LONG-TERM DECLINES AND DECADAL PATTERNS IN POPULATION TRENDS OF SONGBIRDS IN WESTERN NORTH AMERICA, 1979–1999

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Abstract. We analyzed population trends from a constant-effort mist-netting study conducted in central coastal California during the autumns of 1979–1999. Of 31 taxa captured in sufficient numbers, 16 underwent statistically significant declines and none increased. Twice as many species declined from 1989–1999 as compared to 1979–1989. Overall, our results were similar to those of regional Breeding Bird Surveys determined for the same species during the same period. In an attempt to identify possible causes for trends, we grouped species by various life-history categories including nest height, nest type, likelihood of cowbird parasitism, wintering location, winter food preference, and tolerance for human presence on the breeding grounds. All groups underwent significant declines, although high nesters, common cowbird hosts, and Neotropical migrants declined faster than their respective counterparts. While life-history attributes explained differences in trends between groups, there was significant heterogeneity of trends within groups. Capture rates of certain species and groups appeared to be affected by various climate variables, and accelerating declines since 1990 may reflect effects of large-scale climate cycles, particularly on long-distance migrants. We suggest that long-term population trajectories of songbird populations across North America may be better understood in the context of the Pacific Decadal Oscillation. Interpretation of our results is, in some cases, problematic due to the complex interaction of methodological limitations and environmental variables, especially habitat change on the study site. We recommend the use of multiple methods and multiple sites for monitoring trends in songbird population abundance during fall migration.

Key words: climate regime, fall migration, habitat change, migration monitoring, Pacific Decadal Oscillation, population trend, songbird declines.

Disminuciones a Largo Plazo y Patrones Década a Década en Tendencias Poblacionales de Aves Canoras en el Oeste de Norte América, 1979–1999

Resumen. Analizamos las tendencias poblacionales de un estudio de esfuerzo constante con redes de niebla realizado en la costa central de California durante los otoños de 1979 a 1999. De las 31 especies capturadas en números suficientes, 16 sufrieron disminuciones estadísticamente significativas y ninguna aumentó. En comparación con el período de 1979 a 1989, el doble de las especies disminuyeron entre 1989 y 1999. En general, nuestros resultados fueron similares a los determinados para las mismas especies en el mismo período por los censos regionales de aves reproductivas. En un intento por identificar las posibles causas de las tendencias, agrupamos las especies de acuerdo a varias categorías de historias de vida incluyendo altura del nido, tipo de nido, probabilidad de parasitismo por *Molothrus*, localidad de invernada, preferencias alimenticias en el invierno y tolerancia ante la presencia humana en las áreas reproductivas. Todos los grupos sufrieron disminuciones significativas, aunque las aves con nidos altos, los hospederos comunes de *Molothrus* y los migrantes neotropicales disminuyeron más rápidamente que sus respectivas contrapartes. Aunque los atributos de historia de vida explicaron las diferencias de las tendencias entre grupos, existió una heterogeneidad significativa al interior de los grupos. Las tasas de captura de ciertas especies y grupos parecieron ser afectadas por varias variables climáticas, y las disminuciones aceleradas desde 1990 podrían reflejar efectos de ciclos climáticos a gran escala, particularmente en migrantes de larga distancia. Sugerimos que las tendencias poblacionales a largo plazo de las aves canoras a través de Norte América podrían ser mejor entendidas en el contexto de la oscilación década a década del Pacífico. En algunos casos, la interpretación de nuestros resultados es problemática debido a la compleja interacción entre las limitaciones metodológicas y las variables ambientales, especialmente los cambios en el hábitat en el sitio de estudio. Recomendamos el uso de múltiples métodos y sitios para monitorear las tendencias en la abundancia de las poblaciones de aves canoras durante la migración de otoño.

INTRODUCTION

By the late 1980s, many studies indicated long-term declines in songbird populations in eastern North America (e.g., Faaborg and Arendt 1992, Gauthreaux 1992, Sauer and Droege 1992). Most species involved were Neotropical migrants (Robbins et al. 1989, Rappole and Mac-Donald 1994), although some evidence suggested that species wintering in the United States were also declining (Hagan et al. 1992). Equivalent declines were not initially reported in western North America (Sauer and Droege 1992), probably because of a dearth of similar data for the West. However, Pyle et al. (1994) found that 20 species of western migrants experienced long-term declines compared with nine that increased.

These declines stimulated intense study of factors limiting songbird populations, including habitat loss or degradation on breeding, wintering, and migratory stopover areas, suppression of natural disturbance processes, increased cowbird parasitism, influence of pesticides, changes in predation rates or food availability, and other factors brought about by weather or climate change (Sherry and Holmes 1995, Rotenberry et al. 1995, Robinson 1997, Askins 2000). These factors vary with the species, habitats, and geographic areas in question (Martin 1993, Sherry and Holmes 1995, Faaborg 2002).

Here we present songbird population trend estimates from 21 years of standardized capture data collected by the Point Reyes Bird Observatory (PRBO) during the postbreeding and autumn periods (mainly mid-August to late November, hereafter referred to as ''fall'') in central coastal California. We grouped species by various life-history variables in order to gain insight into factors responsible for the observed trends (Robbins et al. 1989, Böhning-Gaese et al. 1993, Pyle et al. 1994). Other investigations at the same study site have implicated variation in breeding productivity as the most likely reason for changes in population sizes in individual species (Johnson and Geupel 1996, Chase et al. 1997, Gardali et al. 2000). Several authors have documented correspondence between regional Breeding Bird Survey (BBS, Robbins et al. 1986) trends and migration counts derived primarily from mist netting (Hagan et al. 1992, Hussell et al. 1992, Pyle et al. 1994). Thus we compare our observations with trends calculated by the BBS during the same years for California and for a larger area including California, Oregon, Washington, and British Columbia, the area in which we assume most of our fall migrants breed.

We also explore the effects of weather and climate on annual capture rates. Annual or seasonal variation in temperature and rainfall may impact fall capture rates by influencing productivity, juvenile survival, or breeding fitness (Perrins 1970, DeSante and Geupel 1987, Dunn and Winkler 1999). We looked for relationships with interannual changes in climate cycles by comparing trends with the Northern Oscillation Index (NOI, Schwing et al. 2002), as well as with respect to a longer-term climate regime by comparison with the Pacific Decadal Oscillation (PDO, Mantua and Hare 2002). The NOI is highly correlated with the Southern Oscillation Index (SOI), with anomalous cycles lasting 1–2 years followed by longer periods of relative stability. It has a higher degree of concordance with climatic events in the Pacific Northwest than the SOI, and has been correlated with various biological indices in the region (Schwing et al. 2002). The PDO is correlated with spring temperatures in northwestern North America, with positive PDO values associated with warmer and earlier springs and negative PDO values associated with colder and later springs, as determined by the phenology of blooming in certain plant species and timing of spring floods (Cayan et al. 2001). A relatively brief shift in the PDO to negative values between 1989 and 1991 has been linked to shifts toward decreased productivity in at least 69 biological time series in eastern Pacific marine ecosystems (Hare and Mantua 2000). We discuss the potential impacts of such climate cycles on landbird populations, particularly in western North America. We also highlight the complexity and methodological challenges associated with interpreting long-term mist-netting data and provide recommendations for monitoring population changes using migration counts.

METHODS

FIELDWORK

The Palomarin Field Station is in north-central coastal California, near the southern end of the Point Reyes peninsula, within Point Reyes National Seashore (37°56′N, 122°45′W). The study

area is primarily coastal scrub (dominated by *Baccharis pilularis* and *Artemisia californica*) and coast live oak (*Quercus agrifolia*) riparian forest. During the 21 years of the study, changes in habitat structure and species composition occurred in the area. These changes were not quantitatively assessed, but they include encroachment of Douglas-firs (*Pseudotsuga menziesii*), reduction of herbaceous cover, and slight increases in height of trees (primarily oaks). These factors may have affected capture probabilities for some bird species (Hussell et al. 1992, Harrison et al. 2000).

Twenty mist nets (12 × 2.6 m) were operated 6–7 days per week for 6 hr per day beginning within 15 min of local sunrise, 1979–1999. The nets were placed at 14 locations, six of which had nets stacked two high. Six nets were situated in coastal scrub, and 14 (six stacked = eight locations) were in mixed hardwood forest. The scrub nets had 36-mm mesh and the forest nets had 30-mm mesh. We checked nets every 20 to 45 min depending on weather conditions and closed them when weather conditions were poor. All birds captured were given a uniquely numbered U.S. Fish and Wildlife Service band and released after several measurements were taken. We recorded high, low, and mean daily temperatures as well as rainfall at the field station 365 days per year. The habitat, net locations, and netting protocol have been described in detail elsewhere (DeSante and Geupel 1987, Johnson and Geupel 1996, Silkey et al. 1999).

STATISTICAL ANALYSES

Species were included in the analyses if they averaged at least five captures per fall and were present in at least 15 of 21 years. For each species we determined a capture window between 1 July and 4 December, during which 90% of individuals were captured (Dunn and Hussell 1995; Table 1). This method clarifies which populations are sampled when both breeding and transient individuals are captured. The migration window limited the numbers of local breeders included in the analyses of migratory species, and allowed us to be confident that, for 18 species, most individuals captured were not from local populations (Table 1). However, for most resident species and for some migrating species, no peak in captures was evident, suggesting that the sampled population was mostly local, or that separation of local breeders from migrating tran-

sients was not possible. For species for which no window was evident, we used data from 18 August to 25 November, a period which begins after locally produced young have already been captured and ends after the last of the migrants have moved through the area (PRBO, unpubl. data). Annual net hours during the default window ranged from 9015 to 11 685 (mean 10 631 ± 691 [SD]), and total days of netting was very consistent, averaging 94 ± 4.7 days per year (range 85–101). We modeled trends in log(total individuals captured per net hour + 1) for each year and compared trends in total captures between decades (1979–1989 and 1989–1999) using linear models controlling for the effect of individual species (Neter et al. 1990). We repeated this decadal comparison for Neotropical migrants separately. We used the log-transformed fall captures per net hour for each year for each species when analyzing individual species trends, and when comparing trends among life-history groups (described below). We also tested higher-order polynomials for better fits in all cases by including $year^2$ and $year^3$ in the models. We evaluated the effects of autocorrelation of the residuals on trend estimation by comparing coefficients and estimates of significance before and after application of the Prais-Winsten transformed regression estimator (Prais and Winsten 1954), which estimates the significance of autocorrelation of residuals.

We evaluated the potential impacts of habitat and change in habitat over time after categorizing net locations as either "forest" (eight net locations, 14 nets) or "scrub" (six net locations, six nets), assuming that the scrub was a more stable habitat and hence capture probabilities would be more consistent there, while captures in the forest nets could be more impacted by habitat changes such as increases in canopy height past the effective capture area of the nets. This habitat descriptor was included in a linear model describing the trends in log(total captures + 1) in each habitat type, controlling for sample sizes of individual species and including the interaction of year and habitat to examine whether trends differed in the two habitats. We did not control for net hours since effort was similar in the two habitats across years and because net-hour data were not available on a net-by-net basis. We determined the percent similarity in proportional abundance of all species captured in each habitat (Krebs 1989). For five species cap-

tured in sufficient quantities in both habitat types, we compared trend estimates derived for scrub nets with those for forest nets in the same way as the combined species model. For Ruby-crowned Kinglets (see Table 1 for scientific names), the most commonly captured species in both habitats and also a commonly captured winter resident, we compared the trend estimates for the wintering population as determined using all nets, and nets from each habitat separately. We defined the winter ''window'' as all captures after the fall migration window and before the rise in spring captures associated with spring migration.

We compared our trends to those from the BBS (1979–1999 and by decade, 1979–1989, 1989–1999) for routes in California and for a larger region including British Columbia, Washington, Oregon, and California (''regional trend analysis'' using the estimating-equations approach, Sauer et al. 2001). This is likely the region where most of the captured individuals bred. The BBS is a breeding-season roadside survey that has been widely used to analyze changes in population sizes of birds in North America (Robbins et al. 1986, 1989, Peterjohn et al. 1995), and as a benchmark against which others have compared population trend estimates derived from other methods (Dunn and Hussell 1995, Dunn et al. 1997, Holmes and Sherry 2001).

We used a principal components analysis to assist in identifying life-history groupings, but the component loadings were broadly distributed, requiring seven components to account for 70% of the variance in the capture rates of the 31 taxa. Therefore we opted for a more subjective approach and assigned each species life-history codes, similar to previous studies (Böhning-Gaese et al. 1993, Pyle et al. 1994), using information contained in species accounts within the *Birds of North America* series (Poole and Gill 1992–2002). We categorized species by most common wintering location (Mexico or Central America versus the United States), typical nest height (ground to 2.5 m versus >2.5 m), nest type (open cup versus other), cowbird parasitism rates (never to uncommon versus common), typical winter food preference (insect, seed, or fruit; omnivores were excluded), and tolerance for human disturbance during the breeding season (usually will versus will not nest in human-altered patches, Table 1).

We then estimated trends in each of these groups separately using linear models controlling for the effect of the individual species, and including the year × species interaction to evaluate differences in capture trends among species within a group. We tested for differences in the slopes of trends comparing groups by including year and the interaction of the group term with year (e.g., wintering location × year). Finding significant differences in trend slopes within three of the groupings, we evaluated the two-way interactions between these trends (e.g., nest height × year compared with wintering location × year) to evaluate whether membership in one or more groups was more influential on trend differences than others. We also evaluated all the possible three-way interactions involving year (e.g., nest height × wintering location × year), and we looked at the three-way species × year × life-history group interactions to quantify the heterogeneity of species trends within each group.

We used linear models to describe relationships between weather variables and log total fall capture rates for all species grouped, Neotropical migrants, winter residents, and for each species individually. We also examined the effect of these weather variables on trends by including year in the models. This means we analyzed detrended data rather than whether the environmental variable predicted variation in capture rates better than the linear trend in time (Box and Jenkins 1976). We controlled for the main effect of individual species numbers by analyzing weather correlates with trends in capture rates of groups of species. To correct significance estimates for multiple comparisons (we made a total of 34 comparisons for each weather variable; i.e., 31 individual taxon capture rates plus the three groupings described above), we used the Šidák adjustment, which is equivalent to using an individual *a priori* P-value of 0.0015, corresponding to an analysis-wide P-value of 0.05 (Stata Corporation 1999). Weather variables included total rainfall (cm) between November and March (winter rain) and between April and July (summer rain), number of winter days with low temperatures below 1°C from 1 December of the previous year to 31 March of the current year (cold winter days), the mean of monthly Northern Oscillation Index means from November of the previous year to March of the current year, year − 1 (previous year) and year

− 2, and mean monthly Pacific Decadal Oscillation mean from November of the previous year to March of the current year, year − 1, and year − 2. NOI data were provided by NOAA's Pacific Fisheries Environmental Laboratory (NOAA 2002) and PDO data were provided by N. J. Mantua, University of Washington (Mantua 2002).

To better understand the relationship between climate cycles and local and regional weather, we compared November to March NOI and PDO values with total November to March rainfall and March to May mean temperatures recorded at Palomarin from 1968 to 2000 using linear regression. We also compared these values with regional ones using data collected at two stations in Oregon (Astoria and Newport, Oregon Climate Service 2003) and one in Washington (Olympia; Western Regional Climate Center 2003). We also used linear regression to describe the relationship at Palomarin between the number of cold winter days, mean December to March temperatures, and mean March to May temperatures, 1979 to 1999.

All statistical calculations were performed using STATA version 6.0 (Stata Corporation 1999). We present means and coefficients ± SE unless SD is indicated, and assumed model significance at $P < 0.05$, marginal significance at $P < 0.10$. The residuals of all models presented were normally distributed, which we determined using a formal test for skewness and kurtosis (STATA: sktest), or by use of diagnostic graphical plots designed for this purpose (STATA: qnorm), depending on sample sizes of individual models (Nur et al. 1999).

RESULTS

TRENDS IN TOTAL CAPTURES

We captured 30 species at least five times per year and in at least 15 of 21 years, totaling 24 611 captures (Table 1). Log total fall captures per 10 000 net hr of these 30 species combined decreased during the study (Fig. 1). Sixteen taxa declined significantly (including two White-crowned Sparrow subspecies analyzed separately), and 15 had no significant or marginally significant trend (Table 1). Trend significance changed (from significant to marginally significant) for only one species (Bewick's Wren) when we controlled for the effects of autocorrelation. Trends for 11 species fit curvilinear re-

lationships, nine quadratic and two cubic (Table 2). Six of the nine quadratic trends were negative, reflecting accelerating declines in capture rates in more recent years. Warbling Vireos had a marginally significant cubic trend indicating a period of increase from 1979–1983, declines from 1984–1996, and increases from 1997–1999 (Table 2). Spotted Towhees exhibited essentially the inverse cubic trend: rapid declines from 1979–1983, increases from 1984–1994, and subsequent sharp declines (Table 2).

EFFECTS OF HABITAT

Trends for captures in forest nets were more pronounced than those for scrub nets (difference in slopes: $\beta = -0.058 \pm 0.009$, $F_{1,1202} = 44.9$, $P < 0.001$, Fig. 2). Proportional species composition by habitat had a coefficient of similarity of 0.45; thus the habitat type (forest or scrub) immediately surrounding a particular net location influenced the species and numbers of captures. For Ruby-crowned Kinglets, Warbling Vireos, Bushtits, Fox Sparrows, and Hermit Thrushes, the only species captured in high numbers in both habitats, trends in forest nets were significantly negative, and significantly more negative than the corresponding trend estimates derived from the scrub nets, which were all nonsignificant. There was no trend in captures for wintering Ruby-crowned Kinglets using all nets or nets in either habitat type. However, the slope of the winter trend estimate from forest nets was significantly more negative than that from the scrub nets ($\beta = -0.054 \pm 0.020$, $F_{1,40} = 4.2$, $P = 0.02$).

COMPARISON WITH BBS

Of the 31 taxa we monitored, BBS reported significant or marginally significant trends for 14 species in either the smaller region, the larger region, or both. Eight of these matched direction and significance of trends observed at Palomarin (Table 3). One species (Western Tanager) showed a significant positive trend according to BBS but a significant negative trend in the Palomarin data.

DECADAL COMPARISONS

Nine species had significant or marginally significant decreasing trends from 1989–1999 compared with five for 1979–1989 (Table 3). Three species (Wrentit, Song Sparrow, and Lincoln's Sparrow) had increasing trends from 1989–1999
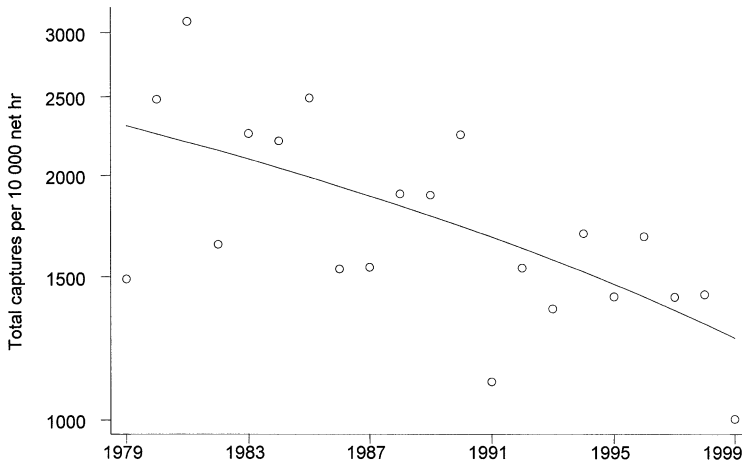
TABLE 1.   Estimated linear trends for species or subspecies captured at least 5 times per fall and in at least 15 of the years 1979 to 1999 at Palomarin field station, California. Mean number of captures per year within the species' peak seasonal capture window, number of years with 0 captures, and life history categories are indicated. Species in bold have significant ($P < 0.05$) or marginally significant ($P < 0.10$) trends. Species marked with an asterisk had identifiable capture peaks, and we calculated 90% capture windows for them to reduce the influence of local breeders in the sample.

Species (mean no. year^{-1}, no. years of 0 captures)	Winter location	Nest height	Nest type	Winter food	Cowbird host	Human tolerant	Linear trend (% chg yr^{-1})	Adjusted r^2	P
Red-breasted Sapsucker (6, 0)* *Sphyrapicus ruber*	resident	high	other	fruit	common	yes	-2.5 ± 1.7	0.06	0.15
Pacific-slope Flycatcher (180, 0)* *Empidonax difficilis*	tropics	high	other	insects	common	yes	-0.5 ± 14.6	-0.05	0.76
Hutton's Vireo (12, 0)* *Vireo huttoni*	resident	high	cup	insects	common	no	-7.7 ± 1.7	0.47	<0.001
Warbling Vireo (47, 0)* *Vireo gilvus*	tropics	high	cup	insects	common	yes	-9.4 ± 2.2	0.43	<0.01
Chestnut-backed Chickadee (24, 0) *Poecile rufescens*	resident	low	other	insects	uncommon	yes	-6.1 ± 2.0	0.27	<0.01
Bushtit (16, 0) *Psaltriparus minimus*	resident	low	other	insects	uncommon	yes	-6.0 ± 1.6	0.37	<0.01
Brown Creeper (16, 0) *Certhia americana*	resident	high	other	insects	uncommon	no	-6.4 ± 2.7	0.17	0.04
Bewick's Wren (10, 0) *Thryomanes bewickii*	resident	low	other	insects	uncommon	yes	-3.0 ± 1.4	0.15	<0.07
Winter Wren (9, 1)* *Troglodytes troglodytes*	resident	low	other	insects	uncommon	no	4.1 ± 2.4	0.09	0.10
Golden-crowned Kinglet (74, 0)* *Regulus satrapa*	resident	high	other	insects	unknown	no	-2.8 ± 3.7	-0.02	0.47
Ruby-crowned Kinglet (201, 0)* *Regulus calendula*	resident	high	other	insects	uncommon	no	-6.5 ± 1.4	0.48	<0.001
Swainson's Thrush (36, 0) *Catharus ustulatus*	tropics	low	cup	fruit	uncommon	no	1.6 ± 1.6	0.004	0.31
Hermit Thrush (109, 0)* *Catharus guttatus*	resident	low	cup	fruit	uncommon	no	-0.3 ± 0.9	-0.05	0.77
Varied Thrush (9, 1) *Ixoreus naevius*	resident	high	cup	fruit	uncommon	no	-1.0 ± 2.9	-0.05	0.75
Wrentit (23, 0) *Chamaea fasciata*	resident	low	cup	insects	uncommon	yes	1.8 ± 1.1	0.09	0.10
Orange-crowned Warbler (8, 1)* *Vermivora celata*	tropics	low	cup	omniv	uncommon	no	-8.5 ± 2.5	0.33	<0.01
Yellow Warbler (19, 0)* *Dendroica petechia*	tropics	low	cup	insects	common	yes	-6.3 ± 2.0	0.29	<0.01
Black-throated Gray Warbler (5, 1)* *Dendroica nigrescens*	tropics	high	cup	insects	unknown	no	-4.9 ± 2.1	0.18	0.03

TABLE 1.   Continued.

Species (mean no. year⁻¹, no. years of 0 captures)	Winter location	Nest height	Nest type	Winter food	Cowbird host	Human tolerant	Linear trend (% chg yr⁻¹)	Adjusted r²	P
Townsend's Warbler *Dendroica townsendi* (39, 0)*	resident	high	cup	insects	uncommon	no	-0.5 ± 1.8	-0.05	0.79
Wilson's Warbler *Wilsonia pusilla* (29, 0)	tropics	low	cup	insects	common	no	-5.8 ± 1.3	0.48	<0.001
Western Tanager *Piranga ludoviciana* (6, 2)*	tropics	high	cup	fruit	common	no	-8.1 ± 2.4	0.33	<0.01
Spotted Towhee *Pipilo maculatus* (18, 0)	resident	low	cup	seeds	common	yes	0.7 ± 1.1	-0.03	0.51
Fox Sparrow *Passerella iliaca* (47, 0)*	resident	low	cup	seeds	unknown	no	0.6 ± 1.7	-0.05	0.74
Song Sparrow *Melospiza melodia* (26, 0)	resident	low	cup	seeds	common	yes	-0.3 ± 1.6	-0.05	0.84
Lincoln's Sparrow *Melospiza lincolnii* (9, 0)*	resident	low	cup	seeds	uncommon	no	2.1 ± 1.6	0.03	0.22
Nuttall's White-crowned Sparrow *Zonotrichia leucophrys nuttalli* (17, 0)	resident	low	cup	seeds	common	yes	-5.4 ± 2.0	0.22	0.02
Puget Sound White-crowned Sparrow *Zonotrichia l. pugetensis* (24, 0)*	resident	low	cup	seeds	uncommon	no	-5.2 ± 2.0	0.22	0.02
Golden-crowned Sparrow *Zonotrichia atricapilla* (76, 0)	resident	low	cup	seeds	uncommon	no	-1.8 ± 1.4	0.03	0.21
Oregon Dark-eyed Junco *Junco hyemalis oreganos* (44, 0)*	resident	low	cup	seeds	unknown	yes	-1.5 ± 1.8	-0.02	0.44
Purple Finch *Carpodacus purpureus* (35, 0)	resident	high	cup	seeds	uncommon	yes	-8.2 ± 1.7	0.50	<0.001
Pine Siskin *Carduelis pinus* (7, 6)	resident	high	cup	seeds	unknown	yes	-12.2 ± 2.9	0.42	<0.01

FIGURE 1.   Total fall captures (of 31 study taxa) per 10 000 net hr at the Palomarin field station, California, 1979–1999. Note that *y*-axis is drawn in log scale. Circles are annual means calculated using individual species' peak capture windows. Line shows values predicted from log-linear regression ($\beta = -0.037 \pm 0.004$, $P < 0.001$)

compared with none for 1979–1989. There was no difference in the slopes of the trend lines for each decade when we looked at all species combined ($P = 0.33$) or winter residents ($P = 0.67$). However, for Neotropical migrants the decline for 1989–1999 was steeper than for 1979–1989 ($\beta = -0.084 \pm 0.031$, $P < 0.01$, Fig. 3). We repeated the model excluding 1999 to evaluate the effect of the extremely low captures that year, and results were similar ($\beta = -0.063 \pm 0.033$, $P = 0.06$). BBS data showed a similar overall pattern, with more species undergoing significant declines from 1989–1999 than 1979–1989 at both the regional level (six species versus one species declining) and for California (six versus four, Table 3).

TRENDS WITHIN LIFE-HISTORY GROUPS

We detected negative trends in all life-history categories when considering the entire study period (Table 4, Fig. 4). For Neotropical migrants, high nesters, and common cowbird hosts, these trends were best modeled with the quadratic term, indicating accelerating declines since approximately 1990 (Fig. 4), and supporting results of the analyses by decade. When we excluded 1999 from the analyses, the quadratic shape was significant only for Neotropical migrants. Differences between the downward linear trends comparing life-history categories were statistically significant for wintering location ($P = 0.01$, Neotropical migrants declining faster than winter residents), nest height ($P \leq$

TABLE 2.   Significant or marginally significant curvilinear trends for species captured at Palomarin field station, California, 1979–1999. Year was coded as $1989 = 0$, $1979 = -10$, $1999 = +10$.

Species	Curvilinear trend (ß ± SE)	Shape	Adjusted R^2	P
Red-breasted Sapsucker	–0.0053 ± 0.0030	quadratic	0.15	0.09
Pacific-slope Flycatcher	–0.0046 ± 0.0026	quadratic	0.06	0.09
Warbling Vireo	0.0015 ± 0.0008	cubic	0.48	0.08
Bewick's Wren	0.0063 ± 0.0023	quadratic	0.37	0.01
Yellow Warbler	–0.0085 ± 0.0036	quadratic	0.42	0.03
Townsend's Warbler	–0.0070 ± 0.0031	quadratic	0.14	0.04
Western Tanager	–0.0087 ± 0.0044	quadratic	0.42	0.07
Spotted Towhee	–0.0008 ± 0.0003	cubic	0.29	0.02
Song Sparrow	0.0050 ± 0.0028	quadratic	0.06	0.10
Golden-crowned Sparrow	0.0046 ± 0.0025	quadratic	0.14	0.08
Purple Finch	–0.0076 ± 0.0031	quadratic	0.60	0.03
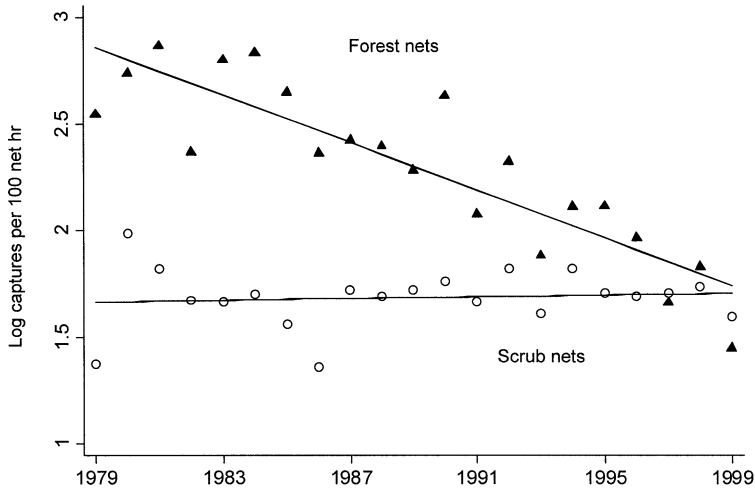
FIGURE 2.   Mist-net capture rates by habitat type at Palomarin field station, California, 1979–1999. Symbols represent total number of captures of 31 taxa. Overall trends in the forest nets (triangles) were significantly more negative than those from scrub nets (circles; $\beta = 0.058 \pm 0.009$, $P < 0.001$).

0.001, medium and high nesters declining faster than ground nesters), and cowbird parasitism ($P = 0.01$, common cowbird hosts declining faster than infrequent hosts, Table 4). Testing the three two-way interactions between these groups, we found that nest height was the most influential characteristic, and that high nesters declined faster than low nesters when controlling for the effect of trends in the other two groups simultaneously (full model statistics: $F_{29,516} = 67.9$, adjusted $r^2 = 0.78$, $P < 0.001$, for the nest height $\times$ year interaction: $F_{1,516} = 9.6$, $\beta = 0.026 \pm 0.008$, $P < 0.01$). The trends differing by wintering location and host likelihood were nonsignificant when controlling for the effect of trends by nest height and each other ($P > 0.05$ for wintering location, $P > 0.30$ for host likelihood). None of the three three-way interactions were significant ($P > 0.60$).

There was significant variability in the severity of slopes for species within each group (all two-way interactions of species $\times$ year, $P < 0.001$), but most species in each group had trends in at least the same direction, and none had significant trends in the opposite (positive) direction, reflecting the individual species' trends presented in Table 1.

WEATHER EFFECTS

The Northern Oscillation Index was negatively correlated with winter rainfall at Palomarin from 1968–2000 ($\beta = -5.58 \pm 1.40$, $P < 0.001$, adj.

$r^2 = 0.35$, Fig. 5), but not with regional winter rainfall (all $P > 0.15$). The Pacific Decadal Oscillation was positively correlated with spring temperatures at Palomarin ($\beta = 1.31$, $P < 0.01$, adj. $r^2 = 0.21$, Fig. 5), and at the regional level ($P < 0.05$). PDO was not related to rainfall at Palomarin ($P > 0.40$, Fig. 5), but it was negatively related to winter rain at the regional scale ($P < 0.05$, except for Newport, where $P = 0.08$). NOI was not related to spring temperatures at Palomarin (Fig. 5), but was negatively correlated with regional spring temperatures (all $P < 0.01$). Mean March to May temperatures were positively correlated with mean December to March temperatures at Palomarin ($\beta = 0.53 \pm 0.22$, $P < 0.03$, adj. $r^2 = 0.19$) but not with the number of cold winter days ($P > 0.50$). At Palomarin, summer rain averaged $10 \pm 4\%$ (SD) of the total annual rainfall and winter rainfall averaged $83 \pm 6\%$ (SD) of total annual rainfall.

Weather variables affected capture rates of several species before accounting for the effect of year (annual trends), but weather effects (coefficients and P-values) were similar whether or not we controlled for annual trends. Therefore, we only present weather effects after controlling for annual trends (Table 5). Considering each species and the six weather variables, 17 out of 186 regressions (31 taxa $\times$ 6 variables) resulted in nominally significant relationships ($P < 0.05$ unadjusted), but none were significant after making the Šidák adjustment. Considering Neo-

TABLE 3. Comparison of trends detected by the North American Breeding Bird Survey (BBS) and by constant-effort mist-netting at Palomarin field station, California, 1979–1999. Species with significant ($P < 0.05$) or marginally significant ($P < 0.10$) trends in either effort are listed. BBS trends were calculated for two areas: California only and a larger region including California, Oregon, Washington, and British Columbia, Canada.

| | 1979–1999 | | | 1979–1989 | | | 1989–1999 | | |
| | BBS | | | BBS | | | BBS | | |
Species	Region	California	Palomarin	Region	California	Palomarin	Region	California	Palomarin
Red-breasted Sapsucker							–3.5+		–12.4*
Pacific-slope Flycatcher								1.4+	–6.1+
Hutton's Vireo			–7.7***						
Warbling Vireo	1.5**	–2.2**	–9.4**		–2.7**		1.86*		
Chestnut-backed Chickadee		–3.8**	–6.0**					–6.2**	–13.0*
Bushtit	–3.1**	–3.2**	–6.0**			–9.2*			
Brown Creeper			–6.4*				–6.2**	–4.1**	
Bewick's Wren			–3.0+			–12.3**	2.2+	2.5+	
Winter Wren	0.9+	2.9*		–4.0***	–4.6***		3.1***	6.9**	
Ruby-crowned Kinglet			–6.5***			–5.4*			–9.6+
Hermit Thrush					5.5*		–1.7+		
Wrentit	–1.1+	–1.1+		3.2+					6.2+
Orange-crowned Warbler	–0.9+		–8.5**				–4.4***	–2.0*	
Yellow Warbler	–1.1+	–2.5+	–6.3**					–2.0*	–12.8+
Black-throated Gray Warbler			–4.9*	1.8*					–11.2*
Wilson's Warbler	–1.3+		–5.8***			–7.0*			
Western Tanager	1.4**		–8.1**	1.6+	2.0*		1.6*		–10.6+
Spotted Towhee	1.2**			1.9**	2.1**				–5.6+
Fox Sparrow					3.5**				
Song Sparrow	4.5*								6.5+
Lincoln's Sparrow									8.0*
White-crowned Sparrow[a]	–1.4**	–3.9+	–5.4*a		–3.3*				
Oregon Junco								2.4**	
Purple Finch			–8.2***				–6.5***	–6.1***	–17.6**
Pine Siskin	–3.3**	–9.3***	–12.2**		–11.2***	–19.8*	–3.3	–12.3**	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, + $P < 0.1$.
[a] Both subspecies (*nuttalli* and *pugetensis*) combined.
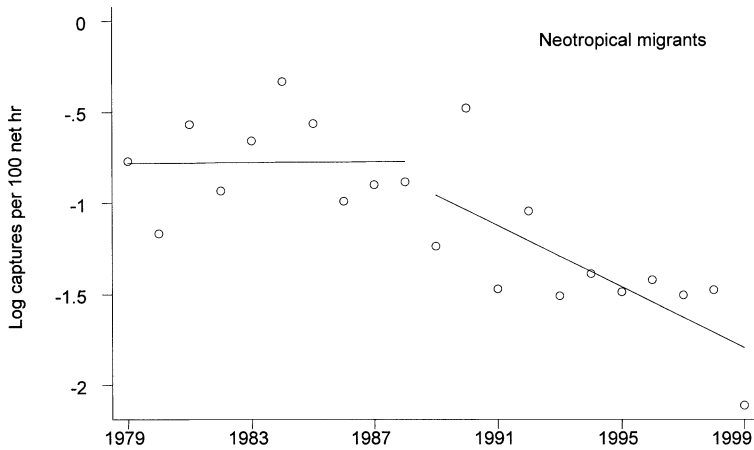
FIGURE 3. Mist-net capture rates for 8 species of Neotropical migrants at Palomarin field station, California, 1979–1999. Lines show best fit of trend by decades: 1979–1989, 1989–1999 and indicate significant declines since 1989 ($P < 0.01$).

tropical migrants, winter residents, and all species, 3 out of 18 regressions (3 groups × 6 variables) were nominally significant, but of those only the negative relationship between the number of cold winter days and captures of Neotropical migrants was significant after adjustment ($\beta = -0.032 \pm 0.010$, $P < 0.05$). We did not detect an effect of NOI (lagged or not) on any species groups. The mean Pacific Decadal Oscillation from November of the previous year to March of the current year was the most consistent weather correlate with capture rates: it was positively related to capture rates of Hutton's Vireo, Swainson's Thrush, Yellow Warbler, all species combined, and Neotropical migrants. The effect of PDO on capture rates of winter

TABLE 4. Estimated linear trends in fall captures of 31 taxa analyzed by life-history groupings, Palomarin field station, California, 1979–1999. All trends were significant at $P < 0.001$ except for the fruit-diet group, which was significant at $P = 0.003$.

Group	df	$\beta \pm SE$	r^2	n (captures)
Wintering location				
Temperate	482	-0.031 ± 0.005	0.02	17 718
Neotropics	167	-0.055 ± 0.008	0.06	6893
Nest height				
Low	377	-0.023 ± 0.005	0.02	11 427
High	272	-0.057 ± 0.007	0.05	13 184
Nest type				
Open cup	461	-0.038 ± 0.005	0.04	13 528
Other	188	-0.034 ± 0.008	0.02	11 083
Cowbird host				
Infrequent	356	-0.028 ± 0.005	0.02	13 460
Common	188	-0.049 ± 0.007	0.06	7425
Winter food				
Insects	314	-0.041 ± 0.006	0.03	14 596
Fruit	104	-0.021 ± 0.010	0.01	3460
Seeds	209	-0.033 ± 0.007	0.03	6392
Human tolerance				
Intolerant	355	-0.031 ± 0.006	0.02	14 696
Tolerant	293	-0.044 ± 0.006	0.05	9915
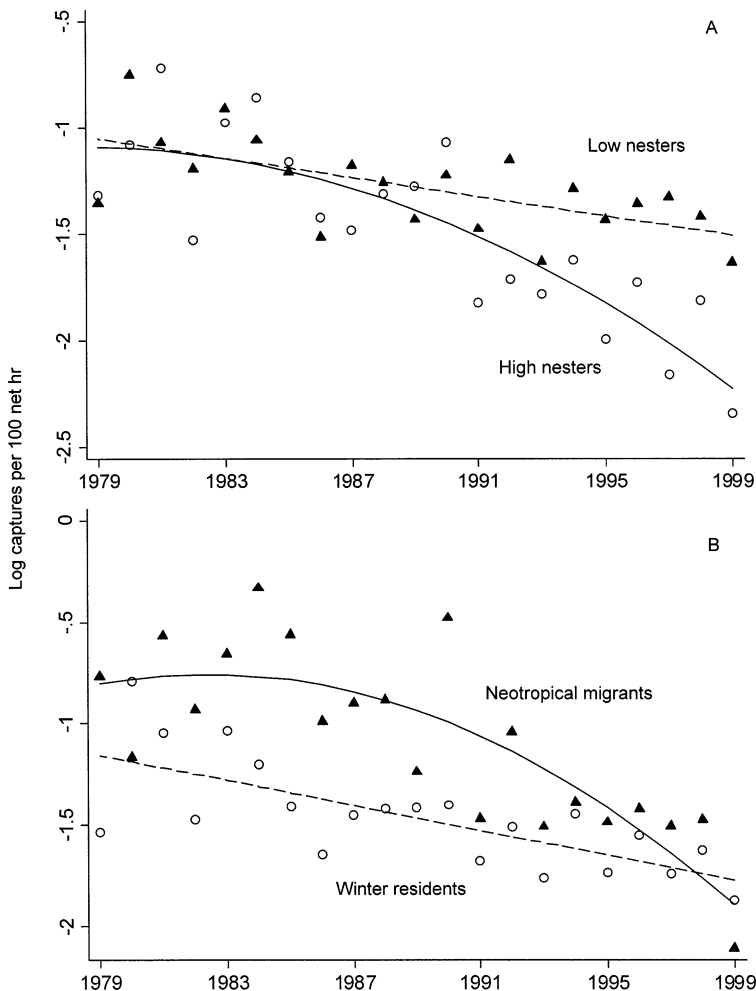
FIGURE 4.   Predicted log-transformed total capture rates for 31 taxa at Palomarin field station, California, 1979–1999, grouped by life-history characteristics. (A) Low nesters (18 species) compared with high nesters (13 species). (B) Winter residents (23 species) compared with Neotropical migrants (8 species). Analyses controlled for the effect of varying sample size by species. High nesters declined faster than low nesters, even while controlling for species' membership in other life-history groups.

residents as a group was also positive, though the uncorrected significance value was marginal ($P = 0.06$).

DISCUSSION

LONG-TERM DECLINES

It is notable that 16 of our 31 study taxa underwent significant declines while none increased from 1979–1999. All life-history groups we identified declined, including 10 winter- or year-round-resident species. Our results, together with those from the BBS, imply regional declines in many species and life-history groups of

western North American songbirds. Interpretation of these results is complicated, particularly by methodological factors and uncertainty regarding the ranges of the populations sampled, but there is strong evidence of agreement between trends derived from mist netting and other counts that use different methods during various times of the year (Dunn and Hussell 1995, Dunn et al. 1997, Silkey et al. 1999, Holmes and Sherry 2001).

Results from Southeast Farallon Island, 36 km offshore from Palomarin, also showed a significant overall linear decline in fall captures of
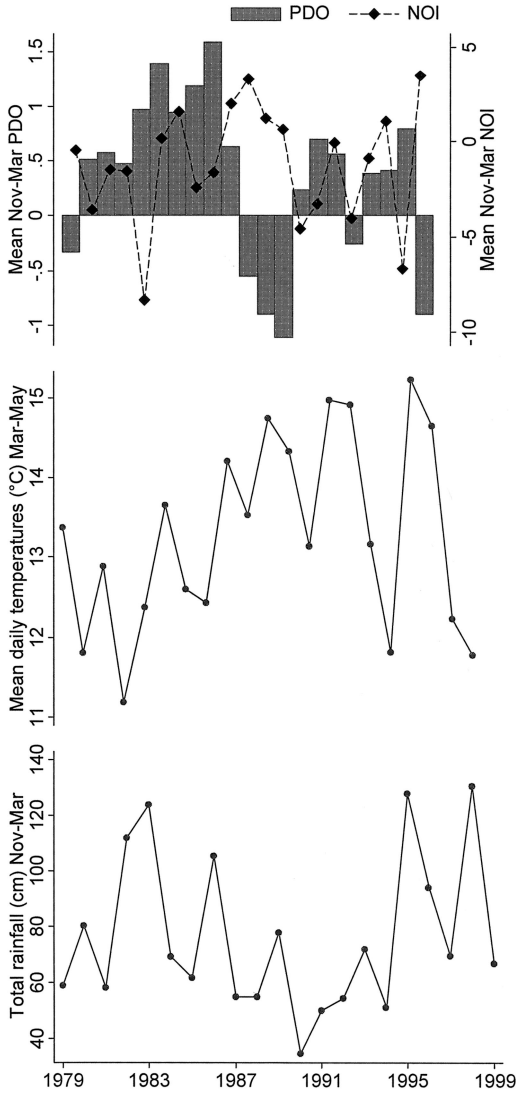
FIGURE 5. Mean monthly Pacific Decadal Oscillation (PDO) and Northern Oscillation Index (NOI) values (November–March), mean daily Palomarin, California, temperatures (March–May), and Palomarin rainfall (November–March) 1979–1999. NOI was negatively correlated with rainfall and PDO was positively correlated with spring temperatures at Palomarin.

species breeding in the "Pacific Coastal" region (Pyle et al. 1994), which is probably the region we sampled. The Farallon time series (1968–1992), partially overlapped our study period, and included 18 of the same species. However, trends were evident in only three of these, and only one, White-crowned Sparrow, showed similar significant decreases, reflected also by BBS

data. Differences between our results could be exacerbated by the sharper decline in 1989–1999 (mostly not covered by the Farallon Island study) than in the previous decade, by habitat differences, or by the use of different survey methods (combination of visual censuses and opportunistic netting on Southeast Farallon Island).

LIFE-HISTORY GROUPS

Unlike Böhning-Gaese et al. (1993) and Rappole and McDonald (1994), who each found specific (though different) guilds were declining, we observed declines in all guilds, making interpretation complex (cf. James et al. 1992, Martin 1993, Sherry and Holmes 1995, Latta and Baltz 1997). Negative trends were statistically stronger for some groups than others and breeding-ground factors (nest height and cowbird host likelihood) seemed to be the most influential, though wintering location was also important. Results support the likelihood that many factors affect songbird populations, and that a systemic factor, such as large-scale climate change or habitat loss, is involved. The quadratic shape of the trend for high nesters, common cowbird hosts, and Neotropical migrants is influenced by the sharp decrease in their captures in 1999, and only further monitoring will determine if this indicates a continuing exponential decrease.

EFFECTS OF HABITAT CHANGE

Habitat change due to succession has likely impacted the numbers of birds visiting or resident to Palomarin, especially those species preferring more herbaceous cover and less tree and shrub cover (Harrison et al. 2000, Holmes and Sherry 2001). This change may explain declines in populations of such species as White-crowned Sparrow and Pine Siskin, as well as the 1989–1999 increases in three shrub-associated species: Wrentit, Song Sparrow, and Lincoln's Sparrow.

Additionally, vegetation changes at the actual net locations may have compromised the sampling effectiveness of some nets (Hussell et al. 1992). This could be especially problematic during migration, when most individuals are transients staying only 1–7 days (Woodrey and Moore 1997, Yong et al. 1998, PRBO, unpubl. data). In summer or winter, resident individuals probably have greater capture likelihood simply because of prolonged exposure to nets in their home ranges. The trees that surround the forest

TABLE 5. Regression coefficients for various weather variables with log-transformed fall capture rates, controlling for year and species effect, Palomarin field station, California, 1979–1999. Summer rain = rainfall (cm) at Palomarin between April 1 and July 31. Cold winter days = number of days with low temperature of $<1°C$, December–March. Northern Oscillation Index (NOI) and Pacific Decadal Oscillation (PDO) values are November–March means. Individual species which had significant pre-Šidák-corrected relationships are indicated in footnotes.

Weather variable Group	$\beta \pm SE$	R^2	P
Summer rainfall[a]			
All species	0.009 ± 0.007	<0.01	>0.90
Winter residents	0.009 ± 0.008	<0.01	>0.90
Neotropical migrants	0.009 ± 0.014	<0.01	1.00
Cold winter days[b]			
All species	-0.009 ± 0.005	<0.01	>0.90
Winter residents	-0.001 ± 0.006	<0.01	1.00
Neotropical migrants	-0.032 ± 0.010	0.01	<0.05
Current-year Northern Oscillation Index[c]			
All species	0.003 ± 0.009	<0.01	1.00
Winter residents	-0.004 ± 0.011	<0.01	1.00
Neotropical migrants	0.020 ± 0.018	<0.01	>0.90
Previous-year Northern Oscillation Index[d]			
All species	-0.008 ± 0.009	<0.01	1.00
Winter residents	-0.011 ± 0.011	<0.01	1.00
Neotropical migrants	0.001 ± 0.019	<0.01	1.00
Two-years-previous Northern Oscillation Index[e]			
All species	-0.011 ± 0.009	<0.01	>0.90
Winter residents	-0.017 ± 0.011	<0.01	>0.90
Neotropical migrants	0.008 ± 0.019	<0.01	1.00
Current-year Pacific Decadal Oscillation[f]			
All species	0.081 ± 0.030	<0.01	>0.20
Winter residents	0.066 ± 0.035	<0.01	>0.80
Neotropical migrants	0.126 ± 0.059	<0.01	>0.70

[a] Wilson's Warbler and Song Sparrow had significant positive relationships with summer rainfall prior to Šidák adjustment.
[b] Golden-crowned Kinglet, Swainson's Thrush, Orange-crowned Warbler, and Western Tanager had significant negative relationships with cold winter days before Šidák adjustment.
[c] Warbling Vireo had a significant positive relationship with current-year NOI before Šidák adjustment.
[d] Red-breasted Sapsucker and Chestnut-backed Chickadee had significant positive relationships and Bewick's Wren had a significant negative relationship with the previous-year NOI before Šidák adjustment.
[e] Before Šidák adjustment, Pacific-slope Flycatcher, Winter Wren, Song Sparrow, and Pine Siskin had significant negative relationships with the NOI 2 years previous.
[f] Hutton's Vireo, Swainson's Thrush, and Yellow Warbler had significant positive relationships with the current-year PDO prior to Šidák adjustment.

nets are primarily slow-growing oaks, and we estimate they grew <1 m during the study; nevertheless, it is possible that canopy-using species passed over nets more often in 1999 than in 1979, resulting in exaggerated trend estimates. In contrast, nets placed in coastal scrub have possibly increased in sampling effectiveness, as the surrounding vegetation had grown but not exceeded net height by 1999. The possibility of negative effects of habitat change on the forest nets was supported by our analyses of capture rates for species commonly caught in both habitats. For these species, trends for forest nets were consistently more negative than for scrub nets, even for the persistent wintering population of kinglets.

The influence of habitat change on capture rates is complicated by the differing species composition in each set of nets: only five species shared sufficient capture numbers in both habitats for comparison. Because capture rates were reduced for both canopy and noncanopy species

in the forest nets compared with the scrub nets, other factors than changes in netting effectiveness are probably involved. Furthermore, effects of incremental habitat change do not satisfactorily explain the abrupt drop-off in capture numbers around 1989, the curvilinear trends in some species and groups, or the trends evident in life-history groupings, which by their diversity should be more robust to the potential impacts of habitat change than single species. The uncertainties related to interpreting the effect of habitat change on netting effectiveness warrant serious consideration, particularly for researchers using only mist nets.

DECADAL COMPARISONS AND COMPARISON WITH BBS

Similar to other studies (Hussell et al. 1992, Peterjohn et al. 1995, Francis and Hussell 1998), we found that trends differed depending on whether we looked at the entire study period or individual decades. Though we recognize that dividing the study period in half is arbitrary, the division serves at least two purposes. First, most studies undertaken so far have only had the benefit of 10 years or less effort; with this longer dataset, we are able to illustrate potential biases evident in either half of our study. Second, the halfway point happens to coincide with a notable shift in the capture rates for several species; drawing attention to more recent trends may justifiably draw conservation concern if causal factors present during the latter part of the study but not in the first can be identified. This was also evident from the higher-order models that best fit some species and group trends and from the BBS results showing many more significant trends in 1989–1999 than 1979–1989. These shifts in trends may reflect normal fluctuations, which would only become obvious after further decades of study.

BBS trends tended to be less severe in magnitude and significance than the corresponding Palomarin trends. This is possibly because most individuals we captured were young (87% of known-aged captures were hatch-year birds, PRBO, unpubl. data), whereas BBS counted only adults. The relationship between numbers of adults in the breeding season and numbers of young in the fall should be nonlinear. Alternatively, the potential effect of habitat change on netting effectiveness could have exaggerated the Palomarin trends in some species.

EFFECTS OF WEATHER

Other authors have used "daily estimated totals" in order to combine data obtained from multiple methods used at a study site, and to account for the potentially large influence a single day's numbers can have on an annual total (Hagan et al. 1992, Hussell et al. 1992, Pyle et al. 1994). These waves of migrants can be influenced by weather and lunar phenomena (Hussell et al. 1992, Pyle et al. 1994). In the data presented here, only one field method was used, and it was very consistent on a daily and annual basis. Further, migrant waves are rare at the study site, where, among the eight species with >100 captures in any year, only 11 days in 21 years of sampling (1931 total banding days) had capture totals of >10% of a species' annual captures.

Seasonal weather patterns and longer-term climate cycles have been shown to impact population sizes and demography, and thus we expected them to influence our capture rates. For example, Sillett et al. (2000) reported that adult survival and an index of fecundity of Black-throated Blue Warblers (*Dendroica caerulescens*) were both lower during El Niño and higher during La Niña years. Forschammer et al. (1998) reported, for some British bird species, changes in timing of breeding and variation in population size related to the North Atlantic Oscillation, a climate cycle with documented impacts to eastern North American and European weather patterns (Barnston and Livezey 1987). The relationships to weather and climate we report are based on exploratory investigations, and are mostly not statistically supported by inference tests (Table 5); given the large numbers of comparisons we made, some of the relationships could be due to chance.

However, it is likely that both seasonal weather variables and large-scale climate cycles impacted some populations in consistent and predictable ways. For example, summer rainfall was positively correlated with capture rates of Wilson's Warblers and Song Sparrows, indicating increased breeding productivity in wet summers. Cold winters were consistently negatively related to capture rates for one winter resident, and three Neotropical migrants. Colder winters corresponded with colder springs at Palomarin, in turn possibly corresponding to depressed productivity (see below). The difference in direction

of Northern Oscillation Index effect depending on time lag may indicate impacts to adult survivorship in some species and impacts to fecundity in others. Since NOI had a negative effect on winter rainfall at Palomarin, but not at the regional scale, it seems likely a relationship could exist for individuals breeding or wintering in the vicinity, but possibly not for individuals from farther away.

The shift in capture rates between decades coincides with a shift in Pacific Decadal Oscillation, from a positive to a negative regime (warm to cool) during 1989–1991 and then back again. This climate regime shift affected weather over a large region, including the Pacific Northwest, Mexico, and Central America, affecting timing and magnitude of stream flows and coastal air temperatures (Hare and Mantua 2000, Cayan et al. 2001). Such shifts in the PDO have been linked to large changes in productivity in salmon and other fish species (Hare and Mantua 2000, Mantua and Hare 2002) and in the onset of spring, with warm phases correlated with earlier springs and cool phases with later springs (Cayan et al. 2001). Further, we demonstrated that negative PDO values corresponded with cooler than average March–May temperatures at Palomarin and at a regional scale. It is possible that such changes impacted productivity in western songbird populations in a stepwise fashion by delaying spring and associated increases in food or vegetation resources through colder than average air temperatures. This may be reflected in our data in the marked drop-off in overall capture rates and in rates for high-nesting species, cowbird hosts, and Neotropical migrants and in the tendency for more individual species to decline in 1989–1999 than 1979–1989.

However, our study occurred mostly within a warm PDO regime (1979–1988, 1992–1993, 1995–1998), which should have been favorable for songbird populations by providing a longer breeding season as well as milder winters and early springs for winter residents (Perrins 1970, Crick et al. 1997). Yet we still saw many long-term declines, implicating something other than the PDO as a primary factor, even though large-scale climate changes may inherently reduce bird populations. Thomas et al. (2001) showed that earlier springs could cause mismatch between food availability and timing of breeding, ultimately causing lower productivity and higher adult mortality in at least one European species.

Inouye et al. (2000) pointed out that changes in timing of spring at lower elevation that are not reflected at higher elevations could cause similar problems for altitudinal migrants in the United States. However, many species have advanced their breeding season to match changes in insect or vegetation phenology associated with warming trends in the latter half of the twentieth century (McCleery and Perrins 1998, Brown et al. 1999, Crick and Sparks 1999, Dunn and Winkler 1999). Also, the positive relationships between capture rates of certain species and species groups and PDO (while controlling for annual trends) suggests that a positive PDO is generally favorable for western songbirds.

CONCLUSION

Our results make apparent the environmental and methodological challenges to interpretation of monitoring data from one site using one method. We advocate combining several count methodologies at migration monitoring stations so that impacts to the effectiveness of any one methodology can be better understood. For example, a system using radar counts combined with flight-call recordings (Millikin 2001, Hobson et al. 2002), standardized area searches (Ralph et al. 1993), and mist netting should be fairly robust to problems with any single sampling methodology. Replication of sampling at multiple stations using similar methodologies within a region would be extremely helpful in clarifying results, provided the sampling protocols were comparable (Dunn and Hussell 1995, Johnson 2002).

While alternative explanations exist, it remains likely that many of the observed species declines are real and thus of conservation concern, replicating declines reported elsewhere in North America. As in other studies, it is uncertain which breeding or wintering subpopulations were impacted. By identifying periods of peak captures for each species we have partitioned the data, particularly for migrants, so that the migratory species data presented here likely represent populations breeding away from the study area. However, many of these species are common breeders throughout the Pacific Northwest. For these reasons it is difficult to evaluate to what extent trends reflected factors on or near the study area and over a much wider area. This issue could be addressed further by using molecular-genetic markers or chemical isotope lev-

els from feather samples, both of which have been used with some success in other songbird populations (Webster et al. 2002).

Results were less equivocal for several species, and therefore we recommend raising their conservation and research priority. For Warbling Vireo (see also Gardali and Jaramillo 2001), Chestnut-backed Chickadee, and White-crowned Sparrow, trends from Palomarin matched BBS trends for California, but not for the larger region, suggesting that California populations, in particular, are declining. For Red-breasted Sapsucker, Bushtit, Brown Creeper, Orange-crowned Warbler, Yellow Warbler, Wilson's Warbler, and Pine Siskin, Palomarin trends reflected BBS trends at a much larger, regional scale, and in some cases at the California level as well, indicating a widespread phenomenon. We encourage investigations of potential factors limiting these species, especially on their breeding grounds.

Robbins et al. (1989), using BBS data, and Hussell et al. (1992), using spring and fall migration data, both reported abrupt changes in trend directions for eastern populations beginning in 1978. Hussell et al. (1992) concluded that fluctuations likely represented normal population dynamics, possibly linked to variability in food availability on the breeding grounds and undescribed climate changes. Since then, climatologists have identified a major PDO shift (from negative to positive) occurring in 1977, and more recent PDO shifts from positive to negative for 1989–1991 and more tentatively for 1998–1999 (Hare and Mantua 2000, Mantua and Hare 2002). These shifts may be linked to stepwise changes in bird population trajectories, the direction of which would depend on species' responses to associated weather variables on their breeding or wintering grounds. Clearly, to take long-term climate cycles into account, datasets spanning at least two decades from multiple locations are necessary. We encourage investigators to consider climate regime shifts when conducting trend analyses, and to consider that the relationships between the Pacific Decadal Oscillation and regional temperatures and precipitation are generally inverse between western and eastern North America (Mantua and Hare 2002).

ACKNOWLEDGMENTS

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