrival dates (see below).

*Female arrival pattern.*—We obtained 37 arrival dates for females. Of these only 4 were from returning, banded individuals, the remainder from unbanded individuals. The combined dates ranged from 17 April to 9 May, with a median arrival date of 26 April (Fig. 1). Most of the arrival dates fell in the ten day period between 21 April and 1 May (28 of 37: 75.7%). Two of the four earliest arrival dates (17 and 20 April) were from returning banded individuals. Because females are cryptic in their plumage and behavior and because we assessed their arrival primarily by pairing with males, our sampling was likely biased toward the earlier arrival dates. Despite this, the median arrival date for females was later than all of the individual male arrival date categories (Mann-Whitney Test:  $U = 3.43$ ,  $P < 0.001$ ; see Fig. 1). We typically observed several males on territory before any females arrived. In several years, most male territories were occupied before any females were seen.

*Age-related male returns.*—We recorded 49 arrival dates from returning banded males and 41 from unbanded males that were later banded. Of the unbanded birds, 21 were of unknown age. The remaining 20 arrival dates were from unbanded birds that occupied territories previously occupied by non-returning banded individuals. Given the high site fidelity for returning individuals, this second category of unbanded replacement birds possibly were second-year adults (SY; first breeding season) which were treated separately in our analysis of age-related returns.

Figure 1 shows the distributions of arrival dates for various age-related classes of males. Because the sample sizes in the three oldest age categories were too small to permit statistical comparison across all age categories, we combined all dates of birds returning after three years into one category (four years or older,  $n = 8$ ). To avoid pseudoreplication, in analysis we averaged dates for individuals that contributed more than one arrival date to this combined category, yielding an effective sample size of 5. A comparison of the four male groups, previously unbanded birds, first returns, second returns, and third + returns, was

significant (Kruskal-Wallis Test:  $H = 11.27$ ,  $P < 0.05$ ). In post hoc (Bonferroni) pairwise comparisons, the only significant difference was between the new (unbanded) arrivals and the first return year ( $Z = 2.77$ ,  $P < 0.05$ ), indicating that the gain in arrival is between the first (banding) year and the first return year. In a more conservative version of this comparison, we compared all returning, banded birds to all unbanded birds. This comparison was also significant, showing arrival dates of all banded birds to be earlier than arrival dates of all unbanded birds (Mann-Whitney Test:  $U = 3.66$ ,  $P < 0.001$ ). In a more direct test, we compared successive dates from individuals for whom we obtained arrival dates in two consecutive years ( $n = 32$  pairs). This comparison was only marginally significant when using all consecutive arrival pairs (Wilcoxon Test:  $Z = 1.465$ ,  $P = 0.074$ ). When this analysis was restricted to consecutive-year pairs starting with the first (unbanded) year, the comparison was significant (Wilcoxon Test:  $Z = 1.80$ ,  $P < 0.05$ ,  $n = 14$ ), showing that birds arrived earlier in the second of these two consecutive years, and reinforcing the finding that the gain in arrival dates is apparent only between the banding and subsequent year. For the 32 pairs of consecutive year arrival dates, we also found that the arrival date of individuals was a significant predictor of its arrival date in the subsequent year ( $r = +0.616$ ,  $P < 0.001$ ). Thus, while a portion of the variability seen in arrival dates can be attributed to age, a substantial portion can be attributed to individual-specific differences in arrival, with early and late arrivers remaining early and late arrivers respectively across seasons (Fig. 2).

*Site fidelity.*—Of the returning banded males, 67 of 69, or 97% of returns were to their previous territory. The two individuals observed to move to non-overlapping territories between years both remained within 800 m of their original territory. Several birds enlarged their territories in subsequent years, occupying areas that included their previous territory. Seven individuals disappeared during the course of a season; three returning birds and four birds in the year they were banded. None of these seven birds was seen in subsequent years. One of the three returning birds lost his territory to human habitat clearing

## Individual Return Dates in Successive Years

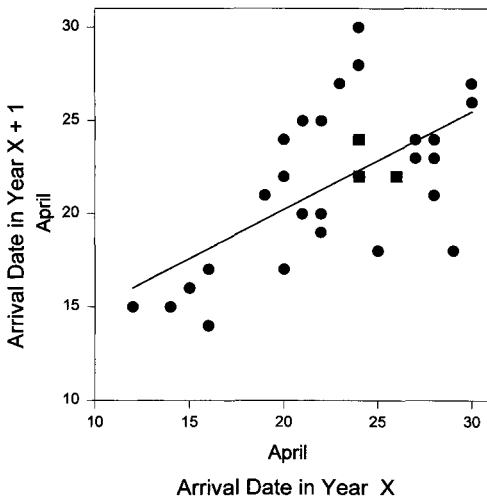


FIG. 2. Scatter plot showing return dates obtained from individual males in successive years. Line depicts best-fitting regression line; squares denote 2 overlapping data points.

during the winter. He was seen in adjacent and nearby territories for only five days following his arrival. Two of the four birds that disappeared during the year they were banded reappeared later in the season. One of these arrived on 22 April in a territory previously occupied by a non-returning banded individual. He was banded on 24 April, disappeared on 2 May, then reappeared on the same territory 7 June where he remained for the season.

For females, all returns were to the same study area where they were first banded, but none to the same territory; none paired with the same male in more than one year. The nearest movement was to an adjacent territory. The farthest moved three territories away, i.e., two intervening territories from the previous year, a distance of about 750 meters.

**Territory use.**—Territory use in this species is a typical "type A" territory (Nice 1941), with males aggressively defending territories against other males, and with the area used for mating, nesting, and feeding for both adults and young during the breeding season. The defense of territory is usually by a series of behavioral displays, including singing, and less frequently by direct contact (see description by Bradley 1980). Most territorial en-

counters occurred early in the season, prior to the arrival and pairing with females; following the onset of nesting activities these territorial encounters were rare.

Individual males could easily be tracked during the season, and adults remained on territory into September; the latest date we recorded a bird on territory in autumn was 6 October. During the last few weeks in the fall the adults increased their singing rate and again became quite responsive to tape-recorded song.

Female use of territory was less easy to observe. On several occasions we observed two females within the same territory, always early in a season. In no case did we observe interactions between females indicating territory defense. On one occasion we observed two females within a few centimeters of each other with no overt behavioral response.

As with females, HY birds were difficult to track carefully during a season. Typically, banded young could be found in their natal territories for 4–5 weeks; often birds from the same brood were found together. After this time, banded HY birds began to disperse from their natal territories mid-August through early September, often being found in other territories within the study site. A few HY birds would defend small territories, responding aggressively to tape-recordings with approach and/or singing. Most HY birds left the region on migration prior to the onset of banded AHY bird departures.

**USFWS encounter data.**—There were 81 total White-eyed Vireo encounter records from the Bird Banding Laboratory. Of these, 22 were both banded and encountered within the 16 May to 16 September period, all of these encountered during the breeding season in the first year after banding. Of these 22, 18 were AHY birds, three were HY, and one was local status (incapable of sustained flight; presumably nestling). Of the 18 adults, 14 were encountered in the same 10' block in which they were banded. Of the four adults encountered outside their initial banding 10' block, three were encountered in the next 10' block of latitude (approximately 19 km on average) and one was encountered in the adjacent 10' block of longitude (approximately 15 km). Of the three HY birds, one was encountered in the original block, and the other two were en-

countered one 10' block of latitude and one 10' block of longitude respectively from where originally banded. The local-status bird was encountered in the same 10' block where it was initially banded. Two other records deserve mention. One HY bird was banded on 17 August and encountered approximately 155 km away in the following year on 14 May. The other, a local bird, was banded on 12 June and encountered the following 13 May, approximately 190 km from initial banding location. As both of these birds were banded and encountered in states near the northern edge of the species' range (Massachusetts and Maryland respectively), these encounters in the middle part of May likely represent an encounter on their breeding ground rather than a point in their migration paths.

### DISCUSSION

*Returns of banded birds.*—Our overall percentage returns of 48.3% for males and 50% for females gives an indication of the baseline returns expected for this species. These can be compared to return rates reported for Black-capped and Bell's vireos. In a long-term study of Black-capped Vireos, Grzybowski (1991) reported male returns of 65% for a study population of approximately 250 birds. Perhaps more directly comparable were his return rates for approximately 130 males from scattered study locations. For these he reported a return rate of 58%, slightly higher than in our study. For females, he reported 52% and 41% encountered for larger and more scattered study groups, respectively. Similarly, for Bell's Vireos, Greaves and Labinger (1998) reported male returns of 62.5% and 58.6% for two separate study areas, and 57.1% and 58.8% for females from the same two study groups. Two notable differences between the studies of both these species and our study are the sample sizes and the study areas. Grzybowski (1991) reported his percentage returns on samples of approximately 250 and 130 males in the main and scattered study areas. The study by Greaves and Labinger (1998) reported on returns from a smaller number of males: approximately 40 and 30. The study areas, however, were considerably larger than in our study. Many researchers have noted that the percentages of birds re-encountered in banding studies is directly related to the size

of the study population, with larger populations affording a higher re-encounter percentage, and that site fidelity is greater in larger study groups (e.g., Temple and Cary 1988, Payne and Payne 1990, Grzybowski 1995). Applied to this study, then, our reported return rates likely represent a low return estimate for the species. The data presented here provide a baseline rate of returns for adult White-eyed Vireos. Because the population densities in this region are relatively low (Price et al. 1995), comparative studies in other areas of this species' range are needed to determine which aspects of the data observed here are shared in other regions, and what factors might affect return rates and survival of White-eyed Vireos.

*Arrival patterns.*—Our finding that older birds arrive sooner than younger birds in spring is consistent with similar reports in other species (e.g., Nolan 1978, Bedard and LaPointe 1984, Hill 1989, Morton and Derickson 1990). An earlier arrival could provide either a longer potential breeding season or better chances of obtaining a mate (see Møller 1990). However, the variation we saw was modest; the only significant difference was approximately 2 days gained between the first (banding) year and the first return year, a pattern seen with both the between-subject and within-subject comparisons. It's difficult to argue strongly for a significant pairing advantage, particularly because most males arrive before most females. We have found that the arrival date itself is not a significant predictor of either pairing date or probability of obtaining a mate. Rather, the age of the individual is more likely a factor, i.e., females are more likely to pair with older (returning) males, regardless of arrival date (SLH, unpubl. data). However, the relation between arrival date and reproductive success in White-eyed Vireos is unknown.

Several studies have identified reasons for earlier arrival dates by older birds, and several of these might pertain to White-eyed Vireos (see Ketterson and Nolan 1983, Woodrey and Chandler 1997 for summaries). First, older birds might winter further north than younger birds. However, the site fidelity of White-eyed Vireos to winter territories (Rappole and Warner 1980) argues against this. Second, older birds might leave earlier for northern mi-

gration in the spring. Third, older birds might be better at finding their territory once they have arrived on the breeding grounds. Finally, it is possible that older birds travel faster during spring migration, either through superior navigational skills or more efficient foraging while enroute.

Our finding that the arrival date for an individual in a given year predicted its arrival in the subsequent year is a pattern that to our knowledge has not been previously reported for any species. The variation seen as a result of individual differences accounts for more of the arrival date variability than that seen for age related return dates. The factors outlined above for age related returns may also be used to explain this result, but with individual rather than age related differences in these abilities being applied to individuals initiating spring migration from a common wintering location. Alternatively, this pattern could result from individuals commencing from a wide range of geographic origins, with more northerly-wintering individuals arriving earlier. The relationship between the winter and breeding locations of individuals is unknown.

*Philopatry and territory use.*—Male White-eyed Vireos show a high degree of territory fidelity. Some researchers have distinguished between site fidelity, where birds return to the study area but to a different territory, and territory fidelity, where birds return to their previous territory (Greenwood 1980, Greenwood and Harvey 1982, Holmes and Sherry 1992). The extent to which birds move between territories in consecutive years has been called breeding dispersal by Greenwood (1980). In our study, the attachment to particular territories is remarkably high and the two tendencies, site and territory fidelity, appear essentially the same. While perhaps uncommon, three lines of evidence may indicate that breeding dispersal movements occur in White-eyed Vireos. First, on two occasions we observed individuals disappear only to reappear in the same territory later within the same season. While we did not locate these birds on other study areas, they obviously relocated for at least a portion of that season. Grzybowski (1995) reported that male Black-capped Vireos sometimes sequentially occupied two non-contiguous territories, and this might also occur in White-eyed Vireos. Second, records

from the BBL show four relocations of adult White-eyed Vireos between breeding seasons, with distances of between 15 and 20 km for each. While these records are limited, they nevertheless show that adult White-eyed Vireos are known to relocate between breeding seasons. Third, we observed three arrival dates of individual males in late May and early June, well outside of the migration dates known for this species (Hopp et al. 1995, Remsen et al. 1996). While circumstantial, these late dates likely reflect instances of relocating individuals rather than first-time arrivals. Taken together, these lines of evidence suggest that at least some portion of adult birds tend to disperse from one breeding territory to another, both within and between seasons. This also suggests that our return percentages represent a low estimate of survival for the species.

We observed that HY birds depart from the breeding grounds before AHY birds. This earlier departure of young may be related to an unusual pattern of molt described for White-eyed Vireos, where juveniles exhibit a partial replacement of primaries prior to fall migration, perhaps facilitating migration in HY birds (Lloyd-Evans 1983). This pattern of molt, however, may vary geographically (George 1973). Whether departures of HY birds precede adults in other parts of their range is unknown. The timing of fall migration between HY and AHY White-eyed Vireos is not significantly different in the southern United States. Woodrey and Moore (1997) found that AHY and HY White-eyed Vireos did not differ in their distribution of arrivals. This timing pattern is in contrast to Red-eyed Vireos (*V. olivaceus*) whose adults depart significantly earlier than the young, and the two age-classes apparently migrate at different rates (Woodrey and Chandler 1997). Perhaps while young White-eyed Vireos depart earlier, the adults minimize the timing differences by the time the two groups reach the southern United States. Alternatively, our observed earlier departure of HY birds may signal the onset of a pre-migration dispersal by young birds, followed by their actual southerly migration some time later.

Our failure to recover any SY birds banded as young may stem from several factors. First, it is possible that young birds tend not to re-

turn to the natal area. For many species, a dispersal of young provides an effective mechanism for avoiding inbreeding (Greenwood and Harvey 1982, Davis and Howe 1992), although some young of other vireo species return to their natal area (see below). Alternatively, since White-eyed Vireos inhabit a successional window of habitat it may be in the best interest of young birds to disperse to other areas, because the optimum successional window will eventually close in their natal area. Young birds may disperse from their natal areas to locate suitable breeding habitat for the following spring (e.g., Brewer and Harrison 1975). Second, it is possible that the combination of a modest number of birds banded and relatively small study areas simply precluded our re-encounter with young. In the BBL encounter records there were six reported recoveries of banded HY birds in later years; two were encountered in the original 10' block, two were encountered 15–20 km of initial banding location, and two were encountered 150–200 km away from the original banding block. These records are equivocal in suggesting a modal pattern of natal dispersal for the species. Instead the pattern appears complex, with distance depending perhaps on other factors, such as habitat size and composition, bird densities, or hatching time of year. In Black-capped Vireos, young birds show a gradient of natal dispersal to at least 21 km (Grzybowski 1991). For this species, the return percentages were directly related to size of the study area, with fewer returns in smaller areas (Grzybowski 1995). In Bell's Vireos, natal dispersal is complex, with some young returning to their natal area, and others dispersing up to 300 km (Kus 1995, Greaves and Labinger 1998). Greaves and Labinger (1998) found that early and late (before and after 15 June, respectively) cohorts of HY Bell's Vireos exhibit significantly different degrees of natal philopatry, with earlier young returning at higher rates. For both Black-capped and Bell's vireos, reported return percentages of young from various studies were 15–27% (Greaves 1987; Grzybowski 1991, 1995; Greaves and Labinger 1998). Our lack of returns provides us with little information on natal dispersal and survival, and instead raises questions about dispersal dynamics of this species.

## ACKNOWLEDGMENTS

We thank J. C. Barlow, R. Greenberg, J. A. Grzybowski, T. Keller, B. Kingsolver, K. Klimkiewicz, B. McClellan, T. Melcer, C. Qualls, and two anonymous reviewers for comments on earlier versions of this manuscript. We thank the Bird Banding Laboratory for providing encounter records for White-eyed Vireos. We thank T. Lloyd-Evans and K. Klimkiewicz for permission to use individual encounter records. We gratefully acknowledge Mr. and Mrs. L. P. Collins, III for their kind permission to conduct our field work on their land. We thank G. McLaren, D. Kegley and C. Carlin for field assistance. The work was partially supported by a Mednick Research fellowship and two Mellon Faculty Development grants to SLH, and a J. J. Murray research award to CAB. This research was conducted while SLH was on the faculty of Emory and Henry College in Emory, Virginia.

## LITERATURE CITED

- ASKINS, R. A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in eastern North America. *Curr. Ornithol.* 7:1–57.
- BARBER D. R. AND T. E. MARTIN. 1997. Influence of alternate host densities on Brown-headed Cowbird parasitism rates in Black-capped Vireos. *Condor* 99:595–604.
- BARLOW, J. C. 1980. Patterns of ecological interactions among migrant and resident vireos on the wintering grounds. Pp. 79–107 in *Migrant birds in the Neotropics: ecology, behavior, distribution and conservation* (A. Keast and E. S. Morton, Eds.). Smithsonian Institution Press, Washington, D.C.
- BEDARD, J. AND G. LAPOINTE. 1984. Banding returns, arrival times, and site fidelity in the Savannah Sparrow. *Wilson Bull.* 96:196–205.
- BIBBY, C. J., N. D. BURGESS, AND D. A. HILL. 1992. *Bird census techniques*. Academic Press, London, U.K.
- BRADLEY, R. A. 1980. Vocal and territorial behavior in the white-eyed vireo. *Wilson Bull.* 92:302–311.
- BRADLEY, R. A. 1981. Song variation within a population of White-eyed Vireos (*Vireo griseus*). *Auk* 98:80–87.
- BREWER, R. AND K. G. HARRISON. 1975. The time of habitat selection by birds. *Ibis* 117:521–522.
- CONNER, R. N., J. G. DICKSON, B. A. LOCKE, AND C. A. SEGELQUIST. 1983. Vegetation characteristics important to common songbirds in East Texas. *Wilson Bull.* 95:349–361.
- DAVIS, G. J. AND R. W. HOWE. 1992. Juvenile dispersal, limited breeding sites, and the dynamics of metapopulations. *Theor. Pop. Biol.* 41:184–207.
- DEGRAAF, R. AND J. H. RAPPOLE. 1995. *Neotropical migratory birds*. Cornell Univ. Press, Ithaca, New York.
- FRANZREB, K. E. 1989. Endangered status and strategies for protection of the Least Bell's Vireo (*Vireo bellii pusillus*) in California. *West. Birds* 18:43–49.



- GEORGE, W. G. 1973. Molt of juvenile White-eyed Vireos. *Wilson Bull.* 85:327–330.
- GRABER, J. W., R. R. GRABER, AND E. L. KIRK. 1985. Illinois birds: vireos. III. *Nat. Hist. Surv. Biol. Notes* 124:1–38.
- GREAVES, J. M. 1987. Nest-site tenacity of Least Bell's Vireos. *West. Birds* 18:50–54.
- GREAVES, J. M. AND Z. LABINGER. 1998. Site tenacity and dispersal of Least Bell's Vireos. *Trans. West. Sect. Wildl. Soc.* 33:18–23.
- GREENBERG, R. 1992. Forest migrants in non-forest habitats on the Yucatan Peninsula. Pp. 273–286 in *Ecology and conservation of neotropical migrant landbirds* (J. M. Hagan, III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- GREENBERG, R., D. K. NIVEN, S. L. HOPP, AND C. BOONE. 1993. Frugivory and coexistence in a resident and a migratory vireo on the Yucatan peninsula. *Condor* 95:990–999.
- GREENBERG, R., M. S. FOSTER, AND L. MARQUEZ-VALDELAMAR. 1995. The role of the White-eyed Vireo in the dispersal of *Bursera* fruit on the Yucatan peninsula. *J. Trop. Ecol.* 11:619–639.
- GREENWOOD, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.* 28:1140–1162.
- GREENWOOD, P. J. AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* 13:1–21.
- GRZYBOWSKI, J. A. 1991. Survivorship, dispersal and population structure of Black-capped Vireos at the Kerr Wildlife Management Area, Texas. *Resour. Protection Div., Texas Parks Wildlife Dept., Austin.*
- GRZYBOWSKI, J. A. 1995. The Black-capped Vireo (*Vireo atricapillus*). In *The birds of North America*, no. 181 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.
- GRZYBOWSKI, J. A., R. B. CLAPP, AND J. T. MARSHALL. 1986. History and current status of the Black-capped Vireo in Oklahoma. *Am. Birds* 34:742–745.
- GRZYBOWSKI, J. A., D. J. TAZIK, AND G. D. SCHNELL. 1994. Regional analysis of Black-capped Vireo breeding habitats. *Condor* 96:512–544.
- HAGAN, J. M. AND D. W. JOHNSTON. 1992. *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, D.C.
- HILL, G. E. 1989. Late spring arrival and dull nuptial plumage: aggression avoidance by yearling males? *Anim. Behav.* 37:665–673.
- 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.
- HOLMES, R. T. AND T. W. SHERRY. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: implications for population dynamics, habitat selection, and conservation. Pp. 563–575 in *Ecology and conservation of neotropical migrant landbirds*. (J. M. Hagan, III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- HOPP, S. L., A. KIRBY, AND C. A. BOONE. 1995. White-eyed Vireo (*Vireo griseus*). In *The birds of North America*, no. 168 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union; Washington, D.C.
- KETTERSON, E. D. AND V. NOLAN, JR. 1983. The evolution of differential bird migration. *Curr. Ornithol.* 1:357–402.
- KUS, B. E. 1995. Status of the Least Bell's Vireo and southwestern Willow Flycatcher at Marine Corps Base Camp Pendleton, California, in 1995. Environmental and Natural Resources Office, Marine Corps Base Camp Pendleton, California.
- LLOYD-EVANS, T. L. 1983. Incomplete molt of juvenile White-eyed Vireos in Massachusetts. *J. Field Ornithol.* 54:50–57.
- LOVEJOY, T. E., III AND D. C. OREN. 1981. The minimum critical size of ecosystems. Pp. 7–12 in *Forest island dynamics in man-dominated landscapes* (R. L. Burgess and D. M. Sharpe, Eds.). Springer-Verlag, New York.
- LYNCH, J. F. 1989. Distribution of overwintering Neartic migrants in the Yucatan peninsula, I: general patterns of occurrence. *Condor* 91:515–544.
- LYNCH, J. F. 1992. Distribution of overwintering Neartic migrants in the Yucatan peninsula, II: use of native and human-modified vegetation. Pp. 178–196 in *Ecology and conservation of neotropical migrant landbirds* (J. M. Hagan, III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- MARVIL, R. E. AND A. CRUZ. 1989. Impact of Brown-headed Cowbird parasitism on reproductive success of the Solitary Vireo. *Auk* 106:476–480.
- MØLLER, A. P. 1990. Male tail length and female mate choice in the monogamous swallow *Hirundo rustica*. *Anim. Behav.* 39:458–465.
- MORTON, E. S. AND K. C. DERRICKSON. 1990. The biological significance of age-specific return schedules in breeding Purple Martins. *Condor* 92:1040–1050.
- NICE, M. M. 1941. The role of territory in bird life. *Am. Midl. Nat.* 26:441–487.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler (*Dendroica discolor*). *Ornithol. Monogr.* 26:1–595.
- PAYNE, R. B. AND L. L. PAYNE. 1990. Survival estimates of Indigo Buntings: comparisons of banding recoveries and local observations. *Condor* 92: 938–946.
- PRICE, J., S. DROEGE, AND A. PRICE. 1995. *The summer atlas of North American birds*. Academic Press, London, U.K.
- RAPPOLE, J. H. 1995. The ecology of migrant birds: a

- Neotropical perspective. Smithsonian Institution Press, Washington, D.C.
- 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 Institution Press, Washington, D.C.
- REMSEN, J. V., JR., S. W. CARDIFF, AND D. L. DITTMANN. 1996. Timing of migration and status of vireos (*Vireonidae*) in Louisiana. *J. Field Ornithol.* 67:119–140.
- ROBBINS, C. S., J. S. SAUER, R. S. GREENBERG, AND S. DROEGE. 1989. Population declines in North American birds that migrate to the Neotropics. *Proc. Natl. Acad. Sci. USA* 86:7658–7662.
- SAUER, J. R. AND S. DROEGE. 1992. Geographic patterns in population trends of Neotropical migrants in North America. Pp. 26–42 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan, III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- SAUER, J. R., G. W. PENDLETON, AND B. G. PETERJOHN. 1996. Evaluating causes of population change in North American insectivorous songbirds. *Conserv. Biol.* 10:465–478.
- TEMPLE, S. A. AND J. R. CARY. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conserv. Biol.* 2:340–347.
- TERBORGH, J. W. 1980. The conservation status of Neotropical migrants: present and future. Pp. 21–30 in *Migrant birds in the Neotropics: ecology, behavior, distribution and conservation* (A. Keast and E. S. Morton, Eds.). Smithsonian Institution Press, Washington, D.C.
- USFWS (UNITED STATES FISH AND WILDLIFE SERVICE). 1986. Endangered and threatened wildlife and plants; determination of endangered status for the Least Bell's Vireo. *Federal Register* 51:16474–16483.
- USFWS (UNITED STATES FISH AND WILDLIFE SERVICE). 1991. Black-capped Vireo (*Vireo atricapillus*) recovery plan. Austin, Texas.
- WOODREY, M. S. AND C. R. CHANDLER. 1997. Age-related timing of migration: geographic and inter-specific patterns. *Wilson Bull.* 109:52–67.
- WOODREY, M. S. AND F. R. MOORE. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *Auk* 114:695–707.