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Monitoring survival rates of Swainson's Thrush *Catharus ustulatus* at multiple spatial scales

DANIEL K. ROSENBERG[1]*, DAVID F. DESANTE[1], KEVIN S. McKELVEY[2] *and* JAMES E. HINES[3] [1]*Institute for Bird Populations, PO Box 1346, Point Reyes Station, CA 94956, USA,* [2]*US Forest Service, Redwood Sciences Laboratory, Arcata, CA 95521, USA,* [3]*US Geological Survey, Biological Rescources Division, Patuxent Environmental Science Center, Laurel, MD 20811, USA*

We estimated survival rates of Swainson's Thrush, a common, neotropical, migratory landbird, at multiple spatial scales, using data collected in the western USA from the Monitoring Avian Productivity and Survivorship Programme. We evaluated statistical power to detect spatially heterogeneous survival rates and exponentially declining survival rates among spatial scales with simulated populations parameterized from results of the Swainson's Thrush analyses. Models describing survival rates as constant across large spatial scales did not fit the data. The model we chose as most appropriate to describe survival rates of Swainson's Thrush allowed survival rates to vary among Physiographic Provinces, included a separate parameter for the probability that a newly captured bird is a resident individual in the study population, and constrained capture probability to be constant across all stations. Estimated annual survival rates under this model varied from 0.42 to 0.75 among Provinces. The coefficient of variation of survival estimates ranged from 5.8 to 20% among Physiographic Provinces. Statistical power to detect exponentially declining trends was fairly low for small spatial scales, although large annual declines (3% of previous year's rate) were likely to be detected when monitoring was conducted for long periods of time (e.g. 20 years). Although our simulations and field results are based on only four years of data from a limited number and distribution of stations, it is likely that they illustrate genuine difficulties inherent to broadscale efforts to monitor survival rates of territorial landbirds. In particular, our results suggest that more attention needs to be paid to sampling schemes of monitoring programmes, particularly regarding the trade-off between precision and potential bias of parameter estimates at varying spatial scales.

Large-scale trends in avian demographic patterns may result from large-scale weather changes or changes in the landscape that affect areas large enough to have similar effects on many local populations. Local changes or trends may result from changes in the vegetation structure, for example, from tree harvest. If the pattern of local environmental change is pervasive, similar regional patterns may result. Understanding the scale of trends will thus be informative for determining future research needed to identify, and solve, specific management problems. Processes that affect patterns in demographic rates are likely to be scale dependent (e.g. productivity[1]); management policies and activities often respond to relatively local issues, although

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*Correspondence author. Present address: Oregon Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA.
Email: Dan.Rosenberg@orst.edu

concern over small-scale patterns may be motivated by documentation of larger-scale phenomena. Thus, monitoring must be effective at multiple scales ranging from 'local' (e.g. national forest or park) through 'regional' (e.g. physiographic strata) to 'large' (e.g. eastern North America or the entire range of the species).

Although there is a large effort to monitor wildlife population trends at small spatial scales, there are few programmes that attempt to monitor trends at larger geographical scales. Understanding patterns at small scales is critical in guiding research and management actions to address local concerns.[2] However, it is difficult to identify likely hypotheses accounting for local demographic changes when large-scale patterns are unknown. The challenge is to design monitoring programmes to provide estimates of parameters of bird populations at large geographical scales, while maintaining adequate precision at small spatial scales.[3]

To examine geographical variation and the effects of spatial scale in identifying and describing variation in survival rates, we used mark–recapture data from Swainson's Thrush *Catharus ustulatus* populations in western North America, collected by the Monitoring Avian Productivity and Survivorship (MAPS) Programme.[4] Swainson's Thrush is a neotropical migrant that is a common breeder in woodlands in western and northeastern North America and winters in Central and South America.[5] We examined the precision of survival-rate estimates and estimated geographical variation of survival rates at various spatial scales. We further explored the question of statistical power to detect geographical and temporal variation in survival rates using simulated data based on our Swainson's Thrush analyses. Data on Swainson's Thrush from MAPS are typical of the data from large-scale monitoring efforts, in that sites are not selected using a probability-based design,[3] the distribution of numbers of captures across stations is highly skewed towards a few sampling sites[6] and the sampling effort is extensive.

METHODS

Collection of data

Stations were established in approximately 20-ha study areas.[4] Those used in the analyses presented here were typically located in forest/meadow edge habitat. Approximately ten permanent net sites were distributed rather uniformly throughout the central 8 ha of the study area, but were placed opportunistically at sites where birds could be captured most efficiently. Generally, one 12-m mist-net of 30 mm mesh 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 usually 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.

A total of 144 stations was operated in each year from 1992–95. For survivorship analyses, we used only stations that were operated for at least half the number of hours normally operated within a ten-day period (60 net hours) for at least three periods that fell within dates appropriate for survival analyses of resident birds. Further, only stations for which at least 50 different individual adult Swainson's Thrushes were captured during 1992–95 in the cluster (defined below) to which the station belonged, were included. Finally, only stations where Swainson's Thrush was considered a breeding species were retained. Forty-two stations met these criteria. They were located from northern California to central Alaska, and from near the Pacific Coast inland to the Rocky Mountain Range. Physiographic Provinces in which stations were located included Southern Pacific Rainforest, Central Rockies, Cascade Range, Dissected Rockies, Northern Rockies and Southern Alaskan Coast.

To investigate patterns of survivorship among spatial scales, we assigned each station to a particular geographical unit within a spatial scale. For example, the Point Reyes Bird Observatory station was assigned to the geographical unit of Southern Pacific Rainforests in the spatial scale of the North American Breeding Birds Survey (BBS) Physiographic Province. Spatial scales, from the smallest to the largest, were: cluster, a grouping of neighbouring stations (e.g. those in Willamette National Forest); BBS Physiographic Province (e.g. South Pacific Rainforests[7]); MAPS Region (e.g. northwest North America[4]); and western North America, the scale at which we pooled all of the stations.

Membership of a specific cluster was determined by the distance of neighbouring stations. A matrix of approximate inter-station distances was computed. To assign stations to clusters, we used all 144 stations and then omitted clusters that did not meet the minimum criteria for sample sizes described above. We used a centroid clustering algorithm[8] to assign all 144 stations into 60 clusters. We chose 60 clusters as this was the number required to place all stations that were subsamples of a given location (e.g. Willamette National Forest) into the same cluster. Thus, stations that were not selected *a priori* as subsamples, but were equally close in distance to other stations as those that were selected as subsamples of a location, were grouped into a cluster. A cluster represented approximately all stations within 100 km of one another. A cluster included from one to 11 stations. Estimates of survival and recapture probabilities at the scale of the individual station typically had large (>19%, with most >50%) coefficients of variation[9] and, for some stations, estimates were unobtainable. Thus, we did not consider models at the spatial scale of individual stations.

Survival analyses

Mark–recapture data were used to estimate survival rates. We fitted time-constrained models to the capture–recapture data using program SURVIV modified to accommodate the transient model described below.[10] We describe these as either 'Resident' models, in which all individuals in the captured population are assumed to be residents, or 'Transient' models. Estimates under our Resident models were those derived under a time-constant model for 1992–95. Several methods have been suggested to reduce the bias of survival rate estimates of resident birds resulting from the presence of transients (i.e. captured individuals which do not remain in the population after the sampling period in which they were captured).[11,12] Our transient models use the method of Pradel *et al.*[12] to estimate the proportion of residents and thus reduce bias of survival estimates. They allow for differences in survival rates of newly marked and previously marked individuals, and are structurally equivalent to the handling-effect model developed by Brownie & Robson.[13] Differences in survival rates between these two groups of individuals may often be due to the presence of transients.[14] In the case of Swainson's Thrush, transients may include individuals searching for breeding territories (i.e. 'floaters'[15]) as well as migratory individuals. Survival estimates from the Transient models are restricted to 'resident' birds and thus are 'after-second-year' individuals.[14] Parameter estimates were constrained to be equal among years. The annual survival rates that we estimated under the Transient models were from the period 1993–95. By including within-year, as well as between-year, recapture information in a revised transient model, we may be able to include an additional year of survival data in the model. The increased precision of the survival estimates expected to result from including this additional year of data, however, may at least partially be negated by the increased number of parameters required by such a transient model.

We compared a total of 25 survival models. These can be categorized as: (1) Resident models that allowed survival rates to vary at the scale of the individual cluster; (2) Resident model that constrained parameters to be equivalent among all stations; (3) Transient models that allowed at least one of the parameters to vary geographically at each of three spatial scales (Cluster, Physiographic Province, Region); and (4) Transient models that constrained parameters to be equivalent among all stations within western North America (Table 1). We focused comparisons on Transient models that allowed survival rate (ϕ), recapture probability (P) and the probability that a newly marked individual is a resident (γ), to vary geographically, and models that constrained one or more of these parameters to be equal among geographical units (Table 1). Model (ϕ_i,P_i,γ_i) (see Table 1 for description) was the most general and allowed survival, recapture probabilities and probability of residency to vary among the i geographical units within a spatial scale. Model (ϕ,P,γ) was the most constrained; each parameter was constrained to be equivalent among all stations. Thus, pooling was done by constraining parameters to be equal among stations within a geographical unit. There were no tests for year-dependence in any of the parameters. We predicted that: (1) capture probabilities would be most likely to vary at small spatial scales due to differences in trap-

Table 1. Description of survival models investigated with MAPS data. Geographical units *i* refer to particular locations within a spatial scale. For all but the most reduced Transient model (ϕ,P,γ), the models are unique for each spatial scale. Parameters were constrained to be equivalent among all years.

Model parameterization	*Description*
ϕ,P	Resident model; no allowance for transients ($\gamma = 1.0$); parameters constrained equal among geographical units
ϕ_i,P	Resident model; only ϕ allowed to vary among geographical units; no allowance for transients ($\gamma = 1.0$)
ϕ_i,P_i,γ_i	Most general Transient model; all parameters allowed to vary among geographical units
ϕ_i,P_i,γ	Transient model with ϕ and P allowed to vary geographically but γ constrained equal among geographical units
ϕ_i,P,γ_i	Transient model with ϕ and γ allowed to vary geographically but P constrained equal among geographical units
ϕ,P_i,γ_i	Transient model with P and γ allowed to vary geographically but ϕ constrained equal among geographical units
ϕ,P,γ_i	Transient model with γ allowed to vary geographically but ϕ and P constrained equal among geographical units
ϕ,P_i,γ	Transient model with P allowed to vary geographically but ϕ and γ constrained equal among geographical units
ϕ_i,P,γ	Transient model with ϕ allowed to vary geographically but P and γ constrained equal among geographical units
ϕ,P,γ	Most reduced Transient model; all parameters constrained equal among geographical units

Spatial scales considered for which there are >1 geographical unit are the Cluster, BBS Physiographic Province and MAPS Region. Geographical units (denoted by *i*) are scale-specific; for example, within the BBS Physiographic Province scale, a geographical unit would be a single province, such as the Northern Rocky Mountains. Parameters include annual survival rate (ϕ), recapture probability (P) and the probability that a newly marked individual is a resident (γ), for the *i*th geographical unit within a spatial scale.

ping intensities;[16] and (2) probability of residency would be most likely to vary among regions (Pacific Northwest and Alaska), with a lower proportion of residents in the Northwest than in Alaska, which is the northernmost part of the range of Swainson's Thrush. We did not predict the scale at which survival rates would vary; mechanisms affecting survival rates of a species could be affected locally by habitat changes or regionally by climate and region-specific wintering grounds,[9] as well as by other factors.

To select the most appropriate model for estimating survival and related parameters, we relied on Akaike's information criterion (AIC) for models in which we did not reject the null hypothesis of model fit ($P > 0.05$).[17] Lower AIC indicates a more appropriate model, based on the trade-off of model fit (describing the data) and the principle of parsimony. Recent work suggests that selecting the model with the lowest AIC results in a more appropriate model than using likelihood-ratio tests;[17] we therefore relied entirely on AIC for model selection. We used the analytical methods described by Burnham *et al.*[18] to compare geographical (spatial) and sampling variance at the scale of the Physiographic Province; geographical variation was estimated as total variance minus sampling variance.

Evaluation of statistical power

To evaluate the statistical power for detecting differences in survival rates among populations and for detecting trends at different spatial scales, we constructed hypothetical populations using survival and recapture values equivalent to those which we estimated from analyses of three years of Swainson's Thrush data.[9] We assumed all birds captured were residents (i.e. $\gamma = 1.0$); this assumption will result in greater statistical power to detect patterns in survival rates than if a proportion of the birds captured were assumed to be transients. We used parameter values of 0.45 and 0.54 for adult survival and recapture probability, respectively, and used population sizes of 83, 241, 731 and 1463 for the spatial scales equivalent to the Cluster, Physiographic

Province, Region and western North America. These population sizes were derived from the average number of individuals captured (45, 130, 395 and 790) during 1992, estimated as $n/\hat{P}$, where n is the number of individuals captured and $\hat{P}$ is the estimated recapture probability.[9] We created three hypothetical populations, each with a different survival rate. Two of the three populations were constructed such that they had survival probabilities:

$$\bar{\phi} = \bar{\phi} + \Delta\phi/2 \text{ and}$$
$$\phi' = \bar{\phi}\ \Delta\phi/2$$

where $\Delta\phi$ represented the effect size, i.e. 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.*[19] We investigated $\Delta\phi$ from 0.05 to 0.40, with $\bar{\phi} = 0.45$, and with three and 12 years of simulated data. Survival and recapture probabilities were set constant across all years. We estimated the statistical power of detecting differences among three populations at each spatial scale (i.e. at different population sizes); models permitting geographical variation in ϕ but not P (model [ϕ_i,P]) were compared to model (ϕ,P) in which all stations were constrained to have equal survival and recapture probabilities. For power approximations we used an analytical 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.*[18]

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 $\phi_t = \phi_1 \times \exp(-\beta \times [t-1])$, where ϕ_t is the survival rate between year t and $t + 1$ ($t = 2 \ldots n - 1$; where n is the number of years), ϕ_1 is the survival rate between year one and two, and β is the annual rate of change in survival (e.g. 0.005 for a 0.5% annual decline). Thus, a survival rate of 0.60 would decline to 0.34 in 20 years under an annual exponential decline of 3%. We investigated the power to detect these trends for various spatial scales. Statistical power was determined using the approach of Burnham *et al.*;[18] the reduced model of equal survival rates among all years (ϕ,P) represented the null hypothesis, while the alternative hypothesis was model (ϕ_d,P), the model with an exponential decline in ϕ but equal and constant P among years.

RESULTS

A total of 2046 adult Swainson's Thrushes were captured during 1992–95 at the 42 stations included in the survival analyses. Under the Transient model for western North America (ϕ,P, γ), we estimated the percentage of residents

Table 2. Estimates of Swainson's Thrush survival probability (ϕ), recapture probability (P) and proportion of residents (γ), with associated estimated standard errors, for a subset of models at multiple spatial scales within western North America.

Scale	*Model*	$\hat{\phi}$	$\widehat{se}(\hat{\phi})$	$\hat{P}$	$\widehat{se}(\hat{P})$	$\hat{\gamma}$	$\widehat{se}(\hat{\gamma})$
Cluster	ϕ_i,P	0.49	0.04	0.51	0.03	1.0[a]	–
	ϕ_i,P,γ	0.60	0.06	0.60	0.03	0.57	0.04
Province	ϕ_i,P,γ	0.60	0.06	0.60	0.03	0.57	0.04
Region	ϕ_i,P,γ	0.56	0.05	0.60	0.03	0.56	0.04
	ϕ,P,γ_i	0.63	0.03	0.60	0.03	0.46	0.06
Western North America	ϕ,P	0.48	0.02	0.51	0.03	1.0[a]	–
	ϕ,P,γ	0.63	0.03	0.60	0.03	0.56	0.04

Estimates, and associated se values, for parameters allowed to vary among the *i* geographical units are the (non-weighted) mean estimate.

[a]The proportion of residents is assumed to equal 1.0 (i.e. these models do not include a transient parameter).

Table 3. Akaike's information criteria (AIC) and goodness-of-fit (GOF) for models investigated with Swainson's Thrush data at multiple spatial scales within western North America

Spatial scale	*Model*	*No. of parameters*	GOF	AIC
Cluster	ϕ_i, P_i	18	0.0001	384.8
	ϕ_i, P	10	0.001	384.7
	ϕ_i, P_i, γ_i	27	0.20	349.4
	ϕ_i, P_i, γ	19	0.27	339.3
	ϕ_i, P, γ_i	19	0.06	350.4
	ϕ, P_i, γ_i	19	0.24	340.3
	ϕ_i, P, γ	11	0.13	338.2
	ϕ, P_i, γ	11	0.08	342.0
	ϕ, P, γ_i	11	0.10	340.2
Province	ϕ_i, P_i, γ_i	18	0.06	350.0
	ϕ_i, P_i, γ	13	0.08	343.6
	ϕ_i, P, γ_i	13	0.09	342.8
	ϕ, P_i, γ_i	13	0.06	345.1
	ϕ_i, P, γ	8	0.12	336.0
	ϕ, P_i, γ	8	0.02	347.7
	ϕ, P, γ_i	8	0.11	337.2
Region	ϕ_i, P_i, γ_i	6	0.05	341.0
	ϕ_i, P_i, γ	5	0.04	341.9
	ϕ_i, P, γ_i	5	0.05	340.5
	ϕ, P_i, γ_i	5	0.05	339.3
	ϕ_i, P, γ	4	0.04	340.6
	ϕ, P_i, γ	4	0.02	345.2
	ϕ, P, γ_i	4	0.05	338.6
Western N.A.	ϕ, P	2	0.0001	395.2
	ϕ, P, γ	3	0.02	345.1

GOF value shown is the probability that the model fits the data.

to be 55.8 (Table 2), suggesting that a large proportion of the captured adults were transient individuals.

The Resident models at the cluster and western North America scale fitted the data poorly and had the highest AIC values (Table 3). The inclusion of the probability of residency as a parameter in the models improved fit and did not appreciably reduce precision (Table 2). The Transient models in which at least one parameter was allowed to vary geographically provided the best fit and had the lowest AICs (Table 2). At the spatial scale of the Cluster and Province, models that allowed only survival rates to vary geographically (model [ϕ_i, P, γ]) were selected. Of the two models, the Physiographic Province scale model had a lower AIC (336.0) than the Cluster scale model (338.2; Table 3). At the scale of the Region, the model that allowed only the proportion of residents to vary (model [ϕ, P, γ_i]) had the lowest AIC. However, models at this scale did not fit the data well ($P \leq 0.05$; Table 3). At each scale, several competing models existed in which one or more parameters varied geographically.

Estimated survival rates under model (ϕ_i, P, γ) at the spatial scale of the Cluster ranged from 0.42 to 0.79 (Fig. 1). Precision was moderate at this scale (Fig. 1); the coefficient of variation (CV) ranged from seven to 20% (mean ± se, 11.3 ± 1.7). Pooling data at the scale of the Physiographic Province, for the two Provinces with more than one cluster, slightly increased the precision of the estimates (compare Figs 1 & 2 for South Pacific Rainforest and Cascades provinces). At the Physiographic Province scale, estimated survival rates ranged from 0.42 to 0.75, with coefficients of variation from 5.8 to 20.0% (11.5 ± 2.5%), under model (ϕ_i, P, γ). At this scale, there was greater geographical variation (53.5%) than sampling variation (46.5%), as estimated by variance components analyses. Scaling up to the Region increased precision (CV = 9.2%) especially for

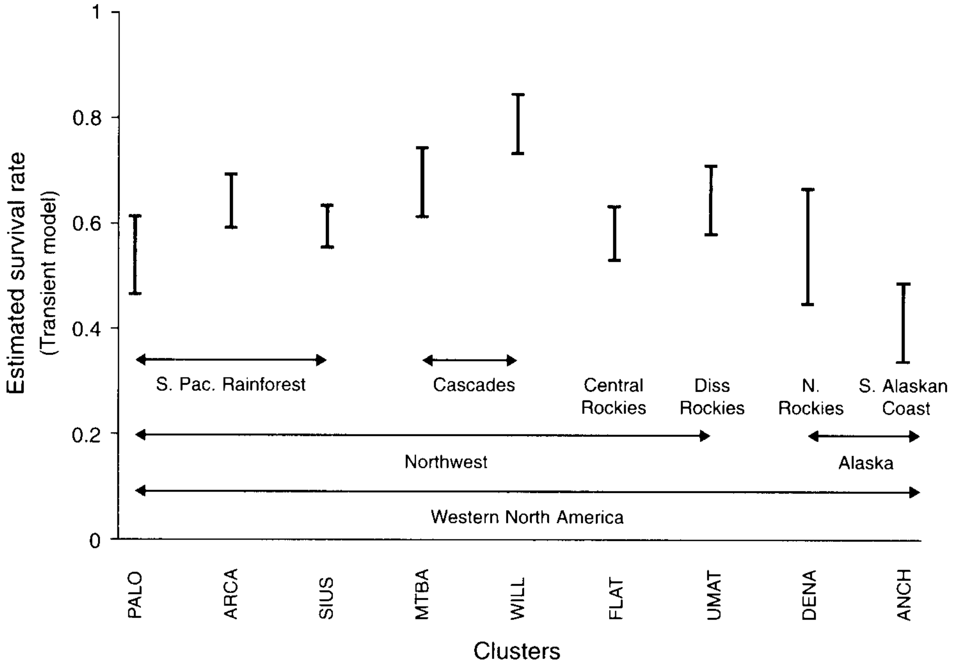

Figure 1. Estimated survival rates for Swainson's Thrush derived from model (ϕ_t,P,γ) at the spatial scale of the cluster. Bars represent estimated survival rates ± 1 se. The nine clusters of stations used in the analyses are shown with the cluster name on the x-axis. Arrows indicate grouping of clusters at larger spatial scales.

the Pacific Northwest (cv = 4.2%; Fig. 3). Many provinces were pooled within this region. The western North America scale had a similar coefficient of variation to the Pacific Northwest (Fig. 2) because most of the data were from that region.

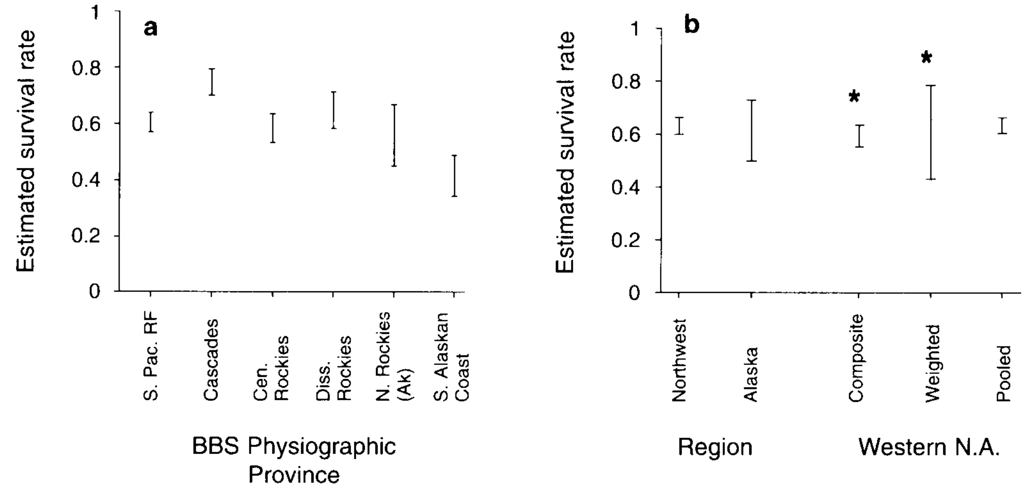

Figure 2. Geographical variation in survival rates of Swainson's Thrush. Estimated survival rates are from the spatial scale of (a) BBS Physiographic Province derived from model (ϕ_t,P,γ) and (b) MAPS Region (model (ϕ_t,P,γ)) and western North America derived from mean and precision-weighted mean of estimates from model (ϕ_t,P,γ) at the Cluster scale, and a pooled estimate (model (ϕ,P,γ)). Bars represent estimated survival rates ± 1$\widehat{se}$, except those indicated by an asterisk which represent the empirical sem survival rate estimates within clusters.

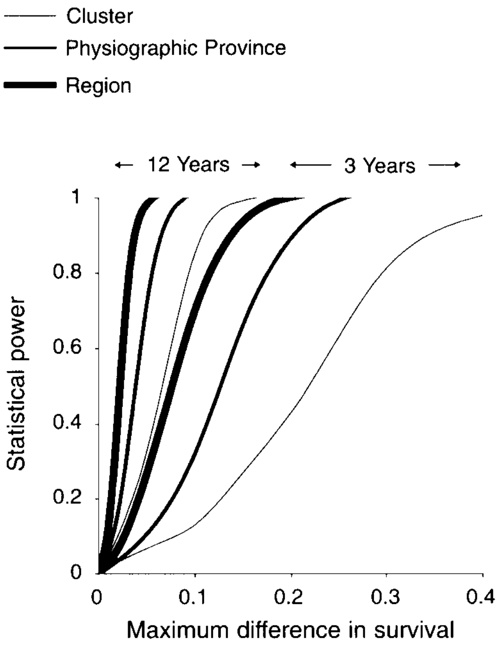

Figure 3. Statistical power to detect differences in survival rates of simulated populations in relation to maximum differences in survival, number of years of monitoring, and spatial scale, which reflects sample size (number of birds released and recaptured).

Evaluation of statistical power

Statistical power to detect spatial differences in survival rates increased with number of years (duration of study), with greater differences in survival rates between groups (effect size) and with larger spatial scales (sample size). With 12 years of simulated data, high power was achieved for small $\Delta\phi$ for the Regional scale (Fig. 3). At the spatial scale of the cluster, adequate power (>80%) was not achieved with three years of simulated data until $\Delta\phi$ was approximately 30%. However, with 12 years of data, adequate power was achieved when $\Delta\phi$ was approximately 10%. Power to detect differences in survivorship for a scale equivalent to Physiographic Provinces was greater than for Clusters but less than for a scale equivalent to a Region (Fig. 3).

The ability to detect trends at different scales is related to three factors: study duration, the magnitude of the decline, and the spatial scale (sample size of ringed birds). Statistical power was inadequate to detect 0.5% annual declines in survivorship (i.e. survival rates each year are 0.5% of those in the previous year) with both 12 and 20 years of data for all sample sizes we examined (Fig. 4). Statistical power was >80%

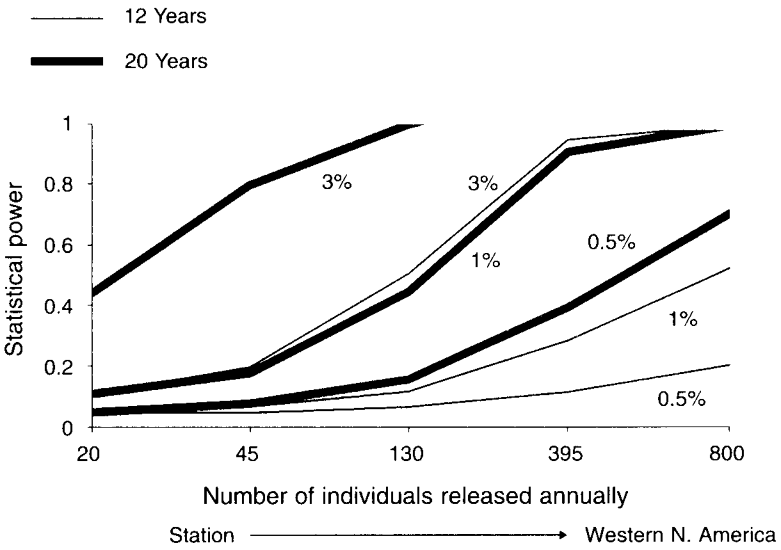

Figure 4. Simulation analysis of the statistical power to detect exponentially declining survivorship in relation to the number of individuals released annually, number of years of monitoring and percentage annual decline. The spatial scale reflects the average number of birds released annually in a geographical unit within a particular spatial scale. Data were simulated to reflect field data on Swainson's Thrush from the MAPS programme.[9] Initial survival rates used in the simulations were 0.45 and recapture probability was 0.54.

for detecting 3% declines with 12 years of data for the larger spatial scales (Fig. 4). Power was increased substantially with 20 years of data. Nevertheless, 20 years of data were necessary to detect 3% annual declines for the sample size of birds that would be typical at the spatial scale of the Cluster; in our example, this would be 45 individuals captured, ringed and released each year. This demonstrates the difficulty of detecting local trends in survivorship.

DISCUSSION

We found strong evidence that survival rates varied geographically for Swainson's Thrush populations; estimated survival rates ranged from 0.42 to 0.75. Although the sampling variance was high, we found greater geographical than sampling variance at the scale of the Physiographic Province. The models at larger geographical scales did not fit the data well, even when allowing one or more parameters to vary geographically. This was presumably because there was spatial heterogeneity in the parameters that was not accounted for at the larger spatial scales. At the smaller spatial scales, models that allowed parameters to vary spatially tended to fit the data. There was sufficient geographical variation in survival rates at the scale of the Physiographic Province that the model that allowed survival rates to vary spatially, but had constant capture probability and proportion of transients, had the lowest AIC and was thus the preferred model.

Although the best models for describing survival rates of Swainson's Thrush with the MAPS data were those that allowed survival rates to vary spatially at the scale of the Province and Cluster, precision was relatively poor at these spatial scales. Similar results were found with most of the commonly captured species from MAPS.[6] Improvements in precision, however, would be achieved with a greater number of years of mark and recapture data[6] or more intensive sampling effort.[3] Station-specific survival and recapture probabilities were estimated by Peach[20] for a nine-year data set on passerines. For example, he reported that the coefficient of variation of survival estimates for Willow Warblers *Phylloscopus trochilus* ranged from 13.5 to 57.8%, with an average of 29.8% at eight sites (computed from Table 4 of Peach[20]). These sites typically had large numbers of individuals captured and recaptured and were operated for nine years, whereas MAPS stations varied considerably in the number of individuals per station and were operated for only four years.[6] Most MAPS stations had few individuals captured; over 25% of Swainson's Thrushes marked were captured from only four stations.[6]

Because we had few stations with large numbers of captures, we considered only spatial scales of the Cluster or larger, even though survival and recapture probabilities may be site-specific, as Peach[20] reported. There is likely to be heterogeneity of recapture probabilities at the scale of the individual station because of station-specific intensities of sampling. For example, recapture probabilities varied among two sites in the Constant Effort Sites programme for Reed and Sedge Warblers (*Acrocephalus scirpaceus* and *A. Schoenobaneus*); the differences were attributed to the different sampling efforts at the two sites.[16] Unfortunately, MAPS data may never permit precise estimation of station-specific variation in recapture probabilities for Swainson's Thrush (or any other territorial landbird species), because only a limited number of territories (probably less than about 15)[21] are likely to be sampled at any single MAPS station. Fortunately, however, potential bias in survival estimates caused by heterogeneous capture probabilities is frequently quite small.[22,23] Results from CES[20] and MAPS (this study) demonstrate the difficulty in obtaining precise, local estimates, especially with a highly clumped frequency distribution of birds. Such distribution patterns may be characteristic of animal populations.[24,25]

Statistical power to detect geographical differences in survival rates was generally low for small differences in survival rates. Power was substantially improved with 12 years of data and at larger spatial scales (which is equivalent to a larger number of releases). We derived the power approximations under a time-constrained model in which the proportion of residents was assumed equal to 1.0. In reality, most samples will include transients and survival rates are likely to vary temporally as well as spatially. Larger sample sizes (number of birds released) will be needed to achieve the power approximations demonstrated in the simulations when transients and time dependence are present and allowed for in the model structure. Our power approximations were for a limited set of conditions. The ability to detect spatial variation in survival rates will vary according to the complexity of the models investigated and the underlying pattern of survival rates, recapture probabilities and proportion of transients.

Important to the issue of monitoring is whether pooling data from large geographical areas masks smaller-scale patterns. Given that patterns of declines in bird abundance are typically on a subregional scale,[26] and are not necessarily reflected in patterns at smaller scales,[27] pooling data from large geographical areas may decrease the ability to detect temporal patterns if they vary geographically. Only for species with large population sizes, high recapture rates and a large proportion of residents, are precise estimates at smaller spatial scales obtainable under sampling strategies that are typical of most large-scale monitoring programmes. In the MAPS data set, Swainson's Thrush had one of the largest samples sizes (number of birds captured) and recapture probabilities of the nearly 200 species captured,[6] yet local estimates, even at the scale of the Physiographic Province, were imprecise. Although trends in survival rates at scales similar to the Physiographic Province have been demonstrated,[28] the statistical power approximations we conducted and the imprecise survival estimates we obtained for Swainson's Thrush suggest that detecting trends in survival rates at small spatial scales will be difficult.

Once additional years of MAPS data have been collected, it may be possible to investigate year-specific variation in some parameters. Moreover, use of a revised transient model that includes within- as well as between-year information may improve accuracy of the survival estimates (by providing a more accurate estimate of the proportion of residents), and may also increase the precision of the survival estimates.

The allocation of effort is equally as important as the total effort expended. Many large-scale monitoring schemes do not have a probability-based sampling design; usually they lack a formal sampling strategy (e.g. CES,[20] MAPS[4]). That few stations contributed most of the information for the Swainson's Thrush data, and for most other species in the MAPS programme,[6] suggests that estimates are unlikely to be representative of spatial scales larger than the actual study sites and may perhaps only be representative of the study area of the few stations that contributed the majority of the data. The potential bias in average survival rates for a geographical area is a concern because of the non-random sampling strategy. If a probability-based design were used, then it could be argued that the dominance of a few stations represents the true distribution of abundance; hence, there may be little bias in the average rates since they reflect the population.

This is unlikely to be the case with data from many monitoring programmes, such as MAPS, that do not utilize a probability-based sampling design. Thus, inferences beyond the specific study sites should only be made with caution. If there were common traits among study sites, hypotheses could then be made relevant to a common trait, such as a specific habitat type. Much more attention needs to be given to the issue of sampling strategy, allocation of effort and the spatial scale of interest, in order to provide rigorous monitoring of demographic rates of birds. In practice, designs that are to be useful must account for the need to capture adequate numbers of birds at individual sampling stations and to incorporate locations that are suitable for mist-netting. This requires some compromise with designs that are statistically ideal. These issues have received little attention despite their importance in providing useful information for the conservation and management of landbirds.

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