Monitoring Survival Rates Of Landbirds At Varying Spatial Scales: An Application Of The MAPS Program

Daniel K. Rosenberg[1,3], David F. DeSante[1], and James E. Hines[2]

ABSTRACT—Survivorship is a primary demographic parameter affecting population dynamics, and thus trends in species abundance. The Monitoring Avian Productivity and Survivorship (*MAPS*) program is a cooperative effort designed to monitor landbird demographic parameters. A principle goal of MAPS is to estimate annual survivorship and identify spatial patterns and temporal trends in these rates. We evaluated hypotheses of spatial patterns in survival rates among a collection of neighboring sampling sites, such as within national forests, among biogeographic provinces, and between breeding populations that winter in either Central or South America, and compared these geographic-specific models to a model of a common survival rate among all sampling sites. We used data collected during 1992-1995 from Swainson's Thrush (*Catharus ustulatus*) populations in the western region of the United States. We evaluated the ability to detect spatial and temporal patterns of survivorship with simulated data. We found weak evidence of spatial differences in survival rates at the local scale of "location", which typically contained 3 mist-netting stations. There was little evidence of differences in survival rates among biogeographic provinces or between populations that winter in either Central or South America. When data were pooled for a regional estimate of survivorship, the percent relative bias due to pooling "locations" was <1%. With the pooled data, we estimated a 44% annual regional survival rate; this low estimated survival rate was likely due to the presence of transients in the population (Rosenberg et al. 1999). Using simulated data, we found that power to detect spatial differences increased considerably with number of years and spatial scale, the latter reflecting larger sample size. Detection of trends at smaller spatial scales required >12 years of monitoring. Detection of spatial patterns and temporal trends in survival rates from local to regional scales will provide important information for management and future research directed towards conservation of landbirds.

INTRODUCTION

Concern over reports of wide-spread declines of neotropical migratory songbirds (e.g., Robbins et al. 1989, Terborgh 1989) motivated the establishment of the Neotropical Migratory Bird Conservation Initiative, "Partners in Flight", an international cooperative program designed to reverse declines in migratory birds (Rogers et al. 1993) and landbirds in general (this volume). An important component of the initiative is to encourage establishment of monitoring programs, such as *MAPS* (Monitoring Avian Productivity and Survivorship [Desante et al. 1993]) to identify trends in species abundance and demographic parameters affecting these trends (Finch and Stangel 1993).

Monitoring temporal trends of primary demographic parameters (fecundity, recruitment, and survivorship) that influence population size is especially important (Temple and Wiens 1989, DeSante and Rosenberg 1998), because environmental factors affect these parameters directly, and thus its impacts can be observed over a short time period. Because of buffering effects of transient individuals and density-dependent responses of populations, there may be substantial time lags between changes in primary demographic parameters and resulting changes in population size or density as measured by census or survey methods (Temple and Wiens 1989). Moreover, because of the vagility of most bird species, local variations in population size may often be masked (George et al. 1992) or accentuated (DeSante 1990) by varying levels of recruitment from a wider area. Thus, density of a species in a given area may not be indicative of population health, due to source-sink dynamics (Pulliam 1988). Primary demographic parameters are thus critical in understanding population dynamics and are directly applicable to population models that can be used to assess land-management practices (Noon and Sauer 1992).

Demographic parameters of avian populations, such as density (Brown et al. 1995), productivity (DeSante and Burton 1994, Robinson et al. 1995), and survivorship (Burnham et al. 1996; Johnson et al. 1992), vary spatially and temporally. Estimating these sources of variation is important for understanding dynamics of populations and for detecting trends that may reflect reduced viability (Wilcove and Terborgh 1984). Lack of knowledge on the extent of temporal variation in demographic parameters often leads to incorrect conclusions regarding population health and makes it difficult to argue that specific population declines are noteworthy and deserve additional attention. Although detection of environmental influences on animal populations is difficult, especially considering the "noisy" nature of time-series data, such as estimated population trajectories (e.g., Botsford and Brittnacher 1992), the detection process can be considered a preliminary search for patterns to be tested in detailed field studies (Holmes and Sherry 1988, Botsford and Brittnacher 1992, Sherry and Holmes, this volume), or to provide information on system state (Nichols, this volume). In this sense, monitoring helps direct priorities for applied research. Furthermore, monitoring, if done in an experimental or quasi-experimental manner (Nichols, this volume), is necessary to determine the effectiveness of management actions designed to reverse population declines or bring about the recovery of small or threatened populations (Noon 1992).

In 1989, The Institute for Bird Populations initiated *MAPS*, a cooperative effort among federal and state agencies, private organizations, and individual bird banders in North America to operate a continent-wide network of constant-effort mist-netting stations (DeSante et al. 1993, DeSante and Burton 1994). The *MAPS* Program was patterned to a large extent after the British Constant Effort Sites (CES) Scheme that has been operated by the British Trust for Ornithology since 1981 (Baillie et al. 1986) and that has become one of the cornerstones of the British Integrated Avian Population Monitoring Scheme (Baillie 1990).

An important aspect of monitoring is the ability to detect demographic trends and investigate the scale at which they may be occurring. Regional trends in annual survivorship may occur due to large-scale weather changes or changes in the landscape that are large enough to affect many local populations similarly. Local changes or trends in annual survivorship, such as may occur in a specific national forest, may occur due to changes in the habitat quality, for example, from increased harvest. Understanding the scale over which demographic parameters are changing will thus be informative for identifying future research needed to isolate problems, and, once identified, determining management solutions.

We evaluated the ability of *MAPS* to detect patterns of avian survivorship at different spatial scales. We view the results herein as a preliminary assessment, using a subset of the *MAPS* data. At the time of the symposia, only data through 1995 were available. Our analyses were restricted to Swainson's Thrush (*Catharus ustulatus*), a neotropical migrant that is a common breeder in western and northeastern North America in woodland environments, and winters in Central and South America (Ehrlich et al. 1988). We chose data from this species because it was one of the most commonly captured species in terms of both the number of stations in which it was captured and the numbers of individuals captured and recaptured.

METHODS

We used data from Swainson's Thrush populations in western North America to investigate patterns of survivorship among spatial scales. We compared variability of survival rates within and among scales. The spatial scales we investigated included: "locations", collections of neighboring stations, similar to the "cluster" (Rosenberg et al. 1999), biogeographic provinces, winter-migration scale (populations that winter in either Central America or South America as delineated by Marshall [1988]), and western U.S., the scale in which we pooled all stations. We used data from Swainson's Thrush that were marked and recaptured at 52 *MAPS* stations during 1992-1994, the only time period in which most stations had three years of data. Stations used in the analyses presented here were located in forest or mixed forest-scrub habitats. Typically, ten permanent net sites were distributed rather uniformly throughout the central 8 ha of the 20 ha study area, but were placed opportunistically at sites where birds could be captured most efficiently. One 12-m, 30-mm-mesh mist net was erected at each net site and the type and location of all nets were kept constant for the duration of the study. The operation of the nets was standardized; most stations were operated for six morning hours, beginning at sunrise, for one day per 10-day period, and for 8-12 consecutive 10-day periods, depending on latitude, from approximately May 1 to August 28. All unbanded birds captured were banded with USFWS bands and an attempt was made to identify all birds captured to age; sex could not be determined reliably for Swainson’s Thrush. DeSante and Burton (1994) provided details of establishment of net sites and their operation.

Mark-recapture was used each year to allow estimation of survival rates. We fit multinomial models to the capture-recapture data using program SURVIV (White 1983). To select the most appropriate model, we used Akaike's information criterion (AIC); we tested the significance between general and constrained models with likelihood ratio tests (Burnham and Anderson 1992, Lebreton et al. 1992). We compared five models that allowed survival rates (ϕ) to vary among geographical units within a spatial scale (Table 1), although each model constrained recapture probabilities (P) to be equal among all stations except for a model that allowed both ϕ and P to vary among locations. A common recapture probability among all stations was deemed appropriate based on earlier model tests (D. Rosenberg, unpubl. data; and see Rosenberg et al. 1999). Model $\{\phi_l , P_l\}$ was the most general, and allowed survival and recapture probabilities to vary among locations. Model $\{\phi_l , P\}$ allowed survival probabilities to vary among locations, but constrained recapture probabilities to be equal among all stations (Table 1). Model {ϕ_b , P} allowed survival rates to vary among biogeographic provinces and Model {ϕ_w , P} allowed survival rates to vary between different wintering-area subpopulations. Model {ϕ, P} was the most restrictive: survival rates and recapture probabilities were constrained to be equal among all stations. Survival estimates from individual stations had large (>19%, with most >50%) coefficients of variation, and, for some stations, estimates were unobtainable. Thus, we did not consider a model of individual stations, although some locations consisted of a single station (Table 2).

Table 1. Comparison of models of annual survival probability for Swainson's Thrush populations in western North America.

		GOF[a]				Likelihood Ratio Test[b]			
Model[c]	No. of parameters	X^2	df	P	AIC[d]	{ϕ_l,P}	{ϕ_b,P}	{ϕ_w,P}	{ϕ,P}
ϕ_l,P_l	34	47.2	34	0.07	264.6	0.81	0.29	0.36	0.37
ϕ_l,P	18	58.1	50	0.20	243.5		0.05	0.10	0.11
ϕ_b,P	7	77.8	61	0.07	241.2			0.64	0.64
ϕ_w,P	3	80.3	65	0.09	235.7				0.36
ϕ,P	2	81.1	66	0.10	234.6				

[a] Goodness-of-fit (GOF) statistics were used to evaluate model fit; larger P-values represent better fit (Lebreton et al. 1992).

[b] Likelihood Ratio Tests were used to determine significance of differences between the more reduced (simple) model (identified at the top of the column, and serves as the null hypothesis), and all other general submodels (listed under "Model," and serves as the alternate hypothesis). Higher P-values suggest little improvement in model fit with the more general model, and thus the reduced (simple) model is the most appropriate.

[c] Models include survival probabilities that are allowed to vary among locations (ϕ_l), among biogeographic provinces (ϕ_b), between winter ranges (ϕ_w), or that are constrained equal among all stations (ϕ) with a common recapture probability (P). Model {ϕ_l ,P_l } allows recapture probability to vary among locations.

[d] Akaike's Information Criteria (AIC); the minimum value represents the most appropriate model (Burnham and Anderson 1992, Lebreton et al. 1992).

Table 2. Summary information on survival estimates among various spatial scales for Swainson's Thrush populations from western North America.

Scale	No. Stations	Biogeographic province	Winter Range[a]	Sample Size[b]	$\hat{\phi}$[c]	$\widehat{SE}(\hat{\phi})$

Location						
ALAS	2	CE Alaska	SA	20	0.45	0.11
DENA	3	CE Alaska	SA	20	0.37	0.10
ARCA	2	Coastal	CA	67	0.50	0.06
BGSR	1	Coastal	CA	2	0.17	0.11
PALA	1	Coastal	CA	36	0.33	0.07
RFSL	6	Coast Ranges	CA	40	0.33	0.07
SISK	3	Coast Ranges	CA	12	0.55	0.14
SIUS	5	Coast Ranges	CA	230	0.43	0.04
MTBA	5	Cascades\Sierras	CA	80	0.40	0.06
TAHO	1	Cascades\Sierras	CA	2	0.27	0.24
WENA	2	Cascades\Sierras	CA	3	0.47	0.27
WILL	6	Cascades\Sierras	CA	84	0.56	0.05
UMAT	6	Basin-Range	SA	57	0.44	0.07
FLAT	6	Rockies	SA	128	0.40	0.05
GRFA	1	Rockies	SA	3	0	0
MESA	1	Rockies	SA	1	0.50	0.40
TSS	1	Rockies	SA	4	0.33	0.20
Biogeographic Zones						
Central Alaska	5		SA	40	0.42	0.08
Coastal	4		CA	105	0.42	0.05
Coast Ranges	14		CA	230	0.43	0.04
Cascades\ Sierra	14		CA	169	0.49	0.05
Basin-Range	6		SA	57	0.45	0.07
Rockies	9		SA	136	0.39	0.05
Winter Range						
Central America	32			556	0.45	0.03
South America	20			235	0.41	0.04
Western North America	52			791	0.44	0.03

[a] Winter range was determined by Marshall (1988).

[b] Sample size is the number of Swainson's Thrush banded and released in year one (1992).

[c] Survival rates were estimated with a recapture probability (0.54) that was estimated from a model of common recapture probabilities among all subpopulations (Table 1).

To evaluate the statistical power for detecting differences in survival rates and for detecting trends among different spatial scales, we constructed hypothetical populations using the approximate parameter estimates for the regional estimate of survival (0.45) and recapture probability (0.54) from the Swainson's Thrush data (see Results). We used the average number of individuals captured in the first year (1992) from the Swainson's Thrush data as the number released each year (total of unmarked and marked individuals) for each spatial scale in the simulated populations (Location: n=45, Biogeographic Zone: n=130, Winter Range: n=395, and Regional: n=790 individuals). We created three hypothetical populations, each with a different survival rate. Two of the three populations were constructed such that they had survival probabilities $\phi = \bar{\phi} + D\phi/2$, $\phi' = \bar{\phi} - D\phi/2$, where $D\phi$ represented the effect size, that is, the difference in survival rates between the populations. The third population was constructed to have the mean survival rate, $\bar{\phi}$. These methods were similar to those in Nichols et al. (1982). We investigated $D\phi$ from 0.05 to 0.40, with $\bar{\phi}=0.45$, and with 3 and 12 years of simulated data. We used the sample sizes (number of individuals banded in year one; assumed to equal the number of releases in each year of the study) listed above for each spatial scale, each reflecting the average number of individual Swainson's Thrushes marked in the first year of sampling. Thus, statistical power comparisons among spatial scales reflect the differences in population size attributed to each scale. We estimated the statistical power of detecting differences among 3 populations at each spatial scale; models permitting geographic variation in ϕ were compared to Model {ϕ, P}, in which all stations were constrained to have equal survival probabilities. For all power approximations we used an analytic approach rather than a Monte Carlo simulation approach. We used the parameter values under the various models and protocols (e.g., number of years) to create expected numbers of birds exhibiting each different capture history. The expectations were then entered into SURVIV as data, and estimator bias and statistical power were computed as described by Burnham et al. (1987:214-217).

We also evaluated statistical power for detecting trends indicating an exponential decline (0.5, 1.0, and 3.0% annual declines) in survival rates with 12 and 20 years of simulated data. An exponential decline would be one in which the survival rate for a given year was a constant fraction of the previous year's survival rate, such that $\phi_t = \phi_1 * \exp(- ß *[t-1])$, where ϕ_t is the survival rate between year t and $t + 1$ (t=2...n-1; where n is the number of years), ϕ_1 is the survival rate between year 1 and 2, and ß is the annual rate of change in survival (e.g., 0.005 for a 0.5% annual decline). We investigated the power to detect these trends for each spatial scale. Statistical power was determined using the approach of Burnham et al. (1987:215-217); the reduced model of equal survival rates among all years (Model {ϕ, P}) represented the null hypothesis, while the alternate hypothesis was Model {ϕ_d, P}, the model with an exponential decline in ϕ, but equal and constant P among all stations and years.

The effect of pooling data when differences among locations are not detected but present was investigated by computing the percent relative bias of the regional survival estimate. We used the estimates for each spatial scale, weighted by number of individuals captured in year one at the scale being investigated to provide a regional (weighted) estimate of survivorship and compared this value to that obtained by pooling all the data and estimating a single regional estimate. If we take the estimates of survival for each Swainson's Thrush population within a geographic scale and treat the estimates as the true survival rate, then percent relative bias can be computed as: 100[$\hat{\phi}$ - ϕ]/ϕ , where $\hat{\phi}$ denotes the estimated survival rates of the pooled populations and ϕ denotes the weighted survival rate, calculated as:

$$\phi = \sum_{i=1}^{k} (\hat{\phi}_i * R_i) / \sum_{i=1}^{k} R_i$$

where $\hat{\phi}_i$ and R_i are the estimated survival rate and number of individuals marked and released at year one, respectively, for a given *ith* population (*i* = 1, *2, . . . , k*) within a spatial scale (e.g., "location"). We then investigated how bias was related to the increase in the difference in survival rates, D ϕ, among locations using hypothetical populations. The 3 "populations" were given the same parameter values and years as was done for the power analyses, and percent relative bias was computed as described above.

RESULTS

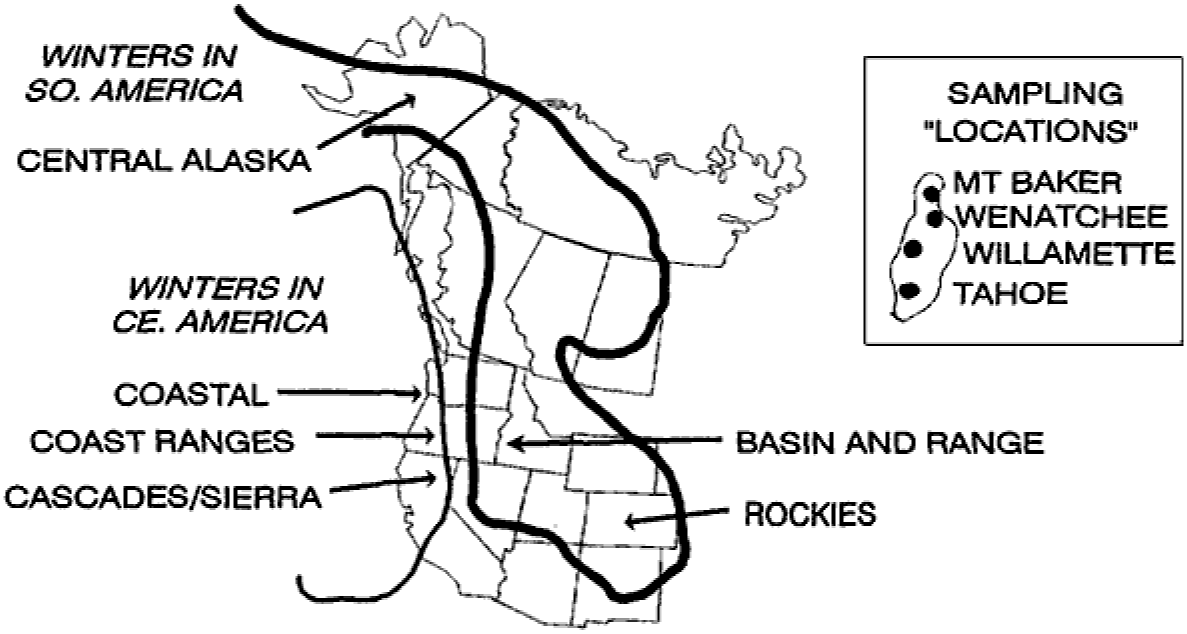
Survival rate estimates varied widely in both point estimates and coefficients of variation for the 52 stations for which Swainson's Thrush data were obtained, and for which there was at least one recapture. Numbers of individuals captured and marked in year one ranged from 1-76 ($\bar{X} \pm \hat{SE}$, 15.8 ± 2.2 individuals) per station. The coefficients of variation ($\hat{SE}/\bar{X}$, a measure of relative precision) for these estimates were typically >50%; this suggests that these (3 year) estimates were not generally very useful. Therefore, we did not consider the spatial scale of the individual station in further analyses, except in cases where the individual station was equivalent to the "location" because there were no other neighboring stations over which to pool data.

There was a total of 17 locations used in the analyses, with 3.1 ± 0.5 stations/location. Number of individuals captured in the first year of banding ranged from 1-230 (46.4 ± 14.6 individuals) per location. Estimates of annual survival varied considerably among locations (Table 2). The coefficient of variation for each location was also fairly large, generally >20%.

We identified 6 biogeographic provinces in which Swainson's Thrush were captured in western North America (Figure 1). Central Alaska included 2 locations, coastal areas in California and the Coast Ranges included 3 locations each, 4 locations were in the mountains of the Cascades and Sierra Nevada, 1 was in the Basin-Range Province, and 4 were in the Rockies. Within the scale of biogeographic provinces, number of individuals captured in the first year ranged from 40-282 (131 ± 35.9 individuals). Survival rate estimates varied from 0.39 to 0.49 (Table 2). Coefficients of variation ranged from 9-19% (13.1 ± 1.5%), reflecting considerable improvements in precision over the results at the scale of the location.

Based on work by Marshall (1988), we identified locations which could be separated by the subpopulations assumed to winter in either Central America or South America (Figure 1). Central American wintering populations included 10 locations (556 individuals marked in year 1) and those from South America included 7 locations (235 individuals marked). We estimated 45% and 41% annual survival rates for the Central and South American wintering populations, respectively. Precision was good for these estimates (Table 2): the coefficients of variation was <10%.

Figure 1. Sampling stratagy for estimating survival rates of Swainson's Thrush populations in western North America. Populations that winter in either Central or South America (Marshall 1988) were pooled for comparisons; these populations were pooled from a collection of biogeographic provinces that included coastal California, Coast Ranges, Cascades and the northern Sierra Nevada, Basin and Range, Rockies, and central Alaska. The subpopulations in the biogeographic provinces were pooled from a collection of "locations," which consist of 1 - 6 stations, each of which consist of a network of mist nets. For example, Swainson's Thrush in the Cascades/Sierra biogeographic province were part of the central America wintering population, and consisted of four locations (Mt. Baker, Wenatchee, Willamette, and Tahoe). Each of these locations consisted of one or more stations where birds were actually captured (Table 2).



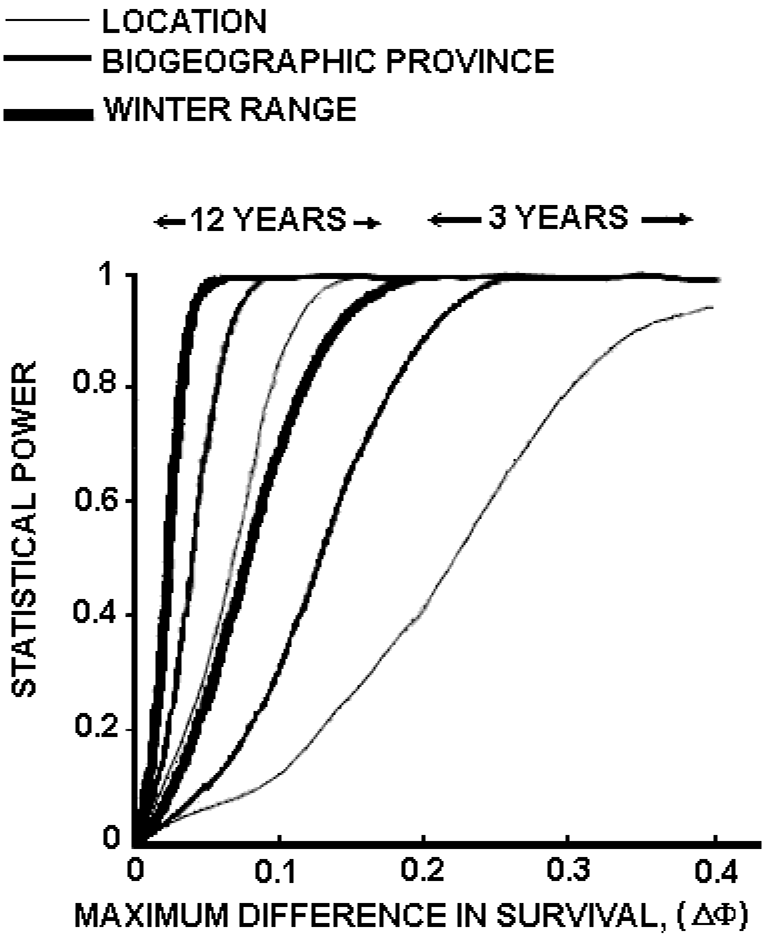
The largest spatial scale was that of the entire sampled area of western North America. A total of 791 individuals were captured in the first year of banding. We estimated a survival rate of 44% for this pooled population (Table 2), with a 7% coefficient of variation. We estimated a recapture probability of 0.54 ± 0.05; this represented the "pooled" recapture probability estimated in all the previous analyses as well.

The model tests, using both AIC and likelihood ratio tests, suggested the most parsimonious, adequate model was that with a common survival rate among all locations (Model $\{\phi, P\}$), although fit was only marginal for this model (Table 2; see Discussion). Model $\{\phi_l, P\}$ fit the data reasonably well, and likelihood ratio tests of this model against nested models with larger geographic groupings suggested that there was reasonable evidence that survival rates varied among locations (Table 2).

However, several models had similar AIC and these can be considered as competing models. The complexity of any chosen model is a function of sample size (Burnham et al. 1987), so it is not surprising that we failed to detect a more complex model, such as one in which capture probability and survival rates vary geographically. From an analysis of a larger data set, we found that the model that allowed geographic variation in survival rates at the scale of the Physiographic Province best described the data (Rosenberg et al. 1999).

Statistical power to detect spatial differences in survival rates increased with number of years (length of study), with greater differences in survival rates between groups (effect size), and with larger spatial scales (sample size). The ability to detect different survival rates between geographic areas was greatest for a scale similar to winter-ranges; with 12 years of simulated data, high power was achieved for small D ϕ for the winter-range scale (Figure 2). At the spatial scale of the individual location, adequate power (>80%) was not achieved with 3 years of simulated data until D ϕ was approximately 30%. With 12 years of simulated data, adequate power was achieved when D ϕ was approximately 10% (Figure 2).

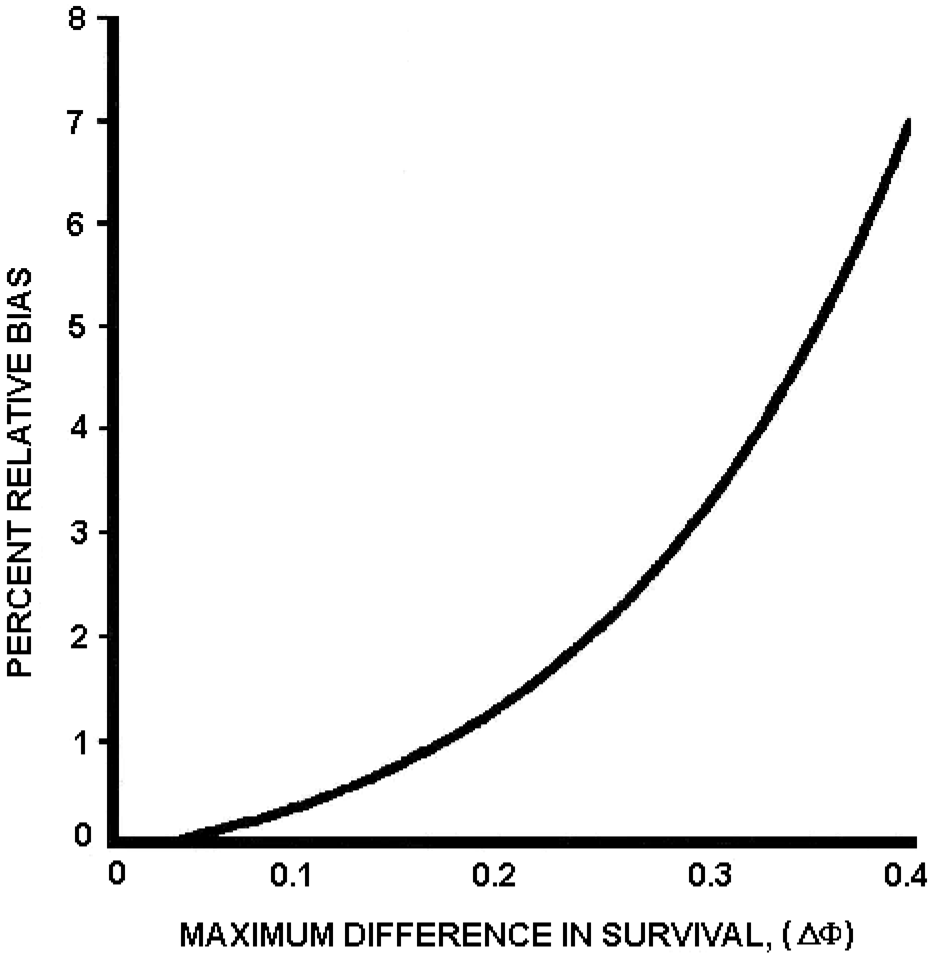
Figure 2. Statistical power to detect differences in survival rates of simulated populations in relation to maximum difference in survival (D ϕ), number of years of monitoring, and spatial scale. Spatial scale differences in statistical power reflect differences in sample sizes among the spatial scales equivilent to that of location, biogeographic province, and winter range. We estimated the statistical power of detecting differences among 3 populations at each spatial scale using methods of Burnham et al. (1987: 215); models with geographic variation were compared to Model {ϕ, *P*} in which all stations were constrained to have equal survival probabilities.



When differences are not detected, but are present, the bias due to pooling heterogeneous samples must be considered. We found that bias of regional estimates is small when pooling data from within spatial scales in which heterogeneity of survival rates is low (Figure 3). However, bias increased with greater differences in survival rates (Figure 2). Fortunately, when large differences existed, the power to detect them was high (Figure 2). Percent relative bias was very low (≤0.7%) with the Swainson's Thrush data; if differences existed, but were not detected, pooling these heterogeneous subpopulations would have negligible effects on regional survival estimates.

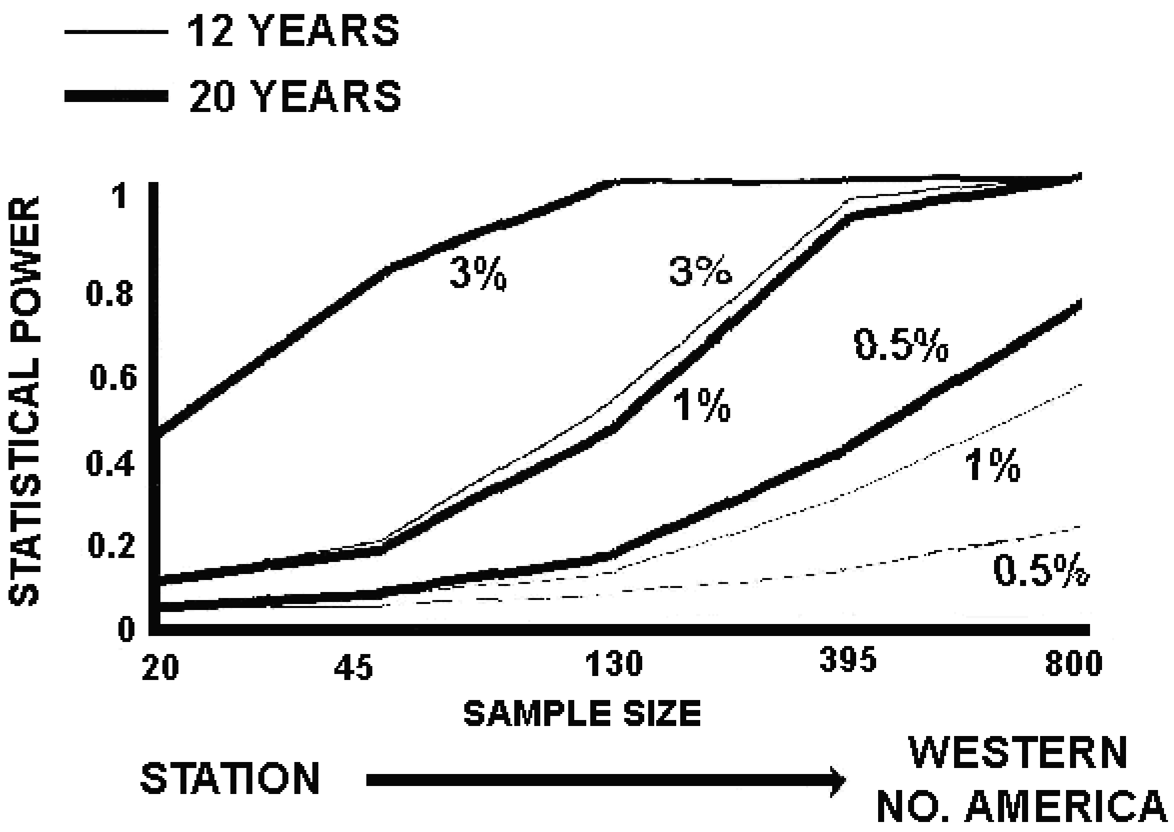
Figure 3. Relationship of percent relative bias due to pooling simulated populations with heterogeneous survival rates. When populations are pooled, but when they have different survival rates, the regional estimate may be biased. Percent relative bias was computed as 100[$\hat{\phi}-\phi$]/ϕ, where $\hat{\phi}$ denotes the estimated survival rates of the pooled populations and ϕ denotes the weighted survival rate, calculated as:

$\phi = \sum_{i=1}^{k} (\hat{\phi}_i * R_i) / \sum_{i=1}^{k} R_i$ where $\hat{\phi}_i$ and R_i are the estimated survival rate and number of individuals marked and released at year one, respectively, for a given *ith* population (*i*=1,*k*) within a spatial scale (e.g., "location"). We found small bias with relatively small differences in survival rates among simulated populations, but this bias increased rapidly with greater differences among populations.



Although detecting spatial differences in survival rates is interesting and important, one of the primary goals of a demographic monitoring program is to detect trends in these rates. The ability to detect trends at different scales is related to three factors: number of years, effect size (magnitude of decline), and spatial scale (sample size of banded birds). Statistical power was inadequate to detect 0.5% annual declines (i.e., survival rates each year are 0.5% lower than they were the previous year) in survivorship with both 12 and 20 years of data for all sample sizes examined (Figure 4). Statistical power was >80% for detecting 3% annual declines with 12 years of data for the larger spatial scales (Figure 4). Power was increased substantially with 20 years of data. Nevertheless, 20 years of data were necessary to detect 3% annual declines for the spatial scale of location; this demonstrates the difficulty of detecting local trends in survivorship.

Figure 4. Statistical power to detect exponentially declining survivorship in relation to sample sizes (e.g., number of birds released at year 1), length of monitoring, and percent annual decline for simulated populations. Power was based on the likelihood ratio test of the negative trend model (ϕ_d, P) against the reduced model of equal survival rates among all years (ϕ, P). Statistical power to detect trends was sensitive to the number of years and sample size; the larger sample sizes were achieved in the field study by pooling among smaller spatial scales, such that a total of approximately 800 Swainson's Thrush were captured in western North America.



DISCUSSION

Survival rates of landbirds may vary spatially and temporally. Examining survival rates in both time and space allows interesting and important management questions to be addressed. Our results suggest that these questions can be explored using a modeling approach with data collected from a monitoring program such as *MAPS*.

We found weak evidence of spatial differences in survivorship for Swainson's Thrush populations in western North America; the most parsimonious model was that of equal survival rates within western North America. The statistical power analyses we performed suggested that geographic differences in survival rates would be difficult to detect with three years of data collected from 3 locations. Power would likely have been higher with a larger number of locations, though many locations typically had lower number of captures than we used in the simulations. The results of the power analyses simply demonstrate the difficulty in detecting differences in survival rates with the sample sizes that are typical at small spatial scales with MAPS data (DeSante and Rosenberg 1998). In cases where survival rates vary geographically, but power to detect such differences is low, the regional estimate from a model of a common survival rate among locations would be chosen as the most appropriate.

If geographical differences in survivorship exist (e.g., among locations, biogeographic provinces, etc.), but are not detected, then pooling data may lead to a biased regional estimate. Fortunately, we found that only negligible bias will result when geographic differences in survivorship are low. When differences in survival rates between groups were sufficiently high to result in biased estimates (due to pooling) statistical power was sufficiently high to detect such differences. Similar results were reported by Nichols et al. (1982), although they reported lower power to detect geographic differences in survival rates than we did; this is likely due to the much higher capture probabilities used (and estimated from our field study) in our power analyses and the differences between band-recovery data vs capture-recapture models and data. In large-scale studies, geographic differences in survival rates should be evaluated prior to pooling data for a single regional estimate. If geographical differences exist, regional estimates could then be computed as averages of estimates from each geographic area. There was sufficient evidence to warrant concern over pooling all locations with the Swainson's Thrush data; however, bias resulting from this was negligible.

Although we explored only bias resulting from pooling heterogeneous samples, an additional source of bias that may be present in the estimates is that resulting from the presence of transient birds in the sampled population (Pradel et al. 1997). Transients will negatively bias survival estimates of resident birds because they, by definition, will not be present at the sampling site in subsequent years (i.e., probability of surviving and being recaptured = 0). For example, in a coastal California site monitored for 7 years, 72% of unmarked Swainson's Thrush were estimated as "transients", resulting in an estimated survival probablity for resident birds of 0.61, compared to an estimate of 0.36 when all birds were assumed to be residents (D. Rosenberg, unpubl. data). The "transient" model (Pradel et al. 1997) requires four sampling periods to provide estimates of annual survival rates of residents, and thus was not used in the analyses presented in this paper because at the time of analyses, only three years of data were available. Use of this model, however, will likely increase the accuracy of survival estimates for resident landbirds at a site when a significant portion of the individuals are transients. In the case of Swainson's Thrush, the transient model fit the data much better ($P = 0.20$) than the model that assumed all individuals were residents ($P = 0.0001$) at a scale equivalent to the "location" in analyses of 1992-1995 MAPS data (Rosenberg et al. 1999). The transient model improved the rather poor fit of the non-transient models used in the analyses we reported here (Rosenberg et al. 1999). The estimated percent of transients for Swainson’s Thrush was 56% (Rosenberg et al. 1999). The survival rates for Swainson’s Thrush under the transient model(0.63) was much higher than reported here (0.44). The large difference in AIC values between transient and non-transient models (Rosenberg et al. 1999) provided strong evidence that transients affected survival rates. Another source of bias of survival rates is emigration (DeSante and Rosenberg 1998). Because we were not able to estimate emigration rates, we do not know how the small study areas of MAPS stations may have biased survival rates. Although models have been developed that allow estimation of survival when movements occur among study areas (e.g., Hestbeck et al. 1991), the low probability of movements between stations under the current MAPS study design will likely prohibit the use of these models.

Detecting trends in survivorship will require long-term monitoring. Our results suggest that local trends of even relatively large annual changes will be difficult to detect. Trends that are regional in scope, however, will likely be detected, especially when the number of years of monitoring is large (e.g., >12). Although we were able to detect relatively large annual declines (3%) of survivorship with moderate sample sizes, such declines are unlikely to persist for long periods of time. What may be more important to investigate is the probability of detecting when survival has reached an *a priori* threshold value reflecting a decline (J. Sauer, pers. commun.). For example, based on a specific productivity, there exists a value of survivorship below which the population can be considered a "sink" rather than a "source" or stable population (Pulliam 1988). The ability to detect when a threshold value is attained may be more important, operationally, than detecting trends. This topic deserves further attention.

The approach we used to evaluate competing hypotheses of variation and trends in survival rates among spatial scales can be a powerful tool to detect environmental variation that directly affects survivorship and thus population dynamics of landbirds. The results highlight limitations and strengths of the sampling methods used in *MAPS*, the only North American program for assessing survivorship of landbirds. The *MAPS* program allowed for large-scale (regional) estimates, but did not adequately estimate rates for local scales with the 3 years of data used in the analyses presented here. Additional years of data will increase power considerably. Large sample sizes, high capture probabilities, and many years of sampling are key to estimating and comparing survivorship among sub-regional spatial scales.

ACKNOWLEDGMENTS

We thank the Biometrics group, especially J. Nichols, at Patuxent Environmental Science Center for their collaboration on methods of analyses for MAPS data, and to the many individuals, organizations, and agencies that have contributed data to the *MAPS* Program, to K. Burton, E. Feuss, D. O'Grady, E. Ruhlen, H. Smith, P. Velez, and B. Walker for preparation of data, and to J. Nichols, C. Conway, B. Cooper, J. Gervais, and N. Nur for constructive comments on earlier drafts of this manuscript. Financial support for the *MAPS* Program has been provided by the National Fish and Wildlife Foundation, The U.S. Fish and Wildlife Service, and Regions 1 and 6 of the U.S.D.A. Forest Service. This is contribution No. 57 of The Institute for Bird Populations.

LITERATURE CITED

Baillie, S. R. 1990. Integrated population monitoring of breeding birds in Britain and Ireland. Ibis 132:151-160.

Baillie, S. R., Green, R. E., Boddy, M., and Buckland, S. T. 1986. An Evaluation of the Constant Effort Sites Scheme. British Trust for Ornithology. Thetford, U.K.

Botsford, L. W., and J. G. Brittnacher. 1992. Detection of environmental influences on wildlife: California quail as an example. Pages 158-169 *in*: McCullough, D. C. & R. H. Barrett (Eds.), Wildlife 2001: Populations. Elsevier Applied Science, London.

Brown, J.H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. Ecology 76:2028-2043.

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

Burnham, K. P., D. R. Anderson, G. C. White. 1996. Meta-analysis of vital rates of the northern spotted owl. Studies in Avian Biology 17:92-101.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5.

DeSante, D. F. 1990. The role of recruitment in the dynamics of a Sierran subalpine bird community. Am. Nat. 136:429-445.

DeSante, D. F. and K. M. Burton. 1994. The Monitoring Avian Productivity and Survivorship (MAPS) Program third annual report (1992). Bird Populations 2:62-89.

DeSante, D. F., and D. K. Rosenberg. 1998. What do we need to monitor in order to manage landbirds. Pages 93-110 *in* J. Marzluff and R. Sallabanks (eds.), Avian conservation: research and management. Island Press, Covelo, CA.

DeSante, D. F., O. E. Williams, and K. M. Burton. 1993. The Monitoring Avian Productivity and Survivorship (MAPS) Program: overview and progress. Pages 208-222 *in* D. M. Finch and P. W. Stangel (Eds), Status and management of Neotropical migratory birds, USDA Forest Service, Rocky Mt. Forest and Range Experimental Station, Ft. Collins, CO. General Technical Report RM-229.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook. Simon and Schuster, Inc. New York.

Finch, D. M., and Stangel, P. W. 1993. Introduction. Pages 1-4 *in* D. M. Finch and P. W. Stangel (Eds), Status and management of Neotropical migratory birds, USDA Forest Service, Rocky Mt. Forest and Range Experimental Station, Ft. Collins, CO. General Technical Report RM-229.

George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. Ecol. Appl. 2:275-284,

Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark0resight data of wintering Canada Geese. Ecology 72:523-533.

Holmes, R. T., and T. W. Sherry. 1988. Assessing population trends of New Hampshire forest birds: local vs. regional patterns. Auk 105:756-768.

Johnson, D. H., J. D. Nichols, and M. D. Schwartz. 1992. Population dynamics of breeding waterfowl. Pages 446-485 *in*: B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu (Eds.), Ecology and managment of breeding waterfowl. University of Minnesota Press, Minneapolic, MN.

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

Marshall, J. T. 1988. Birds lost from a giant sequoia forest during fifty years. Condor 90:359-372.

Nichols, J. D., S. L. Stokes, J. E. Hines, and M. J. Conroy. 1982. Additional comments on the assumption of homogeneous survival rates in modern bird banding estimation models. J. Wildl. Manage. 46:953-962.

Noon, B. R. 1992. Thoughts on the monitoring of terrestrial vertebrates. Pages 49-50 *in* G. S. Butcher and S. Droege (Eds.), Needs Assessment: monitoring neotropical migratory birds. Cornell Laboratory of Ornithology, Ithaca, NY.

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

Pradel, R., J. E. Hines, J.-D. Lebreton, and J. D. Nichols. 1997. Capture-recapture survival models taking into account transients. Biometrics 53:60-72.

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

Robbins, C. S., Sauer, J. R., Greenberg, R. S., and Droege, S. 1989. Population declines in North American birds that migrate to the neotropics, Proceedings of the National Academy of Sciences 86:7658-7662.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990.

Rogers, J. G., Jr., T. J. Dwyer, and C. Martin. 1993. Pages 5-6 *in*: D. M. Finch and P. W. Stangel (Eds), Status and management of Neotropical migratory birds, USDA Forest Service, Rocky Mt. Forest and Range Experimental Station, Ft. Collins, CO. General Technical Report RM-229.

Rosenberg, D. K., D. F. DeSante, K. S. McKelvey, and J. E. Hines. 1999. Monitoring survival rates of Swainson's Thrush (*Catharus ustulatus)* at multiple spatial scales. Bird Study 46 (suppl.):198-208.

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

Terborgh, J. 1989. Where have all the birds gone? Essays on the biology and conservation of birds that migrate to the American tropics. Princeton University Press, New Jersey.

Wilcove, D. S., and J. W. Terborgh. 1984. Patterns of population decline in birds. American Birds 38:10-13.

White, G. C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. Journal of Wildlife Management 47:716-728.

1 The Institute for Bird Populations
P.O. Box 1346
Point Reyes Station
CA 94956

2 U.S. Geological Service
Patuxent Wildlife Research Center
Laurel, MD 20708

3 Present Address:
Oregon Cooperative Fish and Wildlife Research Unit
Department of Fisheries and Wildlife
Oregon State Unversity
Corvallis, OR 97331