Demographic monitoring and the identification of transients in mark-recapture models

Demographic monitoring and the identification of transients in mark-recapture models

M. Philip Nott and David F. DeSante

2000

The Institute for Bird Populations

P.O. Box 1346

Point Reyes Station, CA 94956-1346

Tel: (415) 663-1436 Fax: (415) 663-9482

All correspondence to Dr. Phil Nott (pnott@birdpop.org)

Key words: Demographic monitoring - mark-recapture models - SURVIV – TMSURVIV – LOSSURV – productivity – survival rates – constant effort mist-netting – North American Breeding Bird Survey-MAPS Program– seasonal activity – diurnal activity – transients

Abstract

The demographic causes of avian population change may be identified by demographic monitoring techniques, including mist-netting and nest monitoring, that provide inferences regarding productivity and survivorship parameters. Accurate estimates of these parameters are essential for the construction of predictive population models. Constant-effort mist netting provides spatially-explicit estimates of adult survival rates from mark-recapture modeling of banding data and indices of productivity from the ratio of young to adult birds. This technique provides both within-year and between-year information allowing modifications to be made to mark-recapture models that consider the existence of transient individuals and provide estimates of demographic parameters for the resident proportion of the population. We describe the flexibility of constant effort mist-netting data and outline methods by which the accuracy of estimating demographic parameters can be improved. We examined banding data from the Monitoring Avian Productivity and Survivorship (MAPS) program for ten bird species captured in the northwestern United States at 36 constant-effort banding stations (operated between 1992 and 1998) and determine temporal patterns for three demographic groups of their populations: resident adults, transient adults, and juveniles. We also compared estimates of adult survival rates, recapture probabilities, and proportions of residents obtained from three mark-recapture models (SURVIV, TMSURVIV and LOSSURVIV). LOSSURV, a recent modification of TMSURVIV considers individuals categorized as transients or residents according to a length-of-stay criterion. We found that while TMSURVIV and LOSSURVIV both provide unbiased estimates of adult survival rates, LOSSURVIV provides more precise estimates. We found that both diurnal and seasonal patterns of capture probabilities of the three demographic groups varied by species. The relationship between inter-specific variation in the timing of appearance and numbers of captures of adults and juveniles (productivity), and survival rates was consistent with migration strategy. Tropical-wintering migrants had higher survival but lower productivity than temperate-wintering migrants. Productivity indices are also negatively correlated with adult survival rates, illustrating the trade-off between survival rate and productivity.

Introduction

Methods for monitoring bird populations fall into two categories; population monitoring or demographic monitoring. Population monitoring includes techniques such as point count surveys and area searches that can provide inferences regarding species richness and abundance. Over time these techniques can detect change in population size but may not be able to identify whether the cause(s) of that change are associated with birth or death processes if they do not discriminate between breeding and non-breeding individuals. The demographic causes of population change may be identified by demographic monitoring techniques, including banding and nest monitoring, that provide inferences regarding productivity and survivorship parameters. Accurate estimates of these parameters are essential in the construction of predictive population models. Constant-effort mist netting provides spatially-explicit estimates of survival rates from mark-recapture modeling of banding data (Buckland and Baillie 1987, Rosenberg et al. 1999), and indices of productivity obtained from the ratio of young to adult birds captured (DeSante 1992, DeSante et al. 1995, Peach et al. 1996,). This technique provides both within-year and between-year information allowing modifications to be made to mark-recapture models that consider the existence of transient individuals and provide estimates of demographic parameters for the resident proportion of the population.

Pradel et al. (1997) proposed a method for identifying transients and adjusting survival rate estimates accordingly. This method is incorporated into a modification of the Cormack-Jolly-Seber mark-recapture model (Cormack, 1964; Jolly, 1965; Seber, 1965) called TMSURVIV (Pradel et al. 1997). This model provides estimates of the proportion of residents (γ) in addition to estimates of survival rate (ϕ) and recapture probability (P). Although this method allows that a bird caught in only one year may be a resident, based on the probability of between-year recaptures being less than unity, it ignores within-year information inherent in banding data that is derived from constant effort mist-netting. Analyzing these data requires a more sophisticated mark-recapture model that considers a length-of-stay criterion for individual birds (Pradel et al. 1997). This is provided by LOSSURVIV, a recent modification by J. Hines and J.D. Nichols of TMSURVIV.

In this paper we describe the flexibility of constant effort mist-netting data and outline methods by which the accuracy of estimating demographic parameters can be improved. We utilize banding data from ten bird species (three temperate-wintering, three temperate/tropical- and four tropical-wintering species) captured in the northwestern United States at 36 constant-effort banding stations operated by the Institute for Bird Populations as part of the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante 1992, DeSante et al. 1995). We analyze banding data for the period 1992 to 1998 to provide temporal patterns of the resident adult, transient adult, and juvenile portions of the population. For each species we compare these trends with those obtained from population monitoring data for the western states provided by the North American Breeding Bird Survey (BBS; Peterjohn et al. 1995). We compare estimates of adult survival rates, recapture probabilities, and proportions of residents obtained from three different mark-recapture models (Pollock et al. 1990, Lebreton et al. 1992). These include LOSSURV, a recent modification of SURVIV (White 1983, 1986) that considers individuals categorized as transients or residents according to a length-of-stay criterion. Finally, we explore the relationship between survival rate and productivity as a function of migratory strategy with respect to accepted life history theory for temperate, temperate/tropical and tropical migrants.

Methods

The Monitoring Avian Productivity and Survivorship (MAPS) program collects data from over 500 field stations across the North American continent (DeSante et al. 1998, 1999). This program adopts a "constant-effort mist-netting" protocol to provide survivorship estimates and productivity indices for passerines. Typically, at each station, bird-banding teams operate ten mist nets located within the central 8ha of a 20 ha study plot for six hours following sunrise. Each station is visited on one day within sequential ten-day periods throughout the breeding season (May to August) up to a maximum of 10 periods. Normally, six stations constitute a MAPS "location" which represents a monitoring effort in a national forest, national park or other managed land area. The protocol assumes that captures include adults and young from both the vicinity of the monitoring station early in the breeding season and from the surrounding landscape later in the season as breeding activity ceases and the birds begin to disperse.

Here, we consider a group of 36 stations that allow us to monitor demographic parameters in forested lands under the stewardship of the USDA Forest Service Region 6, which covers the Pacific Northwest region of the United States. Specifically, the locations included are Mount Baker NF and Wenatchee NF in Washington state and Willamette NF, Siuslaw NF, Umatilla NF and Fremont NF in Oregon state. These forests are typically heavily managed and share many plant, animal and bird species. Data were pooled for ten target species (top ten species ranked by total number of captures in each case, represented by over 500 individuals captured) captured at these stations to provide regional survival rate estimates for adult birds.

We selected banding data for the ten most captured species (Table 1) each over the seven-year period from 1992 through 1998 inclusive. Dates of operation vary by station dependent upon latitude and elevation. We only considered captures made between MAPS periods 4 to 10 representing the seven ten-day periods between May 31st and August 8th that were common to all stations.

Demographic groups and indices of productivity

Birds that are caught and banded belong to one of three demographic groups – residents, transients and juveniles. Early in the breeding season the catch includes philopatric individuals returning to breeding territories within the boundaries of the banding station, many of which are caught year after year. The remaining portion of the early season catch is made up of transient individuals passing through the station on their

Table 1. Common names, scientific names, and Breeding Bird Laboratory (BBL) abbreviations for ten bird species represented by over 500 individuals in the MAPS database for USDA Forest Service Region 6.

Common Name	Scientific Name	BBL Abbr.
“Western” Flycatcher	*Empidonax difficilis & E. occidentalis*	WEFL
WinterWren	*Troglodytes troglodytes*	WIWR
Swainson’s Thrush	*Catherus ustulatus*	SWTH
Yellow-rumped (Audubons’s) warbler	*Dendroica coronata audubonii*	AUWA
Townsend’s warbler	*Dendroica townsendi*	TOWA
MacGillivray’s Warbler	*Oporornis tolmiei*	MGWA
Wilson’s Warbler	*Wilsonia pusilla*	WIWA
Song Sparrow	*Melospiza melodia*	SOSP
Lincoln’s Sparrow	*Melospiza lincolnii*	LISP
Dark-eyed (Oregon) Junco	*Junco hyemalis oregonus*	ORJU

way to distant territories, or seeking habitat in which to establish new territories. In the middle of the breeding season the catch consists of resident breeders (whose activity space includes a mist net location) and unpaired adults (floaters) that may be queuing for available territories or passing through in search of otherwise unoccupied breeding habitat. Although some individuals are only caught in one year they may be caught more than once in that year and could be considered as resident birds. Later in the season, as young birds fledge and adult territoriality relaxes, the catch includes dispersing juveniles and adults from the surrounding area.

For each species we constructed temporal activity patterns by categorizing individuals as resident, transient or juvenile individuals according to their capture histories:

Adults Seen Once (ASO) – transient adults include those individuals captured once and once only and those individuals caught in only one year but more than once within a period of less than 7 days.
Between Year Residents (BYRES) – those individuals caught in at least two different years. It is assumed that the probability of any these individuals are merely passing through the site and are caught in more than one year is very low.
Within Year Residents (WYRES) – those individuals caught in only one year but caught more than once in that year. They are only classified as WYRES if the maximum "length-of-stay" between captures exceeded 6 days, otherwise they were assigned to the ASO category.
Known Residents (KNRES) – those individuals classified as BYRES or WYRES; we assume these birds represent the group that are resident at the monitoring site.
Young (YNG) – these are individuals identified in the database as juvenile birds that may have come from the site or from the surrounding landscape.

For each species we estimated linear temporal trends for the annual numbers of all adults, known residents, adults seen once and juveniles. We indexed productivity as the proportion of young in the catch both annually and as a mean annual index for the whole period. We recorded the frequency of captures of birds (pooled across years) in each category by ten-day period, calculated the abundance of each category as a proportion of the total number of captures, and plotted the results as a histogram for each species. Furthermore, to look at the diurnal patterns of activity, we plotted the frequency of captures by hour after sunrise. Henceforth we refer to these histograms as "seasonal capture profiles" and "hourly capture profiles", respectively.

Comparing population trends in MAPS with Breeding Bird Survey data

The North American Breeding Bird Survey (BBS) provides trends of the numbers of birds of all species seen and heard at a number of stops along routes distributed across North America (Peterjohn et al. 1995). We obtained the regional BBS abundance trends (James et al. 1996, Link and Sauer 1998) for ten target species (Table 1) of BC, WA, OR, and CA for the period 1992-1998. For each species, we compared these trends with corresponding trends in the number of adults calculated from MAPS data.

Estimates of survivorship and transience

Birds caught only once may belong to any of the three demographic groups. Adults may be transient individuals, residents that died or left the area by the next year, or residents caught in the latest year of banding that may be caught in future years. The transient individuals cause survivorship estimates to be biased low in closed-population models. Pradel et al. (1997) approached the problem of identifying transients using an *ad hoc* approach to produce unbiased estimates of resident proportions, that effectively ignores the first year of capture for all individuals. This approach is incorporated into TMSURVIV, a modified version of the program SURVIV (White 1983, 1986) that produces estimates of survivorship and capture probabilities for residents, as well as proportions of residents. This approach although unbiased with regard to the recapture probabilities, does not take into account the important "within-year" information that can indicate that an individual captured in only one year is a resident, rather than a transient. Pradel et al. (1997) suggest that the critical parameter in identifying transients is the length-of-stay period and that transients can be detected with a suitable study design in which the interval between capture sessions exceeds that of the maximum length-of-stay of a transient individual. Constant-effort banding studies represent a sampling design appropriate for detecting transients using a length-of-stay method because banding sessions can be separated by an interval which exceeds the period of time a transient might be expected to stay in the area.

For each species, we constructed capture histories for all adult birds. We obtained time-constant estimates of adult survival probability (ϕ), recapture probability (P), and proportion of residents (γ) by entering the capture histories into three different mark-recapture models. The first and oldest model, SURVIV (White 1983) assumes a closed population and does not distinguish between transient and resident individuals. The second model, TMSURVIV, is a modification of SURVIV that provides an unbiased estimate of the resident proportion based on between-year information (Pradel 1997). The final model, LOSSURVIV, is a modification of TMSURVIV that considers additional within-year information. This model requires categorizing capture histories as a) unmarked individuals caught only once in the first year of capture, regardless of how many times they were caught in subsequent years, and b) marked individuals caught more than once seven or more days apart in their first year of capture. We processed these capture histories for each species through a number of permutations of time-constant and time-independent (with respect to ϕ, P and γ) sub-models to ascertain whether the time-constant $\phi P \gamma$ sub-model represented the most (or equally) parsimonious sub-model for estimating demographic parameters. We compared and contrasted the values of demographic parameters resulting from these models.

The relationship between survival rate and productivity

DeSante et al. (1998) presented evidence for the existence of the trade-off between survival rate and productivity suggested by Martin (1995) and found the relationship to be a function of longitude and migration strategy. The underlying theory is that the longer a species lives the fewer offspring it needs to produce to maintain stable population levels. Avian migration to climatically more stable tropical wintering areas may lead to higher over-wintering survival rates relative to those of temperate-wintering species. On the other hand temperate-wintering species can exploit available breeding habitat sooner than tropical-wintering species and potentially produce more clutches. All else being equal, survival rates and productivity indices should correlate negatively and be a function of migration strategy. To explore this relationship we plotted the relationship between survivorship and productivity for the ten species of this study.

Results

Seasonal and hourly capture profiles

Seasonal capture profiles (Figure 1) show the number known resident individuals (KNRES = BYRES+WYRES), individual adults seen once only (ASO), and individual young birds as a function of sequential visits (periods) to the stations throughout the breeding season. Typically, the peak of KNRES captures occurs in period 6 or 7 corresponding to late June or early July, with the exception of Dark-eyed Juncos where the peak capture period occurs in period 4 at the beginning of June. Note that the seasonal capture profiles of KNRES includes, for many individuals, multiple captures of the same birds. The peak of ASO captures relative to the peak of resident captures varies across species, and occurs in the same or a later period, never earlier. The ASO profile for the Western Flycatcher takes a sudden jump from 50 to 80 individuals in period 7 whereas that for the Dark-eyed Junco decreases gently over the entire season. Although the date varies by year, the appearance of young first occurs in period 6 or 7 and generally increases to a peak in periods 9 and 10 for all species except Song Sparrow and Lincoln's Sparrow for which it occurs in periods 9 and 8, respectively.

The hourly capture profiles depicted in Figure 2 also show differences between species but not across demographic groups within a species. Generally, the proportion of total captures decreases as the day progresses. Approximately 45% of MacGillivray's Warbler, Swainson's Thrush and Song Sparrow captures occur in the first two hours (peaking in the second hour), followed by a gradual decline in the hourly capture proportion thereafter. Lincoln's Sparrow captures occur mainly in the first three hours (60% of total) and decline more rapidly thereafter. Hourly capture profiles for Western Flycatcher and Dark-eyed Junco show a more even distribution except that the proportion of Western Flycatcher captures made in the first hour is very low.

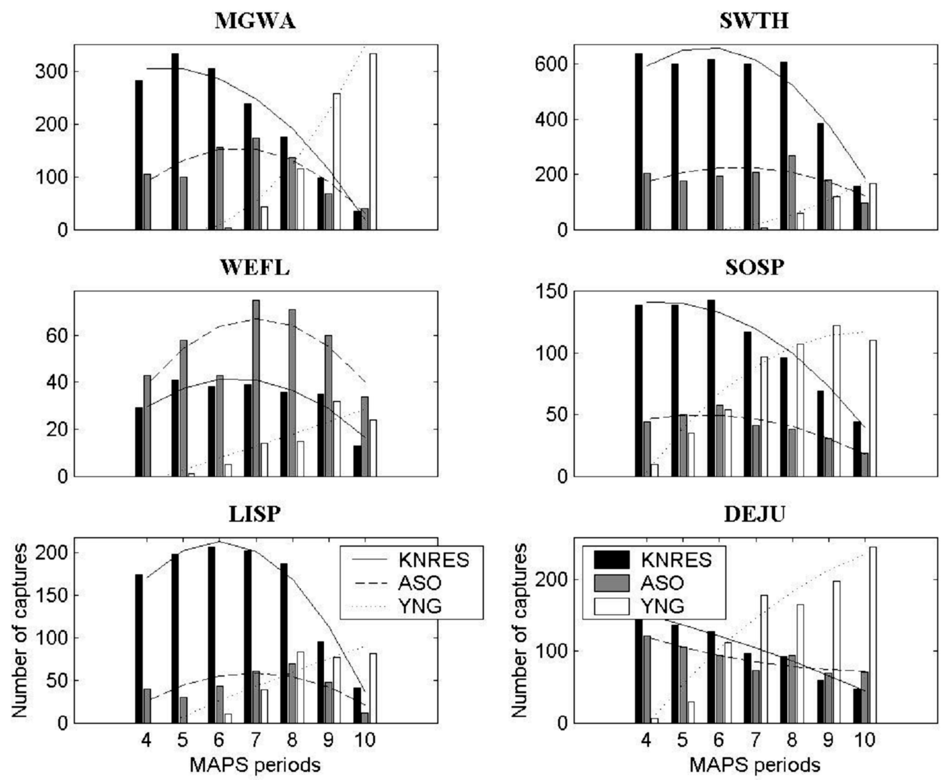

Figure 1. Seasonal capture profiles of the number of individuals caught in mist nets by ten-day periods between May 31st and August 8th. These data are pooled from 36 banding stations across a seven-year period (1992-1998). Six species are represented: MacGillivray's Warbler (MGWA), Swainson's Thrush (SWTH), "Western" Flycatcher (WEFL), Song Sparrow (SOSP), Lincoln's Sparrow (LISP), and Dark-eyed (Oregon) Junco (ORJU) Individuals are categorized into three groups and second order polynomials are fitted to each set of histogram bars. These categories are known residents (black bars, solid line), adults seen once only (gray bars, dashed line), and young birds (white bars, dotted line).

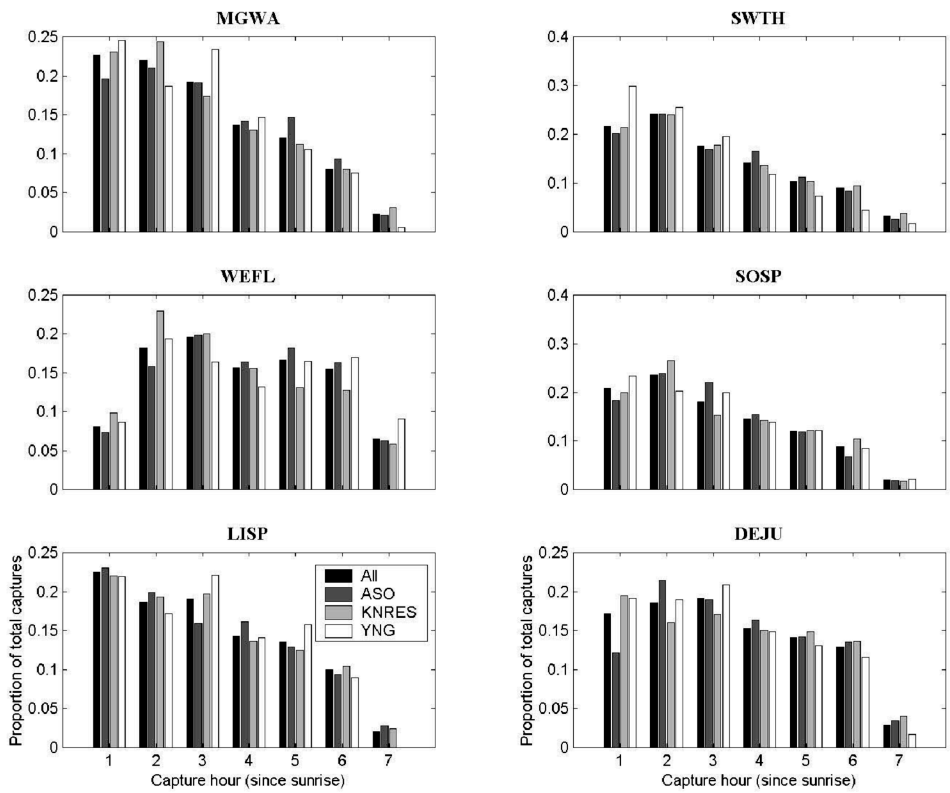

Figure 2. Hourly capture profiles of the proportion of individuals caught in mist nets in each of seven hours after sunrise. These data are pooled from 36 banding stations, visited annually between May 31st and August 8th, across a seven-year period (1992-1998). Six species are represented: MacGillivray's Warbler (MGWA), Swainson's Thrush (SWTH), "Western" Flycatcher (WEFL), Song Sparrow (SOSP), Lincoln's Sparrow (LISP), and Dark-eyed (Oregon) Junco (ORJU). Individuals are categorized into four groups: all adults (black bars), adults seen once only (dark gray bars), known residents (light gray bars), and young birds (white bars).

Population trends in MAPS and Breeding Bird Survey data

Six of the ten species show a negative trend in the total number of adults caught during the period 1992-1998 (Table 2) but only Townsend's Warbler shows a significant trend ($p<0.05$). Generally, these trends are reflected in the trends reported for the KNRES and ASO portions of the captures, as well for the annual numbers of young captured. The increases in the total number of adult Song Sparrows and Winter Wrens appears to be associated with significant increases in the number of adults only seen once. Similarly,

Table 2. Total number and short-term trends (1992-1998) in all adults (Adult), known residents (KNRES), adults seen once (ASO), and young (Young) for ten bird species well represented in the MAPS data covering USDA Forest Service Region 6 (Species abbreviations are WEFL - *Empidonax difficilis & E. occidentalis;* WIWR - *Troglodytes troglodytes;* SWTH - *Catherus ustulatus;* AUWA - *Dendroica coronata audubonii;* TOWA - *Dendroica townsendi;* MGWA - *Oporornis tolmiei;* WIWA - *Wilsonia pusilla;* SOSP - *Melospiza melodia;* LISP - *Melospiza lincolnii; and* ORJU - *Junco hyemalis oregonus).* Regional population trends for the North American Breeding Bird Survey (BBS) for BC, WA, OR, and CA are also shown. The mean annual proportion of young (PI) in the total catch (pooled across all stations) is expressed as (Young/(Adults + Young)).

Code	Adult	trend	KNRES	trend	ASO	trend	Young	trend	BBS	PI
WEFL	470	-4.0	92	-2.2	378	*-1.8	88	0.3	*-2.79	0.14
WIWR	534	1.2	138	-2.8	396	*4.1	266	2.5	*5.57	0.31
SWTH	2213	5.6	947	0.5	1266	5.2	342	-3.2	*-2.25	0.09
AUWA	379	-1.2	55	-2.0	324	0.8	186	-4.0	-1.08	0.29
TOWA	447	*-8.5	68	*-7.1	379	-1.4	469	-6.6	-2.26	0.45
MGWA	1158	-4.8	407	-5.6	751	-0.8	720	-5.9	-0.9	0.32
WIWA	776	-3.5	199	-2.9	557	-0.6	312	-5.7	-1.46	0.28
SOSP	484	5.0	219	0.5	265	*4.5	492	2.5	1.31	0.45
LISP	550	0.9	279	-0.7	271	1.6	267	0.0	*2.37	0.25
DEJU	889	-2.1	277	*-3.7	612	1.7	939	*-18.3	*-1.22	†0.45

* statistically significant ($p<0.05$)
† significantly decreasing productivity ($p=0.01$)

the decline in Western Flycatcher adults is associated with a significant decline in the numbers of adults seen once. Conversely, the declines in Townsend's Warbler and Dark-eyed Junco adults are associated with significant declines in the numbers of known residents. For the Dark-eyed Junco population at least, the overall decline may be driven by a significant decline in the numbers of young. Breeding Bird Survey trends for these species in the western coastal states region agree with the MAPS adult trends in nine out of ten cases. The MAPS trend for adult Swainson's Thrush shows an increase and the BBS trend a decline

Competing mark-recapture models

For each species comparisons of the survivorship probability, capture probability and resident proportion from three competing mark-recapture models: SURVIV, TMSURVIV and LOSSURVIV are shown in Table 3. In all cases the time-independent transient model represents the most (or equally) parsimonious model reported by TMSURVIV or LOSSURVIV based on the values of Aikaike information criteria (Burnham and Anderson 1992) associated with each combination of time dependent and time-independent ϕ, P and γ models. The values of both ϕ and P parameter estimates are significantly greater for both TMSURVIV and LOSSURVIV than for SURVIV ($p < 0.01$, two-tailed t-test), whereas exactly half are greater and half are smaller when comparing TMSURVIV with LOSSURVIV for ϕ and P (non-significant). The ϕ and P increases that result from using LOSSURVIV over TMSURVIV are associated with decreases in the estimates of the resident proportion (γ). Conversely, the ϕ and P decreases that result from using LOSSURVIV rather than TMSURVIV are associated with increases in γ for only three of five species. The percent change in the precision of the estimate of survivorship (ϕ) results from comparing the coefficient of variation (standard error of the estimate of ϕ/estimate of ϕ) from LOSSURVIV with that from TMSURVIV. Precision increased for all species with values ranging from 1% to 29.3% with a mean improvement of ~16% ($P<0.01$, two-tailed t-test), indicating that estimates of survival rate produced by LOSSURVIV are generally more precise than those produced by TMSURVIV.

Table 3: Comparison of estimates of survivorship probability (ϕ), capture probability (P), and resident proportion (γ) from SURVIV, TMSURVIV and LOSSURVIV. These are reported for ten species utilizing MAPS data for the period 1992-98 in USFS Region 6 (Species abbreviations are WEFL - *Empidonax difficilis & E. occidentalis;* WIWR - *Troglodytes troglodytes;* SWTH - *Catherus ustulatus;* AUWA - *Dendroica coronata audubonii;* TOWA - *Dendroica townsendi;* MGWA - *Oporornis tolmiei;* WIWA - *Wilsonia pusilla;* SOSP - *Melospiza melodia;* LISP - *Melospiza lincolnii; and* ORJU - *Junco hyemalis oregonus).* In all cases the time-independent transient model represents the most (or equally) parsimonious model reported by TMSURVIV or LOSSURVIV. Coefficients of variation (standard error/estimate) are calculated for each parameter and shown as percentages (in italics). The percent change in the precision of the estimate of survivorship (ϕ) results from comparing the coefficients of variation from LOSSURVIV with that from TMSURVIV. A positive value indicates that the estimate of survival rate from LOSSURVIV is more precise than that from TMSURVIV.

	SURVIV				TMSURVIV						*LOSSURVIV*						
Species	ϕ	*CV(ϕ)*	P	*CV(P)*	ϕ	*CV(ϕ)*	P	*CV(P)*	γ	*CV(γ)*	ϕ	*CV(ϕ)*	P	*CV(P)*	γ	*CV(γ)*	ΔCV(ϕ)%
WEFL	0.505	*12.7*	0.150	*24.0*	0.553	*13.0*	0.215	*31.2*	0.592	*34.8*	0.561	*11.2*	0.232	*24.1*	0.461	*25.8*	13.7
WIWR	0.233	*18.5*	0.460	*22.8*	0.364	*19.8*	0.648	*16.8*	0.399	*29.3*	0.314	*16.2*	0.593	*17.9*	0.430	*24.4*	17.9
SWTH	0.494	*2.6*	0.533	*3.9*	0.585	*3.2*	0.601	*3.7*	0.660	*5.6*	0.577	*2.6*	0.597	*3.5*	0.546	*5.9*	20.0
AUWA	0.481	*18.5*	0.111	*34.2*	0.582	*17.4*	0.251	*38.2*	0.320	*44.1*	0.549	*17.1*	0.194	*35.1*	0.403	*37.7*	1.3
TOWA	0.349	*16.9*	0.236	*25.8*	0.427	*17.1*	0.370	*27.6*	0.475	*34.9*	0.390	*16.7*	0.315	*28.3*	0.609	*31.9*	2.5
MGWA	0.398	*10.1*	0.523	*7.3*	0.525	*5.9*	0.633	*6.0*	0.533	*9.9*	0.495	*4.8*	0.612	*6.0*	0.487	*9.9*	17.9
WIWA	0.359	*10.0*	0.343	*15.2*	0.425	*11.3*	0.442	*15.8*	0.607	*21.4*	0.445	*9.0*	0.467	*12.8*	0.423	*16.8*	20.4
SOSP	0.371	*8.4*	0.604	*10.6*	0.394	*11.7*	0.626	*11.0*	0.884	*17.9*	0.436	*8.3*	0.658	*9.3*	0.584	*15.6*	29.3
LISP	0.418	*6.0*	0.654	*7.5*	0.427	*8.9*	0.662	*8.0*	0.957	*13.4*	0.439	*6.8*	0.670	*7.3*	0.857	*11.9*	23.2
DEJU	0.413	*7.5*	0.345	*11.9*	0.415	*9.6*	0.347	*15.9*	0.989	*19.3*	0.433	*8.1*	0.373	*12.6*	0.832	*14.5*	16.1
Mean	0.402		0.396		0.470		0.480		0.642		0.464		0.471		0.563		16.2

A plot of the mean annual productivity indices (proportion of young in the catch) derived from Table 2, against the survival estimates from LOSSURV in Table 3, is shown in Figure 3. A regression line reveals a negative relationship in which a high survival rate is associated with a low productivity index and a low survival rate is associated with a high productivity index. Importantly, survival rates of temperate-wintering species tend to be lower than those associated with species with mixed or temperate or tropical-wintering strategies. In turn, survival rates for these species is lower than those associated with tropical-wintering species.

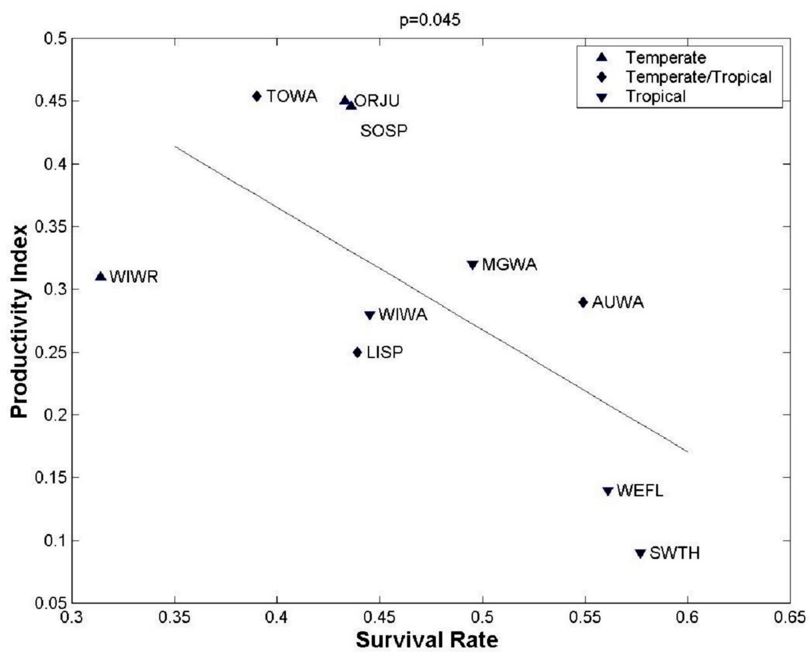

Figure 3. Relationship between mean annual productivity and survival derived from banding data for ten species of passerines breeding in the Pacific Northwest region of the United States. Productivity is expressed as the annual mean of the proportion of young in the total catch from banding data pooled across 36 stations. Survival rates are estimated from a modified Cormack-Jolly-Seber mark-recapture model that considers transient individuals (see text). Three temperate-wintering species (upward pointing triangles), three temperate/tropical-wintering species (downward pointing triangles) and four tropical-wintering species (diamonds) are shown. Linear regression shows a significant negative relationship ($p<0.05$).

Discussion

Analysis of constant effort mist-netting data can detect annual changes in population size and structure, and seasonal or diurnal patterns in the capture rates of resident adult, transient adult and juvenile portions of avian populations. This information can be used to increase the accuracy and precision of demographic parameter estimates. Capture histories derived from these data show inter-specific differences in temporal patterns of activity. For some species the probability of capture peaks during the first few hours of the morning or whereas for others it remains relatively constant over a larger part of the morning. Similarly, the probabilities of capturing young and adults vary by species throughout the season. This strongly suggests that foraging strategies vary by species. Obviously, when indexing productivity by the proportion of young in the total catch the seasonal timing of missing effort can bias the results. If effort is missed early in the season the number of adult captures may be underestimated and bias productivity high. Conversely if effort is missed late in the season the number of young may be underestimated and bias productivity low. Let us assume, for a given species, 100 adults and 40 young should have been captured, 20% of the adults are normally captured in the first banding period and 40% of the young are normally captured in period 10. If half of the effort in the first period were missed then the productivity index (proportion of young in the catch) would be biased 17% higher than expected. If half of the effort in period 10 were missed the productivity index would be 15% lower than expected. Because adult and young captures are a function of both the time of day and the banding period, species-specific temporal patterns of capture probability must be used to adjust productivity indices when banding effort is missing.

In fact, most mist-netting effort is missed early or late in the season due to unfavorable weather, early in the day due to logistic or weather problems, or late in the day due to high ambient temperatures forcing nets to be closed (P.Nott unpubl. data). Because inter-specific diurnal activity patterns vary, effort missed in a particular hour may differentially underestimate numbers of captures among species. It is also likely that these temporal activity patterns vary geographically and with patterns of environmental conditions (e.g. temperature and humidity). We propose that to provide comparisons of annual indices of productivity over many years, corrections for missing effort should be based by region and on the expected proportion of the catch by both hour and by banding period.

The first step in this process involves constructing matrices (hours by periods) expressing the expected proportion of resident, transient, and young captures in each time slot for each species. Young birds, excepting those subsequently recruited into the population, are generally caught only once and therefore generally require only a simple proportional correction as do the number of adults seen once. The relationship between missing effort and changes in the resident proportion of the population is more complex. Many between-year captures are also caught multiple times within a year so would remain classified as residents until considerably more effort is missed. Conversely, as effort increases a portion of the adults seen once may be recaptured in another period and reclassified as within-year residents. The proposed method to obtain species-specific correction rates for each of the time slots and demographic groups is to apply a simple Monte Carlo method. Small increments of effort may be removed randomly (and repeatedly) from existing data, pooled across a number of stations, by period and hour. This process facilitates the formulation of time-specific (diurnal and seasonal) rate equations expressed as the proportion of individuals lost per unit of missing effort. These relationships can then be used to correct for missed effort the numbers of individuals caught at individual banding stations.

Although MAPS adult population trends generally agree with BBS trends it is important to note that the two protocols are very different. BBS point count data is collected from 50km long roadside routes representative of a number of different habitat types and environmental conditions. As such, BBS provides a good indicator of overall numbers of birds of many species. On the other hand, MAPS data is collected from spatially-restricted forest interior or off-road forest edge plots and because it distinguishes between adults and young it can provide indices of productivity, estimates of survivorship, or estimates of the proportion of transient individuals in the numbers of adults detected. In this way, constant-effort bird banding can identify the proximal causes of population changes. In the case of the Oregon Junco it seems likely, from banding data that the number of young produced in a year are declining rapidly. For Swainson’s thrush, the numbers of detections in BBS data are increasing as the numbers of adults seen once are increasing, but the numbers of resident adults captured show no temporal trend.

Perhaps, in cases where there is a great disparity between trends of adults seen once and resident adults, the source-sink dynamics of those populations are changing. Fortunately, morphological data collected from captured individuals allow banders to identify the age (Pyle 1997) and breeding status (identified by brood patch and cloacal protuberance) of captured birds. It is possible that further analysis of the banding data may reveal stations at which, for one or more species, the age of recruited breeding birds has changed over time. In turn, this might suggest a shift from source to sink population or *vice-versa*.

Obviously, open-population mark-recapture models (TMSURVIV and LOSSURVIV) that estimate demographic parameters based on within-year and/or between-year information provide higher values for survival rates and recapture probabilities than the closed-population model, SURVIV. Although the net overall difference in the estimates of survival rate produced by TMSURVIV and LOSSURV is minimal (~1% per species) and statistically insignificant, LOSSURVIV provides a significant improvement in the precision of those estimates (~16%). LOSURVIV also conserves more of the information in the capture histories, which may be responsible for the improvement in precision surrounding survival rate estimates.

Clearly, the negative correlation between survival rates and productivity indices derived from banding data adheres to generally accepted life history theory. In addition to banding, ageing and sexing individual birds, mist-netting protocols allow a series of morphological measurements (e.g., wing chord, weight) to be recorded. We suggest that further research be designed to a) explore the relationship between regional variations in age structure, morphology, survivorship and productivity, and b) test the predictions of the proportions of resident and transient individuals by color banding captured individuals and analyzing re-sight data. These efforts may help toward clarifying both life history theory and source-sink population dynamics.

Acknowledgements

We thank the DoD Legacy Resources Management Program for financial support for this work. We thank Peter Boice and Alison Dalsimer of the Legacy Program, Joe Hautzenroder and Chris Eberly of the DoD Partners in Flight Program, and Robert Johnson of the US Army Corps of Engineers, Huntsville Division for logistical support. We acknowledge the staff of the Patuxent Wildlife Research Center (USGS/BRD Resources Division), especially Jim Nichols and William Kendall for their help in designing TMSURVIV and LOSSURVIV, and Jim Hines for programming these models and subsequent technical support. We would like to thank Rodney Siegel, Amy McAndrews, and Nichole Michel at IBP for their help in crafting this document, along with the many biologists, interns and especially volunteers who diligently operate the monitoring stations every year to provide these valuable data. This is contribution #109 of The Institute for Bird Populations.

References

Buckland, S.T. and S.R. Baillie. 1987. Estimating bird survival rates from organized mist-netting programs. Acta Ornithologica 23:89-100.

Burnham, K. P., and 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.

Cormack, R.M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51429-438.

DeSante, D.F., D.R. O'Grady, and 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.R. O'Grady, K.M. Burton, P. Velez, D. Froehlich, E.E. Feuss, H. Smith, and 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. 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. and M.P. Nott. (in review). Modeling spatial variation in productivity and survivorship, population trends, habitat characteristics, and weather patterns in a monitoring and adaptive management context. Ardea supplement: Proceedings of the 100 years of bird ringing conference, Helgoland 1999.

DeSante, D.F., Burton, K.M., Saracco, J.F., and 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.

James, F.C., McCulloch, C.E. and D.A. Wiedenfeld. 1996. New approaches to the analysis of population trends in land birds. Ecology 77:13-21.

Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225-247.

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

Link, W.A. and J.R. Sauer. 1998. Estimating population change from count data: Application to the North American Breeding Bird Survey. Ecological Applications 8:258-268.

Martin, T.E., and G.R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. J. Field Ornithol. 64(4):507-519.

Peach, W.J., Buckland, S.T. and 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.

Peterjohn, B.G., Sauer, J.R., and 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., Nichols, J. D., Brownie, C., & J. E. Hines. 1990. Statistical inference for capture-recapture experiments, Wildlife Monographs, No. 107.

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

Pyle, P. 1997. Identification guide to North American birds. Part I. Slate Creek Press, Bolinas, California, U.S.A.

Rosenberg, D.K., D.F. DeSante, K.S. McKelvey, and J.E. Hines. (In review) Monitoring survival rates of landbirds from a continental network of mist-net stations. Ecol. Applications.

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

Seber, G.A.F. 1965. A note on the multiple-recapture census. Biometrika 52:249-259.

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

White, G.C. 1986. Program SURVIV User's Manual Version 1.2. Los Alamos: Environmental Science group.