A CENTURY OF AVIFAUNAL CHANGE IN WESTERN NORTH AMERICA

Joseph R. Jehl, Jr. and Ned K. Johnson, editors

Proceedings of an International Symposium at the Centennial Meeting of the COOPER ORNITHOLOGICAL SOCIETY Sacramento, California, April 17, 1993

Studies in Avian Biology No. 15 A PUBLICATION OF THE COOPER ORNITHOLOGICAL SOCIETY

TRENDS IN NOCTURNAL MIGRANT LANDBIRD POPULATIONS AT SOUTHEAST FARALLON ISLAND, CALIFORNIA, 1968–1992

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Abstract. We examined trends in populations and age proportions of nocturnal migrant landbirds arriving on Southeast Farallon Island (SEFI), California during a 25-year period. Trends based on totals statistically adjusted for the effects of weather and lunar cycle on arrival were more precise than those detected with unadjusted annual totals. Significant linear trends were detected in 30 of 70 examined species and each of ten breeding or wintering bioregional groups. Within-season declines outnumbered increases 41 to 16; eight species and four groups showed declines in both seasons whereas only one species and no groups showed seasonally-consistent increases. Directions of slopes of linear trends concurred significantly with those determined with Breeding Bird Survey data, suggesting that both censusing methods may accurately reflect true population trends. Significant curvilinear trends were detected in 21 species and 5 bioregional groups; accelerating declines were detected in two species and no groups. Results based on age proportion suggested that declines in reproductive success could account for decreasing trends detected in four species. Our results of bioregional groups suggest that population declines may be influenced more by changes on the summer grounds than by those on the winter grounds, although changes in both areas are indicated. Increases in eastern "Neotropical migrants" at SEFI, combined with results of age proportion, may indicate that the likelihood of vagrancy in first-year birds of these species is increasing. Reductions of landbird populations breeding (and to a lesser extent wintering) on the Pacific North American coast were most consistent, and may warrant attention.

Key Words: Landbird; trend; population monitoring; migration; productivity.

Declines in North American landbird populations, particularly those that migrate to the Neotropics, have received considerable attention in recent years (Robbins et al. 1989, Hagan and Johnston 1992). Reasons for these declines likely include habitat destruction on the winter grounds (Robbins et al. 1989, Terborgh 1989), increased nest parasitism and predation resulting from forest fragmentation on the breeding grounds (Holmes and Sherry 1988, Askins et al. 1990, Wilcove and Robinson 1990), and other factors (Hagan and Johnston 1992). Population trends can vary geographically and/ or according to habitat (Sauer and Droege 1992, James et al. 1992, Peterjohn and Sauer 1993), indicating that factors affecting trends are not biogeographically concordant. While many recent analyses have examined longterm trends among eastern North American landbirds (Robbins et al. 1989, Hill and Hagan 1991, papers in Hagan and Johnston 1992), only three recent analyses, each using Breeding Bird Survey (BBS) data, have statistically considered long-term trends in the west (Robbins et al. 1986, Sauer and Droege 1992, Peterjohn and Sauer 1993).

The BBS has provided an important database for analyses of population trends, however, some limitations and assumptions exist with this census technique (Hussell 1981, Hagan et al. 1992, Hejl 1994). In order to fully understand the causal components of trends, results derived from a variety of censusing methods should be synthesized. Counts of migrating birds (Dunn 1992), although strongly affected by fluctuation in weather (Richardson 1990), have revealed long-term population trends corresponding to those indicated by the BBS (Hagan et al. 1992), especially after effects of weather and other variables have been statistically controlled (Hussell 1981, Hussell et al. 1992). Migration counts also sample breeding or wintering populations that are difficult to monitor, thus providing additional information for consideration (see Dunn 1992).

For this paper we examined trends of nocturnal migrants recorded during daily censuses on Southeast Farallon Island (SEFI), California, over the 25-year period 1968– 1992. Simple and polynomial regression techniques were applied to totals of 70 species and ten bioregional groups, statistically adjusted for the effects of date, weather, lunar cycle and/or age proportion. We hope that our results, in combination with those of the BBS and other investigations presented in this volume, will be useful in defining western species and biogeographical areas in need of conservation attention.

STUDY SITE AND METHODS

Topographical features and methods of censusing landbirds at SEFI were described by DeSante and Ainley (1980), DeSante (1983), and Pyle and Henderson (1991). Each day Point Reyes Bird Observatory (PRBO) biologists thoroughly censused all landbird migrants and banded as many as possible. Numbers of arrivals of each species and identifiable subspecies (hereafter referred to as "species") were calculated at the end of each day using all available information from banding and observations of plumage variation. If similar unmarked landbirds were encountered on successive days we assumed that a minimum number of individuals were involved (see DeSante and Ainley 1980). Because landbirds concentrated in a few restricted, vegetated areas of this small and barren island, censuses were virtually complete and little biased by variation in observer skills (DeSante and Ainley 1980). Habitat at SEFI remained relatively unchanged during the 25-year period (Pyle and Henderson 1991).

We examined trends in nocturnal migrants (as defined by Pyle et al. 1993) separately in spring (1 March-30 June) and fall (1 August-30 November). Our sample consisted of 77,633 individuals (19,515 in spring and 58,118 in fall) of 197 nocturnal migrant species (see Appendix I). We examined trends in 70 species represented by at least 125 recorded individuals (5/yr); within each season we analyzed trends only if at least 63 individuals (2.5/yr) were recorded. In all cases there were fewer than six years in which zero individuals of a species or group were recorded.

We categorized species into one each of five breeding and five wintering biogeographical groups for analyses of trends (Appendix I). We defined breeding groups as species breeding primarily in areas of the: 1) Pacific coast (PC), 2) lowland interior West (IW) including the Great Basin, 3) montane West (MW), 4) northern taiga or tundra (TT), and 5) eastern deciduous forests (EF). Winter groups included those species found wintering primarily in areas of the: 1) coastal Pacific (CP), 2) the United States (US) away from the Pacific coast, 3) western Mexico (WM), 4) eastern Mexico, the West Indies, and Central America (CA), and 5) South America (SA). Species of which breeding or wintering ranges substantially overlapped two or more bioregions were assigned the group geographically closest to SEFI (in the order of above listings; see DeSante and Ainley 1980).

We investigated temporal trends using linear and polynomial regression on both "unadjusted" and "weather-adjusted" forms of the dependent variable, summed by season and year. Unadjusted totals simply represent the annual number of arrivals of each species or group recorded within each season. These totals were log-transformed in order to normalize the data and because this allowed us to model number of arrivals in a multiplicative fashion rather than with an additive model. In other words, with log(Y) as the dependent variable (where Y = number of arrivals of a species in a given season and year), a constant slope represents a constant proportional change in number of arrivals.

Weather-adjusted indices represent annual totals (log-transformed), statistically adjusted for environmental effects on arrival numbers. These indices were calculated using statistical models, described in Pyle et al. (1993), that estimated the effects of date, weather and lunar variables on logtransformed arrival totals. For analyses of the ten biogeographical groups, we calculated daily arrivals for the appropriate group, adjusting for date, weather and lunar variables (Computing Resource Center 1992). Daily weather-adjusted values were summed over the appropriate season, for each year. Sample sizes of individual species were insufficient to adequately adjust for weather directly. Instead, we adjusted arrival totals for each species using the weather/date/lunar model developed for all nocturnal migrants (Pyle et al. 1993), with each species standardized ($\bar{X} = 0$, sp = 1). For each species, daily weather-adjusted values were back-transformed and summed over the appropriate season, for each year. Similar weather-arrival patterns were generally found among regional and taxonomic subgroups (Pyle et al. 1993), helping to justify this approach.

Our weather-adjustment procedure for biogeographical groups is very similar to the approach used by Hussell (1981); for individual species, direct adjustment was not possible. We recognize that daily arrival totals of each species may be affected by dateadjustment using overall migrants, but consider this point to be of negligible influence on the annual totals. To ensure that longterm changes in weather have not affected landbird arrival at SEFI we examined yearweather interaction terms as additions to our weather models and found no significant interactions between year and those variables that affected arrival (see Pyle et al. 1993). Weather-adjustment of arrivals appeared to reduce variability of arrival totals (see Results), presumably due to reduction of extraneous weather effects, and so we use weather-adjusted indices in analyses presented herein.

For biogeographical groups we examined trends using two different approaches. In "pooled" analyses, we pooled individuals of all representative species (Appendix I) within a defined biogeographical group and then examined trends in annual totals (weather-adjusted). For the second approach we included only the 70 species with adequate sample sizes. The unit of observation is the annual total of each species, and group classification is represented as a categorical variable (see Kleinbaum et al. 1988, chapter 14). This second, "grouped-species" approach allowed us to test for heterogeneity of trends (slopes) within a biogeographical group as well as to examine heterogeneity among groups. Furthermore, an individual species was simultaneously classified according to wintering and summering group, and thus the effect of winter classification could be tested while control-ling for summer classification, and *vice versa*.

We present two different approaches to analyzing the effects of biogeographical groups mainly in order to examine the robustness of our results. Pooling data has its pitfalls (Breslow and Day 1980); however, it also has the advantage that data are used from all representative individuals of each group rather than just those of species with higher samples.

To investigate interannual variation in productivity and its effects on trends in fall we calculated "adult indices" based on annual "HY-proportions" [(first-year birds)/ (adults + first-years)] of nocturnal migrants on SEFI. We assume that HY-proportion provides an index of productivity (Bibby et al. 1992), although we also recognize that this relationship may be partially confounded by age-specific migration strategies (see Pyle et al. 1993). HY-proportions were based on a sample of 20,036 landbirds captured in fall and aged first-year or adult using skull pneumatization, plumage and other criteria (Pyle et al. 1987). Samples were limited to the months August-October (August-September for kinglets and gnatcatchers), when degree of skull pneumatization is a reliable indicator of the two age classes. HY-proportions based on annual samples of <3individuals were excluded from analyses, and analyses were performed only on groups (all) and species (N = 41) with usable proportions in at least 18 of the 25 years. We investigated variation in productivity by examining linear regression on HY-proportion (arcsine square-root transformed), weighted by sample size. Trends of adults in fall were also estimated using adult indices (summed by year: weather-adjusted indices \times adult proportion), and these were compared with trends of all birds in fall; insufficient sample sizes of aged birds (through 1985) prevented estimations of adult trends in spring.

Significant curvilinear effects indicated that a trend was accelerating or decelerating, and/or that there has been significant fluctuations in arrival within our 25-year period. These were estimated by examining the statistical significance of the highest-order trends of quadratic and cubic polynomial regressions. All statistical analyses were performed using the STATA statistics program (Computing Resource Center 1992). Significance was assumed at the P < 0.05level. "Marginally-significant" linear trends are indicated when 0.05 < P < 0.10.

RESULTS

Nocturnal migrant totals decreased overall between 1968 and 1992 (Fig. 1), significantly in spring using weather-adjusted indices ($\beta = -0.044$, se = 0.011, P = 0.001) but not in fall ($\beta = -0.019$, se = 0.013, P = 0.162). These trends were also detected but less precisely (see Fig. 1) using unadjusted totals ($\beta = -0.031$, se = 0.013, P = 0.025 in spring, $\beta = -0.016$, se = 0.013, t = -1.20, P = 0.243 in fall). No significant trend in HY-proportion of all nocturnal migrants was detected; however, the linear decline of adults in fall was "marginally-significant" ($\beta = -0.033$, se = 0.017, P = 0.072).

TRENDS IN INDIVIDUAL SPECIES

Significant linear trends in at least one season were detected using weather-adjusted indices in 30 of 70 species (Table 1). Twenty species showed declines (six in both seasons), nine species increased (one in both seasons), and one showed a decline in spring but an increase in fall. Eight additional mar-



FIGURE 1. Trends in total number of nocturnal migrants recorded on SEFI, using unadjusted and weather-adjusted data, during spring and fall seasons, 1968– 1992. For comparison, indices from both analysis types have been back-transformed, to reflect actual numbers of arrivals. Linear regression lines of best fit, derived from log-transformed weather-adjusted indices, are also presented; note the logarithmic scale.

ginally-significant trends were detected in one of the two seasons, five declining and three increasing. Including significant and marginally-significant results, more declines (20) than increases (2) were detected in spring, whereas in fall there were more increases (13) than declines (11). Two additional species that did not show trends within either season, Western Flycatcher and Ash-throated Flycatcher (see Appendix I for scientific names), showed significant declines when spring and fall totals were combined (0.01 < P < 0.05).

The use of weather-adjusted indices instead of unadjusted totals generally increased the resolution of trends. Of the 46 TABLE 1. LINEAR AND CURVILINEAR TRENDS OF 70 SPECIES USING REGRESSION OF WEATHER-ADJUSTED INDICES; LINEAR TRENDS IN AGE PROPORTION ARE ALSO INCLUDED. SEE APPENDIX I FOR SCIENTIFIC NAMES AND SAMPLE SIZES OF EACH TAXON. SYMBOLS ARE AS FOLLOWS: NT = NOT TESTED DUE TO INSUFFICIENT SAMPLE SIZE WITHIN A SEASON; -NS, -MS, -, --, --- (OR WITH "+"), = INSIGNIFICANT (P > 0.1), MARGINALLY SIGNIFICANT (0.05 < P < 0.1), and Significant (at 0.010 < P < 0.050, 0.001 < P < 0.010, and P < 0.001) Declines (or Increases), Respectively. No Directions are Given for Insignificant (ns) Curvilinear or Age Proportion Trends. Asterisks (*) in Fall Indicate that Analyses of Adults (See Text) Revealed Different Results than Those of All Individuals (Insignificant vs. Significant at P > 0.05, or Vice Versa). Directions of Slopes of Adult Trends Were the Same as Indicated for Each of These Species Except Rose-breasted Grosbeak in Fall, which Was Significantly Negative. Significance Levels of Highest-order terms, Linear (Lin.), Quadratic (Quad) and Cubic (Cub.) are Presented. See Figure 2 for Illustrations of Different Linear and Curvilinear Patterns

		Spring			Fall		
Species	Lin	Quad	Cub		Quad	Cub	_ Age
	Lan.	Quad.	Cuo.	Em.	Quuu.	040.	
Band-tailed Pigeon		ns	ns	_	ns	ns	nt
Red shofted Flicker		ns	ns		ns	ns	nt =1
Oliver sided Fluesteber	nt	nt	nt	-ns	ns	ns	nt
Olive-sided Flycatcher		ns	ns		ns	ns	nt
Western wood-Pewee		ns	ns	-ns	ns	ns	ns
willow Flycatcher	-ns	ns	ns	+ns	+ms	ns	ns
Hammond's Flycatcher	-ms	ns	-ms	nt	nt	nt	nt
Western Flycatcher	-ns	+	ns	-ns	ns	ns	-ms
Black Phoebe	nt	nt	nt	+ms	ns	ns	nt
Say's Phoebe	nt	nt	nt	-ns	ns		nt
Ash-throated Flycatcher	-ns	ns	ns	-ns	ns	ns	nt
Western Kingbird	nt	nt	nt	+ns	ns	ns	nt
Red-breasted Nuthatch	nt	nt	nt	-ns	ns	ns	nt
Brown Creeper	nt	nt	nt	-ns	ns	ns	nt
Rock Wren	nt	nt	nt	-ns	+ms	+ms	nt
House Wren	nt	nt	nt	+ns	+ms	ns	nt
Winter Wren	nt	nt	nt	-ns	ns	ns	nt
Golden-crowned Kinglet	+ns	_	ns	+ns	ns	ns	ns
Ruby-crowned Kinglet	-ns	ns	ns	+*	ns	ns	ns
Swainson's Thrush		+ms	ns	+*	ns	ns	ns
Hermit Thrush	+ns	ns	ns	+ns	ns	ns	ns
American Robin	-ns	ns	ns	+ns	ns	ns	nt
Varied Thrush	-ns	ns	ns	++	ns	ns	nt
Northern Mockingbird	nt	nt	nt	-ns	ns	ns	nt
American Pipit	nt	nt	nt	+	ns	ns	nt
Cedar Waxwing		ns	ns	+ns*	+ms	ns	_
Cassin's Solitary Vireo	nt	nt	nt	+ns	ns	-	ns
Warbling Vireo	+ns	++	ns	+ns*	ns	ns	
Tennessee Warbler	-ns	ns	ns	-ns	ns	ns	ns
Orange-crowned Warbler	-ms	+	ns	+ns	ns	ns	ns
Nashville Warbler	nt	nt	nt	+*	ns	ns	ns
Yellow Warbler	+ns	+	ns	+ns	+ms	ns	ns
Chestnut-sided Warbler	nt	nt	nt	-ns	ns	+ms	nt
Magnolia Warbler	+ns		ns	+	ns	ns	nt
Myrtle Warbler	+ns	ns	ns	++	115	ns	ns
Audubon's Warbler	+ns	ns	15	+ns	+++	115	ns
Black-thr. Gray Warbler	nt	nt	nt	+ms	ns	ns	-ms
Townsend's Warbler		ns	ns	+ns	ns	ns	ns
Hermit Warbler	-ns	ns	-ms	- ns	ns	ns	ns
Palm Warbler	nt	nt	nt	+*	115	115	ns
Blackpoll Warbler	nt	nt	nt	- 75	113	113	ns
American Redstart	+ ns	ns	ne	- 115	ns	113 +	115
Ovenbird	+ms	ne	113	±ne*	113 ne	ne	
MacGillivray's Warbler	1115	115	115	- 115	115	115	76
Common Vollowthroat	<u>н</u> н		115	- 115	115	115	115
Wilcon's Warblar	- -	15	115	+++	115	115	115
Wastern Tonger		+	115	T IIS	115	ns	115
Page brancted Crachesh		+	ns	— ns	ns	ns	ns
Nosc-Dicasted Grospeak	+115	ns	ns	+ ns *	ns	+	+
Black-neaded Grosbeak		ns	ns		ns	-ms	ns

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		Spring			Fall		Ane
Species	Lin.	Quad.	Cub.	Lin.	Quad.	Cub.	prop.
Lazuli Bunting		+	ns		ns	ns	-ms
Rufous-sided Towhee	nt	nt	nt	-ns	ns	ns	ns
Chipping Sparrow		ns	ns	*	+ms	ns	-ms
Clay-colored Sparrow	nt	nt	ns	+++*	ns	ns	ns
Brewer's Sparrow	nt	nt	nt	+ns	ns	ns	nt
Vesper Sparrow	nt	nt	nt	+ns	ns	ns	nt
Lark Sparrow	nt	nt	nt		ns	ns	nt
Savannah Sparrow		ns	ns	-ns	ns	ns	ns
Fox Sparrow	-ns	ns	ns	-	ns	ns	ns
Lincoln's Sparrow	+ns	ns		+ns	ns	ns	ns
White-throated Sparrow	nt	nt	nt	+ns	ns	ns	ns
Golden-crowned Sparrow		+	ns	+ns	ns	ns	ns
White-crowned Sparrow	-ms	ns	ns		_	ns	ns
Oregon Junco		ns	ns	-ns	ns	ns	ns
Lapland Longspur	nt	nt	nt	+ms	ns	ns	nt
Bobolink	nt	nt	nt	+ns	ns	ns	nt
Red-winged Blackbird	nt	nt	nt	+ns	+ms		nt
Western Meadowlark	_	ns	ns	-ms	ns	-ms	nt
Brewer's Blackbird	+ns	ns	+	+ns	++	ns	nt
Brown-headed Cowbird	-ns	ns	ns	+ns	ns	+ms	ns
Bullock's Oriole	-ns	ns	ns	_*		ns	ns

within-season trends detected with weatheradjusted indices, 39 were also detected, in the same direction, with analyses using unadjusted totals. Of these, 29 (74.3%) were more precise (as indicated by lower P values) using the weather-adjusted than the unadjusted analyses. For the remaining seven within-season trends (Orange-crowned Warbler, Lazuli Bunting, White-crowned Sparrow and Oregon Junco in spring; Bullock's Oriole in fall; and Western Meadowlark in both seasons), the unadjusted analyses indicated insignificant trends. By contrast only three fall trends (a significant increase in Rose-breasted Grosbeak and marginally-significant decreases in Blackpoll Warbler and Savannah Sparrow) were detected with the unadjusted totals but not with the weather-adjusted indices (see Table 1).

Trends in HY-proportion were detected in eight species (Table 1); seven proportions declined while only one increased. Trends in HY-proportion coincided with linear trends of migrants in four species (including Western Flycatcher; see above) and was opposite in two species (Table 1). Significance levels of adult trends differed from those of all individuals in 11 species (Table 1). Significant non-linear trends within the 25-year period were detected in 21 species (Table 1). Fall trends of two species, White-crowned Sparrow and Bullock's Oriole, indicated accelerating population declines. Figure 2 illustrates four examples of linear and nonlinear trends among species.

A comparison of our linear trends with those detected with BBS data (Sauer and Droege 1992) indicated a significant degree of conformity between the two methods when directions of slopes were compared (Table 2). Of 42 within-season trends (in 24 species) detected using SEFI data, 32 had slopes in the same direction as detected by the BBS, including all 8 trends (6 species) that were at least marginally-significant according to both analyses. Results of both seasons at SEFI were consistent with those of the BBS, and the fall comparison was similar when adult trends at SEFI were used. Comparison of our results with those of Robbins et al. (1989) and Peterjohn and Sauer (1993) also indicated a high degree of consistency.



FIGURE 2. Four examples of within-season trends of species (see Table 1). Linear and, where significant, curvilinear regression lines based on regressions of log-transformed weather-adjusted indices are presented. Examples of trends include insignificant linear, positive quadratic (Audubon's Warbler); insignificant linear, positive cubic (American Redstart); decreasing linear, positive quadratic (Western Tanager), and decreasing linear, decreasing quadratic (Bullock's Oriole).

TRENDS IN BIOGEOGRAPHICAL GROUPS

Using pooled totals of all recorded species (Appendix I), significant linear trends were detected in at least one season in all ten breeding and wintering bioregional groups (Table 3, Figs. 3-4). Declines were indicated in seven groups in spring and one in fall, while increases occurred with three groups in fall. No significant trends in HY-proportions within groups were detected, and significant fall increases of two groups, eastern forest breeders and Central American winterers, became insignificant when adult indices were used (Table 3). Significant curvilinear trends were detected in six groups (Table 3). The most noteworthy trends occurred with Pacific coastal breeders, the only group to show consistent significant declines in both spring and fall. Trends in this group were also positively curvilinear in both seasons, indicating that most of the decline (within our 25-year period) occurred in the late 1960s and 1970s (see Figs. 3-4). Coastal Pacific winterers also showed linear declines in both seasons, significant in spring and marginally-significant in fall.

The significant declines of Pacific coastal breeders were also evident using the analyses of grouped-species (Table 4), as were the positive curvilinear trends of this group (t = 3.97, P = 0.001 in spring; t = 3.82, P= 0.001 in fall estimated by quadratic year term). These analyses further indicated significant linear declines in interior western breeders and South American winterers in fall, not detected by pooled analyses. Most other group trends estimated with pooled indices were similarly detected with grouped-species analyses, particularly when number of representative species >10.

Tests for heterogeneity of slopes within bioregional groups indicated five withinseason differences among breeding groups and eight among winter groups (Table 4). Differences tended to occur in the groups inhabiting more diverse geographic regions, e.g., most wintering areas and western TABLE 2. COMPARISON OF SLOPE DIRECTIONS OF LONG-TERM TRENDS DETECTED ON SEFI WITH THOSE FOR NEOTROPICAL MIGRANTS DETECTED USING BREED-ING BIRD SURVEY DATA FROM 1966 TO 1988 (SAUER AND DROEGE 1992), IN 24 SPECIES CONSIDERED IN BOTH ANALYSES. COMPARISONS ARE MADE WITH BBS RESULTS OF THE "WESTERN REGION" (P. 36), EXCEPT FOR THREE EASTERN SPECIES WHERE BBS ANALYSES WERE PER-FORMED BY SAUER AND DROEGE ONLY ON POPULATIONS OF THEIR "EASTERN REGION" (PP. 32-33). MARGINALLY-SIGNIFICANT TRENDS (0.05 < P < 0.1)ARE CATEGORIZED AS SIGNIFICANT IN THIS TABLE. FREQUENCY TABLES DIRECTLY COMPARING SLOPE DI-RECTIONS OF THE TWO METHODS INDICATED SIGNIFI-CANT CORRELATIONS IN BOTH SPRING (LIKELIHOOD RA-TIO (G) TEST; LRS = 6.49, P = 0.011) and Fall (LRS = 8.46, P = 0.004). The Fall Comparison was Sim-ILAR WHEN ADULT TRENDS AT SEFI WERE USED

		Direction of slopes				
Trend category using:		Spring		Fall		
SEFI data	BBS data	Same	Dif- ferent	Same	Dif- ferent	
significant	significant	2	0	6	0	
significant	insignificant	6	1	3	1	
insignificant	significant	4	1	2	1	
insignificant	insignificant	_2	_2	7	_4	
Total		14	4	18	6	

breeding bioregions. When slopes of bioregional groups were compared, significant differences were found between breeding groups in both spring and fall, whereas slopes between wintering groups differed significantly in spring but not in fall (Table 5). This was true using both pooled and grouped-species data, and was also true after statistically controlling for trends in the opposite (breeding/wintering) class. In all four classification/season combinations, detected differences were greater after controlling for the opposite classification (Table 5).

DISCUSSION

Analyses of weather-adjusted arrival counts on SEFI revealed trends in total migrants, 30 of 70 species, and all ten biogeographical groups. DeSante and George (1994) examine in more detail possible explanations for these and other trends in western landbirds. Here we examine the validity of our results and interpret the relative strengths of inferred trends.

The separation of SEFI data into seasonal periods provides a measure with which to assess the relative importance of detected trends. Including both significant and "marginally-significant" (0.05 < P < 0.10) results, concordant linear trends in both seasons were detected in nine species (Table 1) and four bioregional groups (according to analyses of pooled totals and grouped-species, combined; Tables 3, 5). This independently-derived seasonal agreement suggests that true population changes may be occurring in these species and groups. Trends in one but not both seasons, detected in 12 species and six bioregional groups, are

TABLE 3. LINEAR AND CURVILINEAR TRENDS OF BIOGEOGRAPHICAL GROUPS AT SEFI USING POOLED, WEATH-ER-ADJUSTED INDICES; TRENDS IN AGE-PROPORTION ARE ALSO GIVEN. SEE APPENDIX 1 FOR GROUP CATEGORI-ZATION. SYMBOLS ARE AS DEFINED IN TABLE 1

		Spring			Fall			
Group	Linear	Quadratic	Cubic	Lin.	Quad.	Cub.	prop.	
Breeding groups								
Pacific Coastal		++	ns		++	ns	ns	
Interior Western		ns		+ns	ns	ns	ns	
Montane Western	-	ns	ns	-ns	ns	ns	ns	
Taiga/Tundra	-	ns	ns	-ns	+ms	ns	ns	
Eastern Forest	+ns	_	ns	+*	ns	ns	ns	
Wintering groups								
Coastal Pacific		ns	ns	-ms	ns	ns	ns	
United States	-ns	ns	ns	+	ns	+	ns	
Western Mexico	_	++	-ms	+ns	ns	ns	ns	
Central America	-ns	ns	ns	+*	-ms	ns	ns	
South America		ns	ns	+ns	— ms	ns	ns	



FIGURE 3. Significant trends in arrival of biogeographical breeding groups at SEFI, according to pooled, weather-adjusted totals. See Table 3 for significance values. Linear and, where significant, curvilinear regression lines based on regressions of log-transformed totals are presented.



Weather-adjusted Indices

FIGURE 4. Significant trends in arrival of biogeographical wintering groups at SEFI, according to pooled, weather-adjusted totals. See Table 3 for significance values. Linear and, where significant, curvilinear regression lines based on regressions of log-transformed totals are presented.

		# of species		Linear	trend	Withi diffe	n-group rences
Group	Total	Positive	Negative	l	Р	F	Р
Spring							
Breeding							
Pacific Coast	25	1	11	-6.42	0.000	2.50	0.000
Interior West	6	0	2	-3.31	0.001	1.93	0.031
Montane West	13	0	6	-3.88	0.000	1.62	0.158
Taiga/Tundra	2	0	1	-1.49	0.141	3.46	0.003
Eastern Forest	6	1	0	0.48	0.635	0.83	0.532
Wintering							
Coastal Pacific	22	1	9	-4.28	0.000	4.12	0.048
United States	2	0	0	0.50	0.348	1.42	0.110
West Mexico	20	0	8	-5.00	0.000	3.03	0.001
Central America	6	1	1	-1.13	0.261	5.87	0.001
South America	2	0	2	-5.65	0.000	2.19	0.002
Fall							
Breeding							
Pacific Coast	29	4	7	-2.38	0.018	2.10	0.001
Interior West	12	0	3	-2.46	0.014	1.28	0.228
Montane West	13	3	1	0.63	0.531	2.95	0.001
Taiga/Tundra	5	3	0	1.48	0.143	0.66	0.619
Eastern Forest	10	3	0	2.84	0.005	1.33	0.246
Wintering							
Coastal Pacific	30	6	5	-1.94	0.053	7.50	0.000
United States	6	2	1	0.97	0.331	2.09	0.003
West Mexico	22	3	4	-0.13	0.898	1.84	0.095
Central America	7	2	0	1.45	0.149	3.01	0.003
South America	4	0	1	-2.13	0.036	1.51	0.045

TABLE 4. SAMPLE SIZES OF SPECIES, LINEAR TRENDS, AND HETEROGENEITY OF SLOPES (WITHIN GROUPS), IN BREEDING AND WINTERING GROUPS USING ANALYSES OF COMMON SLOPES ON WEATHER-ADJUSTED INDICES. LINEAR TRENDS OF SPECIES ARE SUMMARIZED, AND INDICATED POSITIVE AND NEGATIVE TRENDS INCLUDE BOTH SIGNIFICANT AND MARGINALLY-SIGNIFICANT RESULTS (TABLE 1)

more equivocal. For Swainson's Thrush we detected a significant decline in spring but a significant increase in fall. This may reflect occurrence patterns of different subpopulations on SEFI: arrival of western subpopulations may be declining in spring whereas more eastern subpopulations may be increasing in fall (see below and Marshall 1988). The significant degree of consistency between SEFI and BBS results for populations in the west (Table 2) may provide validation of both censusing procedures, and suggests that migration counts, in general, can be used to detect population changes. Some of the species where opposite trends were indicated by the two analyses (e.g., Western Flycatcher, Swainson's Thrush, Wilson's

TABLE 5. DIFFERENCES BETWEEN TRENDS AMONG GROUPS WITHIN BIOREGIONAL CLASSIFICATIONS USING LINEAR MODEL ANALYSES ON POOLED AND SPECIES-GROUP TOTALS (SEE TEXT). ADJUSTED SPECIES-GROUP FIGURES REFER TO DIFFERENCES AMONG GROUPS OF EACH CLASSIFICATION AFTER CONTROLLING FOR THE OPPOSITE (BREEDING/ WINTERING) CLASSIFICATION

				Common slopes					
Bioregional Pooled tot		oled totals Una		djusted	Adj	justed			
class	Season	F	Р	F	Р	F	Р		
Breeding	Spring	3.92	0.005	2.84	0.023	3.64	0.006		
Wintering	Spring	3.11	0.030	3.21	0.012	4.01	0.003		
Breeding	Fall	2.48	0.048	5.00	0.001	5.32	0.000		
Wintering	Fall	1.39	0.250	1.65	0.160	1.97	0.096		

Warbler) have distinct subpopulations which may be unequally represented in the two analyses (see below). A more rigorous statistical comparison of SEFI and BBS data, partitioned taxonomically and geographically, is planned.

It is tempting to think that the greater and more consistent declines detected in spring than in fall reflected changes on the winter rather than the breeding grounds; however, declines in both seasons would be expected from changes at either location. The high proportion of first-year birds recorded in fall on SEFI (DeSante 1983) could be obscuring true population trends based on fall data, although fall and spring results were both consistent with those using BBS data (Table 2). Whether or not population changes were more accurately reflected by adult trends in fall is unclear at this time. Our data suggest that declines in Western Flycatcher, Cedar Waxwing, Lazuli Bunting, and Chipping Sparrow may be caused by decreased productivity on the breeding grounds, as indicated by concordant declines in HY-proportion. A significant increase in HY-proportion of Rose-breasted Grosbeak, coupled with a significant decline in the fall adult trend may indicate a population decrease due to changes on the winter grounds.

Our analyses of bioregional groups suggest that detected trends resulted from changes on both the breeding and the wintering grounds (Table 4). That slopes of group trends differed significantly from each other in three of the four classification/season categories (Table 5) implies that true differences occurred in the trends of populations among these groups. Differences were more evident between breeding groups (significant in both seasons) than wintering groups (significant in spring but not fall), even after controlling for trends in the opposite classification. This suggests that population trends detected at SEFI are caused more by events on breeding grounds than events on winter grounds, although trends due to changes in both areas are indicated.

The increases of eastern forest breeders

and Central American winterers detected on SEFI are interesting, especially in light of the accelerating decreases in these Neotropical winterers detected on their breeding grounds by the BBS (Sauer and Droege 1992, Peterjohn and Sauer 1993, but see Hutto 1988). These combined results and the fact that fall adult trends in these groups were insignificant using SEFI data (Table 3) suggest that the proportion of vagrant individuals may be increasing among first-year birds of eastern forest species, as first suggested by DeSante (1983, see also DeSante and George 1994).

Clearly the strongest and most significant group trends indicated by SEFI data were the long-term decelerating declines in populations breeding (and to a lesser extent wintering) on the Pacific coast. Most of the declines in species of these groups occurred early within our 25-year period but populations have not recovered (see Fig. 3); similar decelerating trends were indicated with BBS data (Sauer and Droege 1992, DeSante and George 1994). Habitat loss due to coastal development and logging, particularly heavy in the 1960s and 1970s (see U.S. Forest Service 1988, Chapter 3), may be the primary cause of declines on SEFI in both breeding and wintering Pacific coast groups; unlike in dryer western bioregions, fire exclusion during this period may not have compensated for habitat loss on the wetter Pacific Slope (see Hejl 1994). Alternatively, the declines in Pacific coastal species may be representative of declines across North America, only appearing to be more significant on SEFI because of higher samples of these species.

The most consistent population declines in western species, as indicated by SEFI and BBS data, occurred in Band-tailed Pigeon, Mourning Dove, Olive-sided Flycatcher (see also Robbins et al. 1986, Marshall 1988), Western Wood-Pewee, Western Tanager, Black-headed Grosbeak, Lazuli Bunting, Chipping Sparrow, White-crowned Sparrow and Bullock's Oriole. Increased attention of these populations may be warranted. On a brighter note, western populations of Nashville Warblers and Common Yellowthroats appear to be increasing in western North America.

ACKNOWLEDGMENTS

The research program on Southeast Farallon Island, part of the Farallon National Wildlife Refuge, is conducted with the cooperation and support of the U.S. Fish and Wildlife Service. The U.S. Coast Guard and the Farallon Patrol also provided logistic support. Farallon weather data for the years 1968-1970, used in weather-adjusted models, were provided by the National Climate Data Center, Asheville, North Carolina; subsequent data were collected by PRBO. The monitoring program for migrant birds has been carried out by numerous PRBO biologists and interns. We again acknowledge those listed in DeSante and Ainley (1980) and Pyle and Henderson (1991); we also thank L. Gilbert and M. Hart for help computerizing 1992 data for inclusion in these analyses. We especially acknowledge the long-term dedication of R. Philip Henderson to the landbird program on SEFI. The manuscript benefitted from comments by D. G. Ainley, E. H. Dunn, D. J. T. Hussell, C. Moore, and W. J. Sydeman. This is PRBO contribution #577.

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APPENDIX I. Nocturnal Migrant "Species" Used in Analyses of Trends, Including Scientific Name, Spring and Fall Sample Sizes, and Breeding and Wintering Biogeographical Groupings. Group Codes Are: Breeding, PC = Pacific Coastal, IW = Interior Western, MW = Montane Western, TT = Taiga/ Tundra, EF = Eastern Forest; Wintering, CP = Coastal Pacific, US = United States (Away from the Pacific Coast), WM = Western Mexico, CA = Eastern Mexico and Central America, SA = South America. A Small Number of Rarer Species Were Not Categorized, as Were Hybrids of Taxa of Parent Species from Different Bioregions

Taxon	Spring total	Fall total	Breeding group	Wintering group
Band-tailed Pigeon (Columba fasciata)	130	170	PC	CP
White-winged Dove (Zenaida asiatica)	0	13		WM
Mourning Dove (Z. macroura)	172	601	PC	CP
Black-billed Cuckoo (Coccyzus erythropthalmus)	0	2	EF	SA
Yellow-billed Cuckoo (C. americanus)	5	9	EF	SA
Lesser Nighthawk (Chordeiles acutipennis)	35	5	IW	WM
Common Nighthawk (C. minor)	1	2	IW	SA
Common Poorwill (Phalaenoptilus nuttallii)	0	7	IW	WM
Lewis' Woodpecker (Melanerpes lewis)	4	3	IW	US
Acorn Woodpecker (M. formicivorus)	0	8	PC	CP
Yellow-bellied Sapsucker (Sphyrapicus varius)	0	1	EF	US
Red-naped Sapsucker (S. nuchalis)	1	3	MW	US
Red-breasted Sapsucker (S. ruber)	2	19	IW	СР
Yellow-shafted Flicker (Colaptes a. auritus)	7	55	EF	US
Intergrade Flicker (C. a. cafer \times auritus)	5	44		US
Red-shafted Flicker (C. a. cafer)	62	260	PC	CP
Olive-sided Flycatcher (Contopus borealis)	103	69	PC	SA
Western Wood-Pewee (C. sordidulus)	1081	450	PC	SA
Eastern Wood-Pewee (C. virens)	1	0	EF	SA
Willow Flycatcher (Empidonax traillii)	120	221	MW	WM
Yellow-bellied Flycatcher (E. flaviventris)	0	5	EF	CA
Least Flycatcher (E. minimus)	6	89	EF	CA
Hammond's Flycatcher (E. hammondii)	113	32	MW	WM
Dusky Flycatcher (E. oberholseri)	77	20	MW	WM
Gray Flycatcher (E. wrightii)	82	14	IW	WM
Western Flycatcher (E. difficilis/occidentalis)	256	700	PC	WM
Black Phoebe (Sayornis nigricans)	13	233	PC	CP
Eastern Phoebe (S. phoebe)	4	14	EF	US
Say's Phoebe (S. saya)	10	188	IW	US
Ash-throated Flycatcher (Myiarchus cinerascens)	66	116	IW	WM
Great Crested Flycatcher (M. crinitus)	0	9	EF	CA
Brown-crested Flycatcher (M. tyrannulus)	0	1	IW	WM
Tropical Kingbird (Tyrannus melancholicus)	1	11		WM
Cassin's Kingbird (T. vociferans)	1	1	IW	WM
Western Kingbird (T. verticalis)	61	95	IW	CA
Eastern Kingbird (T. tyrannus)	12	25	IW	SA
Scissor-tailed Flycatcher (T. forficatus)	1	1	IW	CA
Horned Lark (Eremophila alpestris)	10	97	IW	US
Red-breasted Nuthatch (Sitta canadensis)	32	909	MW	СР

APPENDIX I. CONTINUED

Taxon	Spring total	Fall total	Breeding group	Wintering group
White-breasted Nuthatch (S. carolinensis)	1	1	IW	US
Pygmy Nuthatch (S. pygmaea)	0	1	PC	CP
Brown Creeper (Certhia americana)	2	125	PC	CP
Rock Wren (Salpinctes obsoletus)	23	195	IW	CP
Bewick's Wren (Thryomanes bewickii)	0	3	PC	CP
House Wren (Troglodytes aedon)	36	116	IW	WM
Winter Wren (T. troglodytes)	18	120	PC	CP
Marsh Wren (Cistothorus palustris)	3	21	PC	CP
Dusky Warbler (Phylloscopus fuscatus)	0	2	TT	<u>an</u>
Golden-crowned Kinglet (Regulus satrapa)	80	721	PC	CP
Ruby-crowned Kinglet (R. calendula)	1344	2290	MW	CP
Blue-gray Gnatcatcher (Pollopfila caerulea)	/	14		WM
Northern Wheetern (<i>Computes computes</i>)	0	1		CD
Wortown Physhird (Siglig maxiagna)	1	2		
Mountoin Bluebird (Stalla mexicana)	1	10	PC MW	
Townsend's Solitaire (Myadastas townsandi)	4	16		54
Veery (Catharus fuscascans)	1	10		SA
Gray-cheeked Thrush (C minimus)	1	8		
Swainson's Thrush (C. ustulatus)	182	1160	PC	CA
Hermit Thrush (C. auttatus)	431	1746	PC	CP
American Robin (Turdus migratorius)	237	443	PC	CP
Varied Thrush (Ixoreus naevius)	132	324	PC	CP
Grav Cathird (Dumetella carolinensis)	3	4	FF	CA
Northern Mockingbird (Mimus polyglottos)	48	123	IW	CP
Sage Thrasher (Oreoscontes montanus)	10	41	iw	US
Brown Thrasher (Toxostoma rufum)	6	10	EF	US
Bendire's Thrasher (<i>T. bendirei</i>)	3	2		ŴM
Yellow Wagtail (Motacilla flava)	0	$\overline{1}$	TT	
White/Black-backed Wagtail (M. alba/lugens)	0	1	TT	СР
Red-throated Pipit (Anthus cervinus)	0	21	ΤT	
American Pipit (A. rubescens)	22	3077	TT	СР
Sprague's Pipit (A. spragueii)	0	3	IW	WM
Bohemian Waxwing (Bombycilla garrulus)	0	1	TT	US
Cedar Waxwing (B. cedrorum)	92	837	IW	CP
Phainopepla (Phainopepla nitens)	0	3	IW	US
Brown Shrike (Lanius cristatus)	0	1	TT	
Northern Shrike (L. excubitor)	0	1	TT	US
Loggerhead Shrike (L. ludovicianus)	5	6	IW	US
White-eyed Vireo (Vireo griseus)	1	1	EF	CA
Eastern Solitary Vireo (V. s. solitarius)	0	26	EF	CA
Plumbeous Solitary Vireo (V. s. plumbeous)	0	102		WM
Cassin's Solitary Vireo (V. s. cassinii)	50	102	MW	WM CA
Hutton's Vireo (V. huttoni)	1	25	Er	CR
Workling Vireo (V. nutioni)	12	33		UF WM
Philadelphia Vireo (V. philadelphicus)	102	408	FC	
Red-eved Vireo (V. olivacaus)	47	26	FF	SA SA
Yellow-green Vireo (V flavoviridis)		20	LI	SA
Blue-winged Warbler (Vermivora ninus)	1	Ō	FF	CA
Brewster's Warbler (V ninus × chrysontera)	1	õ	EF	CA
Golden-winged Warbler (V. chrysoptera)	2	2	EF	CA
Tennessee Warbler (V. peregring)	145	159	EF	ČĂ
Orange-crowned Warbler (V. celata)	1158	527	PC	WM
Nashville Warbler (V. ruficavilla)	57	215	MW	WM
Virginia's Warbler (V. virginiae)	6	26	IW	WM
Lucy's Warbler (V. luciae)	0	6		WM
Northern Parula (Parula americana)	31	7	EF	CA
Yellow Warbler (Dendroica petechia)	403	1444	PC	WM
Chestnut-sided Warbler (D. pensylvanica)	36	136	EF	CA

APPENDIX I. CONTINUED

Тахоп	Spring total	Fall total	Breeding group	Wintering group
Magnolia Warbler (D. magnolia)	110	131	EF	CA
Cape May Warbler (D. tigrina)	29	26	EF	CA
Black-throated Blue Warbler (D. caerulescens)	0	78	EF	CA
Myrtle Warbler (D. c. coronata)	215	1551	TT	CP
Audubon's × Myrtle Warbler	12	62		CP
Audubon's Warbler (D. c. auduboni)	1236	1488	MW	CP
Black-throated Gray Warbler (D. nigrescens)	51	319	MW	WM
Townsend's Warbler (D. townsendi)	828	895	MW	CP
Townsend's × Hermit Warbler	1	2		WM
Hermit Warbler (D. occidentalis)	68	223	PC	WM
Black-throated Green Warbler (D. virens)	19	18	EF	CA
Golden-cheeked Warbler (D. chrysoparia)	0	1	IW	WM
Blackburnian Warbler (D. fusca)	5	64	EF	SA
Yellow-throated Warbler (D. dominica)	2	2	EF	US
Pine Warbler (D. pinus)	0	4	EF	
Prairie Warbler (D. discolor)	0	38	EF	
Palm Warbler (D. palmarum)	31	883	EF	05
Bay-breasted Warbler (D. castanea)	29	27 550	EF	SA
Blackpoll Warbler (D. striata)	42	552		SA
Cerulean Warbler (D. cerulea)	50	1	EF EE	SA WM
Black-and-white Warbler (Mniotilia varia)	32	4/	EF	W IVI
American Redstart (Setophaga ruticilia)	83	307	EF FF	
Prothonotary Warbler (Protonotaria citrea)	6	2	Er FF	
Worm-eating wardler (<i>Helmuneros vermivorus</i>)	172	123	EF	CA
Northern Waterthrush (S. novahoracansis)	6	68		WM
Northern Waterthrush (S. motacilla)	1	00	FF	CA
Kentucky Warbler (Operations formasus)	17	3	EF	CA
Connecticut Warbler (O agilis)	3	33	EF	SA
Mourning Warbler (O. nhiladelnhia)	6	36	ĒF	SA
MacGillivray's Warbler (O. tolmiei)	84	288	MW	WM
Common Vellowthroat (Geothlynis trichas)	483	549	PC	CP
Hooded Warbler (<i>Wilsonia citrina</i>)	23	5	EF	CA
Wilson's Warbler (W. nusilla)	3012	969	PC	WM
Canada Warbler (W. canadensis)	11	28	EF	SA
Red-faced Warbler (Cardellina rubrifrons)	0	1	MW	WM
Yellow-breasted Chat (Icteria virens)	30	48	IW	WM
Hepatic Tanager (Piranga flava)	1	1	MW	WM
Summer Tanager (P. rubra)	13	8	EF	CA
Scarlet Tanager (P. olivacea)	1	5	EF	SA
Western Tanager (P. ludoviciana)	186	398	MW	WM
Rose-breasted Grosbeak (Pheucticus ludovicianus)	155	87	EF	CA
Rose-br. × Black-h. Grosbeak	1	3		
Black-headed Grosbeak (P. melanocephalus)	126	141	PC	WM
Blue Grosbeak (Guiraca caerulea)	10	50	IW	WM
Lazuli Bunting (Passerina amoena)	72	2442	IW	WM
Indigo Bunting (P. cyanea)	84	33	EF	CA
Painted Bunting (P. ciris)	0	1 4		
Dickcissel (Spiza americana)	13	14		SA WM
Green-tailed Towhee (Pipilo chlorurus)	8	21	M W	
Rutous-sided Townee (P. erythrophthalmus)	30	455	FC	WM
Cassin's Sparrow (Aimophila cassinii)	16	10	тт	US
Chinging Sporrow (S nassering)	274	1372	MW	ŴМ
Chipping Sparrow (S. passerina) Chipping X Clay-c Sparrow	2/ 4 0	1372	744 44	WM
Chinping × Clay-C. Sparrow	ň	1		WM
Clay-colored Sparrow $(S \ nallida)$	39	342	EF	WM
Brewer's Snarrow (S. broweri)	36	112	ĨŴ	WM
Field Sparrow (S. musilla)	1	0	EF	US
Black-chinned Sparrow (S. atrogularis)	Ô	ĩ	IW	WM
Zien chines oparion (or an ognario)	-	-		

APPENDIX I. CONTINUED

	Spring	Fall	Breeding	Wintering
Taxon	total	total	group	group
Vesper Sparrow (Pooecetes gramineus)	24	238	IW	US
Lark Sparrow (Chondestes grammacus)	29	240	IW	US
Sage Sparrow (Amphispiza belli)	5	3	IW	US
Black-throated Sparrow (A. bilineata)	7	17	IW	US
Lark Bunting (Calamospiza melanocorys)	1	58	IW	WM
Savannah Sparrow (Passerculus sandwichensis)	209	7068	PC	CP
Baird's Sparrow (Ammodramus bairdii)	0	2		WM
Grasshopper Sparrow (A. savannarum)	25	84	PC	WM
LeConte's Sparrow (A. leconteii)	0	7	EF	US
Sharp-tailed Sparrow (A. caudacutus)	0	1	IW	US
Fox Sparrow (Passerella iliaca)	98	1829	PC	CP
Song Sparrow (Melospiza melodia)	16	50	PC	CP
Lincoln's Sparrow (M. lincolnii)	495	1484	MW	WM
Swamp Sparrow (M. georgiana)	6	60	EF	US
White-throated Sparrow (Z. albicollis)	7	213	EF	US
Golden-crowned Sparrow (Z. atricapilla)	460	9185	TT	CP
Golden-c. × White-c. Sparrow	0	2		CP
White-crowned Sparrow (Z. leucophrys)	901	6771	PC	CP
Harris' Sparrow (Z. querula)	2	17	EF	US
Slate-colored Junco (Junco h. hyemalis)	35	66	TT	US
Oregon Junco (J. h. oreganus)	1236	3143	MW	CP
Lapland Longspur (Calcarius lapponicus)	5	204	TT	US
Chestnut-collared Longspur (C. ornatus)	2	47		US
Snow Bunting (Plectophenax nivalis)	0	18	ΤT	US
Bobolink (Dolichonyx oryzivorus)	10	149	EF	SA
Red-winged Blackbird (Agelaius phoeniceus)	37	554	PC	CP
Tricolored Blackbird (A. tricolor)	6	62	IW	CP
Western Meadowlark (Sturna neglecta)	58	1935	PC	CP
Yellow-headed Blackbird (X. xanthocephalus)	24	56	IW	WM
Rusty Blackbird (Euphagus carolinus)	3	8	TT	US
Brewer's Blackbird (E. cvanocephalus)	170	781	PC	CP
Brown-headed Cowbird (Molothrus ater)	477	1825	PC	US
Orchard Oriole (Icterus spurius)	1	36	EF	CA
Hooded Oriole (I. cucullatus)	1	12	IW	WM
Bullock's Oriole (I. bullockii)	124	434	IW	WM
Baltimore Oriole (I. g. galbula)	10	23	EF	CA
Intergrade Northern Oriole	1	3		
Scott's Oriole (I. parisorum)	0	1	IW	WM