Declines in Yosemite's Bird Populations

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Introduction

Birds are sensitive indicators of environmental change in terrestrial ecosystems (Hutto 1998). Long-term monitoring programs, such as the Breeding Bird Survey and the Christmas Bird Count, provide invaluable data on spatial and temporal changes in bird abundances and population trends. However, population-trend data on Neotropical migrant birds, while suggesting alarming declines in some species, provide no information on primary demographic parameters (productivity and survivorship). Without demographic information, population-trend data alone provide no means for determining at what point(s) in the life cycles problems are occurring, or to what extent population trends are driven by causal factors that affect birth rates, death rates, or both (DeSante 1995). The lack of such information for migratory birds in particular is an obstacle to effective conservation actions, as it leaves unresolved whether critical problems that drive population declines are occurring primarily on temperate breeding grounds, during migration, or on distant tropical wintering grounds.

The Monitoring Avian Productivity and Survivorship (MAPS) program was established in 1989 by The Institute for Bird Populations to provide long-term demographic data on birds to aid in identifying the causal factors driving population trends (DeSante et al. 1995). In 1990, the MAPS program was established in Yosemite National Park, and Yosemite now hosts some of the longest-running MAPS stations in the country. Yosemite's MAPS stations provide reference points for assessing the effects of land use and land cover changes on bird populations throughout the larger geographic area (Silsbee and Peterson 1991). These changes may result from regional activities such as land conversion and forest management, or from broader-scale processes such as climate change. Monitoring vital rates and population trends at 'control' sites in national parks is especially important because the parks are among the few sites in the United States where population trends due to large-scale regional or global change patterns are relatively unconfounded with local changes in land-use practices (Simons et al. 1999).

In Yosemite National Park, the MAPS stations target 25 species, including Neotropical-wintering migrants, temperate-wintering migrants, and permanent residents. Using MAPS data, the objectives of this study were (1) to determine if bird populations have changed significantly in Yosemite since the establishment of the Yosemite MAPS stations, (2) to identify proximate demographic causes of those population changes, and (3) to investigate how climate change may be affecting bird population dynamics by examining possible upslope shifts in one group of closely related species.

Methods

We operated five MAPS stations in Yosemite National Park at the same locations each year (Figure 1). The five MAPS stations, located along an elevation gradient in wet montane meadow surrounded primarily by conifer forest (except for Big Meadow which is located in riparian willows and mixed conifer forest that was largely consumed by a stand-replacing fire in 1990) from highest to lowest, were the following: (1) White Wolf Meadow, 2,402 m elevation; (2) Gin Flat Meadow, 2,073 m elevation; (3) Crane Flat Meadow, 1,875 m elevation; (4) Hodgdon Meadow, 1,408 m elevation; and (5) Big Meadow, 1,311 m elevation (Figure 1). The Hodgdon Meadow station was established in 1990, followed by White Wolf, Crane Flat, and Big Meadow in 1993, and Gin Flat Meadow in 1998. Station operation and data collection followed standard MAPS protocol (DeSante et al. 2008).

We identified 25 target species with adequate sample sizes for estimating adult population size, productivity, and survivorship. For each target species and for all species pooled, we examined 16-year trends in adult population size and productivity using data from all five

Figure 1. Locations of five Monitoring Avian Productivity and Survivorship (MAPS) stations in Yosemite National Park, California.

stations combined. For trends in population size, we first calculated adult population indices for each species for each of the 16 years, based on an arbitrary starting index of 1.0 in the first year of station operation or analysis. Year-to-year changes were used to calculate chain indices in each subsequent year by multiplying the proportional change between the two years times the index of the previous year, and adding that figure to the index of the previous year. We then used linear regression to determine the slope of these indices over time. Trends in productivity were calculated in an analogous manner by starting with actual productivity values in 1993 and calculating each successive year's value based on the constant-effort changes in productivity between each pair of consecutive years. For a more detailed explanation of trend analyses, see Pyle et al. (2006).

For each target species, we also calculated annual apparent survival rates of adult birds using modified Cormack-Jolly-Seber (CJS) mark-recapture analyses (Lebreton et al. 1992). These analyses were based only on capture records from the 14-year period 1993–2006. Using the computer program TMSURVIV (Hines, Kendall, and Nichols 2003), we calculated, for each target species, maximum-likelihood estimates and standard errors for adult survival probability, adult recapture probability, and the proportion of residents among newly captured adults using a between- and within-year transient model (Pradel et al. 1997; Hines, Kendall, and Nichols 2003). For a more detailed explanation of survivorship calculations, see Pyle et al. (2006).

In bird species, both productivity and survival vary with body mass: on average, the larger the bird species the lower the annual productivity and the higher the annual survival. To assess whether or not productivity and survival of a given species at Yosemite was as expected, lower than expected, or higher than expected based on its body mass, we regressed productivity indices and survival-rate estimates against body mass (log transformed to normalize the values) for all target species, and compared productivity indices and survival-rate estimates for individual species to the regression lines produced by these fits. We also compared productivity indices and survival estimates for each target species at Yosemite with values obtained from the Northwestern MAPS region as a whole (www.birdpop.org/nbii/NBIIHome.asp).

To investigate the possible role of climate change-driven elevation shifts in driving observed population changes, we focused on *Empidonax* flycatchers, a suite of closely related species in which population changes appear to have been substantial. For dusky flycatcher, willow flycatcher (*Empidonax traillii)*, Hammond's flycatcher (*Empidonax hammondii)*, and Pacific-slope flycatcher (*Empidonax difficilis)*, we assessed trends in demographic parameters at higher- versus lower-elevation MAPS stations, and examined how the abundance of each species relative to one another changed over time at each station.

Results

Populations of 12 species as well as all species pooled showed substantial declining trends ($r \leq -.3$ for a 16-year trend) (Table 1; all tests used $p < .05$ for statistical significance). The declines for golden-crowned kinglet, hermit warbler, chipping sparrow, and lazuli bunting were highly significant; those for western wood-pewee, dusky flycatcher, yellow warbler, dark-eyed junco, and purple finch were significant; that of warbling vireo and black-headed grosbeak were nearly significant, and those of hermit thrush and all species pooled were not significant. In contrast, populations of only five species showed substantial increasing trends ($r \geq .3$), which were highly significant for mountain chickadee, MacGillivray's warbler, and western tanager, and nearly significant for yellow-rumped warbler and song sparrow. Populations of the remaining eight target species showed non-substantial (absolute $r < .3$) trends. The trend for all species pooled is decreasing at a rate of –.9% per year, suggesting that total populations of landbirds in Yosemite have declined by 14.5% over the 16-year period (1993–2008).

For the same 25 target species, five species showed substantially declining productivity trends ($r \leq -.30$), which were highly significant for lesser goldfinch, significant for hermit thrush, marginally significant for Hammond's flycatcher and MacGillivray's warbler, and not significant for western wood-pewee. In contrast, 11 species as well as all species pooled showed substantially increasing productivity trends ($r \geq .30$). Overall, 15 of the 25 target species had positive productivity trends and ten had negative productivity trends. The productivity trend for all species pooled indicated an average annual increase of .027 per year.

Using 14 years of data (1993–2006) from all five stations, we obtained estimates of adult survival and recapture probabilities for 31 breeding species, including the 25 target species. Estimates of annual adult survival rate ranged from a low of .176 for golden-crowned kinglet to a high of .896 for Cassin's finch (*Carpodacus cassinii)*, with a mean of .485. Recapture probability varied from a low of .005 for Cassin's finch to a high of .678 for black phoebe (*Sayornis nigricans)*, with a mean of .263.

Empidonax flycatcher population dynamics changed at each station during the 14-year period 1993–2006 (nine-year period, 1998–2006, at Gin Flat Meadow) (Figure 2). Willow flycatcher has clearly declined in the Yosemite region as a whole, with a regression on adults per 600 net hours at all five stations combined indicating a significant decline ($r = -.735$, $p =$

Table 1. Assessment of vital rates for 18 species showing substantially decreasing or increasing 16-year (1993–2008) population trends at five long-running stations in Yosemite National Park.

Species	Trend and Significance[1]	Productivity	Survival Probability[2]
A. Decreasing Species			
Western Wood-Pewee (*Contopus sordidulus*)	- 3.8 **	slightly low	high
Dusky Flycatcher (*Empidonax oberholseri*)	- 3.2 **	low	slightly low
Warbling Vireo (*Vireo gilvus*)	- 1.5 *	low	expected
Golden-crowned Kinglet (*Regulus satrapa*)	- 6.1 ***	high, increasing	low/high
Hermit Thrush (*Catharus guttatus*)	- 2.7	slightly low	slightly low
Yellow Warbler (*Dendroica petechia*)	- 4.0 **	slightly low, increasing	high/as expected
Hermit Warbler (*Dendroica occidentalis*)	- 4.1 ***	high	high/as expected
Chipping Sparrow (*Spizella passerina*)	- 5.0 ***	low	as expected/high
Dark-eyed Junco (*Junco hyemalis*)	- 1.7 **	slightly high	as expected
Black-headed Grosbeak (*Pheucticus melanocephalus*)	- 3.0 *	slightly high, increasing	as expected
Lazuli Bunting (*Passerina amoena*)	- 6.8 ***	slightly low, increasing	high
Purple Finch (*Carpodacus purpureus*)	- 4.3 **	slightly high, increasing	unknown
B. Increasing Species			
Mountain Chickadee (*Poecile gambeli*)	20.6 ***	as expected, increasing	low
Yellow-rumped Warbler (*Dendroica coronata*)	5.5 *	slightly high	slightly low/low
MacGillivray's Warbler (*Oporornis tolmiei*)	8.3 ***	as expected, decreasing	slightly high/as expected
Song Sparrow (*Melospiza melodia*)	2.9 *	slightly high	unknown
Western Tanager (*Piranga ludoviciana*)	10.3 ***	as expected	high

[1] Significance of the declines in numbers of adults captured (*** $P < 0.01$, ** $0.01 \leq P < 0.05$, * $0.05 \leq P < 0.10$)

[2] Survival assessments are based on two comparisons: (1) with the expected value for the species based on body mass and (2) with survival in the Northwestern Maps region as a whole. When only one assessment is given it indicates that both of these comparisons coincided.

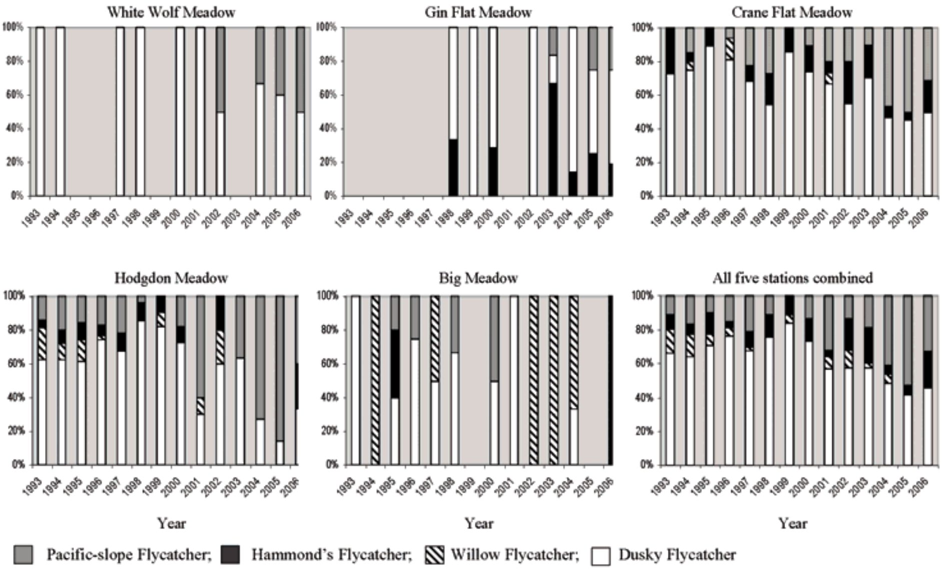

Figure 2. Proportion of the catch of adult *Empidonax* flycatchers comprised by each *Empidonax* species at five MAPS stations in Yosemite National Park, and at all five stations pooled, over the 14 years 1993–2006.

.003). Although still commonly encountered throughout the park, dusky flycatcher has also declined significantly at the Yosemite MAPS stations (r = -.810, p < .001), with the declines most prominent at the lower elevation stations, Hodgdon Meadow (r = –.918, p < .001) and Big Meadow (r = –.472, p = .089). A non-significant decline in Dusky Flycatcher was also noted at Crane Flat (r = –.411, p = .144), whereas at the two higher elevation stations, Gin Flat and White Wolf Meadows, populations show non-significant increases.

For Pacific-slope flycatcher, populations pooled across all stations have increased slightly (r = .353, p = .216), but examination of station-specific trends suggests up-slope shifts: populations have declined non-significantly at the lower elevation stations (Big Meadow and Hodgdon Meadow where the species has historically occurred in greater abundance than at the higher stations), whereas they have increased significantly at all three higher-elevation stations, Crane Flat (r = .675, p = .008), Gin Flat Meadow (r = .735, p = .037), and White Wolf (r = .756, p = .002). Likewise, although no population trends were significant for Hammond's flycatcher, populations have declined at the two lower-elevation stations (Big Meadow and Hodgdon Meadow), and have increased at the two higher-elevation stations where the species is captured, Crane Flat and Gin Flat Meadow.

Discussion

Populations of adult birds of all species pooled at MAPS stations in Yosemite have shown a substantial decrease of –.9% per year from 1993–2008. While this may not seem to be a large annual decline, when compounded over 16 years it represents a 14.5% decline. Sixteen-year population trends were negative at all four long-running stations, with 12 of 25 target species showing declines. In contrast, populations of only five species showed substantial 16-year increasing trends. Comparison of long-term population trends at Yosemite with long-term BBS trends from the Sierra Nevada physiographic strata and MAPS results from elsewhere in the Sierra suggests that population trends of most declining species at Yosemite are part of a broader Sierra-wide decline (DeSante, Pyle, and Kaschube 2005; Siegel and Kaschube 2007).

The estimated annual adult survival rates at Yosemite (calculated only for the period 1993–2006) appear to be relatively high compared with values for the Northwestern MAPS region as a whole (1992–2001; see www.birdpop.org/nbii/surv/default.asp). Estimates are higher than those of the Northwest Region for 20 of 29 species for which this comparison could be made, with a mean annual adult survival rate at Yosemite (.485) that was 3.0% higher than that of the Northwest Region (.471). In addition, DeSante et al. (2005) found that 11 of 17 species showed higher survival at Hodgdon Meadow than at equivalent elevations in Kings Canyon National Park. This suggests that survival of birds breeding at Yosemite is relatively high, overall.

Productivity on the breeding grounds appears to drive population declines or increases in Yosemite more than annual adult survival. We found that lower-than-expected productivity appears to be driving or contributing to the population declines of seven of the 12 declining species, whereas lower-than-expected survivorship appears only to be affecting the declines of one species (Table 1). Similarly, it appears that higher than expected or increasing productivity may be driving the population changes of three increasing species, whereas higher survival may be contributing to increases in two species (Table 1). Thus, overall, it appears that productivity at Yosemite is driving or influencing the population dynamics of ten of the 17 species showing substantial trends. Productivity is presumably affected by events on the breeding ground, thus declines in these species could be within the Park's ability to influence, through stewardship and/or management action.

Willow and dusky flycatchers are clearly declining in the Yosemite region as a whole. For dusky flycatcher, declines are most noticeable and significant at the lower elevation stations (Hodgdon Meadow and Big Meadow) and they are slight and non-significant at the mid-elevation Crane Flat station, whereas at the two higher elevation stations, Gin Flat and White Wolf, we see no evidence of declines. A similar pattern (though non-significant) is apparent for Hammond's flycatcher. For Pacific-slope flycatcher, populations have declined non-significantly at the lower elevation stations where the species has historically been more abundant than at the higher stations; and they have increased significantly at all three higher-elevation stations. Thus, populations of the three more-abundant *Empidonax* flycatcher species appear to be shifting upslope. For Hammond's and Pacific-slope flycatcher, this could suggest that ranges are actually extending up into higher elevations than in previous years. However, for dusky flycatcher, which already nests up to tree-line in the park, our results may indicate the beginning of a contraction in the species' range (with the low-elevation boundary moving upslope), rather than an expansion of the upslope boundary of the range.

If confirmed by more spatially extensive data collection, these upslope shifts are consistent with recent evidence suggesting upslope shifts of other montane taxa throughout North America, associated with global warming (e.g., Parmesan and Yohe 2003; Moritz et al.

2008). Furthermore, they may be bellwethers for more extensive changes in the elevational distribution of Yosemite's landbirds. The recent extirpation of Yosemite's breeding willow flycatchers (Siegel, Wilkerson, and DeSante 2008) and the park's declining bird populations associated with low productivity attest to the potential vulnerability of bird populations even in relatively pristine environments like Yosemite.

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