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# BROWN-HEADED COWBIRD PARASITISM RESULTS IN A SINK POPULATION IN WARBLING VIREOS

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ABSTRACT.—The Warbling Vireo (*Vireo gilvus*) is one of the most heavily parasitized host species of the Brown-headed Cowbird (*Molothrus ater*), suffering up to 80% parasitism in some areas. Warbling Vireo nests that are parasitized by cowbirds typically produce no vireo young. To make predictions about the consequences of brood parasitism on local host populations, we investigated factors that allow such high parasitism to occur. The major factors leading to high levels of brood parasitism on Warbling Vireos in the Okanagan Valley, British Columbia, are habitat overlap with cowbirds and the lack of response of vireos to cowbird eggs. Warbling Vireos responded more strongly to a cowbird dummy placed near the nest than to a dummy of a "neutral" species (junco) or to a common nest predator (crow). Preliminary simulation models based on population parameters obtained from three summers of fieldwork suggest that Warbling Vireos are in danger of extirpation from the Okanagan Valley if little movement of birds occurs between areas with different levels of brood parasitism. The models also indicate the sensitivity of this species to variation in adult and juvenile survival rates and number of successful broods produced per season. Our results emphasize the need for a metapopulation analysis that compares the population ecology of Warbling Vireos at high elevations (and probably with low parasitism) with that at low elevations (high parasitism) and that ascertains whether sufficient dispersal occurs between these populations to prevent extinction at lower elevations. Sufficient dispersal is indicated by apparently stable vireo populations in the Okanagan Valley and by Breeding Bird Survey data that show an overall increasing trend for this species in British Columbia. *Received 19 December 1997, accepted 4 August 1999.*

THE EFFECTS of Brown-headed Cowbirds (*Molothrus ater*) on host populations are highly variable spatially (Robinson et al. 1995, Brawn and Robinson 1996), which may result in the formation of source populations (local recruitment of hosts exceeds mortality) and sink populations (mortality exceeds local recruitment). Here, we report on an apparent sink population of Warbling Vireos (*Vireo gilvus*) in the southern Okanagan Valley, British Columbia. This species is an important host of the Brown-headed Cowbird in western North America (Barlow 1980). We collected data on parasitism frequency and nesting success over three years. To assess whether this vireo population was self-sustaining, we used May and Robinson's (1985) simulation model to make population projections based on our field data. We also recorded habitat preference and cowbird recognition ability of Warbling Vireos to better understand how habitat use and behavioral responses mediate cowbird-host interactions.

Of all the taxa affected by cowbird brood parasitism, vireos appear to be the hardest hit (e.g. Grzybowski et al. 1986; Franzreb 1987, 1990; Ward and Smith 2000). Although Black-capped (*Vireo atricapilla*), Red-eyed (*V. olivaceus*) and Least Bell's (*V. belli pusillus*) vireos have been studied in this regard (Southern 1958, Grzybowski et al. 1986, Franzreb 1990), little information is available concerning brood parasitism on Warbling Vireos. Indeed, little is known of the biology of this widespread species (James 1976, Barlow 1980).

Cannings et al. (1987) summarized parasitism levels by Brown-headed Cowbirds on 41 host species in the Okanagan Valley through 1978. Of these species, the Warbling Vireo experienced the highest level of brood parasitism (79% of 43 nests), and all six Warbling Vireo pairs observed with cowbird fledglings had no young of their own. This is congruent with Rothstein et al.'s (1980) observation in Califor-

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nia that parasitized Warbling Vireos reared no young of their own. The combination of high levels of brood parasitism and an absence of host-chick survival suggests that cowbird parasitism has a large negative effect on Warbling Vireos in the Okanagan Valley.

## METHODS

*Study site.*—We searched for Warbling Vireo nests in the Okanagan Valley, southern British Columbia, from near Okanagan Falls to the United States border 45 km to the south (total area of ca. 1,065 km$^2$). Emphasis was placed on two sites 20 km apart: Shuttleworth Creek Road and Blind Creek Road. The Shuttleworth Creek site is on the east side of the valley at elevations of 700 to 900 m, and the Blind Creek site is on the west side of the valley at 600 to 1,000 m. From 1992 to 1995, we searched for vireos in all habitats in the study area with deciduous trees as part of a larger study of brood parasitism by Brown-headed Cowbirds (Ward and Smith 2000). We attempted to search all habitats equally to minimize detection biases.

*Population monitoring.*—We estimated Warbling Vireo relative abundance by stopping at intervals of 1 km ($n$ = 14) along Blind Creek Road and broadcasting a Warbling Vireo song for 5 min. We recorded response latency and used the reciprocal of response latency as a index of density for between-year comparisons of population size, based on the assumption that the longer the birds take to respond to song playback, the greater the distance between territorial males (i.e. the lower the density of Warbling Vireos). We captured and individually color-banded Warbling Vireos and spot-mapped all territories found. Territoriality was ascertained by observation, and site fidelity and survival were estimated by return rates of marked birds.

*Nest searching.*—When we discovered a nest, we checked it carefully for the presence of eggs and young of cowbirds and the host. Nests were revisited every two to three days to assess their fates. Nests in trees were usually checked using mirrors mounted on extendable aluminum poles. At nests that were too high to be checked, the presence of the parents and the vocalizations of chicks were used to confirm that the nest was active.

*Levels of predation and parasitism.*—Nests were scored as failing if they were preyed upon or deserted before the expected fledging time (i.e. leaving the nest) for the young based on information in Ehrlich et al. (1988). Nests were scored as successful if they contained host nestlings one or two days before the expected fledging time, or if the parents were seen feeding fledglings or carrying food near the nest after the young had fledged. Nests that contained young on the last check but were not checked near the expected time of fledging were dropped from analyses of nesting success. When calculating daily rates of nest failure, we considered nests that raised only cowbirds as successes. Nests were scored as parasitized if they contained cowbird eggs or young at any stage and as nonparasitized if they never contained cowbird eggs when checked during incubation.

Each nest was assigned an exposure score equal to the number of days it was observed and active. When a nest failed between checks, we added half the number of days between the final and penultimate checks to the exposure score. From these data, we calculated failure rates following Hensler and Nichols (1981) and Ward and Smith (2000).

We compared the incidence of brood parasitism at Warbling Vireo nests recorded by Cannings et al. (1987) for the Okanagan Valley with our data to determine whether there were temporal changes in parasitism. The data in Cannings et al. (1987) were gathered mostly in the 1960s at a site about 35 km north of our study area in pine/fir and orchard habitats. Data collection for the studies summarized by Cannings et al. (1987) ended in 1978.

*Dummy cowbird experiments.*—To establish whether brood parasitism of Warbling Vireos is associated with their lack of aggression toward cowbirds, we presented taxidermic mounts of a cowbird (hereafter "dummy"), Dark-eyed Junco (*Junco hyemalis*), and Northwestern Crow (*Corvus caurinus*) near vireo nests. The dummy junco served as a neutral control, and the dummy crow allowed us to distinguish a generalized aggressive response to a nest predator from a response that was specific to cowbirds. Dummies were placed in clear view of each vireo nest 1 m away and at the same height as the nest. We randomly alternated presentation of the different species of dummies to avoid order effects caused by possible learning or conditioning.

We used instantaneous behavior sampling to record vireo behaviors every 10 s for 5 min (Ward and Maclean 1988). We recorded vocalizations of the vireos for the 5-min experiment using a Sennheiser ME 80 unidirectional microphone and a Sony Professional Walkman WM-D6C tape recorder. We used a Kay sonagraph to count the numbers of alarm calls, clicks (low-level aggressive calls), and songs made by the vireos in response to the different dummies.

*Parasitism experiments.*—We artificially parasitized three nests of Warbling Vireos by placing one cowbird egg in each nest. We used instantaneous behavior sampling to record the behavior of the vireos at 15-s intervals for 10 min after placement of the cowbird egg. We then recorded for 20 more min any additional behaviors that might indicate egg recognition by the adult vireos.

*Simulation models of parasitism effects on vireo population persistence.*—We modeled the effects of Brown-headed Cowbird parasitism on Warbling Vireos fol-

TABLE 1. Brood parasitism by cowbirds, nesting success, and fledgling production of Warbling Vireos in the southern Okanagan Valley, 1992 through 1995.

| Year | No. nests found | Parasitism (%)[a] | No. nests failed | No. surviving young[b] |
|---|---|---|---|---|
| 1992 | 11 | 50.0 (3) | — | 3.0 ± 0.00 |
| 1993 | 19 | 64.3 (9) | 7 | 0.8 ± 0.69 |
| 1994 | 18 | 58.8 (10) | 9 | 1.0 ± 0.97 |
| 1995 | 10 | 70.0 (7) | 4 | 0.7 ± 1.06 |
| Total | 58 | 61.7 (29) | 20 | 1.2 ± 0.85 |

[a] Based on total number of nests for which we were sure of parasitism status. The number of nests that contained at least one cowbird egg is shown in parentheses.

[b] Mean number of surviving young in all broods (±SD), including broods found at the postfledging stage.

lowing the methods of May and Robinson (1985). Other modeling approaches are appropriate for such a study (e.g. Pease and Grzybowski 1995), but we consider May and Robinson's (1985) approach to be adequate for our purposes owing to the preliminary nature of the available data (particularly on mortality) for these simulations. Our model was based on a population size of 100 breeding adult female Warbling Vireos, which probably was not very different from that in our study area. Inputs for the model included the number of young fledged by the vireos when parasitized and when not parasitized (Ward and Smith 2000) and different estimates of juvenile survival to breeding age. Survival of adults was assumed to be 0.5 (which is usually considered to be conservative; Ricklefs 1969). Because Warbling Vireo nests usually were placed on thin branches at the tops of young trees, we were unable to reach many nests to band juveniles and measure survival. Therefore, we used a conservative estimate (i.e. likely an overestimate) of juvenile mortality (0.5) for a small passerine (Ricklefs 1969, May and Robinson 1985, Trail and Baptista 1993).

Following May and Robinson (1985), the maximum level of parasitism that this population can sustain is:

$$p_c = \frac{\lambda - [2\mu/(1 - \mu_0)]}{(\lambda - \lambda')}, \qquad (1)$$

where $\lambda$ and $\lambda'$ are the number of young fledged from nonparasitized and parasitized broods, respectively, and $\mu$ and $\mu_0$ are adult and juvenile mortality rates, respectively.

## RESULTS

*Habitat use.*—In the 27 plots surveyed, Warbling Vireos nested mostly in habitats dominated by alder (*Alnus rubra;* nine plots) and Douglas maple (*Acer douglasii;* seven plots). Other dominant species on plots, in order of importance, were willow (*Salix*), paper birch (*Betula papyrifera*), western larch (*Larix occidentalis*), aspen (*Populus tremuloides*), and black cottonwood (*Populus trichocarpa*).

Nest trees tended to be of moderate height ($\bar{x} = 10.5 \pm$ SE of 3.76 m) and small stem diameter ($\bar{x} = 7.7 \pm 1.28$ cm), indicating a preference for young stands. Most of these young trees were in conifer stands that had been clearcut from 1979 to 1982. The mean canopy cover of stands used by Warbling Vireos was 59 ± 3.8%. All of the Warbling Vireo nests that we found were within 15 m of the edge of forest habitat, and all but four were within 5 m of the edge.

Parham (1937) considered Warbling Vireos to be common on the valley floor (300 m) in our study area from about 1900 to 1920, but we found only two nests at this elevation. All other nests occurred between 600 and 1,200 m. In late May, when most Warbling Vireos were arriving at the study area, males sang in riparian woodland on the valley floor for periods up to one week. However, except for the two nests noted above, none of these males stayed to breed.

*Breeding biology and cowbird parasitism.*—The incidence of brood parasitism by cowbirds was high in all years (Table 1) but was consistently lower than the 79% reported by Cannings et al. (1987). Survival of vireo nestlings was low, and on average fewer than two vireo young were produced per nest (Table 1). Warbling Vireo clutch sizes were significantly smaller in parasitized nests ($\bar{x} = 2.75 \pm 0.22$, $n = 24$) than in nonparasitized nests ($\bar{x} = 3.36 \pm 0.22$, $n = 14$), presumably because of egg removal by female cowbirds (see Marvil and Cruz 1989). Of the 24 parasitized nests, 16 contained one cowbird egg and eight had two cowbird eggs.

One obvious difference between the nests in our study and those noted in Cannings et al. (1987) was that our nests were placed substantially higher in trees ($\bar{x} = 6.2 \pm 0.55$ m, $n = 38$)

than were those of Cannings et al. ($\bar{x} = 2.8$ m). We used logistic regression to assess whether cowbirds parasitized low nests more heavily. We found no significant correlation between nest height and whether parasitism occurred ($P > 0.3$), suggesting that the higher level of parasitism recorded by Cannings et al. (1987) was not related to differences in nest height between our respective data sets.

Only 4 of 20 nests parasitized by cowbirds produced vireo fledglings. One nest was parasitized after incubation had begun, and the cowbird egg in another nest did not hatch. No data are available on the timing of cowbird parasitism relative to incubation for the other two nests. The mean number of surviving young was 0.1 ± 0.35 in parasitized nests and 1.7 ± 1.49 young in nonparasitized nests. Renesting was observed in two vireo pairs whose first nests were destroyed by predation (20 of 58 nests failed owing to predation). Otherwise, pairs nested only once per season, although it is possible that some pairs dispersed and renested outside of the study area.

*Return frequencies of birds.*—Thirty-eight Warbling Vireos, all but two of which were territorial males, were color banded in 1992 through 1994. Thirteen birds were recaptured or resighted in 1993 and 1994 (return percentage = 34.2%). Three males caught in 1992 were recaptured in both 1993 and 1994. Site fidelity in males was high; all 13 resighted birds were found in the same territories in subsequent years.

*Indices of density.*—Response to song playback at Blind Creek suggested that vireo densities fluctuated little over the study period. Mean response latency to playback was 181 ± 28.7 s in 1992, 182 ± 34.3 s in 1993, and 164 ± 32.1 s in 1994. This result was supported by data from spot mapping. Twenty-five vireo pairs were recorded along Blind Creek (ca. 14 km$^2$) in 1993 and 24 pairs in 1994. Similarly, we found 13 pairs at the Shuttleworth Creek site (ca. 15 km$^2$) in both 1993 and 1994. We found a single pair of vireos at each of three other sites from 1992 to 1994.

*Reactions to dummy birds and experimental cowbird eggs.*—All eight vireo pairs attacked the cowbird dummy ($\bar{x} = 4.9 \pm 1.10$ attacks/5 min). In contrast, only two vireo pairs attacked the junco dummy, and none attacked the crow dummy. The type and number of vocalizations given by vireos in the presence of the crow and the junco dummies were similar, but vireos increased their rate of alarm-calling in the presence of the cowbird dummy (Fig. 1). Because vireos reacted differently to the crow dummy than to the cowbird dummy, we conclude that their behavior toward cowbirds was not a generalized aggressive response.

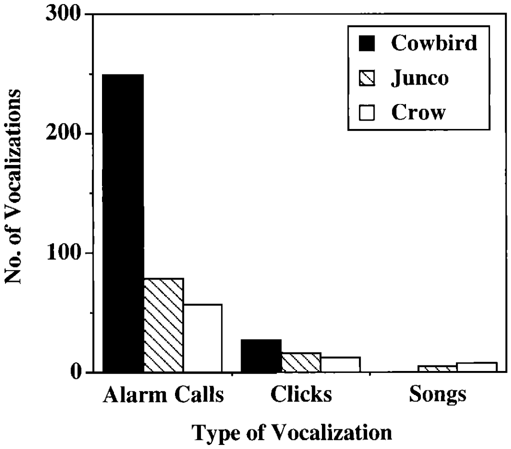

FIG. 1. Median number of vocalizations per 5 min given by Warbling Vireos in response to dummy cowbirds, juncos, and crows placed near their nests. Alarm calls consisted of growls and preceded dive-bombing of the dummy. Clicks appeared to be an intermediate response associated with behaviors such as wing-flicks. Vireos did not sing in the presence of the cowbird dummy.

Following experimental placement of a cowbird egg in the nest, all three vireo parents returned to the nest immediately and resumed incubation. These birds made no attempt to examine or manipulate the eggs during the 30 min after the cowbird egg had been placed in the nest.

*Simulation models of the effect of cowbird parasitism.*—Using the models outlined above (May and Robinson 1985), persistence of a population of 100 adult female Warbling Vireos ranged from 21 to 31 years, assuming that (1) the mean number of fledglings produced per nonparasitized brood was equal to that we measured (i.e. 1.60), or the true (population) mean number of fledglings was at the upper 95% confidence limit (i.e. 1.90); (2) no vireo fledglings were produced in parasitized broods; and (3) no immigration occurred.

We also modeled the population using the 79% parasitism rate of Cannings et al. (1987).

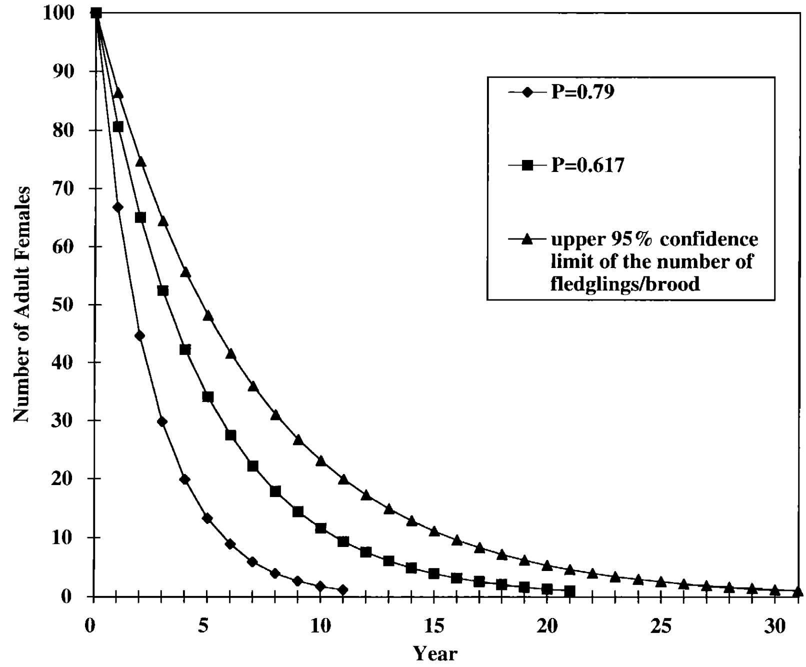

FIG. 2. Simulation model of the effects of different levels of parasitism and different numbers of successful fledglings per brood for a hypothetical population of Warbling Vireos. Adult and juvenile mortality rates were assumed to be 0.5 in all cases, and the birds were considered to raise only one brood per season.

At this level of parasitism, the vireo population would go extinct in 11 years (Fig. 2). For the Okanagan vireos, the maximum sustainable level of parasitism ($p_c$) is 37.5%, assuming that adult and juvenile survival rates are 0.5 and 1.6 fledglings are produced per brood. The maximum sustainable level of adult mortality that will allow the population size to remain at equilibrium or to increase is 0.31, assuming the first (and only) brood fledges 1.6 offspring and parasitism frequency is 0.617 (Table 1). If the true mean number of fledglings produced lies at the upper 95% confidence limit (1.9), a maximum adult mortality of 0.36 can be sustained at equilibrium.

## DISCUSSION

*Factors associated with vulnerability to cowbird parasitism.*—A number of aspects of the life history and habitat use of Warbling Vireos make them particularly susceptible to parasitism by Brown-headed Cowbirds. Warbling Vireos nest in a habitat that is considered to be the preferred habitat of Brown-headed Cowbirds, the forest edge (Brittingham and Temple 1983). Moreover, vireos nest in trees that are on the edge of this habitat, usually trees near roads and firebreaks. Thus, it is not surprising that the level of parasitism experienced by this species is high.

Barlow (1980) considered habitat destruction to be a major source of concern for the conservation of vireos in North America. This appears to be true in light of the almost complete loss of riparian woodland in the Okanagan Valley, where Red-eyed Vireos and Warbling Vireos have declined in recent times. However, Warbling Vireo habitat at higher elevations appears to be increasing as a result of recent extensive clearcutting of conifers.

Warbling Vireos showed a strong behavioral response to cowbirds near their nests, yet they did not reject cowbird eggs nor even recognize them. The behavior of vireos toward the dummy cowbirds was compatible with the aggressive-defense hypothesis (Robertson and Norman 1977); i.e. a high level of brood parasitism was associated with aggressive (albeit ineffective) behavior by the host species.

It is unlikely that vireos accepted cowbird eggs because they could not distinguish them from their own eggs, because no overlap occurs in egg size (cowbird eggs are larger) or egg coloration between Warbling Vireos and Brown-headed Cowbirds. Small-billed birds are more likely to accept cowbird eggs than are large-billed birds (Rothstein 1982, Rohwer and Spaw 1988), perhaps because small-billed birds may be unable to grasp and eject a cowbird egg. Rohwer and Spaw (1988) suggested that acceptance of cowbird eggs has reached an evolutionary equilibrium in many small-billed hosts because the alternative strategy available to the hosts is to desert and renest, which may be excessively costly. In the case of the Warbling Vireo, the equilibrium argument is untenable because this species has very few surviving young when parasitized (Rothstein et al. 1980, Cannings et al. 1987, this study). Thus, in theory it would always pay for them to desert the attempt and renest elsewhere.

Sealy (1996) has shown that the eastern subspecies (*V. gilvus gilvus*) of Warbling Vireo in Manitoba recognizes and removes cowbird eggs, which makes it the smallest bird known to eject cowbird eggs. Rejection behavior may account for the low incidence of parasitism (1.6%; $n = 62$ nests) recorded for this species in Ontario (Peck 1975). Sealy's findings are further evidence that small bills do not necessarily constrain rejection behavior (contra Rohwer and Spaw 1988).

*Breeding biology, brood parasitism, and the likelihood of extinction.*—Our simple population models suggest that current levels of brood parasitism in our study area are sufficient to drive small populations of Warbling Vireos to extinction without substantial emigration from nonparasitized populations. Furthermore, our data indicate that nesting success of Warbling Vireos is fairly poor, even without cowbird parasitism (Table 1). We stress that our models represent only preliminary estimates of the population dynamics of this species. It will be especially important to obtain accurate estimates of adult and juvenile survival rates as well as the frequency of renesting after nest failures.

Concentration of the vireo population at higher elevations (i.e. away from high densities of cowbirds; Ward and Smith 2000) owing to loss of riparian habitat may explain the 17% reduction in parasitism levels between our study and those summarized by Cannings et al. (1987). Most of the data in Cannings et al. (1987) were collected from the valley floor, where Warbling Vireos are no longer common. We found very few Warbling Vireos on the valley floor, and only moderate densities of them at middle elevations. Warbling Vireos seem to be locally common in young stands of deciduous trees (5 to 10 years old) at elevations between 1,300 and 1,600 m. Our data suggest that habitat loss and perhaps cowbird parasitism have been factors in the near extirpation of Warbling Vireos at low elevations in the Okanagan Valley, and that, on a small spatial scale, vireo numbers may have been enhanced at high elevations by forestry operations.

Our models and breeding data contrast with Sauer et al.'s (1997) analysis of Breeding Bird Survey data for this species. Sauer et al. (1997) recorded a nonsignificant ($P = 0.46$) mean decline of 1.40% per year for Warbling Vireos across British Columbia between 1966 and 1979 and a significant ($P < 0.01$) increase of 2.90% per year from 1980 to 1996; a significant increase of 2.20% per year (95% confidence limits 0.8 and 3.6%) occurred for the entire period. This lack of congruence between our results and those of Sauer et al. (1997) may be caused by different spatial scales of measurement. In contrast to our data, Sauer et al.'s data were region-wide and did not consider variation in population size at a local spatial scale. Merging our results with those of Sauer et al. leads to the conclusion that Warbling Vireos on the floor and middle elevations of the Okanagan Valley are part of a sink population maintained by emigration from source populations at higher elevations or from other areas. Verner and Rothstein (1988) showed that the relative abundance of Warbling Vireos and Brown-headed Cowbirds in their Sierra Nevada study area was inversely correlated and that many Warbling Vireos nested in remote areas away from human influence and cowbirds and thus experienced little risk of parasitism. These populations of Warbling Vireos may be important "sources" for sink populations.

We believe that it will be fruitful to continue monitoring populations of Warbling Vireos in the Okanagan Valley (and elsewhere) from a metapopulation perspective. Source populations, with high survival and low parasitism, may exist at high elevations and elsewhere in extensive forested habitats where few cowbirds exist (Ward and Smith 2000). However, if emigration from source populations to sink populations is rare, there may indeed be considerable cause for concern about the conservation status of some populations of Warbling Vireos.

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