Identifying the Proximate Demographic Cause(s) of Population Change by Modeling Spatial Variation in Productivity, Survivorship, and Population Trends

David F. DeSante, M. Philip Nott & **Danielle R. O'Grady**

The Institute for Bird Populations, P.O. Box 1346,

Point Reyes Station CA 94956-1346 USA.

Email: ddesante@birdpop.org, pnott@birdpop.org, dogrady@birdpop.org

ABSTRACT

We proposed and evaluated a technique for identifying the proximate demographic cause(s) of population decline at two spatial scales. The approach involves modeling spatial variation in vital rates (productivity and survivorship) as a function of spatial variation in population trends. We modeled productivity indices (using logistic regression) and time-constant annual adult survival-rate estimates (using modified Cormack-Jolly-Seber mark-recapture analyses) from the Monitoring Avian Productivity and Survivorship (MAPS) Program.

For the larger scale, we modeled productivity and survivorship of Gray Catbird (*Dumetella carolinensis*) during 1992-1998 from stations located in areas comprised of physiographic strata (as defined by the North American Breeding Bird Survey [BBS]) where the 1992-1998 BBS population trend for Gray Catbird was significantly ($P<0.01$) positive or negative. We used AIC to select the appropriate models for both productivity and survivorship. We found that adult survival-rate estimates were area-dependent while productivity indices were independent of area. We used a simple demographic model to estimate modeled population changes for each area based on the selected models. Differences in modeled population changes for the two areas for Gray Catbird agreed well with difference in BBS population trends, although the modeled population changes for both areas were substantially more negative than the BBS population trends. This suggests that MAPS productivity indices (and, possibly, adult survival-rate estimates) are biased low. These results also suggest that the proximate demographic cause of population decline in catbirds in physiographic strata where they are declining was low survival of adults, and that management strategies to reverse the declines in catbirds by increasing their productivity will not be successful.

At the smaller scale, we modeled productivity and survivorship during 1994-1999 of five selected target species (Carolina Chickadee - *Poecile carolinensis*, Gray Catbird, Ovenbird - *Seiurus aurocapillus*, Yellow-breasted Chat - *Icteria virens*, and Field Sparrow - *Spizella pusilla*) from stations located on US Department of Defense installations in both the western (Kansas and Missouri) and eastern (Indiana and Kentucky) Midwest. The selected species were those whose trend in adult captures over the six years 1994-1999 was significantly ($P<0.05$) positive or negative in one area (eastern or western Midwest) and of the opposite sign (but not necessarily significant) in the other area. Again, we used AIC to

select the appropriate models for the vital rates for each species, and used the vital rates from the selected models to calculate the modeled population change for each species in each area. The regression of modeled population change on trend in adult captures showed a significant (P=0.028) positive relationship, although the y-intercept was negative (-0.418). This again suggests that MAPS productivity indices (and, possibly, survivorship estimates) are biased low, but that the biases are relatively constant between areas and among species. These results also allowed us to suggest likely causes of population decline for each of the target species.

Finally we discussed difficulties and short-comings of this approach, including the difficulty of obtaining precise estimates of vital rates at smaller spatial scales, the potential failure of some stations to adequately represent the larger-scale habitat, the lack of consideration of the survival of first-year birds, and the lack of consideration of the effects of density-dependent processes. We conclude that the approach is indeed useful for identifying the proximate demographic cause of population change, but that an optimal approach would include consideration of both spatial and temporal variation in vital rates and population trends. This underscores the critical importance of large-scale, long-term demographic monitoring to provide the capability for robust investigations of the causes of population decline.

INTRODUCTION

Integrated avian population monitoring is an approach whereby information from programs that monitor vital rates (e.g., productivity and survivorship) and programs that monitor population trends are integrated through analyses that attempt to model the dynamics of populations over varying spatial scales (Baillie 1990, Greenwood et al. 1994). The monitoring of vital rates, as well as population size, is a critical component of integrated population monitoring for several reasons. First, environmental stressors and management actions tend to affect vital rates directly and, often, without lengthy time lags caused by the buffering effects of non-breeding individuals and the density-dependent responses of populations (Temple & Wiens 1989). Second, vital rates provide crucial information about the stage of the life cycle at which population change is being effected (DeSante 1992). Third, monitoring vital rates provides critical information about the 'health' of the population being monitored and about the quality of the habitat or landscape that the population inhabits. Indeed, because of the vagility of most bird species, local variations in population size may often be masked by recruitment from a wider region (George et al. 1992) or accentuated by lack of recruitment from a larger area (DeSante 1990). Thus, density of a species in a given area may not be indicative of population health because of source-sink dynamics (Van Horne 1983, Pulliam 1988). Data on vital rates can provide information regarding potential sources and sinks, although additional data on immigration, emigration, and density-dependent dispersal are needed to distinguish true sinks from pseudo-sinks (Watkinson & Sutherland 1995). Estimating vital rates is therefore critical for understanding population dynamics and is directly applicable to population models designed to assess the effects of land-management practices upon those parameters (Noon & Sauer 1992).

Ringing studies provide an important tool for monitoring vital rates (Baillie this volume). Indeed, ringing (or other marking) and recovery, recapture, or resighting of marked birds provides the only useful way to monitor survival rates (Lebreton this volume).

The multiple objectives of an integrated avian population monitoring strategy should be to: (1) identify the proximate demographic cause of population change; (2) aid the formulation of testable hypotheses regarding the ultimate environmental cause of population change; and (3) aid the identification of management actions and/or conservation strategies to maintain stable or increasing populations and reverse population declines (DeSante 1995). In

addition, a truly successful avian population monitoring strategy must be intimately integrated with land management (DeSante & Rosenberg 1998). Such integration adds two additional objectives to avian population monitoring: (4) to evaluate the effectiveness of those management actions and/or conservation strategies actually implemented; and (5) to aid in the modification of those management actions and conservation strategies in an adaptive management cycle.

This paper focuses on the first objective of integrated population monitoring, identification of the proximate demographic cause(s) of population change. Baillie & Peach (1992) showed how a modification of the concept of key factor analysis (Varley & Gradwell 1960, Krebs 1970) could be used to identify causes of population change in birds. In this approach, multi-year temporal patterns in indices of productivity and estimates of survival rates are compared to analogous temporal patterns in population size (Peach et al. 1995). To gain further insight, multi-year temporal patterns in various components of productivity (clutch size, hatching success, fledging success) and survival (juvenile survival, adult survival) can be compared to analogous patterns of population trends. A major difficulty of this approach is that a long time series of data is needed and strong evidence for the proximate demographic cause of the decline can generally be obtained only following many years of decline.

Green (1995, 1999) outlined and described additional methods for diagnosing causes of bird population declines and paid particular attention to methods that rely on comparisons among geographical regions and/or time periods with different population trends. He emphasized that comparisons of breeding productivity and survival among regions or time periods can provide a valuable check on other diagnoses or hypotheses of external causes of decline indicated by correlations with population trend (Green 1999). DeSante & Rosenberg (1998) suggested that substituting space for time in comparing differences in vital rates as a function of differences in population trends could increase the efficiency with which demographic causes of population change can be identified, because long-term data on temporal differences in population trends are not needed. Green (1999), however, pointed out the difficulties of detecting changes in vital rates associated with population declines, especially if the demographic rate which changes is density-dependent. He suggested that

these considerations likely apply also, or even especially, to efforts that rely on spatial, rather than temporal, differences.

Here we describe and illustrate an analytical framework for integrating spatial variation in vital rates with spatial variation in population trends to provide inferences as to the proximate demographic causes of population declines for target species at multiple spatial scales. The basic approach is to identify geographic areas where a target species has a negative population trend and analogous areas where the species has a positive trend. We then model productivity (using logistic regression) and survivorship (using modified Cormack-Jolly-Seber mark-recapture analyses) both as a function and not as a function of these areas and use AIC for model selection. If, for example, we find that productivity is best modeled as independent of area, that survival rates are best modeled with area-dependence, and that the differences in survival are sufficient to bring about the observed differences in population trends, we can conclude that low survival rate is the proximate demographic cause of the population decline in the area in which the population is declining. Opposite results will lead to the opposite conclusion.

We apply this approach at two spatial scales and discuss the results obtained on several target species. We discuss the limitations of this approach and discuss several of its difficulties and short-comings, including lack of consideration of the survival of first-year birds and lack of consideration of the effects of density-dependent processes. We close by suggesting how the approach could be improved by including consideration of temporal, as well as spatial, variation in vital rates and population trends.

METHODS

We obtained productivity indices and adult survival-rate estimates from the Monitoring Avian Productivity and Survivorship (MAPS) program, a cooperative network now consisting of over 500 constant-effort mist netting and banding stations across North America (DeSante et al. 1995, 1998, 2000). Although MAPS was initiated in 1989, 1992 was the first year of completely standardized operation and a widespread continental distribution of stations. Each MAPS station typically consists of about ten permanent net-sites located opportunistically, but rather uniformly, within the interior eight ha of a 20-ha study area. Typically, one 12-m, 36-mm-mesh mist net is operated at each net site for six

morning hours per day, and for one day during each of six to ten consecutive 10-day periods (numbered 1-10). Starting dates vary between May 1 and June 10 (later at more northerly latitudes and higher elevations) and operation continues through August 8. All data used in this paper were collected at stations that start in Period 3 or 4. All birds captured during the program are identified to species, age, and sex according to criteria in Pyle (1997) and, if unmarked, are marked with a uniquely numbered aluminum ring provided by the US Geological Survey/Biological Resources Division Bird Banding Laboratory or the Canadian Wildlife Service Bird Banding Office.

Following Peach et al. (1996), we calculated productivity indices as the proportion of young in the catch (number of young individuals/total number of aged individuals).   We estimated annual adult survival rates and capture probabilities from modified Cormack-Jolly-Seber (CJS) mark-recapture models (Clobert et al. 1987, Pollock et al. 1990, Lebreton et al. 1992) that included both a "between-year transient" model (Pradel et al. 1997) and a "within-year length-of-stay transient" model (Nott & DeSante in press). These modifications were incorporated into the computer program SURVIV (White 1993). They permit estimation of the proportion of residents among newly captured birds and provide survival-rate estimates that are unbiased with respect to transient individuals (Pradel et al. 1997). The incorporation of the length-of-stay modification has the further advantage of increasing the precision of the survival-rate estimates (Nott & DeSante in press). Because four consecutive years is the minimum needed to employ the "between-year transient" modification (Pradel et al. 1997) of the CJS mark-recapture model, we only included data in productivity and survivorship models from stations that were operated for at least four consecutive years during the particular period of years under consideration.

MAPS protocol (DeSante et al. 2000) requires station operators to record the probable breeding/summer resident status of all avian species seen, heard, or captured at each station on every day of operation using methods similar to those employed in breeding bird atlas projects; and to assign a composite breeding/summer resident status for every species at the end of the season based on those daily records. Data for a given species were included in productivity and survivorship analyses only from stations where the species was determined to be a breeding, summer resident species during more than half of the years the station was operated. Stations fulfilling this requirement for a given species and that were operated for at

least four consecutive years during the period of interest were defined as "qualified stations" for that species.

We modeled productivity indices and survivorship estimates as functions of population trends at two spatial scales. For the larger-scale approach, we used 1992-1998 population-trend data derived from the North American Breeding Bird Survey (BBS; Robbins et al. 1986, Peterjohn et al. 1995), which consists of over 4000 fixed 39.4-km survey routes (of which up to about 3000 were operated in any given year) that were randomly located along secondary and tertiary roadsides. Fifty fixed points were established at 0.8-km intervals along each route, and one 3-min fixed-radius (0.4-km) point count was conducted at each point each year during the height of the breeding (singing) season. Spatial patterns of population trends were based on pre-established BBS physiographic strata (Robbins et al. 1986). For the smaller-scale approach, we determined 1994-1999 population trends from MAPS data on the numbers of adult birds captured at three US Department of Defense (DoD) military installations in the western Midwest (Kansas and Missouri) and three installations in the eastern Midwest (Indiana and Kentucky).

Because the temporal runs of data studied here were either six or seven years, and four years is the minimum required to obtain even time-constant estimates of annual adult survival rates, we did not include time (year) as a factor in any of our analyses. Indeed, Pyle et al. (1999) found that time-dependent models of adult survival were selected over time-constant models of adult survival for none of 25 species studied at western Midwest DoD installations using six consecutive years of data, and were equivalent to time-constant models for only two species. We suggest that at least eight years of data might be necessary to model both spatial and temporal variation in survival rates with data sets of the extent presented here.

Larger-scale Analyses: BBS Physiographic Strata

For the larger-scale analyses, we calculated 7-year (1992-1998) population trends for Gray Catbird (*Dumetella carolinensis*) for each physiographic stratum in which the species occurred using the estimating equations method (Link & Sauer 1996) available on the BBS website (Sauer et al. 1999). We selected Gray Catbird for this analysis because it is a common, widely distributed species that is frequently captured at MAPS stations and that
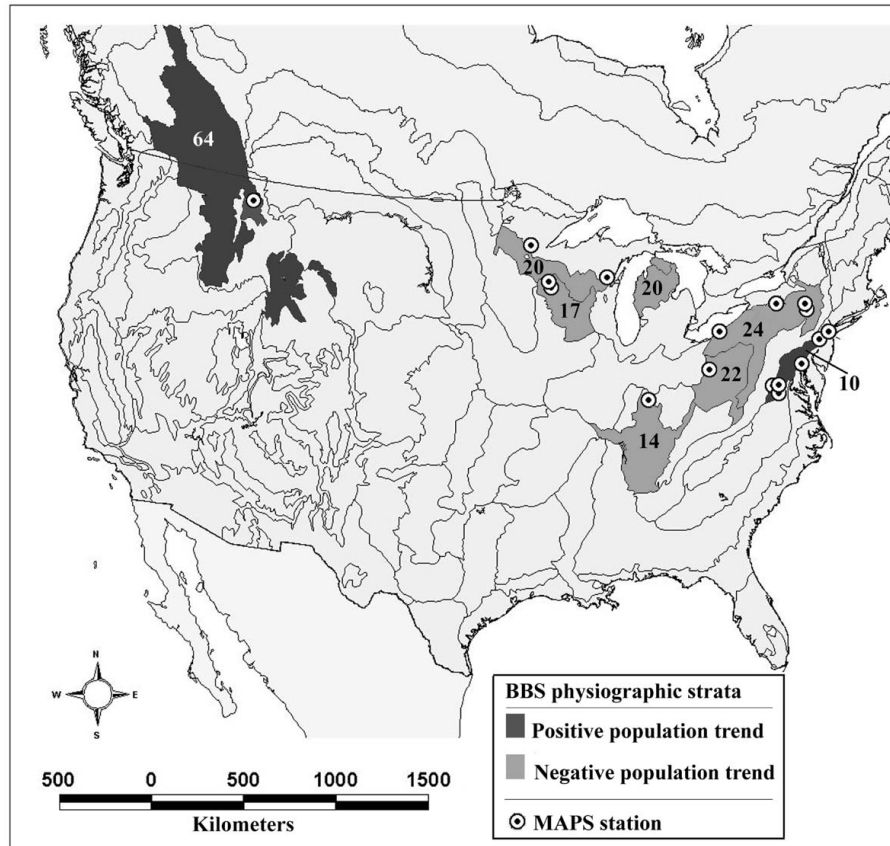
Figure 1. Map of a portion of North America showing the physiographic strata defined by the North American Breeding Bird Survey (BBS) and indicating those strata for which Gray Catbird (*Dumetella carolinensis*) had significantly (P<0.01) positive (dark shading) and negative (light shading) 7-year (1992-1998) BBS population trends. Also shown are the locations of MAPS stations in those physiographic strata which were operated for at least four consecutive years during the period 1992-1998, and at which Gray Catbirds were determined to be a breeding, summer resident species during more than half the years the station was operated.

shows substantial geographic variation in population trends. We used the period 1992-1998 because that was the period for which we had data from the entire MAPS Program. We then identified the set of qualified MAPS stations for Gray Catbirds located within each physiographic strata where catbirds showed a significant (*P*<0.01) positive 7-year BBS population trend. We next identified the analogous set of qualified stations located within each strata where catbirds showed a significant (*P*<0.01) negative 7-year BBS population trend. All these BBS strata and their associated MAPS stations are listed in Appendix 1 and shown geographically in Figure 1. Most of the stations used in these catbird analyses were operated by independent operators, rather than by IBP personnel.

We calculated the number of young (hatching-year) and adult (after-hatching-year) individual catbirds captured during each year that each station was operated, and pooled these numbers over all years at each station to provide station-specific productivity indices. We then used a *t*-test to assess the difference between the mean station-specific productivity index for stations in strata with significant positive population trends versus the mean station-specific productivity index for stations in strata with significant negative population trends. We also calculated a pooled productivity index for positive strata by pooling the numbers of adult and young catbirds over all stations located in positive strata, and an analogous pooled productivity index for negative strata.

We also used logistic regression to model productivity as a function of the underlying population trend for catbirds. In these analyses, the logit was the probability that an individual sampled at random from the pooled data was a young bird. Because productivity indices are strongly dependent upon the extent and timing of netting effort, we included five different netting effort variables (net-hours/period, net-hours/paired period [periods 3-4, 5-6, 7-8, 9-10], net-hours/triplet period [periods 3-5, 6-8, 9-10], net-hours/superperiod [periods 3-7, 8-10], and total net-hours [periods 3-10]) in the logistic regression models. We defined the reference stations as those in strata where catbird population trends were significantly positive. An odds-ratio <1.0 indicates that productivity in strata with positive trends tended to be higher than productivity in strata with negative trends. An odds-ratio >1.0 indicates the reverse. We also modeled catbird productivity independent of increasing or decreasing strata. We used Akaike Information Criteria (AIC) to select the appropriate (strata-dependent or strata-independent) model(s) (Burnham & Anderson 1992) where the selected model was the one with the lowest AIC. We considered competing models that had AICs within 2.0 AIC units of each other to be equivalent models (Anderson & Burnham 1999).

In a similar manner, we modeled adult survival-rate (ϕ), adult capture probability (P), and proportion of residents among newly banded adults (γ) as a function (or not as a function) of area. The eight possible combinations of area-dependence and non-dependence are shown in Table 1. Capture probabilities, of course, are dependent on netting effort; but because capture probabilities are estimated, netting effort does not need to be modeled separately. Again we used AIC to select the appropriate model(s).

Table 1. Model selection for Gray Catbird (*Dumatella carolinensis*) as a function (and not as a function) of BBS physiographic strata (area = A) where catbirds have significant (P<0.01) positive and negative BBS population trends for (1) Productivity (modeled using logistic regression) and (2) Survivorship (modeled using modified Cormack-Jolly-Seber mark-recapture analyses).

1. Productivity

Model	AIC		Odds ratio (SE)	Z	P	Positive strata	Both	Negative strata
							Proportion of young (SE)	
Effort (period), Area	2791.2	*	1.186 (0.146)	1.388	0.165	0.270		0.320 (0.039)
Effort (period)	2791.1	**					0.295	

2. Survivorship

Model	AIC	ϕ (SE) Positive	ϕ Both	ϕ Negative	P (SE) Positive	P Both	P Negative	γ (SE) Positive	γ Both	γ Negative
ϕ, P, γ	276.8		0.523 (0.028)			0.445 (0.037)			0.434 (0.047)	
ϕ(A), P, γ	262.4*	0.571 (0.032)		0.398 (0.039)		0.451 (0.037)			0.450 (0.049)	
ϕ, P(A), γ	270.3		0.532 (0.029)		0.479 (0.043)		0.311 (0.043)		0.455 (0.050)	
ϕ, P, γ(A)	263.6		0.522 (0.028)			0.446 (0.037)		0.542 (0.063)		0.272 (0.049)
ϕ(A), P(A), γ	264.4	0.571 (0.033)		0.400 (0.049)	0.452 (0.042)		0.447 (0.077)		0.450 (0.049)	
ϕ(A), P, γ(A)	261.6**	0.555 (0.033)		0.443 (0.048)		0.451 (0.037)		0.496 (0.061)		0.333 (0.071)
ϕ, P(A), γ(A)	265.3		0.525 (0.028)		0.455 (0.043)		0.416 (0.062)	0.531 (0.065)		0.286 (0.058)
ϕ(A), P(A), γ(A)	263.4*	0.558 (0.034)		0.432 (0.052)	0.441 (0.042)		0.486 (0.081)	0.500 (0.062)		0.324 (0.071)

** Selected model (model with lowest AIC value)
* Equivalent model (model with AIC value within 2.0 units of that for selected model)

Finally, using the productivity indices and survivorship estimates from the selected models, we modeled the population change of adults (*MPC*) for each stratum using a simple demographic model following DeSante et al. (1999):

$$MPC = (\phi + R*\phi_y) - 1.0$$

where ϕ is the annual survival rate of adults, ϕ_y is the survival rate of young (from the time that the juveniles are ringed, generally during their juvenile dispersal, to recruitment into the next year's breeding population; this was modeled as $\phi_y = 0.75\phi$; see DeSante et al. 1999); and *R* is the reproductive index (young per adult) which is related to *PI* the productivity index (young per total aged birds) by $R = PI/(1\text{-}PI)$.

Smaller-scale Analyses: DoD Installations

For the smaller-scale analyses, we pooled data for target species over the 6-year period (1994-1999) from all 18 MAPS stations on three DoD military installations in the western Midwest (Fort Riley, KS; Fort Leavenworth and Sunflower Army Ammunition Plant, KS; and Fort Leonard Wood, MO) and separately for all 18 stations on three DoD installations in the western Midwest (Jefferson Proving Ground, IN; Crane Naval Weapons Support Center, IN; and Fort Knox, KY). The period 1994-1999 was chosen for these analyses because 1994 was the first year of operation for five of the 18 stations in the western Midwest (12 of the other stations started in 1993 and one started in 1995) and for 17 of the 18 stations in the eastern Midwest (the other station started in 1996). Thus, 34 of the 36 stations were operated from 1994-1999 and all 36 were operated by trained field biologist interns from The Institute for Bird Populations. Target species were initially defined as those having at least 42 adult individuals captured during the six years (an average of seven individuals per year) at all stations pooled in each of the western Midwest and eastern Midwest areas.

For each initial target species, we calculated year-to-year changes in the number of pooled individual adults captured at MAPS stations in each of the western and eastern Midwest areas in a rigorous, constant-effort manner, by using net-opening and –closing times and net-check times on a net-by-net and period-by-period basis to excluded captures that occurred in a given net in a given period in one year at a time when that net was not operated in that period in the other year. We estimated 6-year (1994-1999) trends in adult captures (*TAC*) by "chain-indexing" the constant-effort year-to-year changes and defining *TAC* as the

slope (additive change per year) of the linear regression of the chain-index on year (DeSante et al. 1999). We used these *TAC*s as the estimated population trends for each species in each area. We then examined the estimated population trends of the initial target species in each area and selected those species for which the estimated population trend in one area was significantly (*P*<0.05) positive or negative, and the estimated trend in the other area had the opposite sign. Five species (Appendix 2) fulfilled this requirement: Carolina Chickadee (*Poecile carolinensis*), Gray Catbird, Ovenbird (*Seiurus aurocapillus*), Yellow-breasted Chat (*Icteria virens*), and Field Sparrow (*Spizella pusilla*).

For each of these five species, we followed analytical procedures similar to those used for the Gray Catbird analyses described above. First, we pooled data from the subset of stations in each area and modeled productivity (using logistic regression and including the same five effort variables in the models) both as a function of area and not as a function of area. We defined the set of stations in the western Midwest area as the reference set of stations and again used AIC to select the appropriate model(s). Next, using modified CJS mark-recapture analysis, we modeled all eight combinations of the three parameters associated with survivorship (ϕ, P, γ) both as a function of area and not as a function of area, and again used AIC to select the appropriate model(s). Then, in a manner analogous to that described above for Gray Catbird, we modeled population change in adult birds of each species in each area, and ran regression analyses of the modeled populations changes (*MPC*s) on the corresponding estimated population trends (*TAC*s).

RESULTS

Larger-scale Analyses: Gray Catbirds in BBS Physiographic Strata

We identified seven qualified MAPS stations in two strata where Gray Catbirds had significant (*P*<0.01) positive BBS population trends during the 1992-1998 period, and ten analogous stations in five strata where they had significant (*P*<0.01) negative BBS population trends (Fig. 1). The numbers of young and adult catbirds captured at each of these stations, along with station-specific productivity indices (proportion of young in the catch) and station-specific adult survival-rate estimates are also presented in Appendix 1. It is apparent that data were sparse at a number of stations in both areas. A rule of thumb we have found is that an average of seven adult individuals per year need be captured to obtain any kind of reasonable estimates for annual survival rates using a "transient" modification of

the CJS mark-recapture model even when constraining survival in all years to be equal (Pyle et al. 1999). Applying this guideline, only five of seven stations in strata with positive population trends and six of ten stations in strata with negative population trends were considered to have an adequate sample of adult birds captured for survivorship analyses. Using data only from these stations, we found that the mean annual adult survival rate at stations in strata with positive population trends (ϕ=0.568) was nearly significantly greater than the mean at stations in strata with negative population trends (ϕ=0.384; t=2.204, df=9, P=0.055). In contrast, again using data only from these stations, we found that there was no difference in mean productivity between stations in strata with positive population trends (*PI*=0.264) and strata with negative trends (*PI*=0.311; t=-0.546, df=9, P=0.598).

When data from all stations were pooled in each area and productivity was modeled using logistic regression, we found that the model that included area as a variable was equivalent to the model that excluded area as a variable (Table 1). The odds ratio suggesting that productivity in strata with negative trends (*PI*=0.270) was 1.186 times that in strata with positive trends (*PI*=0.320) was not significant (P=0.165). This method, which allows effort to be included as a variable but ignores the underlying spatial structure of the data within each area, provided a result that is very similar to that obtained from the *t*-test presented above. In contrast, all three of the equivalent mark-recapture models included adult survival rates that varied with area. The selected model had both survival rate and proportion of residents varying with area and suggested that survival in strata with positive trends (ϕ=0.555) was higher than survival in strata with negative trends (ϕ=0.443). This method, which permits capture probability and proportion of residents to be modeled as a function of area but, again, ignores the underlying spatial structure of the data within each area, also produced a result quite similar to that obtained from the *t*-test presented above.

Table 2 presents the modeled population change (*MPC*) for each area obtained using the productivity indices and adult survival-rate estimates for each area from the selected logistic regression and CJS models. The 1992-1998 BBS population trends are also presented for comparison. Although modeled population changes were substantially more negative than the BBS population trends, suggesting that productivity indices or survival rate estimates or both were biased low, the relationship between the two areas for modeled trends agreed with the BBS trends and the magnitude of the differences was also similar.

Table 2. Vital rates (from the selected models; see Table 1) and population trends for Gray Catbird from MAPS data pooled from stations in BBS physiographic strata where catbirds nave significant (P<0.01) positive and negative BBS population trends.

	Positive strata	Negative strata	Difference (pos - neg)
Productivity index [a]	0.295	0.295	0.000
Adult survival rate estimate[b]	0.555	0.443	0.112
Modeled population change[c]	-0.271	-0.418	0.147
BBS population trend [d]	0.102	-0.055	0.157

[a] Proportion of young in the catch, modeled using logistic regression
[b] Modeled using modified Cormack-Jolly-Seber mark-recapture analyses.
[c] Annual change; see text.
[d] Annual change; see text.

Smaller-scale Analyses: Five Target Species on DoD Installations

Estimated trends in adult captures are presented for the five selected target species from MAPS stations in both the western and eastern Midwest (Fig. 2, Table 4). Because adults of four of these five species (all but Gray Catbird) were captured in sufficient numbers to provide meaningful survival-rate estimates at very few individual stations (Table 3), we pooled data from all stations in each area in order to model productivity (using logistic regression) and survivorship (using modified CJS models) both as and not as a function of area. The results of all of these models are presented in Appendix 2 and summarized in Table 4.

Table 3. Number of year-unique adults (summed over 1994-1999) captured at MAPS stations on US Department of Defense installations in the western and eastern Midwest for selected target species.

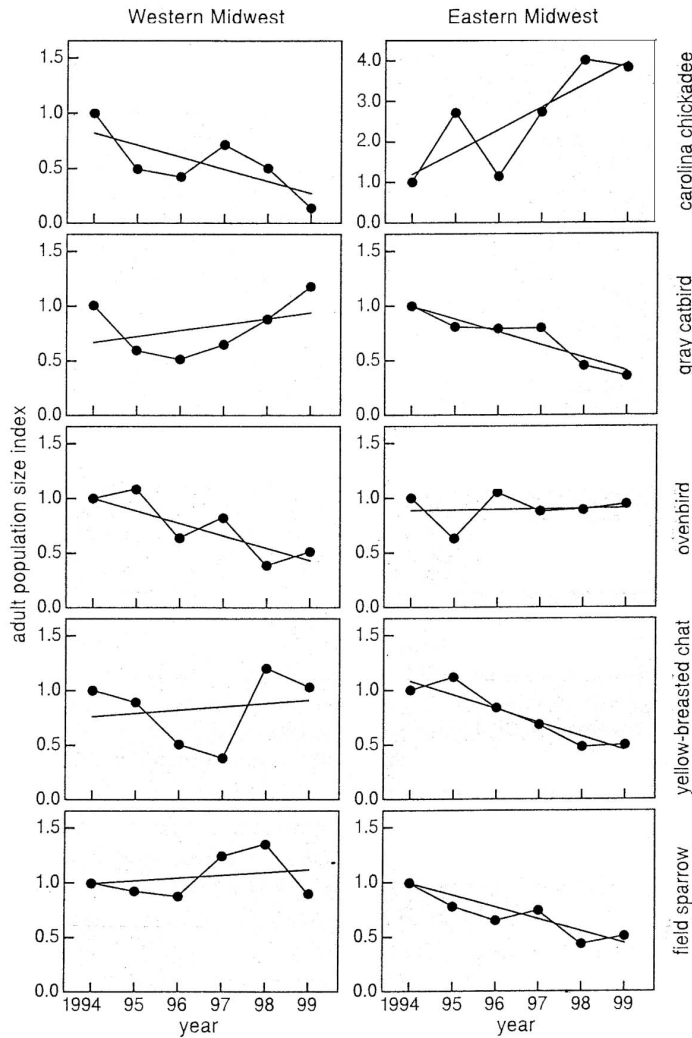| Species	Western Midwest			Eastern Midwest		
		No. of stations			No. of stations	
	No. of adults	Total	with ≥ 42 adults	No. of adults	Total	with ≥ 42 adults
Carolina Chickadee	48	6	0	104	17	0
Poecile carolinensis						
Gray Catbird	564	5	4	527	8	6
Dumatella carolinensis						
Ovenbird	47	3	0	321	12	1
Seiurus aurocapillus						
Yellow-breasted Chat	224	3	2	257	11	1
Icteria virens						
Field Sparrow	404	9	3	128	8	1
Spizella pusilla						

Figure 2. Adult population size index as a function of year for five selected target species as determined from MAPS data from 18 stations on U.S. Department of Defense (DoD) installations in the western Midwest (Kansas and Missouri) and 18 stations on DoD installation in the eastern Midwest (Indiana and Kentucky). The slope of the regression line was used as the trend in adult captures (*TAC*; see Table 4).

For Gray Catbird and Yellow-breasted Chat, the two species with highly significant ($P<0.01$) decreasing trends in the eastern Midwest and non-significant increasing trends in the western Midwest, area-dependent models were strongly selected for both productivity and survival. For both species, productivity and survival were each much lower in the eastern than in the western Midwest. For Field Sparrow, which showed a significant ($P<0.05$) decline in the eastern Midwest and a non-significant increase in the western Midwest, area-dependent models were found to be equivalent to area-independent models for both productivity and survival. Both productivity and survival tended to be higher in western than in the eastern Midwest, but the differences were not significant.

Ovenbird differed sharply from the three previous species and showed a significant ($P<0.05$) decline in the western Midwest and a non-significant increase in the eastern Midwest. Area dependent models for Ovenbird for both productivity and survival were

Table 4. Vital rates (SE) from selected models (see Appendix 2) and population trends (SE) for five selected target species from MAPS data pooled from stations on US Department of Defense installations in the western Midwest (Kansas and Missouri) and eastern Midwest (Indiana and Kentucky).

Species	Area	Productivity [a]	Survival [b]	Modeled population change [c]	Trend in adult captures [d]	
Carolina Chickadee						
Poecile carolinensis						
	Western	0.250	0.476 (0.127)	-0.405	-0.114 (0.052)	*
	Eastern	0.494 (0.161)	0.476 (0.127)	-0.176	0.553 (0.196)	**
Gray Catbird						
Dumatella carolinensis						
	Western	0.270	0.634 (0.051)	-0.190	0.055 (0.063)	
	Eastern	0.160 (0.026)	0.283 (0.041)	-0.677	-0.123 (0.023)	***
Ovenbird						
Seiurus aurocapillus						
	Western	0.170	0.489 (0.073)	-0.436	-0.125 (0.039)	**
	Eastern	0.344 (0.134)	0.489 (0.073)	-0.319	0.004 (0.039)	
Yellow-breasted Chat						
Icteria virens						
	Western	0.164	0.610 (0.067)	-0.300	0.027 (0.084)	
	Eastern	0.034 (0.017)	0.329 (0.062)	-0.662	-0.133 (0.025)	***
Field Sparrow						
Spizella pusilla						
	Western	0.179	0.453 (0.063)	-0.473	0.033 (0.051)	
	Eastern	0.119 (0.031)	0.453 (0.063)	-0.501	-0.100 (0.022)	**

[a] Proportion of young in the catch, modeled using logistic regression.
[b] Modeled using modified Cormack-Jolly-Seber mark-recapture analyses.
[c] Annual change; see text.
[d] Annual change; see text.
* $0.05 \leq P < 0.10$
** $P < 0.05$
*** $P < 0.01$

found to be equivalent to area-independent models, although area-dependence in productivity was the selected model and productivity in the eastern Midwest was nearly significantly ($P=0.071$) greater than in the western Midwest. The same general pattern of increasing and decreasing trends also characterized Carolina Chickadee, which, however, showed a significant ($P<0.05$) increase in the eastern Midwest and a nearly significant ($0.05<P<0.10$) decrease in the western Midwest. Area-dependence in productivity was unambiguously selected in Carolina Chickadee and productivity in the east was significantly ($P<0.05$) greater than in the west. Area-independence in survival was the selected model for Carolina Chickadee, although one area-dependent model, which showed higher survival in the western than eastern Midwest, was equivalent to it.
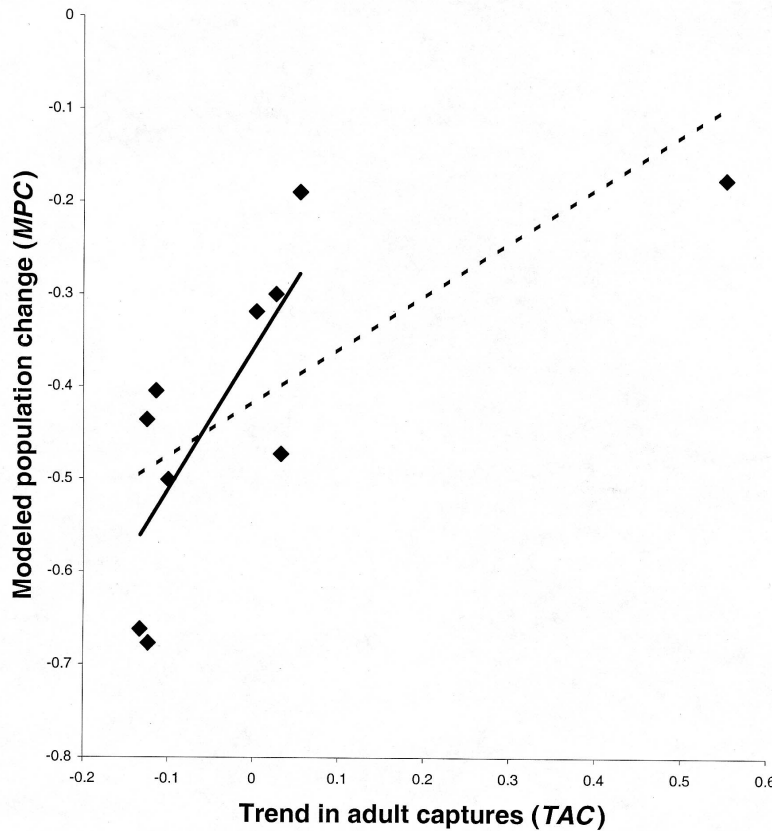
Figure 3. Regression of modeled population change (MPC) on trend in adult captures (TAC) for five selected target species (Carolina Chickadee, Gray Catbird, Ovenbird, Yellow-breasted Chat, Field Sparrow) from 1994-1999 MAPS data from 18 stations on DoD installation in the western Midwest (Kansas and Missouri) and 18 stations on DoD installation in the eastern Midwest (Indiana and Kentucky). The regression for all ten points (dashed line) -- *slope*=0.580, *y-intercept*=-0.418, *r*=0.688, *P*=0.028; the regression for nine points (solid line; eliminating Carolina Chickadee eastern Midwest) -- *slope*=1.507, *y-intercept*=-0.361, *r*=0.747, *P*=0.021.

In summary, when only the selected models were considered (the ones with the single lowest AIC; Table 4), differences between the western and eastern Midwest for both productivity and survivorship agreed, at least in direction, with differences in population trends (*TAC*) for all five species. Furthermore, a significant correlation was found between modeled population change (*MPC*) and population trends as indicated by trends in adult captures (*TAC*) for all species-area combinations (*r*=0.688, *df*=8, *P*=0.028). The y-intercept of the regression of *MPC* on *TAC* (Fig. 3) was negative (-0.418), again suggesting that productivity or survival or both were biased low. When the possible outlier (Carolina Chickadee in the eastern Midwest, the only species-area combination for which the standard error of the trend was >0.1 [actually, 0.196]) was eliminated (Fig. 3), the correlation was improved (*r*=0.747, *df*=7, *P*=0.021), but the y-intercept remained negative (-0.361).

DISCUSSION

An interesting and important aspect of the results presented above is that the modeled population changes derived from indices and estimates of vital rates from MAPS were always considerable more negative than the population changes derived from BBS population trends or MAPS trends in adult captures. This indicates that either productivity indices or survival-rate estimates from MAPS (or both) were biased low. Because the modified CJS mark-recapture models used provide estimates of capture probability and proportion of residents among newly captured adults, MAPS survival-rate estimates are unbiased with respect to variation among stations in capture effort, behavioral differences within and among species with respect to ease of capture, and the presence of transient individuals in the populations sampled. Survival-rate estimates from MAPS, however, are estimates of "apparent survival" which include an unknown component of emigration. Because all five target species examined in this study are territorial breeding species that are suspected to exhibit relatively high rates of breeding site fidelity, it is likely that the proportion of annual non-survival attributable to emigration is small compared to the proportion that is attributable to mortality. Thus, the bias in adult survival rates is likely to be relatively small.

Productivity indices, on the other hand, are likely biased substantially low. This is because the adult and young birds captured at MAPS stations include individuals breeding and produced within the 20-ha area of the station itself as well as dispersing individuals from the surrounding landscape. However, while relatively few of the locally produced young are captured (they generally disperse away from the station before being captured), a great many of the locally breeding adults are captured because they are resident within the boundaries of the station for much of the MAPS period of operation (Nur & Geupel 1993). This has the effect of substantially lowering any productivity index based on proportion of young in the catch.

Although MAPS productivity indices (and possibly survival-rate estimates) were biased low, the fact that modeled population changes based on these indices and estimates were significantly correlated with population trends based on BBS data or captures of adult birds, suggests that the biases were relatively constant between areas and among the five selected target species studied here. The fact that these five species include permanent resident, temperate-wintering, and tropical wintering species, as well as cavity-, ground, and shrub-nesting species, makes this result even more robust.

The relative spatial and between-species consistency of the biases in vital rates also suggests that these data can provide a useful aid in identifying the proximate demographic cause(s) of population change in the species studied. Indeed, at the scale of the BBS physiographic strata, the decline in Gray Catbird clearly seems to involve low adult survival and not low productivity. This suggests that efforts to reverse the decline in catbirds by managing for increased productivity are not likely to succeed, because productivity of Gray Catbirds in physiographic strata where they are significantly declining is already at least as high (if not higher) than in strata where they are increasing. Rather, management actions designed to reverse the decline in catbirds need to address causes of the low adult survival.

Although conventional wisdom often suggests that survival in passerine birds is effected primarily during the non-breeding season, and especially on the wintering grounds of migratory species, one cannot assume this to be the case in all or even any species. Indeed, it has recently been suggested that mortality during migration can play a major role in population regulation, at least during some years of unfavorable weather (Butler 2000). Furthermore, it is possible that adult survival could primarily be effected on the breeding grounds and during the breeding season. Thus, a change in annual survival rate could reflect a change in recruitment of adults back into the breeding population (e.g., returning adults unable to establish territories due to habitat loss would be forced to emigrate elsewhere and would appear as local mortalities). A change in annual survival rate could also reflect survival through the breeding season (e.g., food shortages could increase the mortality associated with costs of breeding), although in this latter case, one might also expect productivity indices to be lower and thus to co-vary with adult survival rates which, for Gray Catbird at the scale of the BBS physiographic strata, they clearly did not.

The point is, however, that when low adult survival rates are identified as the proximate demographic cause of population declines, additional information is needed to identify the exact location where the low survival is being effected. One promising approach is the use of molecular markers, especially mitochondrial and microsatellite DNA sequences, to link breeding and wintering populations of migratory birds (Girman et al. in press). If areas where a species is declining and increasing can be linked to specific wintering areas, and if monthly survival rates for the species in the areas where individuals from increasing populations winter can be shown to be greater than monthly survival rates in the areas where individuals from declining populations winter, then it can be suggested that low survival on the wintering grounds is the proximate demographic cause of the decline.

Results from the five selected target species on DoD installations in the western and eastern Midwest also provide strong suggestions as to the proximate demographic cause(s) of population decline in the areas where they are declining. For Gray Catbird and Yellow-breasted Chat, both low productivity and low adult survival rates are strongly implicated in the highly significant declines on DoD installations in the eastern Midwest. For Field Sparrow, it is likely that low productivity and possibly also low adult survival are contributing to the declines in the eastern Midwest, although the strength of these determinations is much lower than for the catbird and chat. For Carolina Chickadee, the decline in the western Midwest seems clearly related to the low productivity there and survivorship does not seem to be a factor in the decline; indeed, if survivorship does vary spatially, it is higher in the western than eastern Midwest. This latter result was the same as for Ovenbird, although the difference between productivity in the western and eastern Midwest was not as strong as for the chickadee.

In summary, the results presented here suggest that modeling spatial variation in vital rates as a function of spatial variation in population trends can provide a strong indication of the proximate demographic cause(s) of population declines. It is prudent at this point, however, to emphasize the difficulties of interpreting spatial variation in vital rates, even if they can be measured with sufficient precision to actually detect real spatial differences. The smaller scale approaches, where vital rates and population trend data are taken at the same sites often suffer from limited precision in indices and estimates of vital rates. On the other hand, an important difficulty with the larger-scale approaches is that the habitat at stations at which demographic data are collected may not be representative of overall habitat in the larger region over which the population trend is measured. The inclusion of aspects of a probability-based selection system for siting stations will help alleviate this problem.

Another important difficulty of this approach is that no account is taken of survival of young birds from juvenile dispersal through recruitment into the breeding population the following year, ϕ_y. In our equation for modeled population change, we modeled this first-year survival as $\phi_y = 0.75\phi$ and assumed it to be constant over all areas and among all species, an untenable simplification. Indeed, recent work on the Song Thrush (*Turdus philomelos*) suggests that long-term changes in the first-year annual survival rates were sufficient to account for the observed population decline in the species (Thomsen et al. 1997). It is difficult to obtain estimates for first-year survival except through extensive

mark-recovery data, which generally exist for small landbirds only in areas with high human population densities and very large volunteer ringing efforts.

Perhaps the most pervasive problem of all may well be the existence of density-dependent processes, which, as pointed out by Green (1999), can make the detection of temporal changes or spatial differences in the vital rates difficult. If long-term temporal data are available, then there is some possibility of modeling the effects of density-dependence. If the analysis is limited to modeling spatial data, the inclusion of the effects of density-dependence will be very difficult. The most powerful analyses along these lines will be those which attempt to account for both temporal and spatial variation in population dynamics. This provides a strong justification for large-scale, long-term demographic monitoring to give the capability for robust investigations of the cause(s) of population declines. Caughley (1994) pointed out that the declining-population paradigm, which deals with the cause of small population size and its cure, is urgently in need of more theory and a unifying set of models. Clearly data to test those models can only come from broad-scale long-term demographic monitoring.

ACKNOWLEDGEMENTS

REFERENCES

Anderson D.R. & K.P. Burnham 1999. General strategies for the analysis of ringing data. Bird Study 46(suppl.): S261-270.

Baillie, S.R. 2000. Why bird conservation needs ringing studies. *This Volume*.

Baillie, S.R. 1990. Integrated population monitoring of breeding birds in Britain and Ireland. Ibis 132: 151-166.

Baillie S.R. & W.J. Peach 1992. Population limitation in Palearctic-African migrant passerines. Ibis 134, Suppl. 1: 120-132.

Burnham K. P. & D.R. Anderson 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. Pp. 16-30 in McCullough, D.C. and R.H. Barrett, (eds.), Wildlife 2001: Populations, Elsevier Applied Science, London, U.K.

Butler R.W. 2000. Stormy seas for some North American songbirds: are declines related to severe storms during migration? Auk 117: 518-522.

Caughley G. 1994. Directions in conservation biology. J. Anim. Ecol. 63: 215-244.

Clobert J., J.-D. Lebreton & D. Allaine 1987. A general approach to survival-rate estimation by recaptures or resightings of marked birds. Ardea 75: 133-142.

DeSante D.F. 1995. Suggestions for future directions for studies of marked migratory landbirds from the perspective of a practitioner in population management and conservation. J. Appl. Stat. 22: 949-965.

DeSante D.F. 1992. Monitoring Avian Productivity and Survivorship (MAPS): a sharp, rather than blunt, tool for monitoring and assessing landbird populations. In: D. R. McCullough and R. H. Barrett (eds.), Wildlife 2001: Populations, pp. 511-521. (London, U.K.: Elsevier Applied Science).

DeSante D.F. 1990. The role of recruitment in the dynamics of a Sierran subalpine bird community. Amer. Naturalist 136: 429-455.

DeSante D.F., K.M. Burton, P. Velez & D. Froehlich 2000. MAPS Manual: 2000 Protocol. The Institute for Bird Populations, Point Reyes Station, CA, USA.

DeSante D.F., K.M. Burton, J.F. Saracco & B.L. Walker 1995. Productivity indices and survival rate estimates from MAPS, a continent-wide programme of constant effort mist-netting in North America. J. Appl. Stat. 22: 935-947.

DeSante D.F., D.R. O'Grady, K.M. Burton, P. Velez, D. Froehlich, E.F. Feuss, H. Smith & E.D. Ruhlen 1998. The monitoring Avian Productivity and Survivorship (MAPS) program sixth and seventh annual report (1995 and 1996). Bird Populations 4: 69-122.

DeSante D.F., D.R. O'Grady & P. Pyle 1999. Measures of productivity and survival derived from standardized mist-netting are consistent with observed population changes. Bird Study 46 (suppl.): S178-188.

DeSante D.F. & D.K. Rosenberg 1998. What do we need to monitor in order to manage landbirds? In: J. Marzluff and R. Sallabanks (eds.), Avian Conservation: Research Needs and Effective Implementation, pp. 93-106. Island Press, Washington, DC.

George T.L., A.C, Fowler, R.L. Knight & L.C. McEwen 1992. Impacts of a severe drought on grassland birds in western North America. Ecological Applications 2: 275-284.

Girman D.J., M. Kimura, B. Mila, P. Wade & T.B. Smith In press. Population structure and the use of molecular markers to link wintering sand breeding populations of Wilson's warbler (*Wilsonia pusilla*), a Neotropical migrant. Molecular ecology.

Green R.E. 1999. Applications of large-scale studies of demographic rates to bird conservation. Bird Study 46 (suppl.): S 279-288.

Green R.E. 1994. Diagnosing causes of bird population declines. Ibis 137 (suppl.): S47-55.

Greenwood J.J.D., S.R. Baillie, R.D. Gregory, W.J. Peach & R.J. Fuller 1994. Some new approaches to conservation monitoring of British breeding birds. Ibis 137 (suppl.): S16-28.

Krebs J.R. 1970. Regulation of numbers in the Great Tit (Aves: Passeriformes), Journal of Zoology 162: 317-333.

Lebreton J.-D. 2000. The use of bird rings in the study of survival. *This Volume*.

Lebreton J.-D., K.P. Burnham, J. Clobert & D.R. Anderson 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies, Ecological Monographs 62: 67-118.

Link W.A. & J.R. Sauer 1994. Estimating equations estimates of trends. Bird Populations 2: 23-32.

Noon B.R. & J.R. Sauer 1992. Population models for passerine birds: structure, parameterization, and analysis. In Wildlife 2001: Populations. D.C. McCullough and R.H. Barrett (eds), pp. 441-464. Elsevier Applied Science, London.

Nott M.P. & D.F. DeSante In press. Demographic monitoring and the identification of transients in mark-recapture models. In Scott, J.M. & P. Heglund (eds.) Predicting Species Occurrences. Island Press, New York, USA.

Nur N. & G.R. Geupel 1993. Evaluations of nest monitoring, mist-netting, and other methods for monitoring demographic processes in landbird populations. Pp. 237-44. in Finch, D.M. & P.W. Stangel (eds.). Status and Management of Neotropical Migrant Birds. USDA Forest Service Publication: GTR RM-229, Fort Collins, CO, USA.

Peach W.J., S.T. Buckland & S.R. Baillie 1996. The use of constant mist-netting to measure between-year changes in the abundance and productivity of common passerines. Bird Study 43: 142-156.

Peach W.J., H.Q.P. Crick & J.H. Marchant 1995. The demography of the decline in the British willow warbler population. J. Appl. Stat. 22: 905-922.

Peterjohn B.G., J.R. Sauer & C.S Robbins 1995. Population trends from the North American Breeding Bird Survey. In Ecology and Management of Neotropical Migratory Birds. T.E. Martin and D.M. Finch (eds.), pp. 357-380. Oxford University Press, New York

Pollock K.H., J.D. Nichols, C. Brownie & J.E. Hines 1990. Statistical inference for capture-recapture experiments, Wildlife Monographs, No. 107.

Pradel R., J. Hines, J.-D. Lebreton & J.D. Nichols 1997. Estimating survival probabilities and proportions of 'transients' using capture-recapture data. Biometrics 53: 60-72.

Pulliam H.R. 1988. Sources, sinks, and population regulation. Amer. Naturalist 132: 652-661.

Pyle P. 1997. Identification Guide to North American Birds, Part 1. Slate Creek Press, Bolinas, CA, USA.

Pyle P., D.R. O'Grady & D.F. DeSante 1999. The 1998 Annual Report of the Monitoring Avian Productivity and Survivorship (MAPS) Program on Military Installations and Other Federal lands in the Midwest and East. The Institute for Bird Populations, Point Reyes Station, CA, USA.

Robbins C.S., D. Bystrak & P.H. Geissler 1986. The Breeding bird Survey: Its First Fifteen Years, 1965-1979. Resource Publication 157, U.S. Fish and Wildlife Service, Washington, D.C.

Sauer J.R., J.E. Hines, I. Thomas, J. Fallon & G. Gough 1999. The North American Breeding Bird Survey, Results and Analysis 1966-1998. Version 98.1, USGS Patuxent Wildlife Research Center, Laurel, MD, USA.

Temple S.A. & J.A. Wiens 1989. Bird populations and environmental changes: can birds be bio-indicators?. Amer. Birds 43: 260-270.

Thomson D.L., S.R. Baillie & W.J. Peach 1997. The demography and age-specific annual survival of song thrushes during periods of population stability and declines. J. Anim. Ecol, 66: 414-424.

Van Horne B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47: 893-901.

Varley G.C. & G.R. Gradwell 1960. Key factors in population studies. J. Anim. Ecol. 29: 399-401.

Watkinson A.R. & W.J. Sutherland 1995. Sources, sinks and pseudo-sinks. J. Anim. Ecol. 64: 126-130.

White G.C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. J. Wildl. Manage. 47: 716-728.

Appendix 1. Station-specific productivity (proportion of young in catch) and survivorship (from modified Cormack-Jolly-Seber mark-recapture analyses: ϕ = annual adult survival rate, P= recapture probability, γ = proportion of residents among newly captured adults) for Gray Catbird (*Dumatella carolinensis*) in BBS physiographic strata where catbirds have a significant (P<0.01) 1992-1998 (A) positive or (B) negative BBS population trend.

Stratum	Station	Years operated	Productivity [a]			Survivorship [a]				
			No. of adults	No. of young	Prop. of young	No. of indiv.	No. of returns	ϕ (SE)	P (SE)	γ (SE)
A. Strata with positive population trends										
10	15504[b]	92-98	360	133	0.270	294	66	0.491 (0.057)	0.604 (0.083)	0.604 (0.083)
10	15507[b]	92-98	335	97	0.225	255	80	0.635 (0.051)	0.377 (0.056)	0.647 (0.121)
10	15533[b]	92-98	112	7	0.059	90	22	0.503 (0.099)	0.481 (0.137)	0.635 (0.236)
10	15548	93-98	13	1	0.071	12	1	0.091 (3.661)	1.000 (39.933)	1.000 (2.473)
10	15550[b]	93-98	89	29	0.246	70	19	0.564 (0.122)	0.472 (0.145)	0.581 (0.228)
10	15592[b]	92-96	103	112	0.521	100	3	0.647 (0.402)	0.031 (0.056)	1.000 (1.556)
64	11136	92-98	9	1	0.100	7	2	1.000 (0.400)	0.304 (0.273)	0.331 (0.358)
Pooled			1021	380	0.271	828	193			
Mean (SD of mean)					0.213 (0.161)			0.562 (0.269)	0.467 (0.297)	0.685 (0.240)
Mean (SD of mean) for stations marked [b]					0.264 (0.166)			0.568 (0.073)	0.393 (0.218)	0.693 (0.173)
B. Strata with negative population trends										
14	16629[b]	94-98	65	13	0.167	60	5	0.200 (1.286)	1.000 (6.667)	0.306 (0.265)
17	13305	92-98	42	6	0.125	40	2	0.745 (0.429)	0.034 (0.106)	1.000 (3.158)
17	13335[b]	95-98	47	9	0.161	36	11	0.563 (0.141)	0.760 (0.200)	0.326 (0.192)
20	13302	92-98	23	3	0.115	27	2	0.200 (1.954)	1.000 (10.134)	0.227 (0.310)
20	13324	93-98	20	9	0.310	18	2	1.000 (4.374)	1.000 (4.259)	0.063 (0.088)
22	15546[b]	93-98	79	61	0.436	77	2	0.489 (0.319)	0.185 (0.245)	0.118 (0.160)
24	15512[b]	92-98	161	107	0.399	133	28	0.564 (0.082)	0.430 (0.106)	0.404 (0.136)
24	15524[b]	92-98	88	39	0.307	78	10	0.214 (0.796)	1.000 (3.853)	0.366 (0.223)
24	15529[b]	92-97	89	59	0.399	81	8	0.272 (0.156)	0.475 (0.321)	1.000 (0.801)
24	15543	92-96	1	0	0.000	1	0	-	-	
Pooled			615	306	0.332	551	70			
Mean (SD of mean)					0.242 (0.148)			0.472 (0.279)	0.654 (0.384)	0.423 (0.345)
Mean (SD of mean) for stations marked [b]					0.312 (0.122)			0.384 (0.174)	0.642 (0.332)	0.420 (0.301)
C. All strata										
Pooled			2322	686	0.295	1379	263			
Mean (SD of mean)					0.230 (0.149)			0.511 (0.270)	0.572 (0.350)	0.538 (0.323)
Mean (SD of mean) for stations marked [b]					0.290 (0.138)			0.467 (0.163)	0.529 (0.302)	0.544 (0.279)

[a] No. of adults (under productivity) represents the number of year-unique adult captures over all years of operation and equals the sum of the number of individuals plus the number of returns (under survivorship).

[b] Station with an average of at least 7 adults captured/year.

Appendix 2. Model selection for five target species (Carolina Chickadee – *Poecile carolinensis*; Gray Catbird – *Dumatella carolinensis*; Ovenbird – *Seiurus aurocapillus*; Yellow-breasted Chat - *Icteria virens*; Field Sparrow - *Spizella pusilla*) on US Department of Defense installations in the western Midwest (Kansas and Missouri) and eastern Midwest (Indiana and Kentucky). Two demographic parameters (1) Productivity (modeled using logistic regression), and (2) Survivorship (modeled using modified Cormack-Jolly-Seber mark-recapture analyses) are modeled as a function (and not as a function) of these areas (A).

Carolina Chickadee

1. Productivity

Model	AIC		Odds ratio (SE)	Z	P	Proportion of young (SE)		
						Western Midwest	Both	Eastern Midwest
Effort (sup-per), Area	326.1	**	1.981 (0.645)	2.099	0.036	0.250		0.494 (0.161)
Effort (sup-per)	328.6						0.372	

2. Survivorship

Model	AIC	φ (SE) W. Midwest	φ (SE) Both	φ (SE) E. Midwest	P (SE) W. Midwest	P (SE) Both	P (SE) E. Midwest	γ (SE) W. Midwest	γ (SE) oth/Both	γ (SE) E. Midwest
φ, P, γ	64.9**		0.476 (0.127)			0.402 (0.158)			0.392 (0.182)	
φ(A), P, γ	66.6*	0.518 (0.162)		0.438 (0.141)		0.406 (0.159)			0.398 (0.185)	
φ, P(A), γ	66.7*		0.471 (0.125)		0.361 (0.200)		0.465 (0.187)		0.378 (0.173)	
φ, P, γ(A)	66.1*		0.472 (0.126)			0.407 (0.158)		0.536 (0.293)		0.310 (0.173)
φ(A), P(A), γ	67.3	0.618 (0.204)		0.352 (0.136)	0.262 (0.171)		0.610 (0.259)		0.392 (0.182)	
φ(A), P, γ(A)	68.0	0.441 (0.185)		0.498 (0.161)		0.403 (0.158)		0.590 (0.418)		0.292 (0.172)
φ, P(A), γ(A)	65.6*		0.458 (0.122)		0.196 (0.181)		0.623 (0.220)	1.000 (0.947)		0.229 (0.123)
φ(A), P(A), γ(A)	67.4	0.522 (0.216)		0.413 (0.146)	0.163 (0.157)		0.657 (0.243)	1.000 (0.993)		0.247 (0.140)

Appendix 2. (cont.)

Gray Catbird

1. Productivity

Model	AIC		Odds ratio (SE)	Z	P	Proportion of young (SE)		
						Western Midwest	Both	Eastern Midwest
Effort (period), Area	1424.9	**	0.591 (0.096)	-3.222	0.001	0.270		0.160 (0.026)
Effort (period)	1433.4						0.215	

2. Survivorship

Model	AIC	φ (SE)			P (SE)			γ (SE)		
		W. Midwest	Both	E. Midwest	W. Midwest	Both	E. Midwest	W. Midwest	oth	E. Midwest
φ, P, γ	185.2		0.480 (0.038)			0.469 (0.053)			0.491 (0.070)	
φ(A), P, γ	162.3	0.601 (0.048)		0.346 (0.041)		0.485 (0.053)			0.490 (0.069)	
φ, P(A), γ	182.9		0.503 (0.039)		0.499 (0.067)		0.342 (0.053)		0.512 (0.074)	
φ, P, γ(A)	171.7		0.483 (0.038)			0.464 (0.053)		0.658 (0.105)		0.374 (0.067)
φ(A), P(A), γ	158.9**	0.634 (0.051)		0.283 (0.041)	0.419 (0.058)		0.694 (0.104)		0.490 (0.069)	
φ(A), P, γ(A)	164.2	0.606 (0.051)		0.339 (0.049)		0.486 (0.053)		0.477 (0.080)		0.515 (0.120)
φ, P(A), γ(A)	178.6		0.479 (0.038)		0.456 (0.073)		0.487 (0.073)	0.674 (0.126)		0.338 (0.069)
φ(A), P(A), γ(A)	160.7*	0.627 (0.053)		0.292 (0.045)	0.412 (0.060)		0.703 (0.104)	0.516 (0.091)		0.449 (0.104)

Appendix 2. (cont.)

Ovenbird

1. Productivity

Model	AIC		Odds ratio (SE)	Z	P	Proportion of young (SE)		
						Western Midwest	Both	Eastern Midwest
Effort (sup-per), Area	559.7	**	2.022 (0.788)	1.808	0.071	0.170		0.344 (0.134)
Effort (sup-per)	561.4	*					0.257	

2. Survivorship

Model	AIC	φ (SE) W. Midwest	φ (SE) Both	φ (SE) E. Midwest	P (SE) W. Midwest	P (SE) Both	P (SE) E. Midwest	γ (SE) W. Midwest	γ (SE) oth	γ (SE) E. Midwest
φ, P, γ	92.0**		0.489 (0.073)			0.377 (0.090)			0.481 (0.133)	
φ(A), P, γ	93.4*	0.559 (0.120)		0.467 (0.077)		0.377 (0.090)			0.493 (0.138)	
φ, P(A), γ	93.9*		0.489 (0.073)		0.387 (0.159)		0.373 (0.094)		0.483 (0.135)	
φ, P, γ(A)	93.3*		0.489 (0.073)			0.377 (0.090)		0.300 (0.213)		0.505 (0.142)
φ(A), P(A), γ	95.1	0.603 (0.157)		0.456 (0.079)	0.306 (0.156)		0.401 (0.105)		0.490 (0.137)	
φ(A), P, γ(A)	93.0*	0.658 (0.139)		0.433 (0.079)		0.370 (0.090)		0.200 (0.149)		0.601 (0.190)
φ, P(A), γ(A)	94.9		0.492 (0.074)		0.456 (0.205)		0.342 (0.094)	0.256 (0.195)		0.542 (0.167)
φ(A), P(A), γ(A)	95.0	0.659 (0.158)		0.432 (0.081)	0.368 (0.174)		0.371 (0.106)	0.200 (0.151)		0.600 (0.196)

Appendix 2. (cont.)

Yellow-breasted Chat

1. Productivity

Model	AIC		Odds ratio (SE)	Z	P	Western Midwest	Both	Eastern Midwest
						Proportion of young (SE)		
Effort (tri-per), Area	334.3	**	0.208 (0.101)	-3.224	0.001	0.164		0.034 (0.017)
Effort (tri-per)	345.5						0.099	

2. Survivorship

Model	AIC	φ (SE) W. Midwest	Both	E. Midwest	P (SE) W. Midwest	Both	E. Midwest	γ (SE) W. Midwest	oth	E. Midwest
φ, P, γ	149.4		0.501 (0.058)			0.352 (0.068)			0.580 (0.128)	
φ(A), P, γ	136.7**	0.610 (0.067)		0.329 (0.062)		0.365 (0.068)			0.645 (0.140)	
φ, P(A), γ	142.5		0.532 (0.060)		0.411 (0.084)		0.183 (0.051)		0.675 (0.150)	
φ, P, γ(A)	145.8		0.501 (0.058)			0.351 (0.068)		0.839 (0.210)		0.415 (0.117)
φ(A), P(A), γ	138.7	0.611 (0.072)		0.327 (0.082)	0.364 (0.076)		0.369 (0.131)		0.645 (0.141)	
φ(A), P, γ(A)	138.4*	0.622 (0.072)		0.306 (0.076)		0.364 (0.068)		0.604 (0.155)		0.752 (0.285)
φ, P(A), γ(A)	144.5		0.530 (0.060)		0.408 (0.087)		0.194 (0.069)	0.691 (0.182)		0.634 (0.241)
φ(A), P(A), γ(A)	140.4	0.619 (0.073)		0.313 (0.086)	0.371 (0.078)		0.340 (0.139)	0.600 (0.155)		0.777 (0.327)

Appendix 2. (cont.)

Field Sparrow

1. Productivity

Model	AIC		Odds ratio (SE)	Z	P	Proportion of young (SE)		
						Western Midwest	Both	Eastern Midwest
Effort (total), Area	629.8	**	0.661 (0.172)	-1.588	0.112	0.179		0.119 (0.031)
Effort (total)	630.5	*					0.149	

2. Survivorship

Model	AIC	φ (SE) W. Midwest	φ (SE) Both	φ (SE) E. Midwest	P (SE) W. Midwest	P (SE) Both	P (SE) E. Midwest	γ (SE) W. Midwest	γ (SE) oth	γ (SE) E. Midwest
φ, P, γ	122.7**		0.453 (0.063)			0.255 (0.064)			0.954 (0.245)	
φ(A), P, γ	123.5*	0.475 (0.068)		0.385 (0.084)		0.256 (0.064)			0.945 (0.243)	
φ, P(A), γ	124.7		0.454 (0.063)		0.257 (0.067)		0.243 (0.082)		0.956 (0.246)	
φ, P, γ(A)	124.7		0.454 (0.063)			0.255 (0.064)		0.961 (0.257)		0.932 (0.323)
φ(A), P(A), γ	123.7*	0.505 (0.074)		0.272 (0.094)	0.226 (0.063)		0.464 (0.204)		0.944 (0.243)	
φ(A), P, γ(A)	124.9	0.496 (0.071)		0.361 (0.113)		0.275 (0.066)		0.797 (0.213)		1.000 (0.501)
φ, P(A), γ(A)	126.7		0.456 (0.063)		0.259 (0.073)		0.232 (0.114)	0.940 (0.273)		1.000 (0.509)
φ(A), P(A), γ(A)	125.5	0.513 (0.075)		0.267 (0.104)	0.238 (0.066)		0.453 (0.223)	0.865 (0.246)		1.000 (0.553)

** Selected model (model with lowest AIC value)
* Equivalent model (model with AIC value within 2.0 units of that for selected model)