

Assessing Landbird Monitoring Programs and Demographic Causes of Population Trends

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ABSTRACT Population trend data from the North American Breeding Bird Survey (BBS) have been used to identify conservation priorities and justify major conservation initiatives. Yet the BBS has been criticized for potential habitat bias and reliance on abundance indices to estimate trends. We compared 1992–2003 BBS trend estimates to trend estimates derived from bird-banding data collected as part of the Monitoring Avian Productivity and Survivorship (MAPS) program for 36 wood warbler species. Similarity in trends between the 2 monitoring programs at the survey-wide and program-wide scales suggested that each program can provide accurate trend information. The MAPS program, however, was designed primarily to complement (rather than duplicate) count-based efforts, such as the BBS, by providing estimates or indices of demographic rates. Demographic data from MAPS can be used to lend insight into proximate (demographic) causes of population trends and inform management. We illustrate this with analyses of 1992–2003 MAPS data for yellow warbler (*Dendroica petechia*). We used reverse-time capture–recapture models to evaluate importance of new recruits (including immigrating adults and young from the previous year) relative to surviving adults in explaining variation in trend among BBS physiographic strata. We included the number of young per adult captured (an index of productivity) as a covariate in models to assess effects of productivity on trends. Survival was the key demographic driver of recent population trends. Comparison of MAPS productivity indices and adult apparent survival rate estimates to BBS trend estimates largely confirmed this inference. We suggest that increased MAPS coverage, better coordination between MAPS and the BBS, and continued development of analytical methods that link the 2 programs will enhance the value of these monitoring efforts to land managers and conservation planners working at a variety of spatial scales. (JOURNAL OF WILDLIFE MANAGEMENT 72(8):1665–1673; 2008)

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Birds are sensitive indicators of environmental quality and ecosystem health and are the focus of broad-scale volunteer-based monitoring efforts such as the North American Breeding Bird Survey (BBS; Morrison 1986, Hutto 1998). The BBS utilizes count data collected at randomly selected roadside survey routes to provide information on spatial and temporal variation in abundance and population trend for approximately 420 bird species (Robbins et al. 1986). Trend estimates from the BBS have been central to establishing major conservation initiatives (e.g., Partners in Flight; Finch and Stangel 1993) and setting research, conservation, and management priorities for landbirds (Rich et al. 2004). Yet the validity of BBS data have been questioned due to sampling focused on roadside habitats (Droege 1990, Bart et al. 1995, Keller and Scallan 1999) and inability to estimate detection probabilities under the current BBS sampling design (Pollock et al. 2002).

Abundance and trend, even when estimated accurately and precisely, are not always the best metrics for guiding management and conservation (Van Horne 1983, DeSante and Rosenberg 1998, Nichols and Williams 2006). Source–sink dynamics and ecological traps could result in high abundance in low-quality habitats (Pulliam 1988, Donovan et al. 1995, Donovan and Thompson 2001, Schlaepfer et al. 2002, Bock and Jones 2004). Territorial exclusion by dominant individuals could lead to aggregation of subordinates in low-quality habitats (Fretwell and Lucas 1970). The link between abundance and habitat quality in

migratory species may be further obscured by limiting factors acting at times other than when abundance is measured (e.g., limitation on wintering grounds but abundance measured on breeding grounds; Marra et al. 1998, Nott et al. 2002).

Effective management of habitats and conservation of bird populations would be facilitated by monitoring demographic rates (i.e., reproduction, recruitment, survival) in addition to abundance and trend (DeSante et al. 2005a). Advantages of demographic monitoring are manifold. First, demographic monitoring emphasizes processes, rather than the resulting patterns. Because it is the process (demographic rate), not the pattern (abundance), that is directly affected by environmental factors (e.g., stressors or management actions), changes in vital rates will more accurately and sensitively reflect short-term and local environmental change (Temple and Wiens 1989, DeSante and George 1994). Information on demographic rates can lend insight into stages of the life cycle that are most important for limiting bird populations, particularly for migratory species (Sherry and Holmes 1995, Green 1999, Peach et al. 1999, DeSante et al. 2001). Finally, demographic rates can be modeled as functions of environmental variables (e.g., land uses, habitat, climate; DeSante et al. 2005a), and these relationships can be incorporated into predictive population models to assess the viability of populations (Noon and Sauer 1992).

Application of standardized constant-effort mist netting and modern capture–recapture analytical techniques can be

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an effective means of monitoring demographic rates of many landbird species (Pollock et al. 1990, Lebreton et al. 1992, DeSante et al. 2004, Peach et al. 2004). Such an effort was initiated in North America by The Institute for Bird Populations (IBP) in 1989 with the establishment of the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante 1992). The MAPS program currently consists of nearly 500 monitoring stations sampled annually (see DeSante et al. 2004, 2007 for details of field methods); many of these stations (227, or nearly 25% of all stations that have ever registered with the program) have been operated for ≥ 10 years. Although it is difficult to use a strictly probabilistic sampling strategy to select sites for establishment of MAPS stations, some element of randomness can be maintained in most cases. Approximately 80% of MAPS stations are operated by independent bird banders (i.e., trained citizens), governmental agencies, or non-governmental organizations. Remaining stations are operated by biologists and interns recruited and trained by IBP (Burton and DeSante 1999).

The MAPS program provides estimates of adult apparent survival and recruitment rates and indices of productivity for about 150 landbird species (DeSante et al. 1995, 2004). Other population metrics, including indices and estimates of population size and trend, can also be derived from MAPS data (Pollock et al. 1990, Silkey et al. 1999, Williams et al. 2002, Dunn and Ralph 2004). Although MAPS can provide information on abundance and trend, it was designed principally to complement count-based efforts such as the BBS by providing information on demographic rates. Our objectives here are to 1) assess the ability of MAPS and the BBS to provide accurate information on landbird population trends at survey-wide (BBS)–program-wide (MAPS) scales; and 2) provide an example of how MAPS alone, and in combination with the BBS, can lend insight into proximate (demographic) causes of population change.

METHODS

Comparison of BBS and MAPS Trends

To compare BBS and MAPS survey-wide and program-wide population trends, we estimated 1992–2003 trends for wood-warblers (Parulidae) from data collected as part of each program. We included 34 species and 2 subspecies groups (Audubon's warbler [*Dendroica coronata auduboni*] and myrtle warbler [*D. coronata coronata*]), which represented all taxa for which we could obtain estimates from both programs.

We took a Bayesian hierarchical approach to estimating trends, which enabled us to minimize effects of sampling variances on individual species trend estimates (Link and Sauer 1996, Sauer and Link 2002). We used estimating equations BBS trends and variances from the BBS website as our initial (i.e., non-Bayes) estimates of BBS trends and variances (Link and Sauer 1994, Sauer et al. 2005). We estimated initial time-constant population growth rates (λ) and variances from MAPS data using reverse-time capture–recapture models (Pradel 1996). We implemented models

with the survival and lambda option in Program MARK (White and Burnham 1999). For each species, we only included MAPS data from stations where the species was known, or strongly suspected, to be a usual breeder (i.e., stations where it was listed as a probable or confirmed breeder in $>50\%$ of the years the station was operated) and from stations that were operated ≥ 4 years. We set recapture probabilities to zero whenever years were missed or stations stopped operating prior to 2003. We considered 8 models for each species, including all combinations of time-varying and time-constant adult apparent survival rate (ϕ) and recapture probability (p); we also considered models allowing p to vary by station or as a linear function of station-specific mean within-season capture rate of individuals (Julliard 2004). We calculated model-averaged time-constant program-wide population growth rates (and estimates of SEs) based on Akaike's Information Criterion (AIC_c) model weights (Burnham and Anderson 2002). To facilitate direct comparison of BBS and MAPS data, we converted MAPS estimates of λ to trend estimates (% change/yr) using the formula $\text{trend} = 100 \times (\lambda - 1)$. We converted variances of $\hat{\lambda}$ to trend variances using the delta method (Williams et al. 2002).

We incorporated initial trend estimates and variances into 2 separate hierarchical models (one for MAPS, the other for BBS) following Sauer and Link (2002). For each data set, we specified sampling distributions for initial population trend estimates, $\hat{\beta}_s$, as normal with mean β_s and variance σ_s^2 , where $s = 1, 2, \dots, 34$ warbler species. We modeled trend variance estimates $\hat{\sigma}_s^2$ as multiples of a chi-squared distribution with v_s degrees of freedom. Multipliers for this chi-squared distribution were σ_s^2/v_s . We set v_s equal to the number of BBS routes (for the BBS model) or the number of MAPS stations (for the MAPS model) sampled. We assumed species trends (i.e., β_s) to be normally distributed (representing trends for warblers) with hyperparameters μ and τ^2 . We specified noninformative prior distributions for each parameter and hyperparameter (diffuse normal for β_s and μ ; flat inverse gamma for σ_s^2 and τ^2).

We obtained posterior distributions for parameters and hyperparameters by sampling full conditional distributions (full conditionals for our models are defined in Sauer and Link 2002, appendix A) using Markov chain Monte Carlo (MCMC) methods (Gilks et al. 1996), as implemented in WinBUGS (Spiegelhalter et al. 2003). Following Sauer and Link (2002), we denote Bayes trend estimates as β_s^B . We used a burn-in of 5,000 observations; we based posterior distributions on the subsequent 100,000 observations.

We examined the relationship between BBS and MAPS trends by calculating Pearson's correlation coefficients (denoted as r_B) between trend estimates from BBS and MAPS trend at each iteration of the MCMC simulation. We inferred the mean and 95% credible interval for r_B from the distribution of correlation coefficients. We also report standard Pearson's correlation between posterior trend mean estimates. In addition, we calculated the median number of increasing species, N_{inc}^B and 95% credible interval from posterior trend distributions for each program.

Linking Trends to Demographic Rates

To link population change and important demographic rates, we considered spatial variation in trend and demographic parameters at the scale of BBS physiographic strata (Droege and Sauer 1989). We focused on one wood warbler species, yellow warbler (*D. petechia*), which had broad geographic coverage by both the BBS and MAPS (it had the largest number of captures among wood warblers in the MAPS data base). We excluded strata with <14 BBS routes sampled or that had a mean detection rate of <1.0 birds/route (following criteria for the highest BBS trend credibility measure; Sauer et al. 2005). In addition, we excluded strata with <3 MAPS stations with a mean number of years of operation of <5 years/station and strata with <120 adult captures (i.e., 10 birds/yr for the 12-yr period). We only included data from MAPS stations where yellow warblers were usual breeders (defined above) and that operated for ≥ 4 years (with effort spanning the breeding season).

We used 2 approaches to link demographic rates and population trends. First, we applied reverse-time capture-recapture methods (Pradel 1996) to MAPS capture-recapture data. We considered 9 model parameterizations (3 parameterizations of $\phi \times 3$ parameterizations of $\lambda \times$ one parameterization of p). We modeled p as station specific (p_{sta}) because no other parameterization of p (i.e., p as constant across stations or as a function of within-season capture rate of individuals) was supported in our initial range-wide analyses for this species (see above). We modeled ϕ and λ as either constant across strata (ϕ , λ) or strata specific (ϕ_{strata} , λ_{strata}), or as linear functions of the strata-specific MAPS reproductive index (RI_{strata} ; ϕ_{RI} , λ_{RI}), where RI_{strata} is the proportion of young to adult birds in the constant-effort catch averaged across years.

We calculated model-averaged time-constant estimates of ϕ_{strata} and λ_{strata} (and their SEs) based on AIC_c model weights (Burnham and Anderson 2002). We also estimated recruitment rates, f_{strata} ($\hat{\lambda}_{strata} - \hat{\phi}_{strata}$) and seniority parameters γ_{strata} ($\hat{\phi}_{strata}/\hat{\lambda}_{strata}$) and their variances (using the delta method; Williams et al. 2002).

We inferred relative contributions of adult apparent survival rate, productivity, and first-year survival-recruitment to strata-specific population trends based on 1) magnitude of $\hat{\gamma}_{strata}$ and its complement $1 - \hat{\gamma}_{strata}$ (Nichols et al. 2000, Nichols and Hines 2002), 2) levels of statistical support for the various models, 3) direction and significance of the linear relationship between RI_{strata} and $\hat{\lambda}_{strata}$ (Nichols et al. 2005), and 4) magnitude and direction of correlations between estimates of the various parameters (Julliard 2004).

We expected that if strata-scale population trends for this species were determined primarily by adult survival rates, we would find high values of $\hat{\gamma}_{strata}$ (relative to $1 - \hat{\gamma}_{strata}$), strong statistical support (in terms of AIC_c wt) for the model in which both ϕ and λ were constrained to vary as a function of strata (spatial variation in λ effected via ϕ) or the model in which ϕ and λ were modeled as constant across space (program-wide λ effected via survival), and positive correlation between $\hat{\phi}_{strata}$ and $\hat{\lambda}_{strata}$. If productivity was

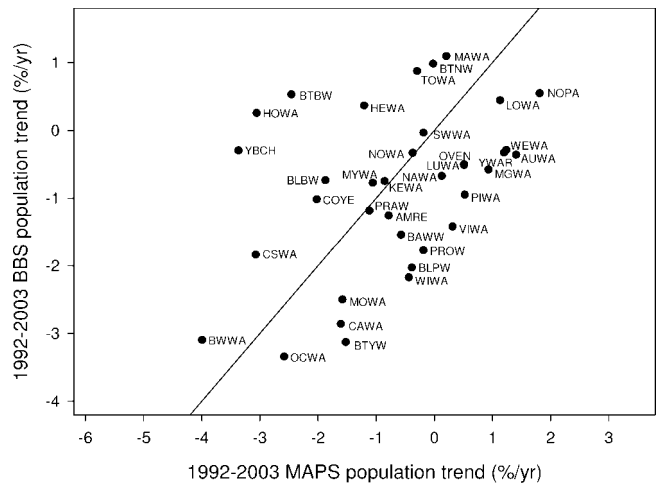


Figure 1. Scatterplot of program-wide Monitoring Avian Productivity and Survivorship (MAPS) and survey-wide North American Breeding Bird Survey (BBS) 1992–2003 Bayes population trend estimates. Four-letter species codes denote species identity (see Table 1). The reference line indicates a one-to-one relationship.

the most important demographic determinant of trends, we would expect low values of $\hat{\gamma}_{strata}$, strong statistical support for models in which λ_{strata} varies as a function of RI_{strata} and for models in which ϕ_{strata} varies independently of λ_{strata} , a weak relationship between ϕ_{strata} and λ_{strata} , and positive correlation between RI_{strata} and \hat{f}_{strata} and $\hat{\lambda}_{strata}$. Finally, we would infer support for recruitment-driven population change from specific combinations of support for the survival and productivity models. For example, high values of $1 - \hat{\gamma}_{strata}$, support for models where $\hat{\phi}_{strata}$ and $\hat{\lambda}_{strata}$ positively covary, positive correlation between \hat{f}_{strata} and $\hat{\lambda}_{strata}$, and positive correlation between \hat{f}_{strata} and RI_{strata} and little support for models where $\hat{\lambda}_{strata}$ is constrained to vary as a function of RI_{strata} would suggest recruitment limitation affected primarily by first-year survival.

As a second (visual) approach to identifying demographic drivers of population change, we compared spatial patterns in BBS population trend estimates and MAPS productivity indices and adult apparent survival rate estimates. By considering both MAPS and BBS data we took advantage of the particular strengths of each program (i.e., trend estimation from the BBS and vital rate information from MAPS). We obtained estimating equations (Link and Sauer 1994) 1992–2003 BBS trends from the BBS website (Sauer et al. 2005). To provide more realistic estimates of (time-constant) adult apparent survival, we used the ad hoc Robust Design transient model described by Nott and DeSante (2002) and Hines et al. (2003). This parameterization differs from the one used for the Pradel (1996) model described above in that it reduces (negative) bias associated with the presence of transient individuals in the data set (thus increasing the magnitude of survival-rate estimates).

RESULTS

MAPS and BBS population trends for the 36 warbler species were positively correlated (Fig. 1), although the 95%

Table 1. Bayes estimates of 1992–2003 population trends for wood-warblers (Parulidae). We derived trend estimates from North American Breeding Bird Survey (BBS) and Monitoring Avian Productivity and Survivorship (MAPS) data.

| Species | Code | BBS ^a | | | | MAPS ^b | | | | |
|--|------|------------------|-------------|------|-----------------------|-------------------|-----------|-------------|------|-----------------------|
| | | n_{rte} | β_i^B | SD | 95% credible interval | n_{sta} | n_{ind} | β_i^B | SD | 95% credible interval |
| Blue-winged warbler (<i>Vermivora pinus</i>) | BWWA | 343 | -3.10 | 0.70 | -4.49, -1.73 | 36 | 1129 | -3.99 | 1.59 | -7.15, -0.93 |
| Orange-crowned warbler (<i>V. celata</i>) | OCWA | 392 | -3.34 | 0.64 | -4.60, -2.09 | 73 | 4479 | -2.58 | 1.24 | -5.06, -0.18 |
| Nashville warbler (<i>V. ruficapilla</i>) | NAWA | 620 | -0.67 | 0.69 | -2.03, 0.68 | 34 | 1313 | 0.13 | 1.88 | -3.48, 3.93 |
| Virginia's warbler (<i>V. virginiae</i>) | VIWA | 84 | -1.42 | 1.20 | -3.84, 0.91 | 10 | 499 | 0.32 | 2.15 | -3.76, 4.80 |
| Lucy's warbler (<i>V. luciae</i>) | LUWA | 34 | -0.50 | 1.13 | -2.71, 1.74 | 7 | 382 | 0.51 | 1.70 | -2.87, 3.86 |
| Northern parula (<i>Parula americana</i>) | NOPA | 903 | 0.55 | 0.36 | -0.15, 1.25 | 44 | 476 | 1.81 | 1.42 | -0.92, 4.65 |
| Yellow warbler (<i>Dendroica petechia</i>) | YWAR | 2,066 | -0.33 | 0.24 | -0.79, 0.14 | 149 | 12099 | 1.20 | 0.37 | 0.48, 1.92 |
| Chestnut-sided warbler (<i>D. pensylvanica</i>) | CSWA | 709 | -1.84 | 0.41 | -2.65, -1.03 | 22 | 910 | -3.07 | 1.16 | -5.32, -0.77 |
| Magnolia warbler (<i>D. magnolia</i>) | MAWA | 458 | 1.10 | 0.57 | -0.01, 2.21 | 17 | 649 | 0.21 | 1.47 | -2.66, 3.12 |
| Black-throated blue warbler (<i>D. caerulescens</i>) | BTBW | 337 | 0.53 | 0.97 | -1.34, 2.48 | 7 | 134 | -2.46 | 2.14 | -6.89, 1.55 |
| Audubon's warbler (<i>D. coronata auduboni</i>) | AUWA | 471 | -0.36 | 0.44 | -1.22, 0.51 | 65 | 3788 | 1.41 | 0.65 | 0.13, 2.69 |
| Myrtle warbler (<i>D. coronata coronata</i>) | MYWA | 546 | -0.77 | 0.64 | -2.04, 0.49 | 33 | 1182 | -1.06 | 1.17 | -3.35, 1.25 |
| Black-throated gray warbler (<i>D. nigrescens</i>) | BTYW | 218 | -3.13 | 0.74 | -4.61, -1.68 | 20 | 174 | -1.52 | 1.75 | -5.04, 1.88 |
| Black-throated green warbler (<i>D. virens</i>) | BTNW | 573 | 0.98 | 0.55 | -0.08, 2.06 | 22 | 474 | -0.02 | 1.37 | -2.72, 2.67 |
| Townsend's warbler (<i>D. townsendi</i>) | TOWA | 171 | 0.87 | 0.80 | -0.68, 2.46 | 29 | 1191 | -0.29 | 1.08 | -2.42, 1.83 |
| Hermit warbler (<i>D. occidentalis</i>) | HEWA | 107 | 0.37 | 0.67 | -0.94, 1.69 | 33 | 1307 | -1.21 | 2.00 | -5.27, 2.65 |
| Blackburnian warbler (<i>D. fusca</i>) | BLBW | 393 | -0.74 | 0.65 | -2.00, 0.55 | 5 | 46 | -1.87 | 2.19 | -6.44, 2.28 |
| Pine warbler (<i>D. pinus</i>) | PIWA | 787 | -0.95 | 0.44 | -1.80, -0.10 | 31 | 236 | 0.53 | 1.78 | -2.89, 4.15 |
| Prairie warbler (<i>D. discolor</i>) | PRAW | 593 | -1.18 | 0.50 | -2.17, -0.2 | 27 | 674 | -1.12 | 1.67 | -4.45, 2.14 |
| Blackpoll warbler (<i>D. striata</i>) | BLPW | 44 | -2.03 | 1.37 | -4.84, 0.56 | 7 | 160 | -0.38 | 1.94 | -4.23, 3.47 |
| Black-and-white warbler (<i>Mniotilta varia</i>) | BAWW | 933 | -1.54 | 0.55 | -2.63, -0.45 | 85 | 1368 | -0.57 | 0.87 | -2.29, 1.15 |
| American redstart (<i>Setophaga ruticilla</i>) | AMRE | 1,030 | -1.26 | 0.40 | -2.03, -0.48 | 71 | 3930 | -0.78 | 0.51 | -1.79, 0.21 |
| Prothonotary warbler (<i>Protonotaria citrea</i>) | PROW | 306 | -1.77 | 0.63 | -3.02, -0.53 | 22 | 739 | -0.18 | 1.96 | -4.03, 3.76 |
| Worm-eating warbler (<i>Helminthos vermivorus</i>) | WEWA | 271 | -0.29 | 1.05 | -2.32, 1.80 | 32 | 927 | 1.24 | 1.04 | -0.83, 3.28 |
| Swainson's warbler (<i>Limnithlypis swainsonii</i>) | SWWA | 79 | -0.03 | 1.39 | -2.68, 2.81 | 8 | 150 | -0.18 | 1.99 | -4.07, 3.81 |
| Ovenbird (<i>Seiurus aurocapilla</i>) | OVEN | 1,197 | -0.51 | 0.24 | -0.99, -0.04 | 126 | 4688 | 0.51 | 0.45 | -0.37, 1.39 |
| Northern waterthrush (<i>S. noveboracensis</i>) | NOWA | 427 | -0.33 | 0.63 | -1.56, 0.90 | 23 | 625 | -0.37 | 1.84 | -3.99, 3.28 |
| Louisiana waterthrush (<i>S. motacilla</i>) | LOWA | 378 | 0.44 | 0.82 | -1.16, 2.08 | 37 | 683 | 1.14 | 1.21 | -1.24, 3.53 |
| Kentucky warbler (<i>Oporornis formosus</i>) | KEWA | 536 | -0.75 | 0.53 | -1.78, 0.29 | 62 | 2191 | -0.85 | 0.71 | -2.24, 0.54 |
| Mourning warbler (<i>O. philadelphia</i>) | MOWA | 435 | -2.50 | 0.57 | -3.62, -1.39 | 9 | 272 | -1.58 | 2.05 | -5.78, 2.35 |
| MacGillivray's warbler (<i>O. tolmiei</i>) | MGWA | 403 | -0.58 | 0.69 | -1.94, 0.79 | 101 | 7536 | 0.94 | 0.36 | 0.24, 1.64 |
| Common yellowthroat (<i>Geothlypis trichas</i>) | COYE | 2,505 | -1.02 | 0.18 | -1.37, -0.67 | 211 | 11337 | -2.02 | 0.29 | -2.59, -1.44 |
| Hooded warbler (<i>Wilsonia citrina</i>) | HOWA | 526 | 0.25 | 0.49 | -0.70, 1.21 | 51 | 1526 | -3.05 | 0.86 | -4.74, -1.38 |
| Wilson's warbler (<i>W. pusilla</i>) | WIWA | 369 | -2.17 | 0.71 | -3.57, -0.8 | 86 | 11339 | -0.44 | 1.43 | -3.25, 2.39 |
| Canada warbler (<i>W. canadensis</i>) | CAWA | 323 | -2.86 | 0.92 | -4.71, -1.09 | 12 | 389 | -1.61 | 2.04 | -5.82, 2.30 |
| Yellow-breasted chat (<i>Icteria virens</i>) | YBCH | 1,051 | -0.30 | 0.27 | -0.83, 0.24 | 77 | 3927 | -3.37 | 0.57 | -4.49, -2.23 |

^a No. of BBS routes surveyed (n_{rte}) and Bayes trends (β_i^B), SDs, and 95% credible intervals derived from BBS data.

^b Sample sizes and Bayes trends (β_i^B), SDs, and 95% credible intervals derived from MAPS data. Sample sizes are given for both the no. of MAPS stations (n_{sta}) and no. of individuals (n_{ind}). We combined stations <1 km apart. All stations were operated for ≥ 4 years.

credible interval did include zero ($r_B = 0.26$; 95% credible interval: $-0.02 \leq r_B \leq 0.51$). There were 3 conspicuous outliers: black-throated blue warbler (*D. caerulescens*), hooded warbler (*Wilsonia citrina*), and yellow-breasted chat (*Icteria virens*; Fig. 1). Excluding these improved the correlation somewhat ($r_B = 0.35$; 95% credible interval: $0.05 \leq r_B \leq 0.61$). We found even scatter around the one-to-one relationship (mean difference in trend estimates = 0.18) and broad overlap in 95% credible intervals for all species (Table 1), suggesting that both programs can provide accurate trend information. Indeed, lack of significant Bayesian correlation probably reflects imprecision of estimates (particularly MAPS estimates, for which credible intervals spanned BBS credible intervals in most [22] cases) rather than lack of a relationship, as suggested by significant standard correlation between the two ($r = 0.42$, $P = 0.01$ with all species included; $r = 0.64$, $P < 0.001$ with the 3 outliers excluded).

Mean warbler trend estimates were negative for both programs. The MAPS trend estimates tended to be higher than BBS trend estimates ($\mu^B = -0.686$ for MAPS v. $\mu^B = -0.866$ for BBS), although trend distributions overlapped greatly (MAPS 95% credible interval: $-1.65 \leq \mu^B \leq 0.26$; BBS 95% credible interval: $-1.41 \leq \mu^B \leq -0.32$). Similarly, the estimated median number of increasing species, N_{inc}^B , was also higher for MAPS than for the BBS (14 vs. 9), although again, credible intervals overlapped broadly ($9 \leq N_{inc}^B \leq 20$ for MAPS; $6 \leq N_{inc}^B \leq 13$ for BBS).

Reverse-time capture-recapture models of MAPS data suggested high variation among physiographic strata in average population change (λ) for yellow warblers (Table 2). Just 2 of 9 models accounted for 100% of the statistical support; both of these constrained λ to vary by strata.

Adult apparent survival rate appeared to be an important demographic driver of differences in population trend among strata. Estimated contributions of adult apparent

Table 2. Model-averaged estimates of population parameters and standard errors from reverse-time and transient capture–recapture models applied to Monitoring Avian Productivity and Survivorship (MAPS) data, mean MAPS reproductive index values and standard errors, and North American Breeding Bird Survey (BBS) trend estimates and standard errors for yellow warbler over 1992–2003 in 15 physiographic strata.

| Stratum | Reverse–time model ^c | | | | | | | | | | Transient model ^d | | BBS ^f | | | | |
|------------------------------|---------------------------------|------------------------|--------------------------|------|-----------------------|------|--------------------|------|-------------------------|------|------------------------------|------|-----------------------------------|------|-----------|------------------------|------|
| | n_{sta} ^a | n_{ind} ^b | $\hat{\lambda}_{strata}$ | SE | $\hat{\phi}_{strata}$ | SE | \hat{f}_{strata} | SE | $\hat{\gamma}_{strata}$ | SE | $\hat{\phi}_{strata}$ | SE | RI _{strata} ^e | SE | n_{rte} | $\hat{\beta}_{strata}$ | SE |
| Southern New England | 4 | 139 | 0.93 | 0.02 | 0.47 | 0.06 | 0.46 | 0.06 | 0.50 | 0.07 | 0.56 | 0.07 | 0.11 | 0.04 | 43 | 1.62 | 2.12 |
| Great Lakes Plain | 9 | 1,301 | 0.98 | 0.01 | 0.41 | 0.03 | 0.56 | 0.03 | 0.42 | 0.03 | 0.48 | 0.02 | 0.53 | 0.09 | 108 | 0.76 | 0.56 |
| St. Lawrence River Plain | 4 | 350 | 0.86 | 0.02 | 0.42 | 0.04 | 0.44 | 0.04 | 0.49 | 0.04 | 0.57 | 0.03 | 0.24 | 0.08 | 72 | −0.04 | 0.62 |
| Allegheny Plateau | 4 | 243 | 0.93 | 0.02 | 0.35 | 0.10 | 0.58 | 0.11 | 0.38 | 0.11 | 0.37 | 0.10 | 0.45 | 0.80 | 110 | −3.58* | 0.55 |
| Northern Spruce–Hardwoods | 4 | 181 | 1.08 | 0.02 | 0.38 | 0.08 | 0.70 | 0.09 | 0.35 | 0.08 | 0.38 | 0.06 | 0.52 | 0.14 | 240 | −2.21* | 0.79 |
| Aspen Parklands | 5 | 205 | 0.95 | 0.02 | 0.28 | 0.15 | 0.67 | 0.15 | 0.29 | 0.16 | 0.19 | 0.04 | 0.43 | 0.09 | 110 | 0.60 | 0.79 |
| Southern Rockies | 6 | 1,513 | 1.09 | 0.01 | 0.47 | 0.03 | 0.61 | 0.03 | 0.44 | 0.03 | 0.59 | 0.02 | 0.54 | 0.79 | 58 | 1.65 | 1.75 |
| Central Rockies | 8 | 468 | 1.09 | 0.02 | 0.45 | 0.03 | 0.65 | 0.03 | 0.41 | 0.03 | 0.56 | 0.03 | 0.28 | 0.81 | 107 | 0.16 | 0.68 |
| Dissected Rockies | 6 | 578 | 1.05 | 0.01 | 0.48 | 0.04 | 0.57 | 0.04 | 0.46 | 0.04 | 0.60 | 0.03 | 0.59 | 0.79 | 48 | −0.06 | 0.63 |
| Sierra Nevada | 9 | 636 | 0.99 | 0.01 | 0.44 | 0.02 | 0.55 | 0.02 | 0.45 | 0.02 | 0.55 | 0.03 | 0.48 | 0.07 | 20 | 1.90 | 4.48 |
| Cascade Mountains | 4 | 211 | 0.98 | 0.02 | 0.47 | 0.04 | 0.51 | 0.04 | 0.48 | 0.04 | 0.57 | 0.04 | 0.27 | 0.04 | 19 | −0.87 | 1.60 |
| Pitt-Klamath Plateau | 6 | 368 | 1.04 | 0.02 | 0.45 | 0.03 | 0.59 | 0.03 | 0.43 | 0.03 | 0.57 | 0.04 | 0.41 | 1.08 | 25 | −2.03 | 1.63 |
| Wyoming Basin | 3 | 918 | 1.04 | 0.01 | 0.48 | 0.03 | 0.57 | 0.04 | 0.46 | 0.03 | 0.59 | 0.02 | 0.21 | 1.28 | 28 | 4.29* | 2.07 |
| Basin and Range | 9 | 1,005 | 1.01 | 0.01 | 0.44 | 0.03 | 0.57 | 0.03 | 0.44 | 0.03 | 0.52 | 0.03 | 0.35 | 0.81 | 23 | 1.40 | 3.89 |
| Southern Pacific Rainforests | 10 | 758 | 1.05 | 0.01 | 0.46 | 0.03 | 0.59 | 0.03 | 0.44 | 0.02 | 0.56 | 0.03 | 0.29 | 0.04 | 38 | 0.93 | 2.03 |

^a No. of MAPS stations included in capture–recapture analyses. We combined stations <1 km apart. All stations were operated for ≥ 4 yr. For 4 strata (Southern New England, Aspen Parklands, Central Rockies, and Southern Pacific Rainforests), the no. of stations that actually contributed information for population change (and vital rate) estimation was 2 fewer than indicated here because of sparse recapture data and inestimable recapture probability at the station level.

^b No. of individual birds included in capture–recapture analysis. As indicated above, the actual no. of individuals contributing information to estimates was reduced in 4 strata. The actual no. of individuals was reduced by 47, 73, 44, and 15 for the Southern New England, Aspen Parklands, Central Rockies, and Southern Pacific Rainforests, respectively.

^c Reverse-time capture–recapture model is Pradel (1996) model. Parameters estimates include the time-constant (i.e., average) rate of population change ($\hat{\lambda}_{strata}$), (nontransient) ad apparent survival rate ($\hat{\phi}_{strata}$), recruitment rate (both young from previous yr and immigrating ad; \hat{f}_{strata}), and the relative contribution of ad apparent survival rate to the rate of population change ($\hat{\gamma}_{strata}$; the complement of this value [i.e., $1 - \hat{\gamma}_{strata}$] is the relative contribution of recruitment rate to the rate of population change).

^d Transient model refers to the ad hoc robust design model described in Hines et al. (2003); $\hat{\phi}_{strata}$ is the time-constant adult apparent survival-rate estimate.

^e Reproductive index, calculated as the mean ratio of young to ad birds captured at MAPS stations during constant-effort mist netting.

^f No. of BBS routes surveyed (n_{rte}) and estimating equations BBS trend estimate ($\hat{\beta}_{strata}$; from Sauer et al. 2005). Asterisks indicate statistically significant ($P < 0.05$) trend estimates.

survival to λ approached or equaled contributions of recruitment (mean $\hat{\gamma}_{strata} = 0.43$; Table 2). Additional evidence supporting the importance of adult apparent survival to population trend included 1) strong statistical support for the model with both ϕ and λ varying by strata (AIC_c wt = 0.61); 2) positive (albeit weak) correlation between estimates of adult apparent survival rate, $\hat{\phi}_{strata}$, and estimates of population growth rate $\hat{\lambda}_{strata}$ ($r = 0.35$, $n = 15$, $P = 0.20$); and 3) good correspondence between adult apparent survival rates estimated from the transient (ad hoc robust design) model and BBS population trends, especially for the 2 strata with statistically significant BBS population declines (Table 2; Fig. 2).

Recruitment of new individuals onto MAPS study areas, \hat{f}_{strata} , contributed even more to variation in population trend than did adult apparent survival rate (mean $1 - \hat{\gamma}_{strata} = 0.57$). The importance of new recruits was reinforced by strong correlation between \hat{f}_{strata} and $\hat{\lambda}_{strata}$ ($r = 0.67$, $n = 15$, $P < 0.01$). Note, however, that our measure of recruitment represents components of both productivity and survival (both first-year survival and survival of ad immigrating onto study areas). Although our index of productivity, RI_{strata}, was positively correlated with estimates of recruitment rate \hat{f}_{strata} ($r = 0.52$, $n = 15$, $P < 0.05$), productivity appeared to

have had little influence on population trend (summed AIC_c wt for models including RI_{strata} as a covariate = 0.00). Taken as a whole, variation in population change for yellow warblers among strata over this time period appears to have been largely effected via variation in survival rather than productivity.

DISCUSSION

We demonstrated that the BBS and MAPS can provide similar estimates of trend for many wood-warbler species at the survey-wide–program-wide scale, which is quite remarkable given differences in sampling design, gaps in geographic coverage, and methods. Although improvement of the BBS by sampling non-road-side habitats (Droege 1990, Bart et al. 1995, Keller and Scallan 1999) and estimating detection probabilities (Pollock et al. 2002, Simons et al. 2007) is clearly desirable, our results suggest that the current BBS provides estimates of trend that can be broadly useful for conservation. Concordance between the BBS and MAPS also suggests that MAPS data are representative of real populations despite distributions of stations that are not completely random.

Although our intention was not to specifically compare MAPS and BBS trend estimates at the physiographic strata

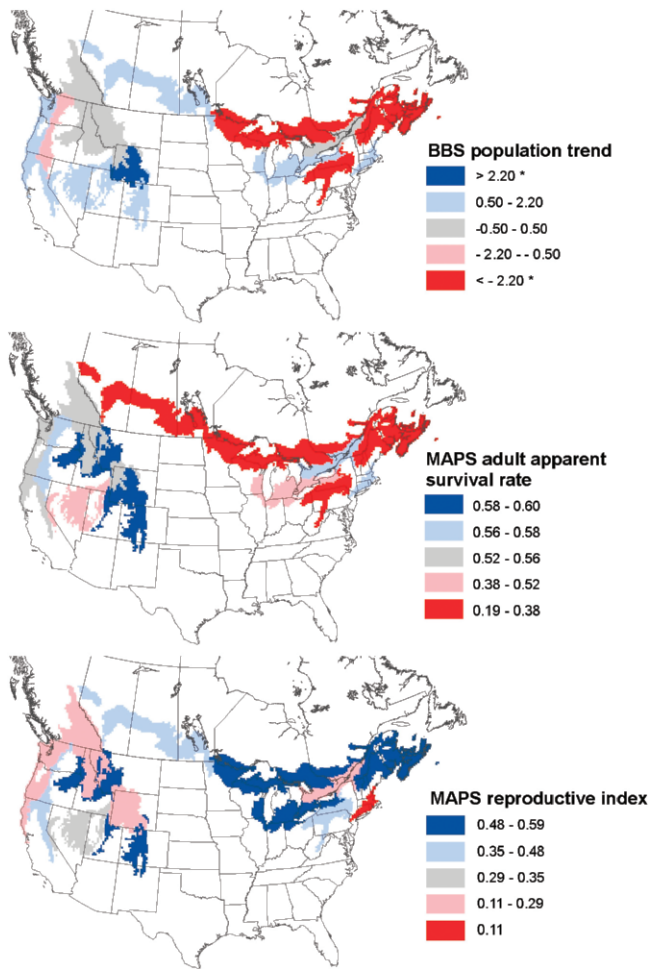


Figure 2. North American Breeding Bird Survey (BBS) population trend estimates, Monitoring Avian Productivity and Survivorship (MAPS) adult apparent survival-rate estimates (from transient model; Hines et al. 2003), and MAPS reproductive index (ratio of young to ad birds captured during constant-effort mist netting) for yellow warbler in 15 physiographic strata 1992–2003. Dark blue and red BBS trend classes denote statistically significant ($P < 0.05$) trends (blue = increasing; red = declining). We determined color divisions for MAPS data by Jenks' natural breaks.

scale, it is notable that strata-scale trend estimates for yellow warbler were quite different between MAPS and the BBS in many cases. The BBS trend estimates were less variable and more precise than the MAPS estimates of population change. Divergence between the 2 programs undoubtedly reflects differences in geographic coverage for this species at this spatial scale. For example, the largest differences in yellow warbler trend estimates were in strata with relatively poor MAPS coverage but extensive BBS coverage. Positive correlation between MAPS survival-rate estimates and BBS population trend estimates suggests that survival rates reflect broad-scale environmental conditions, whereas recruitment rates may reflect processes within local landscapes (e.g., source–sink dynamics). Greater MAPS coverage and better coordination between MAPS and the BBS within individual strata (or within similar regions of conservation interest; e.g., North American Bird Conservation Regions) would improve our ability to link information between the 2 programs.

Although knowledge of trends can be useful for identifying species or species groups in need of management or conservation action, they may not provide the best information for directing such efforts. Demographic monitoring can provide greater focus for directing research into where and what types of management are most likely to yield the greatest conservation benefit (DeSante and Rosenberg 1998, DeSante et al. 2005a). Demographic monitoring can provide land managers with information as to whether management should be directed at increasing survival rates or increasing productivity; distinguishing between these options is critical for migratory species because factors affecting productivity and survival may largely act at different times of the year and in distinct geographic areas.

Variation in adult apparent survival rate was an important determinant of differences in 1992–2003 yellow warbler population trends among physiographic strata. The MAPS capture–recapture analysis suggested that adult apparent survival contributed less to population trend than did recruitment (based on the magnitude of $\hat{\gamma}_{\text{strata}}$; Nichols et al. 2000); however, differences in the relative contributions of the two were not large, and the importance of survivors from study areas was undoubtedly underestimated because nonresident (i.e., transient) birds were not distinguished from breeding residents under the Pradel (1996) model. Furthermore, knowledge of the importance of new recruits is of relatively limited use because the recruitment parameter (f_{strata}) includes components of both productivity and survival (first-year survival and survival of adults that immigrate from outside the study area). We attempted to determine the relative importance of productivity in influencing yellow warbler population trends by including the RI from MAPS constant-effort mist netting as a covariate of λ_{strata} . We found no statistical support for models including the RI covariate, suggesting that the survival component of recruitment was more important in driving trends. First-year survival may be especially important because most recruits are second-year birds (D. F. DeSante, The Institute for Bird Populations, unpublished data).

It could be argued that RI might not accurately reflect productivity (Sauer and Link 2004). Available evidence suggests otherwise. For example, capture rates often compare favorably with count data and indices of productivity are often positively correlated with local or regional nest success (Bart et al. 1999, Dunn and Ralph 2004). Differences in RI among nesting migratory guilds are often consistent with differences expected from theory and nest monitoring data (DeSante 1999), and RI often correlates with weather and habitat variables in expected ways (Nott et al. 2002; M. P. Nott, The Institute for Bird Populations, unpublished report). Additional support comes from the strong positive relationship between $\text{RI}_{\text{strata}}$ and \hat{f}_{strata} for yellow warbler that we report here. Although further investigation into the relationship between reproductive indices from mist-netting data and other productivity

measures (e.g., estimates of nest success) is warranted, we suggest that sufficient evidence exists to be reasonably confident in the ecological significance of our RI.

Our comparison of MAPS survival-rate estimates (from models that account for the presence of transient individuals) and RIs to BBS estimates of population trend within 15 BBS physiographic strata largely confirmed the findings of our MAPS analysis. This comparison could be followed up with formal joint modeling of MAPS and BBS data (e.g., Thomas et al. 2005, Besbeas and Freeman 2006); however, the simple visual representation we presented provides a good exploratory view of spatial overlap between trends and vital rates. Although spatial correspondence between adult apparent survival-rate estimates and population trend estimates was not perfect, it was clearly better than the spatial correspondence between RI and population trend.

Although trends for yellow warbler were stable in most strata we considered (based on BBS data), we suggest that successful efforts to reverse declines in strata where they are declining will hinge on the identification of habitat characteristics that promote high survival rates. Mortality in long-distant migrants such as yellow warbler may largely occur during migration (Sillett and Holmes 2002); however, habitat conditions during premigratory periods, particularly late winter, may be critical (Sillett et al. 2000, Nott et al. 2002). We are currently investigating spatial variation in, and habitat correlates of, apparent overwintering survival rates of yellow warblers and other migratory bird species that winter in the northern Neotropics (DeSante et al. 2005*b*).

MANAGEMENT IMPLICATIONS

The MAPS program represents a viable cost-effective method for obtaining demographic monitoring data for landbird species that are easily captured in ground-level mist nets. Such data complement count-based data and can better inform management. Many species monitored with MAPS methodology are focal species or species of conservation concern in state Wildlife Action Plans, Partners in Flight Physiographic Area Plans, and descriptions of United States North American Bird Conservation Initiative Bird Conservation Regions. As few as 4 years of MAPS data can be used to detect biologically meaningful differences in vital rates for a target species between clusters (e.g., representing distinct habitat types or regions) of just a few MAPS stations each (Rosenberg et al. 1999). This level of effort requires just 2–4 trained interns (to operate 6–12 stations) and a supervisory biologist working during 2 (at high latitudes) to 3 (at lower latitudes) months during the breeding season. At larger spatial and temporal scales, we estimate that 20 years of data from the current network of about 470 MAPS stations is sufficient to detect meaningful differences in adult apparent survival rates between populations or linear trends in survival rates for 19–47 species at MAPS regional scales (similar to United States Fish and Wildlife Service regions; DeSante 1992) and for 105 species at the program-wide scale (J. F. Saracco, D. F. DeSante, D. R. Kaschube, J. E. Hines, M. P. Nott, and R. B. Siegel, The

Institute for Bird Populations, unpublished report). Nevertheless, habitat- and region-specific demographic data are lacking for many landbird species that are potentially monitorable by MAPS. We suggest that the full potential of MAPS will only be realized with 1) a clear vision for improvement and growth to better monitor species and habitats of conservation concern and under-represented regions; 2) better integration with spatially extensive counting efforts (e.g., the BBS) within regions of conservation interest (e.g., Bird Conservation Regions); 3) integration of MAPS into a program of coordinated bird monitoring, which would help foster a commitment from federal, state, and private land managers to implement MAPS; and 4) continued development and implementation of analytical techniques that formally link many sources of monitoring data. Realization of these goals will provide better guidance to private and public land managers as to the implementation of MAPS to best meet both local monitoring needs (e.g., in relation to a particular management action) and the needs of the broader avian conservation community.

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