*The Auk* 113(4):911–923, 1996

# IMPLICATIONS OF VAGRANT SOUTHEASTERN VIREOS AND WARBLERS IN CALIFORNIA

MICHAEL A. PATTEN[1,3] AND CURTIS A. MARANTZ[2]

[1]*Department of Biology, University of California, Riverside, California 92521, USA; and*
[2]*Department of Biology, University of Massachusetts, Amherst, Massachusetts 01003, USA*

ABSTRACT.—An unprecedented influx of vagrant vireos and wood-warblers into California occurred in the spring and summer of 1992. The seven species involved (White-eyed Vireo [*Vireo griseus*], Yellow-throated Vireo [*V. flavifrons*], Northern Parula [*Parula americana*], Yellow-throated Warbler [*Dendroica dominica*], Worm-eating Warbler [*Helmitheros vermivorus*], Kentucky Warbler [*Oporornis formosus*], and Hooded Warbler [*Wilsonia citrina*]) all breed primarily in the southeastern United States, suggesting a common factor for the influx. Furthermore, all seven species have been recorded in California with increasing frequency over the past two decades, suggesting a common trend in the populations of these species. We examined five hypotheses that could explain the increasing number of California records of these species: (1) observer bias, (2) pesticide-caused misorientation, (3) shifts in winter range, (4) anomalous weather conditions (including global warming and El Niño-Southern Oscillation), and (5) range expansions into the western United States and/or dramatic population increases in the southeastern United States. We found little or no support for the first three hypotheses. Anomalous weather conditions probably accounted for the magnitude of the 1992 influx, but the final hypothesis is needed to explain the overall trend. Although available data are not sufficient to distinguish between summer distributional shifts and population increases within the "normal" breeding ranges of these species, the possibility of westward range expansion is intriguing. *Received 15 March 1996, accepted 25 June 1996.*

MIGRATION CAN be considered an adaptive response that allows birds to exploit seasonally abundant food resources in breeding areas that lack those resources at other times of the year (Terrill 1991). By contrast, vagrancy has been regarded as maladaptive, because out-of-range individuals probably do not reproduce successfully. For this reason, vagrant birds often are treated as anomalies that have little or no biological significance (e.g. Bock 1979).

Vireos (Vireonidae) and American wood-warblers (Parulinae) with primarily eastern North American ranges are well-documented vagrants to California (e.g. McCaskie and Banks 1964; McCaskie 1968, 1970b, 1970c; Austin 1971; DeBenedictis 1971; DeSante 1973; DeSante and Ainley 1980; Roberson 1980; DeSante 1983). However, some species initially believed to be vagrants have proven to be scarce transients: Black-and-white Warbler (*Mniotilta varia*; McCaskie and Banks 1964, Austin 1971), American Redstart (*Setophaga ruticilla*; Pulich and Phillips 1953, McCaskie 1970a; cf. Root 1962), Northern Waterthrush (*Seiurus noveboracensis*; Mans and Peyton 1962, Austin 1971, Binford 1971), and, perhaps, Tennessee Warbler (*Vermivora peregrina*; McCaskie and Banks 1964, Austin 1971), Palm Warbler (*Dendroica palmarum*; Austin 1971), and Ovenbird (*Seiurus aurocapillus*; Austin 1971). Other species of eastern warblers and vireos generally are treated as vagrants, although some vagrants occur regularly in sizeable numbers (e.g. Blackpoll Warbler [*Dendroica striata*]; McCaskie 1970b, DeSante and Ainley 1980).

Grinnell (1922) predicted that "accidentals" were a mechanism "by which the species keeps aware of the possibility of a real expansion." Strictly speaking, the group-selectionist idea presented by Grinnell generally is considered invalid (see Williams 1966, Maynard Smith 1976). However, even considering range expansion to be an emergent property of individual selection, this prediction is difficult (if not impossible) to explore without many decades of comparable field data, unless expansion has been sufficiently rapid to be documented in a relatively short time (see Johnson 1994). Recent examples include the incursion of the Shiny Cowbird (*Molothrus bonariensis*) into the southeastern United States (Post et al. 1993) and the range expansions of various species noted by Johnson (1994). Presumably because short-term

[3] E-mail: patten@citrus.ucr.edu

trends like these are difficult to detect (Holmes et al. 1986), especially in sparsely distributed species, DeBenedictis (1971) concluded that "there is little indication of range expansion in the records of 'accidentals' in California." Increasing numbers of certain vireos and warblers from the southeastern United States have been recorded recently in California, which suggests that such an expansion may be taking place. Alternatively, numbers of these southeastern species may have increased by such a dramatic amount (even though their ranges have not changed) that the number of vagrants now being recorded in California reflects this increase. Finally, weather conditions or other environmental factors could be responsible for the observed pattern.

In this paper, we document an unprecedented incursion into California in the spring and summer of 1992 of seven species of vireos and wood-warblers from the southeastern United States. We provide a more thorough summary of the 1992 incursion than did Terrill et al. (1992), whose summary was necessarily brief and explored only weather-related hypotheses (which they felt explained the magnitude of the influx). Furthermore, we demonstrate that records of these species have been increasing steadily in California for 20 years, even though records of vagrants in general either have not been increasing or have increased at a much slower rate. Also, occurrences of these species have tended to covary with one another. We close by presenting a series of potential explanations for this trend, discussing the implications of each of them.

## METHODS

California records of White-eyed Vireo (*Vireo griseus*), Yellow-throated Vireo (*V. flavifrons*), Worm-eating Warbler (*Helmitheros vermivorus*), Yellow-throated Warbler (*Dendroica dominica*), and Kentucky Warbler (*Oporornis formosus*) were obtained from the California Bird Records Committee (CBRC). Records not accepted by the CBRC were excluded from analyses. Records of Northern Parula (*Parula americana*) and Hooded Warbler (*Wilsonia citrina*), species that are not reviewed by the CBRC, were obtained from regional reports in *Audubon Field Notes* and *American Birds* and from unpublished observations. We also discuss trends of four other parulines from the southeastern United States: Blue-winged Warbler (*Vermivora pinus*), Pine Warbler (*Dendroica pinus*), Prothonotary Warbler (*Protonotaria citrea*), and Louisiana Waterthrush (*Seiurus motacilla*).

California records of these species were analyzed in an attempt to distinguish between range expansion and vagrancy. We used three measures to detect such differences: (1) length of stay, (2) timing of occurrence, and (3) locality. For each of the seven species, the total number of occurrences in spring and summer was plotted by year. The overall trend in number of records was determined using Spearman rank correlation (year vs. occurrences) for each species from 1972 to 1994. Northern Parula records extended only through 1993 because we lacked sufficient data to include 1994. We used 1972 as a cutoff to ensure that observer bias would be minimized (by this time California birders had been actively searching for vagrants for nearly a decade [Roberson 1980]). Each species had been recorded in spring and summer in California before 1972, so the potential for occurrence in California was known. To avoid biases from inclusion of 1992 spikes, correlations also were calculated for each species with that year excluded.

The timing of occurrence of these seven species was analyzed qualitatively from 1972 to 1994 to detect seasonal trends, specifically for summering birds. For the two species with sufficient and complete data, a mean date of occurrence was calculated per record, either for all records (Kentucky Warbler) or for records from 1979 to 1994 (Hooded Warbler). These mean dates were regressed against year to elucidate any trend toward occurrence later in the spring and summer period.

The fact that migrant birds concentrate in isolated patches of vegetation, whether on the coast or in the desert, has been known for decades (Roberson 1980). Much effort is devoted to searching for vagrants at such locations. As a result of this observer bias, the vast majority of California records of these species has occurred at such "vagrant traps." We analyzed qualitatively the records for each of the seven vireos and warblers treated herein by comparing 1992 locations of occurrence with those from previous years. In doing so, we noted whether a 1992 location was a known vagrant trap or, based on biogeography, if it would have been considered one (e.g. a coastal promontory, desert oasis, or other distinct habitat island).

## RESULTS

Each of the seven species we examined is discussed briefly below in a separate account, followed by a composite discussion of Blue-winged Warbler, Pine Warbler, Prothonotary Warbler, and Louisiana Waterthrush. We provide information regarding the status of each species in California, a summary of spring and summer records for 1992, and a note on spring and summer records for 1993, 1994, and, if available, 1995. Trends of occurrence for each species also are provided, with and without the 1992 data.

TABLE 1. Number of records of southeastern vireos and warblers in California during spring and summer 1992 compared with the 10-year average ($\bar{x} \pm$ SD; range in parentheses) of spring and summer records from 1982 to 1991. Numbers differ from those published in Terrill et al. (1992) because some records reported during spring and summer 1992 were not documented, some overcounting likely occurred, and some records were reported late. The numbers in this table are probably a more accurate reflection of the 1992 influx.

| Species | 1982–1991 | 1992 |
|---|---|---|
| White-eyed Vireo (*Vireo griseus*) | 0.6 ± 0.84 (0–2) | 10 |
| Yellow-throated Vireo (*V. flavifrons*) | 1.2 ± 1.23 (0–3) | 9 |
| Northern Parula (*Parula americana*) | 18.3 ± 9.74 (6–36) | 138 |
| Yellow-throated Warbler (*Dendroica dominica*) | 1.7 ± 1.95 (0–6) | 6 |
| Prothonotary Warbler (*Protonotaria citrea*) | 1.0 ± 1.25 (0–3) | 3 |
| Worm-eating Warbler (*Helmitheros vermivorus*) | 0.9 ± 0.99 (0–3) | 8 |
| Kentucky Warbler (*Oporornis formosus*) | 3.3 ± 4.11 (0–13) | 36 |
| Hooded Warbler (*Wilsonia citrina*) | 6.3 ± 3.56 (2–14) | 76 |

*White-eyed Vireo.*—During spring and summer 1992, 10 White-eyed Vireos, all but one singing, were recorded in California between 10 May and 14 August (Heindel and Patten 1996). This number was well above the average number of spring and summer occurrences for this species (Table 1). Five were singing individuals found between 23 June and 14 August in areas not generally considered to be vagrant traps. Both the spring and summer of 1993 and 1994 again saw above-average numbers of this species, with four and three records, respectively. The rate of spring and summer records of White-eyed Vireos in California has increased since 1972 (Fig. 1), although the trend is only marginally significant (Table 2).

*Yellow-throated Vireo.*—Nine Yellow-throated Vireos were reported between 28 April and 9 July 1992 (Table 1). Five were singing (Heindel and Patten 1996) and three were from areas that were not vagrant traps. Both 1993 (three) and 1994 (two) also showed an above-average number of records (Fig. 1), including the first probable oversummering individual for California (CBRC 125-1994). The rate of spring and summer records of Yellow-throated Vireos in California has increased since 1972, but the trend is not quite significant (Table 2).

*Northern Parula.*—An unprecedented 138 birds were located between 3 April and the end of July 1992 (Table 1). At least three pairs nested in California that year, including the first for southern California (McCaskie 1992). Forty-six birds were recorded in the spring and summer of 1993, the second-highest total ever. Spring and summer records for 1994 were not available, but 20–30 Northern Parulas were recorded, and they probably nested again in Marin County.

Between 1972 and 1993, the frequency of spring and summer records of Northern Parula in California has increased significantly (Table 2, Fig. 1). Furthermore, although this species nested in California only twice prior to the mid-1980s (Williams et al. 1958, Winter and Morlan 1977), confirmed nesting has been recorded in most years since 1984, mainly along the coast of central California from Marin County south to San Mateo County (see Shuford 1994). Summering individuals are recorded with increasing frequency, with many found in foothill-riparian areas and other locations that are not typical vagrant traps.

*Yellow-throated Warbler.*—Two Yellow-throated Warbler subspecies have been recorded in California, with the western subspecies *D. d. albilora* accounting for the vast majority of records. Six were found from 8 May through 3 July 1992 (Heindel and Patten 1996; Table 1, Fig. 1), three of which were singing and at least three of which were identified as *albilora* (the subspecific identity of the other three is unknown). Five were at known vagrant traps, and the sixth, a singing male in Monterey County on 24 May 1992 (CBRC 147-1992), was in coastal coniferous forest. None of the birds in 1992 was known to have summered, although a singing male in Humboldt County on 3 July was later than a typical "spring" vagrant. The only confirmed record of oversummering in California was in 1981. This individual often was accompanied by a singing male Northern Parula (Binford 1985). Unlike the other species we discuss, the Yellow-throated Warbler has shown no clear trend in the number of spring and summer records (Table 2, Fig. 1).

*Worm-eating Warbler.*—Eight Worm-eating Warblers were found 7 May through 28 June

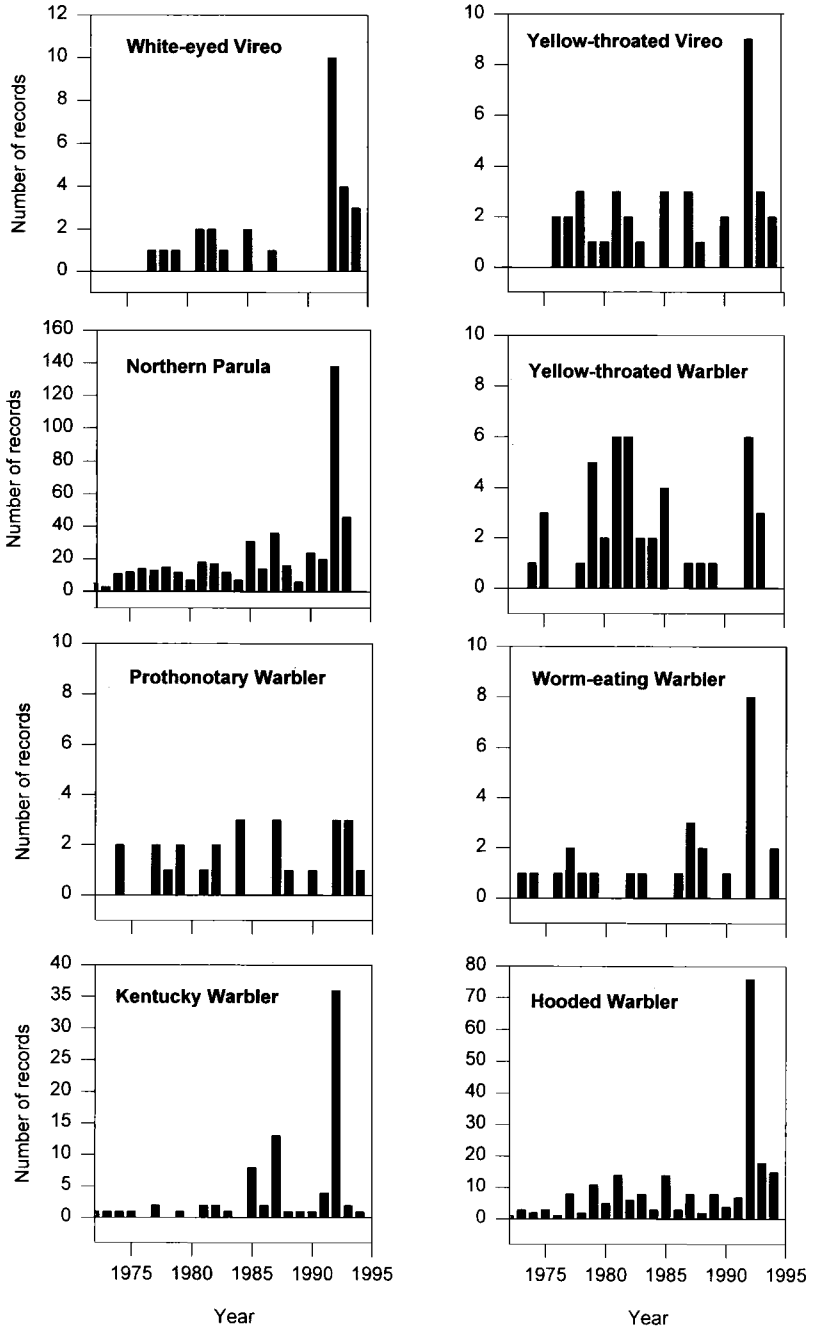


FIG. 1. Spring and summer records in California (1972–1994) of White-eyed Vireo, Yellow-throated Vireo, Northern Parula (1972–1993), Yellow-throated Warbler, Prothonotary Warbler, Worm-eating Warbler, Kentucky Warbler, and Hooded Warbler.

1992 (Table 1), all at typical vagrant traps (Heindel and Patten 1996). Although birds in 1977 (CBRC 66-1977) and 1978 (CBRC 94-1978) may have oversummered, one banded and photographed at Coyote Creek Riparian Station, Santa Clara County, 17 June–26 August 1992 (CBRC 69-1993) was the first unequivocal summering record for California. The Worm-eating War-

TABLE 2. Trends in the rate of spring and summer records in California of southeastern vireos and warblers. Trend correlations were calculated by comparing number of spring and summer records vs. year of occurrence from 1972 to 1994 using Spearman rank correlation.

| Species | 1972–1994 | | 1972–1994 (1992 excluded) | |
|---|---|---|---|---|
| | $r_s$ | $P$ | $r_s$ | $P$ |
| White-eyed Vireo (*Vireo griseus*) | 0.383 | 0.07 | 0.290 | 0.19 |
| Yellow-throated Vireo (*V. flavifrons*) | 0.344 | 0.11 | 0.259 | 0.24 |
| Northern Parula (*Parula americana*) | 0.671 | 0.001 | 0.623 | 0.002 |
| Yellow-throated Warbler (*Dendroica dominica*) | 0.085 | 0.70 | −0.010 | 0.96 |
| Prothonotary Warbler (*Protonotaria citrea*) | 0.275 | 0.20 | 0.186 | 0.41 |
| Worm-eating Warbler (*Helmitheros vermivorus*) | 0.154 | 0.48 | 0.049 | 0.82 |
| Kentucky Warbler (*Oporornis formosus*) | 0.423 | 0.04 | 0.356 | 0.10 |
| Hooded Warbler (*Wilsonia citrina*) | 0.606 | 0.002 | 0.552 | 0.008 |

bler has shown a modest, albeit nonsignificant, increase in the frequency of spring and summer records in California since 1972 (Table 2).

*Kentucky Warbler.*—An unprecedented 36 Kentucky Warblers were reported 4 May through 11 August 1992 (Table 1), including at least 11 along the upper Santa Ynez River drainage in Santa Barbara County (10 of which were banded there and most of which spent the entire summer in the area [Heindel and Patten 1996]). Most of the individuals found in 1992 were singing males and were recorded away from areas considered to be vagrant traps. The number of records in spring and summer 1993 and 1994 returned to recent "normal" levels, with two summering birds in 1993 (both at atypical locations for vagrant landbirds) and one in spring 1994 (Fig. 1). The rate of spring and summer records of Kentucky Warbler in California has increased significantly between 1972 and 1994 (Table 2, Fig. 1). No trend was found in mean date of occurrence since 1968 ($r = 0.047$, $n = 81$, $P > 0.05$).

*Hooded Warbler.*—Seventy-six Hooded Warblers were found between 18 April and 11 September 1992 (Table 1). An adult female banded in San Bernardino County in mid-September likely summered and is considered in our 1992 total. The first breeding records of Hooded Warblers for California occurred in 1992, with one nest in Los Angeles County (two young fledged on 9 August; McCaskie 1992, K. L. Garrett pers. comm.), and three nesting attempts from a minimum of two pairs that summered at the South Fork Kern River Preserve, Kern County (McCaskie 1992). Additional records included a singing male and a female at the same Riverside County location, a male in San Bernardino County in mid-June (ca. 1 km from the September female noted above), and two males and a female at the same location in San Luis Obispo County.

The number of Hooded Warbler records in spring and summer 1993 and 1994 again was much higher than average, with 18 and 15 birds recorded, respectively (Fig. 1). These records included birds summering again at the South Fork Kern River Preserve. The frequency of spring and summer records of Hooded Warblers has increased significantly in California since 1972 (Table 2, Fig. 1). Furthermore, although the first oversummering individual was recorded as recently as 1985 (Campbell et al. 1985), nearly 20 have oversummered in California during the 1990s, many in locations not typically frequented by vagrant landbirds. Despite this qualitative increase in summering records, no trend was detected for mean date of occurrence between 1979 and 1994 ($r = 0.022$, $n = 183$, $P > 0.05$).

*Other southeastern warblers.*—Blue-winged Warblers have occurred in California at least nine times in the past decade (CBRC data), including two in May 1992 (Heindel and Patten 1996), a number that matched the previous maxima in spring 1984 and 1987. Nearly half (10 of 21) of all California records are from spring.

No Pine Warblers were recorded in California during spring or summer in 1992, but their rate of occurrence has increased in recent years (Patten and Erickson 1994). Only eight were recorded before 1983, but Pine Warblers have occurred in California each year thereafter, with a total of 52 records through January 1995 (all but two or three in fall and winter; CBRC data).

There have been slightly more than 100 accepted records of Prothonotary Warblers in the state. Three occurred in California between 1

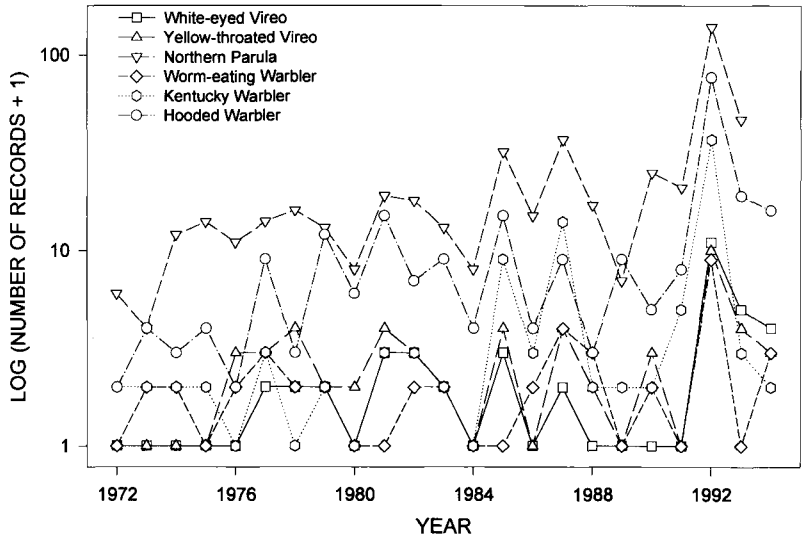


FIG. 2. Spring and summer occurrences in California of White-eyed Vireo, Yellow-throated Vireo, Northern Parula, Worm-eating Warbler, Kentucky Warbler, and Hooded Warbler. Note how peaks and valleys in occurrence tend to match across species.

and 17 May 1992, which equaled the previously recorded maximum for a single spring (Fig. 1). Three Prothonotary Warblers also were recorded during spring 1993, but only one bird was recorded in spring 1994. One of the birds in 1993 oversummered, the first such record for California (McCaskie 1993, 1994). The frequency of spring records in California did not increase significantly from 1972 to 1994 (Table 2).

Only two Louisiana Waterthrushes were recorded in California before 1990. Six occurred between 1990 and 1995, including four in spring (CBRC 85-1990, 78-1991, 119-1992, 61-1995).

## DISCUSSION

Our results demonstrate clearly two different but related phenomena. The first is the steady increase in the number of southeastern vireo and warbler species reaching California each year, and the second is the unprecedented influx into California (and other western states) of many of these species during the spring and summer of 1992. Furthermore, both Northern Parula and Hooded Warbler nested successfully in California in 1992 (Hooded Warbler for the first time), and it is possible that Kentucky Warblers also attempted to nest. A number of hypotheses may explain the steady increase in the frequency of California records of these species, in addition to the 1992 influx; some of these hypotheses were discussed by Terrill et al. (1992). That occurrences of these species covary, particularly White-eyed Vireo, Yellow-throated Vireo, Northern Parula, Kentucky Warbler, and Hooded Warbler (Table 3, Fig. 2), is an important consideration, as is the fact that those species with the most marked rates of increase (Table 2) are the most highly intercorrelated (Table 3). Here we discuss five potential causative factors.

*Observer bias.*—The efforts and skills of observers in finding vagrant birds in California have increased tremendously since the early 1960s (Shuford 1981). Thus, the marked increase in southeastern vireo and warbler records in California could be directly related to observer effort. Whereas effort and skill increased sharply in the early 1960s, both factors have remained relatively constant since the mid-1970s (see Roberson 1980). Furthermore, despite the increase in observer coverage and awareness, many northern-breeding species, most notably Cape May Warbler (*Dendroica tigrina*) and Bay-breasted Warbler (*D. castanea*) (but also Red-eyed Vireo [*Vireo olivaceus*], Tennessee Warbler, Black-throated Green Warbler [*D. virens*], and Blackburnian Warbler [*D. fusca*]) have been recorded with decreasing frequency in California. Although the decrease in Tennessee, Cape May, and Bay-breasted warbler numbers may be due in part to a natural re-

TABLE 3. Spring and summer occurrences of eight vireo and warbler species in California from 1972–1993. Data represent Spearman rank correlation coefficients by year ($n$ = 22 years) for each pairwise combination of species, followed by $P$-values associated with these coefficients (in parentheses). WEVI, White-eyed Vireo; YTVI, Yellow-throated Vireo; NOPA, Northern Parula; YTWA, Yellow-throated Warbler; POWA, Prothonotary Warbler; WEWA, Worm-eating Warbler; KEWA, Kentucky Warbler; HOWA, Hooded Warbler.

| | WEVI | YTVI | NOPA | YTWA | POWA | WEWA | KEWA |
|---|---|---|---|---|---|---|---|
| YTVI | 0.8155 | | | | | | |
| | (0.0001) | | | | | | |
| NOPA | 0.6314 | 0.7701 | | | | | |
| | (0.002) | (0.0001) | | | | | |
| YTWA | 0.6808 | 0.4360 | 0.2991 | | | | |
| | (0.0005) | (0.042) | (0.176) | | | | |
| POWA | 0.5127 | 0.4649 | 0.4203 | 0.3846 | | | |
| | (0.015) | (0.029) | (0.052) | (0.077) | | | |
| WEWA | 0.2003 | 0.3389 | 0.2744 | −0.1426 | 0.4134 | | |
| | (0.371) | (0.123) | (0.216) | (0.527) | (0.056) | | |
| KEWA | 0.5806 | 0.3926 | 0.6731 | 0.2311 | 0.2628 | 0.2108 | |
| | (0.005) | (0.071) | (0.001) | (0.301) | (0.237) | (0.346) | |
| HOWA | 0.7519 | 0.5282 | 0.5103 | 0.5938 | 0.3365 | −0.0242 | 0.6618 |
| | (0.0001) | (0.012) | (0.015) | (0.004) | (0.126) | (0.915) | (0.001) |

duction from inflated population levels during the 1970s and early 1980s that resulted from spruce budworm (*Choristoneura fumiferana*) outbreaks (Morse 1989, Patten and Marantz unpubl. data), a similar explanation cannot be invoked for decreases in other northern species. For example, even some scarce transients like Black-and-white Warbler, American Redstart, Rose-breasted Grosbeak (*Pheucticus ludovicianus*), and Indigo Bunting (*Passerina cyanea*) have shown a general decrease in numbers in California during spring and summer, whereas others have remained fairly constant (Table 4). Conversely, with the exception of Yellow-throated Warbler, which shows no trend, the more southerly breeding vireos and warblers discussed herein all have recently occurred in California with increasing frequency. It is unlikely that the dramatic increase in the number of records of these southerly species is a function of observer bias.

*Pesticide contamination.*—Pesticides are prevalent in today's environment, and it has been suggested that their ingestion may lead to misorientation in migrant birds. However, the impact of pesticides on migrants is not well known (Berthold and Terrill 1991), although in some cases, e.g. DDT, the debilitating effects have been well documented (Carson 1962). Furthermore, DeSante (1983) noted that "there is no good evidence linking pesticide contamination to orientation or navigation errors in birds," but he warned that "the possibility should not be unequivocally dismissed." That the majority of vagrants are hatching-year birds suggests that pesticide contamination, if it is responsible for the misorientation of migrants, is more likely transmitted to the young as a genetically inherited abnormality (via mutations of the germ line through biomagnification or increased exposure). However, exposure on the wintering grounds may play a more immediate role, es-

TABLE 4. Average number of occurrences in California in spring and summer for selected Neotropical migrants breeding mainly across Canada and in the northeastern and northern United States. Data for Philadelphia Vireo and Golden-winged Warbler are from the California Bird Records Committee. Data for other species taken from Roberson (1980) and regional reports in *American Birds*.

| Species | 1975–1979 | 1982–1991 |
|---|---|---|
| Philadelphia Vireo (*Vireo philadelphicus*) | 0.6 | 0.4 |
| Golden-winged Warbler (*Vermivora chrysoptera*) | 0.6 | 1.0 |
| Black-and-white Warbler (*Mniotilta varia*) | 27.6 | 24.7 |
| American Redstart (*Setophaga ruticilla*) | ca. 59 | 29.3 |
| Ovenbird (*Seiurus aurocapillus*) | 17.3 | 17.4 |
| Rose-breasted Grosbeak (*Pheucticus ludovicianus*) | 59.8 | 45.9 |
| Indigo Bunting (*Passerina cyanea*) | 38.5 | 31.2 |

pecially for spring migrants. Even if pesticide residues account, in part, for the gradual increase of southeastern migrants in the western United States, they provide a poor explanation for the 1992 influx.

*Shifts in winter range.*—Another possibility is that the wintering distributions of these species are changing, with increasing numbers wintering in western Mexico. Recent data from the San Blas (Nayarit) Christmas Bird Count show that many southeastern warbler species (but not vireos) are present in small numbers in western Mexico (Pashley and Martin 1989). Although these counts demonstrate the occurrence of species in a region where they were not known previously (Miller et al. 1957), the numbers documented on these counts probably have not increased over the past 10 years to an extent that would account for the increase in California.

*Weather patterns.*—We explore two related hypotheses regarding weather: El Niño-Southern Oscillation (ENSO), and anomalous weather conditions in 1992. Global warming could be another weather-related factor, but there is no solid evidence regarding warming trends or their influence on passerine movements, and therefore any predictions from it are not clear.

Anomalous warm water appearing in the coastal and equatorial waters off of Peru and Ecuador is termed the El Niño. This periodic episode is accompanied by an atmospheric force known as the Southern Oscillation (Rasmusson and Wallace 1983). The profound effects of ENSO events are well-documented for seabirds (Ainley and Lewis 1974, Bock and Larson 1983, Ainley et al. 1988) but not for terrestrial birds. Although Schreiber and Schreiber (1984) suggested that ENSO conditions "may extend to nonmarine species far from the Pacific," Hall et al. (1988) were the first to attempt a synthesis of existing information, much of which is "circumstantial, but highly suggestive." Despite Hall's (e.g. Hall 1984a, 1984b) long-term studies of Neotropical migrants in the eastern United States showing a correlation between ENSO events and low numbers of breeding birds, other studies have not shown such a correlation (e.g. Holmes et al. 1986). Even so, the sparse evidence ". . . suggests that ENSO events result in lower populations of Neotropical migrants" (Hall et al. 1988).

Whether ENSO conditions can result in the subsequent displacement of Neotropical migrants is difficult to ascertain. An increase in precipitation in the highlands of central Mexico, leading to colder-than-normal conditions during winter months and a decrease in food availability for insectivores, may prove to be too great a barrier during the return migration for species wintering in western and southern Mexico. By contrast, large amounts of rainfall during mid-winter may improve rather than hurt a bird's chances of survival. What seems more likely is that fronts associated with this rainfall may move in an abnormal direction that might shift migrants concomitantly (see below).

Species that normally cross the highlands from their wintering grounds to reach their breeding grounds in the southeastern United States might be "forced" to take an alternate lowland path, possibly leading them up the western coast of Mexico into the southwestern United States. Whereas such a westerly displacement is speculative, the idea seems plausible (Terrill et al. 1992, P. Pyle pers. comm.). ENSO events should be considered in future, large-scale displacements of eastern birds to the west.

By contrast, the 1992 influx may represent a transient phenomenon unrelated to ENSO events, and one without bearing on long-term demography of southeastern vireo and warbler species. Weather, particularly wind, plays a major role in bird migration, affecting food availability and energy requirements, and even forcing birds out of normal migratory routes (Lack 1960, Bagg 1970, Richardson 1978, Pyle et al. 1993). Most migrants await favorable tailwinds before commencing migration (Richardson 1978, Terrill 1991; cf. Pyle et al. 1993), and it has been shown that migrants tend to head downwind regardless of the direction of flow (Lowery 1951, Gauthreaux and Able 1970).

Typically, atmospheric high-pressure dominates the Gulf of Mexico in April and May, leading to persistent northerly winds throughout migration (Lowery 1951). These air masses are usually slightly west of due north in the western Gulf of Mexico, and are northeasterly on average in the central Gulf States and in the lower Mississippi Valley. This high pressure region occasionally is broken by northerly cold fronts (which lead to spring "waves" or "fallouts" on the Gulf Coast), which occur less often as the season progresses (Lowery 1951). A high-pressure system stalled over the western United States, coupled with a low-pressure system over the Gulf of Mexico, leads to prolonged easterly

or northeasterly winds that could drive many trans-Gulf migrants westward. This situation did exist in mid-April 1992, when relatively strong east and northeast winds blew across the Gulf (Terrill et al. 1992). Although this condition may have driven some birds westward, it probably was not strong enough to bring birds to the West, largely because of the distance involved. In the last week of April 1992, however, a strong Canadian high produced north, northeast, and east winds in the Gulf of Mexico that appeared to carry to California the first southeastern vireos and warblers. Furthermore, a strong low-pressure system stalled over southeastern California and southwestern Arizona for most of May 1992. In addition to bringing steady easterly and southeasterly winds to the region throughout the month, this system brought monsoon-like conditions to Arizona well before their typical appearance in July (Terrill et al. 1992). These conditions probably led to the tremendous westward displacement of trans-Gulf migrants, and they may have played an important role in at least the magnitude of the influx of southeastern vireos and warblers that occurred in the western United States (see Terrill et al. [1992] for more information).

*Population trends and habitat availability.*—If the species involved in the 1992 incursion experienced either an exceptionally productive breeding season in 1991 or much higher than normal survivorship on their wintering grounds (or a combination of these two factors), then the resultant swelled populations could have led to a higher incidence of dispersal to the western United States. Alternatively, loss of habitat in the southeastern United States may be forcing birds to disperse in search of available habitat elsewhere. Thus, there are two possible hypotheses: (1) increased population levels of these species are causing more birds to disperse, or (2) habitat loss in the Southeast is causing birds to seek sites elsewhere.

With regard to the first hypothesis, two important predictions result. The first is that an increase in population levels of vireos and warblers in the southeastern United States must be demonstrable. Many recent sources, however, suggest that the population trends for these species are downward (e.g. Sauer and Droege 1992, Böhning-Gaese et al. 1993, Peterjohn and Sauer 1994, Taper et al. 1995). Nevertheless, James et al. (1992) indicated that population levels of these species are increasing in lowland areas in the southeastern United States, and Taper et al. (1995) presented data indicating that these species are increasing in some regions.

The second prediction is that the number of vagrant vireos and warblers reaching California directly reflects population levels of these species within their normal range. This idea appears to have merit based on correlations between numbers of visible migrants and breeding bird populations (Svensson 1978). In considering Pine Warbler, for example, Patten and Erickson (1994) suggested that the increased number of California records reflected a population increase in the southeastern United States noted by Böhning-Gaese et al. (1993); a similar correlation appears to exist for Blue-winged Warbler. Likewise, Roberson (1980) discussed population fluctuations of certain species (e.g. Cape May Warbler) affecting the number of vagrants found along the west coast of North America. Although breeding population size seems to be associated with the number of records of vagrants in California, more work is needed to determine how widespread this relationship is. If the frequency of vagrancy to California is a valid measure of population size, then the increase in rate of occurrence of these species suggests that James et al. (1992) have uncovered the real trend.

The tremendous displacement of the various southeastern vireos and warblers into the southwestern United States may be part of a long-term trend toward range expansion. In the past three decades, various passerines have appeared with increased frequency in the western United States, particularly in California (DeSante 1973, Pyle et al. 1993). DeBenedictis (1971) noted that range expansion of birds is possible under two circumstances: (1) through amelioration of environmental conditions such that more suitable habitat becomes available to a given species or set of species adapted to those conditions; or (2) by movement across unsuitable habitat to areas of suitable, unoccupied habitat. He further assumed that vagrancy leading to range expansion occurred primarily through the latter mode.

The notion of "unoccupied habitat" is critical to this argument. Individuals dispersing to California in the past probably found suitable habitat already "filled" by native species, such as Willow Flycatcher (*Empidonax traillii*), Bell's Vireo (*Vireo bellii*), Warbling Vireo (*V. gilvus*), Yellow Warbler (*Dendroica petechia*), and Mac-

Gillivray's Warbler (*Oporornis tolmiei*). The sharp decrease in many riparian-breeding birds in the western United States (Gaines 1974) may have opened habitats for these vagrants. Unoccupied habitat in the West, coupled with habitat loss in the Southeast, could lead to an increase in the number of records of these species in California.

A first step in testing the "increased source-pool hypothesis" versus the "westward expansion hypothesis" is to obtain reliable population trends for the species involved. Beyond this effort, California records can be analyzed in an attempt to distinguish between expanding species ranges and vagrancy. We propose three measures to detect such differences: (1) length of stay, (2) timing of occurrence, and (3) locality. Length of stay should be longer for birds expanding their range into an area because migrants, particularly in spring, stay only for rest or brief re-fueling (Blake 1950, Lavee et al. 1991). Timing of occurrence should be later for birds expanding their range, although this measure is a function of length of stay (Lavee et al. 1991). Lastly, a species expanding its range should occur with increasing frequency in areas that are not vagrant traps, but with relatively constant frequency at vagrant traps. This measure is strongly affected by observer bias, because most effort invested in finding vagrants occurs in areas that are known to concentrate migrants.

Even though mean date of occurrence was not correlated with year of occurrence for all seven of the species considered here (Kentucky Warbler and Hooded Warbler did not show this trend), many of the vagrants found in California during 1992 not only stayed for extended periods, but several species nested or remained on territories. Because using mean date of occurrence ignores variance (i.e. length of stay), it is perhaps not surprising that these results were not significant. Qualitatively, there has been a trend toward increasing frequency of summering individuals of Kentucky and Hooded warblers and of Northern Parulas. Furthermore, many of the individuals found in 1992 were in foothill riparian areas, localities seldom checked for vagrants but heavily used by many of California's breeding birds (Gaines 1974). Although not visited often by birders, many riparian areas have been surveyed steadily since the late 1970s and early 1980s for Least Bell's Vireo (*V. b. pusillus*) and other endangered species. Yet, the increase in southeastern vireos and warblers at these locations has been noted only recently.

## CONCLUSIONS

Some bird species show remarkable plasticity in their breeding ranges. Individuals that find themselves in California in potentially suitable habitat and with potential mates often attempt to nest. An event like the 1992 influx thus has major implications on the dispersal of these species, because the potential for a breeding population to become established perhaps is only an "influx or two away," a concept fulfilling Grinnell's (1922) predictions. The general lack of returns in 1993 (some Northern Parulas and Hooded Warblers likely did return) suggests either that most birds did not survive to the next year, or that they attempted to nest elsewhere, perhaps within their normal breeding ranges. The implication is that if these birds were shifted off-course by an anomalous event, they may have attempted to return to their normal ranges in the following year.

The huge influx of southeastern vireos and warblers into California may be explained in part by anomalous weather conditions that forced these trans-Gulf migrants westward. However, given the general increase of records of these species in California, contrasted with a general decrease in records of more northerly breeding vireos and warblers, we feel that: (1) the southeastern species are expanding westward; and/or (2) their populations are increasing, thus increasing the source pool for vagrants to California. These hypotheses are not mutually exclusive. Indeed, if "forced dispersal" (either through habitat loss or density dependence) is a factor, then it is possible that an increase in population levels of southeastern vireos and warblers would lead to range expansion (both westward and northward).

Distinguishing between westward expansion and increased source pool is not simple, although the three predictions described above (increased length of stay, later mean time of occurrence, and non-vagrant-trap locality) could be analyzed qualitatively to distinguish between vagrants and potential colonizing individuals. For most of the species discussed herein, there has been a general trend toward an increase in the rate of spring and summer records, with a concomitant increase in the frequency of summering individuals (this affects

both the length of stay and the timing of occurrence) and an increase in occurrence in foothill riparian areas, montane areas, and other locations not typical of vagrant traps.

Each of the species treated herein has recently summered and/or nested in California, and Northern Parula has become relatively well-established as a regular (albeit scarce) member of California's breeding avifauna. If we truly are witnessing a westward range expansion of these species, then the frequency of occurrence and the number of summering individuals should continue to increase, as should the number of nesting attempts. Only a long-term analysis, with a few more decades of data, can be used to test this hypothesis.

ACKNOWLEDGMENTS

Guy McCaskie and David G. Yee supplied numerous unpublished 1992 records of Northern Parula and Hooded Warbler. Stephen F. Bailey, Kimball L. Garrett, John D. Goodman, and Stephen J. Myers supplied additional unpublished information. Scott B. Terrill provided much useful information and many hours of stimulating discussion. Louis R. Bevier, Mary K. Chase, Kimball L. Garrett, Richard L. Hutto, William B. Kristan III, Donald E. Kroodsma, Jeff Marks, Peter Pyle, C. J. Ralph, J. V. Remsen, Jr., and Jeffrey V. Wells improved drafts of this manuscript. The California Bird Records Committee was an invaluable source of documentation for the rarer vagrants discussed herein. All records reviewed by the CBRC are archived at the Western Foundation of Vertebrate Zoology, Camarillo, California.

LITERATURE CITED

AINLEY, D. G., AND T. J. LEWIS. 1974. The history of Farallon Island marine bird populations 1854–1972. Condor 76:432–446.

AINLEY, D. G., H. R. CARTER, D. W. ANDERSON, K. T. BRIGGS, M. C. COULTER, F. CRUZ, J. B. CRUZ, C. A. VALLE, S. I. FEFER, S. A. HATCH, E. A. SCHREIBER, R. W. SCHREIBER, AND N. G. SMITH. 1988. Effects of the 1982–1983 El Niño-Southern Oscillation on Pacific Ocean bird populations. Pages 1747–1758 *in* Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). Ottawa, Ontario, 1986. National Museum of Natural Science, Ottawa.

AUSTIN, G. T. 1971. On the occurrence of eastern wood warblers in western North America. Condor 73:455–462.

BAGG, A. M. 1970. The changing seasons: A summary of the 1969 fall migration season, with special attention to eruptions of various boreal and montane species and an analysis of correlations between wind flows and migration. Audubon Field Notes 24:4–13.

BERTHOLD, P., AND S. B. TERRILL. 1991. Recent advances in studies of bird migration. Annual Review of Ecology and Systematics 22:357–378.

BINFORD, L. C. 1971. Northern and Louisiana waterthrushes in California. California Birds 2:77–92.

BINFORD, L. C. 1985. Seventh report of the California Bird Records Committee. Western Birds 16:29–48.

BLAKE, C. H. 1950. Length of stay of migrants. Bird-Banding 21:151–152.

BOCK, C. E. 1979. Joseph Grinnell and the Christmas Bird Count. American Birds 33:693–694.

BOCK, C. E., AND D. LARSON. 1983. The changing seasons: Winter 1982–3, wherein the unexpected and the unexplained prove how very normal the season was. American Birds 37:275–277.

BÖHNING-GAESE, K., M. L. TAPER, AND J. H. BROWN. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? Conservation Biology 7:76–86.

CAMPBELL, K. F., R. A. ERICKSON, AND S. F. BAILEY. 1985. The summer season, Middle Pacific Coast Region. American Birds 39:956–961.

CARSON, R. 1962. Silent spring. Fawcett Publishing, Greenwich, Connecticut.

DEBENEDICTIS, P. 1971. Wood warblers and vireos in California: The nature of the accidental. California Birds 2:111–128.

DESANTE, D. F. 1973. An analysis of the fall occurrences and nocturnal orientations of vagrant wood warblers (Parulidae) in California. Ph.D. dissertation, Stanford University, Palo Alto, California.

DESANTE, D. F. 1983. Annual variability in the abundance of migrant landbirds on Southeast Farallon Island, California. Auk 100:826–852.

DESANTE, D. F., AND D. G. AINLEY. 1980. The avifauna of the South Farallon Islands, California. Studies in Avian Biology No. 4.

GAINES, D. 1974. A new look at the nesting riparian avifauna of the Sacramento Valley, California. Western Birds 5:61–80.

GAUTHREAUX, S. A., JR., AND K. P. ABLE. 1970. Wind and the direction of nocturnal songbird migration. Nature 228:476–477.

GRINNELL, J. 1922. The role of the "accidental." Auk 39:373–380.

HALL, G. A. 1984a. Population decline of Neotropical migrants in an Appalachian forest. American Birds 38:14–18.

HALL, G. A. 1984b. A long-term bird population study in an Appalachian spruce forest. Wilson Bulletin 96:228–240.

HALL, G. A., H. L. GIBBS, P. R. GRANT, L. W. BOTSFORD, AND G. S. BUTCHER. 1988. Effects of El Niño-Southern Oscillation (ENSO) on terrestrial birds.

Pages 1759–1769 *in* Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). Ottawa, Ontario, 1986. National Museum of Natural Science, Ottawa.

HEINDEL, M. T., AND M. A. PATTEN. 1996. Eighteenth report of the California Bird Records Committee: 1992 records. Western Birds 27:1–29.

HOLMES, R. T., T. W. SHERRY, AND F. W. STRUGES. 1986. Bird community dynamics in a temperate deciduous forest: Long-term trends at Hubbard Brook. Ecological Monographs 56:201–220.

JAMES, F. C., D. A. WIEDENFELD, AND C. E. MCCULLOCH. 1992. Trends in breeding populations of warblers: Declines in the southern highlands and increases in the lowlands. Pages 43–56 *in* Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.

JOHNSON, N. K. 1994. Pioneering and natural expansion of breeding distributions in western North American birds. Pages 27–44 *in* A century of avifaunal change in western North America (J. R. Jehl., Jr., and N. K. Johnson, Eds.). Studies in Avian Biology No. 15.

LACK, D. 1960. The influence of weather on passerine migration. A review. Auk 77:171–209.

LAVEE, D., U. N. SAFRIEL, AND I. MEILIJSON. 1991. For how long do trans-Saharan migrants stop over at an oasis? Ornis Scandinavica 22:33–44.

LOWERY, G. H., JR. 1951. A quantitative study of the nocturnal migration of birds. University of Kansas Publications of the Museum of Natural History 3:361–472.

MANS, M., AND G. S. PEYTON. 1962. Spring migration, Middle Pacific Coast Region. Audubon Field Notes 16:442–446.

MAYNARD SMITH, J. 1976. Group selection. Quarterly Review of Biology 51:277–283.

MCCASKIE, G. 1968. Noteworthy vireo records in California. Condor 66:442–443.

MCCASKIE, G. 1970a. The American Redstart in California. California Birds 1:41–46.

MCCASKIE, G. 1970b. The Blackpoll Warbler in California. California Birds 1:95–104.

MCCASKIE, G. 1970c. Occurrence of the eastern species of *Oporornis* and *Wilsonia* in California. Condor 72:373.

MCCASKIE, G. 1992. The summer season, Southern Pacific Coast Region. American Birds 46:1177–1180.

MCCASKIE, G. 1993. The summer season, Southern Pacific Coast Region. American Birds 47:1149–1152.

MCCASKIE, G. 1994. The autumn migration, Southern Pacific Coast Region. American Birds 48:151–155.

MCCASKIE, R. G., AND R. C. BANKS. 1964. Occurrence and migration of certain birds in southwestern California. Auk 81:353–361.

MILLER, A. H., H. FRIEDMANN, L. GRISCOM, AND R. T. MOORE. 1957. Distributional check-list of the birds of Mexico, part II. Pacific Coast Avifauna No. 33.

MORSE, D. H. 1989. American warblers: An ecological and behavioral perspective. Harvard University Press, Cambridge, Massachusetts.

PASHLEY, D. N., AND R. P. MARTIN. 1988. The contribution of Christmas Bird Counts to knowledge of the winter distribution of migratory warblers in the Neotropics. American Birds 42:1164–1176.

PATTEN, M. A., AND R. A. ERICKSON. 1994. Fifteenth report of the California Bird Records Committee. Western Birds 25:1–34.

PETERJOHN, B. G., AND J. R. SAUER. 1994. Population trends of woodland birds from the North American Breeding Bird Survey. Wildlife Society Bulletin 22:155–164.

POST, W., A. CRUZ, AND D. B. MCNAIR. 1993. The North American invasion pattern of the Shiny Cowbird. Journal of Field Ornithology 64:32–41.

PULICH, W. M., AND A. R. PHILLIPS. 1953. A possible desert flight line of the American Redstart. Condor 55:99–100.

PYLE, P., N. NUR, R. P. HENDERSON, AND D. F. DESANTE. 1993. The effects of weather and lunar cycle on nocturnal migration of landbirds at Southeast Farallon Island, California. Condor 95:343–361.

RASMUSSON, E. M., AND J. M. WALLACE. 1983. Meteorological aspects of the El Niño/Southern Oscillation. Science 222:1195–1202.

RICHARDSON, W. J. 1978. Timing and amount of bird migration in relation to weather: A review. Oikos 30:224–272.

ROBERSON, D. 1980. Rare birds of the West Coast. Woodcock Publications, Pacific Grove, California.

ROOT, R. B. 1962. Comments on the status of some western specimens of the American Redstart. Condor 64:76–77.

SAUER, J. R., AND S. DROEGE. 1992. Geographic patterns in population trends of Neotropical migrants in North America. Pages 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.

SCHREIBER, R. W., AND E. A. SCHREIBER. 1984. Central Pacific seabirds and the El Niño Southern Oscillation: 1982 to 1983 perspectives. Science 225: 713–716.

SHUFORD, W. D. 1981. A note on assessing the status of vagrant warblers on the California coast. American Birds 35:264–266.

SHUFORD, W. D. 1994. The Marin County breeding bird atlas: A distributional and natural history of coastal California birds. Bushtit Books, Bolinas, California.

SVENSSON, S. E. 1978. Efficiency of two methods for

monitoring bird population levels: Breeding bird censuses contra counts of migrating birds. Oikos 30:373–386.

TAPER, M. L., K. BÖHNING-GAESE, AND J. H. BROWN. 1995. Individualistic responses of bird species to environmental change. Oecologia 101:478–486.

TERRILL, S. B. 1991. Evolutionary aspects of orientation and migration in birds. Pages 180–201 *in* Orientation in birds (P. Berthold, Ed.). Birkhäuser Verlag, Basel, Switzerland.

TERRILL, S., K. P. ABLE, AND M. A. PATTEN. 1992. The changing seasons: Summer 1992. American Birds 46:1109–1111, 1182.

WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, New Jersey.

WILLIAMS, L., K. LEGG, AND F. S. L. WILLIAMSON. 1958. Breeding of the Parula Warbler at Point Lobos, California. Condor 60:345–354.

WINTER, J., AND J. MORLAN. 1977. The nesting season, Middle Pacific Coast Region. American Birds 31: 1183–1188.

*Associate Editor: R. L. Hutto*