



Minimum capture-recapture rates and years of banding station operations to obtain reliable adult annual survival estimates

Tasas mínimas de captura-recaptura y años de funcionamiento de la estación de anillamiento para obtener estimaciones confiables de la supervivencia anual de los adultos

*Danielle R. Kaschube*¹, *James F. Saracco*¹, *Chris Ray*¹, *Christine M. Godwin*², *Kenneth R. Foster*² and *Peter Pyle*¹

ABSTRACT. We examined variability in adult annual survival rate estimates for 33 breeding bird species, using 2011–2019 data from a 38-station Monitoring Avian Productivity and Survivorship (MAPS) program in Alberta, Canada. Using coefficient of variation (CV) as a metric, we provide recommendations for number of years a station should be operated and numbers of captures and between-year recaptures required to achieve acceptable levels of precision for adult survival estimation. Our primary aim was to provide minimum sample-size guidelines for MAPS banding station operators. The proportion of individual species \times spatial scale scenarios for which we could obtain adult survival estimates, as well as the precision of those estimates, increased substantially once six years of data were collected, and we recommend six years as a target minimum level of continuity for banding station operation. Across 33 species analyzed, averages of 23.4 captures (3.9/yr) and 2.1 recaptures (0.4/yr) were needed to yield marginally precise survival estimates (CV of 20% to 30%, inclusive), while averages of 89.2 captures (14.9/yr) and 6.3 recaptures (1.1/yr) were needed to achieve more precise estimates (CV < 20%). We suggest these as guidelines for minimum capture and recapture rates at the scale of individual banding stations and for clusters of stations, e.g., multiple stations operated in a selected habitat type or sampling region, respectively. It should be noted, however, that sample-size requirements will vary markedly among species. For example, reliable estimates of survival for species with low between-year site fidelity, e.g., Tennessee Warbler (*Leiothlypis peregrina*), will not be obtainable at any sample size; while species with high inter-annual site fidelity and recapture probabilities, e.g., some flycatchers, thrushes, sparrows, and wood warblers, will require smaller sample sizes than those proposed here as guidelines.

RESUMEN. Examinamos la variabilidad en las estimaciones de la tasa de supervivencia anual de adultos para 33 especies de aves, con datos entre 2011 y 2019 provenientes de un programa de 38 estaciones de Monitoreo de Productividad y Supervivencia Aviar (MAPS) en Alberta, Canadá. Utilizando el coeficiente de variación (CV) como métrica, proporcionamos recomendaciones sobre el número de años que debe funcionar una estación y el número de capturas y recapturas entre años que se requieren para lograr niveles aceptables de precisión para la estimación de la supervivencia de los adultos. Nuestro objetivo principal era proporcionar directrices sobre el tamaño mínimo de muestra para los operadores de las estaciones de anillamiento del MAPS. La proporción de especies individuales \times escala espacial para los que pudimos obtener estimaciones de supervivencia de adultos, así como la precisión de dichas estimaciones, aumentó sustancialmente una vez que se colectaron seis años de datos, y recomendamos seis años como el nivel mínimo de continuidad para el funcionamiento de la estación de anillamiento. Para las 33 especies analizadas, se necesitaron en promedio 23,4 capturas (3,9/año) y 2,1 recapturas (0,4/año) para obtener estimaciones de supervivencia marginalmente precisas (CV del 20% al 30%, inclusivos), mientras que se necesitaron en promedio 89,2 capturas (14,9/año) y 6,3 recapturas (1,1/año) para lograr estimaciones más precisas (CV < 20%). Sugerimos estos datos como directrices para las tasas mínimas de captura y recaptura a escala de estaciones de anillamiento individuales y para grupos de estaciones, por ejemplo, múltiples estaciones operadas en un tipo de hábitat seleccionado o región de muestreo, respectivamente. Sin embargo, hay que tener en cuenta que el tamaño de muestra variará notablemente entre las especies. Por ejemplo, las estimaciones confiables de la supervivencia de especies con baja fidelidad interanual, e.g., *Leiothlypis peregrina*, no podrán obtenerse con ningún tamaño de muestra; mientras que las especies con alta fidelidad interanual y probabilidad de recaptura, por ejemplo, algunos atrapamoscas, mirlos, gorriones y reinitas, requerirán tamaños de muestra más pequeños que los propuestos aquí como directrices.

Key Words: *landbirds; MAPS; mark-recapture; sample size; survival*

INTRODUCTION

Birds are sensitive indicators of ecosystem health and are the focus of broad-scale monitoring efforts. Many of these efforts such as the North American Breeding Bird Survey (Robbins et al. 1986) and others involving point-count or line-transect surveys estimate relative abundance and population trends; however, additional data on vital rates, in particular adult survival, productivity, and

recruitment into breeding populations, are needed to identify causes of trends (DeSante et al. 2005, Saracco et al. 2008, Wilson et al. 2018, Saracco and Rubenstein 2020). Estimates of vital rates can help identify whether population declines are caused by factors on breeding grounds or during migratory and wintering periods, leading to more effective and targeted management of habitats and other bird-conservation efforts (Wilson et al. 2018).

¹The Institute for Bird Populations, ²Owl Moon Environmental Inc.

Application of standardized constant-effort mist netting combined with modern capture-recapture analytical techniques are effective means of monitoring demographic rates of landbird species across broad spatial scales (Peach et al. 2004, DeSante et al. 2015). In North America, such an effort was initiated in 1989 with the establishment of the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante 1992). The MAPS program database includes over 2 million records of banded birds from more than 1300 monitoring stations, of which approximately 300 stations are operated annually according to standardized procedures (DeSante et al. 2019). Data collected from 1992 through 2006 provided sufficient sample sizes to calculate a full suite of vital-rate estimates for 158 North American species (DeSante et al. 2015).

Annual adult survival is a key vital rate estimated from MAPS capture-recapture data, and requires larger sample sizes than most other parameters, e.g., productivity. Adult survival is also needed for mechanistic models projecting population dynamics (Ryu et al. 2016, Saracco and Rubenstein 2020). In declining migratory species, for example, relatively low adult survival (compared to similar but non-declining species) may indicate that conservation management is required away from breeding grounds (during migration, at stopover locations for molt, or on the winter grounds), whereas high adult survival suggests that declines may be driven by factors on breeding grounds, such as low reproductive success (Faaborg et al. 2010). The primary means of estimating adult survival from banding data is with transient Cormack-Jolly-Seber (CJS) capture-recapture models (Hines et al. 2003, DeSante et al. 2015). Transient CJS models require a minimum of four consecutive years of data to estimate time-constant demographic rates, and precision of these estimates usually increases with an increase in years of data on captures and between-year recaptures of each species (DeSante et al. 2015). An increase in the number of years of data also allows for more robust analyses of temporal trends and spatial variation in vital rates.

Planning for data analysis and conservation applications using capture-recapture models requires assessing minimum sample sizes in terms of years of data and the number of captures and recaptures needed per species to obtain meaningful survival estimates. As capture-recapture programs evolve to contribute to the needs of avian monitoring, an evaluation of the statistical power of the program to provide vital-rate estimates with known confidence is often required. Specifically, assessment of minimum sample sizes needed for capture and recapture rates at multiple scales (at individual stations and program-wide) can help guide the development of MAPS sampling design (DeSante and Saracco 2009, DeSante et al. 2009).

Here we provide such an assessment using the coefficient of variation (CV) in survival probability estimates for each of 33 breeding bird species from CJS models based on nine years (2011–2019) of MAPS data collected at 38 stations in the boreal forest of northeastern Alberta, Canada (Boreal MAPS program). Prior analyses of these data have provided insights on effects of habitat and regional human-footprint indices on the population trends of boreal forest landbirds (Foster et al. 2017, Wilson et al. 2018, Pyle et al. 2020). We assess the number of years of data and minimum sample sizes of captured and recaptured individuals needed for precise survival estimates, and we examine how these estimates vary among species.

METHODS

Boreal MAPS program

Our analyses are based on data collected during the Boreal MAPS program in the oil sands region of northeastern Alberta (Foster et al. 2017). The program was initiated in 2011 with the establishment of six MAPS stations, and this program has since expanded to include 33–38 stations operated annually from 2014 to 2019. Boreal MAPS stations were established in predominantly upland habitat to reduce data variability in capture rates associated with habitat type. MAPS stations were operated in accordance with the standardized protocols developed for the program (DeSante et al. 2019). At the latitudes of the Boreal MAPS program, station operation began by 5 June, concluded by 7 August, and included six days of operation per station each year. On each day of operation, 8 to 14 12-m mist-nets were opened for six hours beginning at local sunrise. Station operation avoided periods of inclement weather, e.g., rain or high wind, and nets were closed when conditions deteriorated to the point of compromising bird safety. For each newly captured bird a uniquely numbered Canadian Wildlife Service band was fitted and for each capture and recapture, birds were aged as either hatching-year or older (“adult”), following criteria presented by Pyle (1997). Survival analyses are restricted to adult birds.

We used data collected in 2011–2019, during which 28,841 captures of adults of 85 bird species were recorded. These totals included 19,508 uniquely marked adult individuals, of which 5191 individual adults (26.6%) were subsequently recaptured in the year(s) following initial banding; 4142 within-year recaptures were excluded from analyses. Capture rates for each bird species were calculated as the number of year-unique adult individuals divided by the number of years of the study (nine), and recapture rates were calculated in the same manner but divided by the number of between-year intervals (eight). We performed analyses on 33 species that met our minimum data requirement of at least 2.5 new captures of adults per year and 2 between-year recaptures overall of species considered to be breeding at a station or program-wide (DeSante et al. 2015).

Estimating annual adult survival

Annual adult survival was estimated from a single time/space constant CJS model accounting for transients in the sample (Hines et al. 2003). Survival analyses were performed at both the individual station level and at the program-wide level (all Boreal MAPS stations pooled). Variable numbers of analyses were performed each year based on the number of stations and species meeting the minimum data requirements. We evaluated minimum sample sizes for survival analyses for six multiyear periods, based on four years (2011–2014), five years (2011–2015), six years (2011–2016), seven years (2011–2017), eight years (2011–2018), and nine years (2011–2019) of data collection at the program-wide level. Individual stations may include different sets of years depending on when the station started operation, e.g., a four-year station may have run 2016–2019. For the first three sets of multiyear analyses, all models were fitted using the computer program TMSURVIV (White 1983, Hines et al. 2003) and for the remaining analyses, models were fitted using Program MARK (White and Burnham 1999) via the RMark package (Laake 2013) in R (R Core Team 2020). The underlying models and calculations are the same in both programs but TMSURVIV does not allow for missing sampling years, which was necessary after the first few

years of analyses of this data set. Coefficients of variation (CVs), which indicate the precision of the estimates, were calculated from the model outputs. We refer here to “model outputs” rather than “survival rate estimates” because, in some cases, survival rates are inestimable using the time/space constant mark-recapture models. This problem can occur for a variety of reasons, including too few recaptures, heterogeneity in survival that is not accounted for by the model, incompatibility between the selected model and the distribution of the data, or parameter values that lie near the boundaries of parameter space (DeSante et al. 2015). Here, we quantify the relationships in both the production of meaningful survival rate estimates and the CVs of those estimates, as captures and recaptures accumulate by year.

To represent the general relationship between CV and the number of captures or recaptures per year with data points pooled from all 33 species, we used generalized additive models (Hastie and Tibshirani 1990) in which CV was a cubic-spline smooth function of the log of captures or recaptures per year. To represent the relationship between CV and capture or recapture data from each individual species, we used a generalized linear (“log-linear”) model appropriate for Poisson-distributed response variables.

Ecologists regard CVs of less than 20% as providing reasonable precision of estimates for studies based on mark-recapture models (Pollock et al. 1990, Krebs 2014), and avian adult survival probability estimates with CVs in the 10–20% range have been reported in the literature. For example, CVs of 10–20% were reported for nearly one-third of species in a meta-analysis of 949 avian survival rate estimates from 204 studies (Scholer et al. 2020). Additionally, survival rate estimates with CVs in this range have been used in a variety of applications, including comparisons of survival among sites or habitats (Ruiz-Gutiérrez et al. 2008), comparison among ecological trait groups (Bellier et al. 2018), and for incorporation into integrated population models (Schaub and Kéry 2021). Although less commonly reported (e.g., 18% of studies in Scholer et al. 2020), survival rate estimates with CVs > 20% can still be useful in ecological studies, and estimates with this lower level of precision have also been used in comparisons of survival among habitats and regions (e.g., Whitaker et al. 2008, Wolfe et al. 2014). For this analysis, we therefore regard CVs of < 20% as a useful threshold for defining “precise” estimates of survival from CJS models. We also refer to CVs of 20–30% as indicating “marginally precise” survival estimates that we consider useful in some contexts, particularly for species that may exhibit more spatial or temporal variation and therefore require higher capture and/or recapture rates to obtain biologically meaningful levels of precision.

RESULTS

We produced a total of 470 adult annual survival model outputs from 33 species among the 38 stations during the nine years of operation; 178 outputs were generated at the program level (data from all stations pooled), and 292 outputs were generated at the individual station level. Survival rates were inestimable for 111 model outputs, 29 at the program-wide level and 82 at the station level. In total, 359 models produced survival estimates, 149 at the program-wide level and 210 at the station level (Table 1). The number of stations at which adults were captured ranged from three stations for Savannah Sparrow (see Table 1 for scientific names) to 34 stations for White-throated Sparrow. Mean new

captures per year ranged from 12.3 for Purple Finch to 484.3 for Tennessee Warbler, and mean between-year recaptures ranged from 0.4 for Western Tanager to 41.5 for White-throated Sparrow (Table 1).

Proportion of species with estimable adult survival

Adult survival estimates were obtained at the program-wide level for all 33 species, ranging from one estimate for Yellow-bellied Sapsucker and Western Tanager to the maximum of six estimates (one per multiyear period of analysis) for seven species (Table 1). Survival estimates at the station level were obtained for 22 species, ranging from two estimates for Tennessee Warbler to 37 estimates for White-throated Sparrow, and total outputs ranged from one for Western Tanager to 43 for White-throated Sparrow (Table 1).

Most model outputs that were based on > 100 captures or > 10 recaptures produced survival estimates (Fig. 1a-b); however, in some cases outputs from such models did not produce estimates. Likewise, some outputs based on < 20 captures and < 10 recaptures produced estimates (albeit with high CVs) while most did not produce estimates. Species that regularly produced estimates from lower numbers of captures and recaptures included Chipping Sparrow, Red-eyed Vireo, Swainson’s Thrush, and Yellow-rumped Warbler, whereas four model outputs each based on > 100 captures of White-throated Sparrow and Yellow-bellied Sapsucker did not produce estimates.

As with overall captures, the ability to estimate survival rates usually increased with increased capture rates (Fig. 1c-d). The proportion of models failing to yield survival rates dropped considerably after 20 captures per year and/or two recaptures per year were recorded, and few inestimable results were observed with > 60 captures or > six recaptures per year. Depending on the inter-annual variability in capture and recapture rates across species, models can produce estimates with as few as five captures and one recapture per year, while survival rates can be inestimable with as many as 61 captures and 4.5 recaptures per year.

As expected, there was a higher proportion of inestimable rates when models were fit to only four years of data, and the proportion of estimates increased as models were fit to six or more years of data (Fig. 1e). The largest improvements in the number of estimates were achieved when increasing from four to five and from five to six continuous years of data collection.

Precision of survival estimates (CV)

The precision of the estimates increased with corresponding increases in numbers of captures through seven years of data collection but levelled off thereafter (Fig. 2, Table 2). Survival estimate CVs from models based on four years of data did not approach 20% and reached 30% only in one case when a minimum of 4.3 recaptures was recorded (for Swainson’s Thrush; Fig. 3, Table 2). Once six years of data were collected, at least 23.4 captures (3.9 per year) and 2.1 recaptures (0.35 per year) resulted in marginally precise estimates. To achieve CVs of < 20%, however, 89.2 captures (14.9 per year) and 6.3 recaptures (1.05 per year) were needed once six years of data had been collected. In either case, based on the fitted curves, it again appears that a minimum of six years of continuous data collection is a good threshold for achieving reasonable precision.

Table 1. Bird species in the Boreal MAPS program used in capture-recapture analysis. Minimum requirements for inclusion were 2.5 or more year-unique adult captures per year and 2 or more between-year recaptures. For each species we present the number of stations that operated for at least four consecutive years at which the species breeds, mean numbers of captures and recaptures per year over all nine years of data collection (2011–2019), number of models that produced adult annual survival estimates at the station and program-wide levels, and number of models that did not produce survival estimates.

Common Name	Species Code	Scientific Name	No. Stations	Captures Per Year (mean)	Recaptures Per Year (mean)	Number of Models			
						Estimable Survival Rates			Inestimable
						Program-wide	Station [†]	Total	
Yellow-bellied Sapsucker	YBSA	<i>Sphyrapicus varius</i>	21	50.7	4.4	1	3	4	5
Alder Flycatcher	LEFL	<i>Empidonax alnorum</i>	30	202.3	13.3	5	14	19	15
Least Flycatcher	LEFL	<i>Empidonax minimus</i>	23	93.9	3.3	6	6	12	0
Red-eyed Vireo	REVI	<i>Vireo olivaceus</i>	27	95.7	8.8	5	10	15	1
Canada Jay	CAJA	<i>Perisoreus canadensis</i>	24	15.9	2.8	5	0	5	0
Black-capped Chickadee	BCCH	<i>Poecile atricapillus</i>	29	41.2	6.3	6	0	6	0
Boreal Chickadee	BOCH	<i>Poecile hudsonicus</i>	23	20.8	2.8	4	0	4	2
Swainson's Thrush	SWTH	<i>Catharus ustulatus</i>	33	172.2	18.6	6	26	32	4
Hermit Thrush	HETH	<i>Catharus guttatus</i>	14	18.6	2.4	2	3	5	3
American Robin	AMRO	<i>Turdus migratorius</i>	33	84.6	8.9	5	9	14	0
Purple Finch	PUFI	<i>Haemorhous purpureus</i>	7	12.3	0.8	2	0	2	4
Chipping Sparrow	CHSP	<i>Spizella passerina</i>	32	142.6	7.3	6	19	25	1
Clay-colored Sparrow	CCSP	<i>Spizella pallida</i>	15	136.7	8.3	5	8	13	2
Savannah Sparrow	SAVS	<i>Passerculus sandwichensis</i>	3	46.3	7.0	3	6	9	0
Song Sparrow	SOSP	<i>Melospiza melodia</i>	8	27.7	3.4	2	0	2	6
Lincoln's Sparrow	LISP	<i>Melospiza lincolni</i>	29	139.7	12.1	6	14	20	10
Swamp Sparrow	SWSP	<i>Melospiza georgiana</i>	16	66.1	3.5	3	3	6	5
White-throated Sparrow	WTSP	<i>Zonotrichia albicollis</i>	34	408.2	41.5	6	37	43	21
Dark-eyed Junco	DEJU	<i>Junco hyemalis</i>	10	21.6	2.1	5	0	5	0
Ovenbird	OVEN	<i>Seiurus aurocapilla</i>	27	100.6	5.1	5	4	9	8
Northern Waterthrush	NOWA	<i>Parkesia noveboracensis</i>	10	19.8	3.1	5	0	5	1
Black-and-white Warbler	BAWW	<i>Mniotilta varia</i>	22	46.6	4.0	5	0	5	1
Tennessee Warbler	TEWA	<i>Leiothlypis peregrina</i>	33	484.3	2.1	5	2	7	6
Mourning Warbler	MOWA	<i>Geothlypis philadelphia</i>	12	60.7	8.9	5	0	5	1
Common Yellowthroat	COYE	<i>Geothlypis trichas</i>	19	47.6	4.5	5	4	9	0
American Redstart	AMRE	<i>Setophaga ruticilla</i>	8	33.6	4.5	5	4	9	0
Magnolia Warbler	MAWA	<i>Setophaga magnolia</i>	15	70.7	6.9	5	3	8	3
Yellow Warbler	YEWA	<i>Setophaga petechia</i>	9	59.4	8.1	6	12	18	0
Yellow-rumped Warbler	MYWA	<i>Setophaga coronata</i>	20	54.0	5.8	5	11	16	3
Canada Warbler	CAWA	<i>Cardellina canadensis</i>	14	59.8	5.1	5	9	14	5
Wilson's Warbler	WIWA	<i>Cardellina pusilla</i>	12	32.9	1.4	4	3	7	1
Western Tanager	WETA	<i>Piranga ludoviciana</i>	14	8.2	0.4	1	0	1	3
Rose-breasted Grosbeak	RBGR	<i>Pheucticus ludovicianus</i>	16	19.9	1.4	5	0	5	0
All Species Pooled			35	2894.8	218.5	149	210	359	111

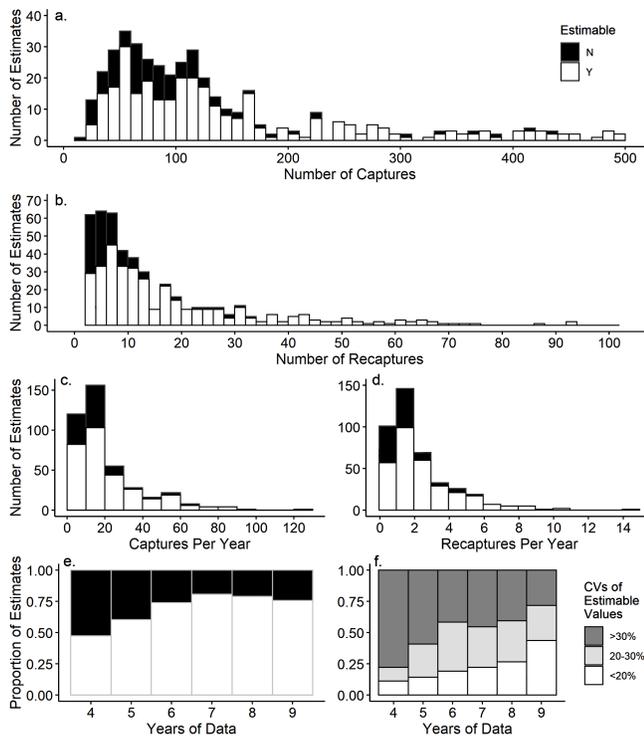
[†] The number of estimates can exceed the station count if estimates were calculated for more than one year.

When considering the CV values directly, both minimum numbers of new captures and between-year recaptures needed for precise and marginally precise survival estimates continued to decrease through nine continuous years of data collection. This is also shown by a consistent increase in the proportions of precise and marginally precise estimates between four and nine years of data collection (Fig. 1f). Thus, survival estimate precision continues to improve through at least nine years of data collection.

We plotted CV values according to captures per year for 12 species with 10 or more survival estimates (Fig. 4) and we indicate the values at which each fitted curve crossed CV thresholds of 20% and 30% (Table 3). As expected, CV declined with data accumulation but there were some exceptions. For example, the distribution of data for Least Flycatcher resulted in a relatively

constant CV regardless of data accumulation, and very high capture-rate targets (> 100 per year) to achieve CVs at both < 20% and from 20% to 30%. Similar but less extreme insensitivities in CV resulted in very high capture-rate values necessary to achieve the < 20% CV threshold for Alder Flycatcher, Chipping Sparrow, Clay-colored Sparrow, Lincoln's Sparrow, and White-throated Sparrow. Targets for precise estimates among the remaining six species ranged from 41 (Yellow Warbler) to 85 (Red-eyed Vireo) with a mean of 66.1 captures per year, and from four (Canada Warbler) to eight (American Robin and Yellow-rumped Warbler) with a mean 6.33 recaptures per year (Table 3). For 11 species (not including Least Flycatcher with a very high capture-rate target), the sampling targets to achieve marginally precise estimates (CV of 20% to 30%) ranged from eight (Clay-colored

Fig. 1. Distribution of estimable adult annual survival rates at different levels of precision by captures, recaptures, and years of data. Models producing survival estimates are shown in white, models failing to produce estimates in black. Estimates were derived from analyses at both the program-wide and station levels during six periods (2011–2014, 2012–2015, 2011–2015, etc., through 2011–2019). To emphasize the proportions obtained from analyses of smaller sample sizes, graphs a and b omit results from analyses based on > 500 captures (n = 55) and > 100 recaptures (n = 7), all of which were estimable. Models based on ≥ 40 recaptures, ≥ 70 captures per year, or ≥ 6 recaptures per year were all estimable.

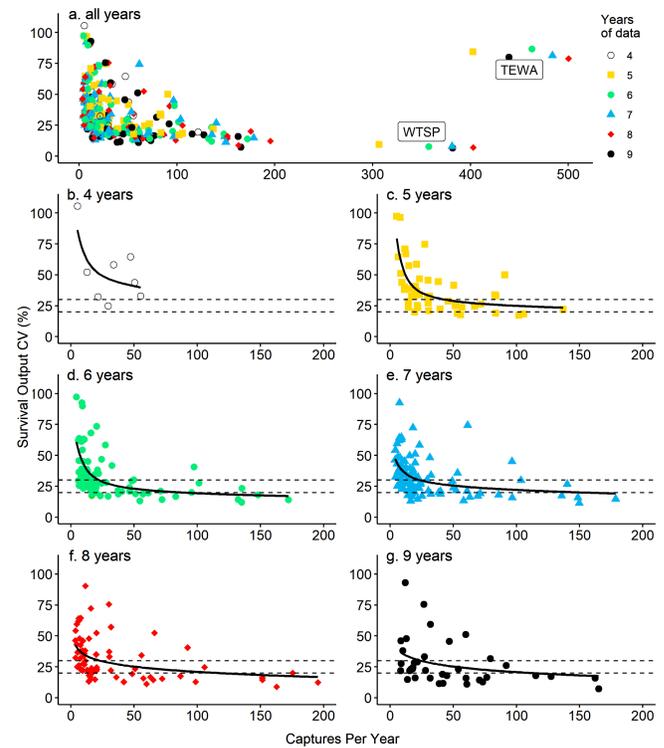


Sparrow) to 75 (Chipping Sparrow) with a mean of 31.6 captures per year, and from two (Clay-colored Sparrow, White-throated Sparrow, Yellow Warbler, and Canada Warbler) to five (Yellow-rumped Warbler) with a mean of 3.0 recaptures per year.

DISCUSSION

With up to nine years of capture-recapture data from 38 bird-banding stations we were able to obtain adult annual survival estimates for 33 bird species at the program-wide level and for 22 of these 33 species at the station scale. We were able to estimate survival from most models based on > 100 captures or > 10 recaptures, and in some cases we estimated survival from models based on < 20 captures and < 10 recaptures. Species for which we regularly produced estimates with lower numbers of captures and recaptures included Chipping Sparrow, Red-eyed Vireo, Swainson's Thrush, and Yellow-rumped Warbler. These species may be more faithful to breeding territories and are thus more consistent in their capture and between-year recapture patterns. Species for which we sometimes could not estimate survival

Fig. 2. Coefficient of variation (CV) of adult annual survival estimates according to capture rates for 33 species at Boreal MAPS program-wide and station levels. Top panel (a) displays all 359 estimates, while bottom panels (b-g) show estimates by number of data-years and curves fitted using a generalized additive model. The lower panels omit the estimates based on Tennessee Warbler (TEWA; *Leiothlypis peregrina*) and White-throated Sparrow (WTSP; *Zonotrichia albicollis*) to better illustrate the decline in CV with increasing capture and recapture rates across the majority of species. Table 2 lists the points at which each curve crosses CV thresholds of 20% and 30%.



despite high capture rates (White-throated Sparrow, Yellow-bellied Sapsucker) may have more inter-annual variability in capture and recapture patterns. Heterogeneity in survival or recapture probabilities among stations may hinder the ability to estimate survival in program-wide, i.e., multi-station, analyses, even with seemingly sufficient sample sizes. Such inconsistent program-wide capture patterns could explain these results for White-throated Sparrow in the Boreal MAPS program, and appears to be the case for woodpeckers in general (DeSante et al. 2015). Adapting models for individual species, for example with random (hierarchical) station effects, may alleviate such issues and produce increased accuracy and precision in survival estimates without sample size increases.

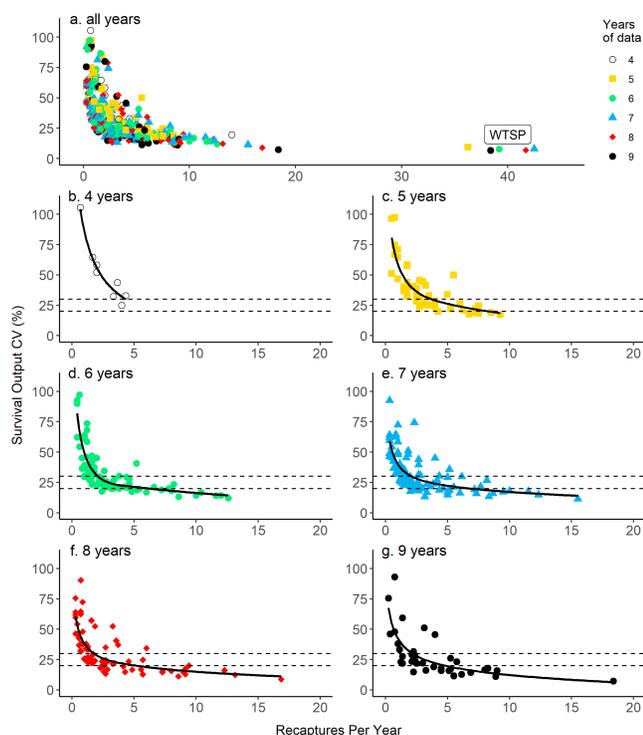
Our results indicate that both the proportion of estimable survival rates and the precision of these estimates increase, and the required minimum capture and recapture rates decrease, once six years of continuous data collection has been achieved, and that precision continues to improve with up to nine years of data

Table 2. Mean captures and recaptures per year needed to achieve precise ($CV < 20\%$) and marginally precise ($20\% \leq CV \leq 30\%$) adult annual survival estimates (see Fig. 2).

Years of Data	No. Species	No. Survival Estimates		Precise Estimates [†] CV < 20%		Marginally Precise Estimates [†] 20% ≤ CV < 30%	
		Program-wide	Station	Captures	Recaptures	Captures	Recaptures
4	8	7	1	NA	NA	NA	4.3
5	26	22	25	NA	8.4	45.2	3.8
6	30	27	55	89.2	6.3	23.4	2.1
7	30	28	69	151.9	6.9	23.9	2.3
8	32	28	49	117.7	5.3	25.4	1.8
9	28	26	11	113.5	4.8	26.2	2.3

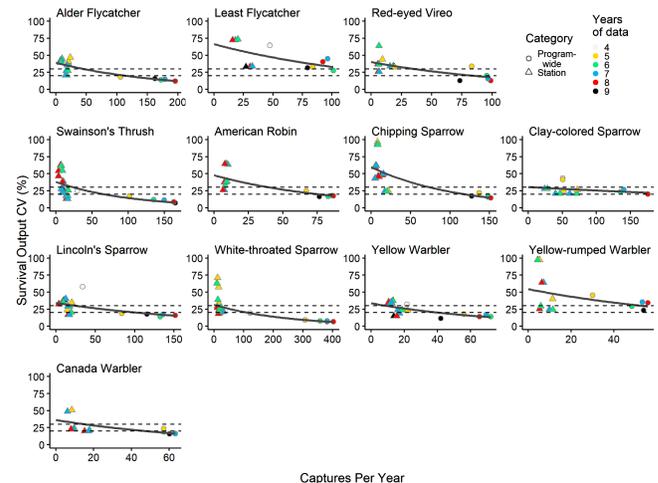
[†]NA (not achieved) indicates that fitted curves did not reach the indicated threshold.

Fig. 3. Coefficient of variation (CV) of adult annual survival estimates according to recapture rates for 33 species at Boreal MAPS program-wide and station levels. Top panel (a) displays all 359 estimates, while bottom panels (b–g) show estimates by number of data-years and curves fitted using a generalized additive model. The lower panels omit the White-throated Sparrow (WTSP; *Zonotrichia albicollis*) to better illustrate the decline in CV with increasing capture and recapture rates across the majority of species. Table 2 lists the points at which each curve crosses CV thresholds of 20% and 30%.



collection. To maximize the number of species for which survival estimates can be calculated and to increase the precision of these estimates, we therefore recommend that MAPS stations be operated for at least six continuous years and as many continuous years as possible thereafter. Continent-wide simulation analyses of MAPS data during the years 1992–2006 indicates that

Fig. 4. Coefficient of variation (CV) in adult annual survival estimates related to captures per year for 12 species. Dashed horizontal lines represent precision thresholds for $CV < 20\%$ (lower line) and $20\% < CV < 30\%$ (upper line). Intersections between these thresholds and the regression lines indicate the number of captures required for these levels of precision in survival rate estimates. Note that samples can represent various annual intervals, e.g., 2011–2015, 2012–2016, etc. See Table 1 for species scientific names.



minimum capture rates needed to produce survival estimates continued to decrease with up to at least 15 years of data collection (DeSante and Saracco 2009, DeSante et al. 2009, 2015). Missed years of data collection can be accommodated in the analyses; however, multiple consecutive missed years can be problematic for inferences regarding shorter-lived species, because the probability of an individual surviving across the skipped years may be low.

Once six continuous years of data had been collected, means of 23.4 captures (3.9 per year) and 2.1 recaptures (0.35 per year) resulted in marginally precise (CV of 20% to 30%) survival estimates. Within the Boreal MAPS program such capture and recapture numbers were obtained for 166 species-station combinations and 23 species when all stations were combined, and we recommend these minimum values (after six years of data

Table 3. Capture and recapture rates needed to achieve precise ($CV < 20\%$) and marginally precise ($20\% \leq CV < 30\%$) adult annual survival estimates for 12 species at the station and program-wide levels. Species included are those for which there were 10 or more survival estimates. The regression line used to identify each threshold in CV as a function of capture or recapture rate was a Poisson loglinear model (see Fig. 4). See Table 1 for species scientific names.

Species	No. Model Outputs		Precise Estimate CV < 20%		Marginally Precise Estimate 20% ≤ CV < 30%	
	Program-wide	Station	Captures Per Year	Recaptures Per Year	Captures Per Year	Recaptures Per Year
Alder Flycatcher	5	14	114	7	45	3
Least Flycatcher	6	6	172	8	114	5
Red-eyed Vireo	5	10	85	7	35	3
Swainson's Thrush	6	26	67	6	26	3
American Robin	5	9	76	8	40	4
Chipping Sparrow	6	19	118	6	75	4
Clay-colored Sparrow	5	8	232	13	8	2
Lincoln's Sparrow	6	14	103	8	26	3
White-throated Sparrow	6	37	114	12	14	2
Yellow Warbler	6	12	41	5	10	2
Yellow-rumped Warbler	5	11	81	8	53	5
Canada Warbler	5	9	47	4	16	2

collection) as good targets for obtaining reasonably precise survival estimates using data from individual MAPS stations. To achieve more precise estimates ($CV < 20\%$), means of 89.2 captures (14.9 per year) and 6.3 recaptures (1.05 per year) were needed once six years of data had been collected. Within the Boreal MAPS program such capture and recapture numbers were obtained for 63 species-station combinations and seven species when all stations were combined but only for 14 species at the individual station level. We anticipate that such capture rates will be obtained for good samples of species within programs that include a cluster of stations within similar habitats and ecological region. Precisions of $CV < 20\%$ from data collected at single stations in more unique habitats will be less common and we recommend these data be pooled with data from the larger MAPS program if possible. However, CVs of 20–30% are more easily attainable from single-station data, as demonstrated here. For example, 22 of the 210 station level estimates in this study had CVs of less than 20% but an additional 81 estimates had CVs of 20–30%.

Because of variation in capture patterns among species (see above), minimum capture rates needed to obtain precise and marginally precise survival estimates varied by species. Among 12 species for which survival estimates could be obtained with 10 or more models, one species (Least Flycatcher) showed weak relationships between CV and years of data and very high (> 100 per year) or incalculable capture-rate targets to achieve precise ($CV < 20\%$) or marginally precise (CV of 20% to 30%) estimates. These values result from a mixing of station-specific and program-wide models, the latter containing higher capture rates which, if not substantially more precise than those of the station-specific models, will add error to the CV response curve. For Least Flycatcher we anticipate that the observed CV response may be an artefact within our data and that marginally precise estimates may be obtainable at stations or programs with different inter-annual capture patterns.

Models for Tennessee Warbler resulted in high CVs regardless of capture rate or years of data because the proportion of between-

year recaptures was very low (16 recaptures; two per year) compared to 4002 captures (445 per year). This species seeks outbreaks in spruce budworm (*Choristoneura fumiferana*) populations to breed (Rimmer and McFarland 2020, Moisan Perrier et al. 2021) and, because these outbreaks show substantial geographic variation from year to year, few adults return to breeding sites of the previous year, minimizing between-year captures. Thus, it is unlikely that meaningful survival estimates can be obtained for species that lack between-year fidelity to breeding sites, such as Tennessee Warbler.

Among the other 11 species with at least 10 survival estimates, sufficient capture and recapture rates at the program level appear to provide marginally precise survival estimates for all 11 species, and sufficient rates to obtain precise estimates were achieved for six species: Red-eyed Vireo, Swainson's Thrush, American Robin, Yellow Warbler, Yellow-rumped Warbler, and Canada Warbler. Some of these species likely show favorable capture-recapture patterns including high inter-annual fidelity to breeding territories resulting in higher recapture rates. It should also be noted that we were able to obtain precise estimates for some species with fewer captures and recaptures, such as Savannah Sparrow, Lincoln's Sparrow, American Redstart, and Magnolia Warbler, which may show similarly favorable capture and recapture patterns. For any given species it is not possible to predict future capture and recapture numbers with certainty; however, these results will provide general guidelines for MAPS program evolution, given target species at each station.

Mist-nets may be added, or existing nets moved, to increase capture rates overall or for given species. MAPS protocols ask for this change to occur between the first and second season of operation, when possible, to minimize introduced variability. However, within the Boreal MAPS program, we plan to re-align station placement or net placement within stations after up to 10 years of operation to better achieve more precise survival estimates. Station realignment will occur according to the Oil Sands Monitoring Program's Before-After-Dose-Response (BADR) design, with the goal of integrating terrestrial

monitoring programs within the oil sands region (Arciszewski et al. 2021). We will be using the results reported herein to both guide our repositioning of mist nets within existing stations and to guide the establishment of new stations within the BADR design, with the intent of operating reconfigured and new stations for six or more consecutive years.

In conclusion, we recommend that operators of relatively large banding programs strive for precise ($CV < 20\%$) survival estimates for their target species at their program level, and all operators strive for marginally precise (CV of 20% to 30%) estimates at the station level regardless of the number of stations in their programs. At either the station or the program level, after six years of continuous data collection, MAPS operators should generally strive for 3.9 captures and 0.35 recaptures per species per year to obtain marginally precise estimates, and 14.9 captures and 1.1 recaptures per year to obtain precise estimates. Annual rates of initial captures necessary for precise estimation were more difficult to obtain than those of recaptures, therefore initial capture-rate thresholds should be the focus for target species. Substantially more data from MAPS stations are required to estimate survival than to estimate other vital rates such as productivity (DeSante et al. 2015); therefore, focusing on capture-rate thresholds will also result in sufficient data for other demographic analyses. Regardless of the number of stations operated by an individual MAPS operator, the data acquired by each operator are fundamental to the ability to derive landbird vital rates at the continental scale, and continued annual incorporation of MAPS data into continental databases will allow for calculation and updating of the vital rates presented by DeSante et al. (2015). Even for species for which sufficient captures and between-year recaptures for meaningful survival estimation are not achievable, indices of productivity, adult population size trends, and other vital-rate metrics can help managers assess the reasons for population change.

Responses to this article can be read online at:
<https://journal.afonet.org/issues/responses.php/71>

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Data Availability:

Data that support the findings of this study are openly available:
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LITERATURE CITED

- Arciszewski, T. J., D. R. Roberts, K. R. Munkittrick, and G. J. Scrimgeour. 2021. Challenges and benefits of approaches used to integrate regional monitoring programs. *Frontiers in Environmental Science* 9:666698. <https://doi.org/10.3389/fenvs.2021.666698>
- Bellier, E., M. Kéry, and M. Schaub. 2018. Relationships between vital rates and ecological traits in an avian community. *Journal of Animal Ecology* 87:1172-1181. <https://doi.org/10.1111/1365-2656.12826>
- DeSante, D. F. 1992. Monitoring avian productivity and survivorship (MAPS): a sharp, rather than blunt, tool for monitoring and assessing landbird populations. Pages 511-521 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001: populations*. Springer, Dordrecht, The Netherlands. https://doi.org/10.1007/978-94-011-2868-1_39
- DeSante, D. F., K. M. Burton, P. Velez, D. Froehlich, and D. Kaschube. 2019. MAPS Manual, 2019 Protocol. The Institute for Bird Populations, Point Reyes Station, California, USA.
- DeSante, D. F., D. R. Kaschube, and J. F. Saracco. 2015. Vital rates of North American landbirds. The Institute for Bird Populations, Point Reyes Station, California, USA. [online] URL: <https://www.VitalRatesOfNorthAmericanLandbirds.org>
- DeSante, D. F., D. R. Kaschube, J. F. Saracco, and J. E. Hines. 2009. Power to detect differences and trends in apparent survival rates. *Bird Populations* 9:29-41.
- DeSante, D. F., M. P. Nott, and D. R. Kaschube. 2005. Monitoring, modeling, and management: why base avian monitoring on vital rates and how should it be done? Pages 795-804 in C. J. Ralph and T. D. Rich, editors. *Bird conservation implementation and integration in the Americas*. U.S. Forest Service General Technical Report PSW-GTR191. Pacific Southwest Research Station, Albany, California, USA.
- DeSante, D. F., and J. F. Saracco. 2009. Power of the MAPS Program to detect differences and trends in survival and a vision for program expansion. *Bird Populations* 9:42-75.
- Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, Jr., P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, P. P. Marra, C. L. Merkord, E. Nol, S. I. Rothstein, T. W. Sherry, T. S. Sillett, F. R. Thompson III, and N. Warnock. 2010. Conserving migratory land birds in the New World: Do we know enough? *Ecological Applications* 20:398-418. <https://doi.org/10.1890/09-0397.1>
- Foster, K. R., C. M. Godwin, P. Pyle, and J. F. Saracco. 2017. Reclamation and habitat-disturbance effects on landbird abundance and productivity indices in the oil sands region of Northeastern Alberta, Canada. *Restoration Ecology* 25:532-538. <https://doi.org/10.1111/rec.12478>
- Hastie, T., and R. Tibshirani. 1990. *Generalized additive models*. Chapman and Hall, New York, New York, USA.

- Hines, J. E., W. L. Kendall, and J. D. Nichols. 2003. On the use of the robust design with transient capture-recapture models. *Auk* 120:1151-1158. <https://doi.org/10.2307/4090285>
- Krebs, C. J. 2014. *Ecological methodology*. Third edition. Addison-Wesley Educational Publishers, Menlo Park, California, USA.
- Laake, J. L. 2013. RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01. Seattle, Washington, USA.
- Moisan Perrier, J., D. Kneeshaw, M.-H. St-Laurent, P. Pyle, and M.-A. Villard. 2021. Budworm-linked warblers as early indicators of defoliation by spruce budworm: a field study. *Ecological Indicators* 125:107543. <https://doi.org/10.1016/j.ecolind.2021.107543>
- Peach, W. J., S. R. Baillie, and S. T. Buckland. 2004. Current practices in the British Trust for Ornithology Constant Effort Sites scheme and comparison with temporal changes in mist-net captures with changes in spot-mapping counts at an extensive scale. *Studies in Avian Biology* 29:46-56.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107:3-97.
- Pyle, P. 1997. *Identification guide to North American birds*. Part 1. Slate Creek, Bolinas, California, USA.
- Pyle, P., K. R. Foster, C. M. Godwin, D. R. Kaschube, and J. F. Saracco. 2020. Yearling proportion correlates with habitat structure in a boreal forest landbird community. *PeerJ* 8:e8898. <https://doi.org/10.7717/peerj.8898>
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [online] URL: <https://www.R-project.org/>
- Rimmer, C. C., and K. P. McFarland. 2020. Tennessee Warbler (*Leiothlypis peregrina*), version 1.0. In A. F. Poole, editor. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.tenwar.01>
- Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. *The Breeding Bird Survey: its first fifteen years, 1965-1979*. U.S. Fish and Wildlife Service Resource Publication 157, Washington, D.C., USA.
- Ruiz-Gutiérrez, V., T. A. Gavin, and A. A. Dhondt. 2008. Habitat fragmentation lowers survival of a tropical forest bird. *Ecological Applications* 18:838-846. <https://doi.org/10.1890/07-1090.1>
- Ryu, H. Y., K. T. Shoemaker, É. Kneip, A. M. Pidgeon, P. J. Heglund, B. L. Bateman, W. E. Thogmartin, and H. R. Akçakaya. 2016. Developing population models with data from marked individuals. *Biological Conservation* 197:190-199. <https://doi.org/10.1016/j.biocon.2016.02.031>
- Saracco, J. F., D. F. DeSante, and D. R. Kaschube. 2008. Assessing landbird monitoring programs and demographic causes of population trends. *Journal of Wildlife Management* 72:1665-1673. <https://doi.org/10.2193/2008-129>
- Saracco, J. F., and M. Rubenstein. 2020. Integrating broad-scale data to assess demographic and climatic contributions to population change in a declining songbird. *Ecology and Evolution* 10:1804-1816. <https://doi.org/10.1002/ece3.5975>
- Schaub, M., and M. Kéry. 2021. *Integrated population models*. Academic, London, UK. <https://doi.org/10.1016/C2019-0-02015-8>
- Scholer, M. N., M. Strimas-Mackey, and J. E. Jankowski. 2020. A meta-analysis of global avian survival across species and latitude. *Ecology Letters* 23:1537-1549. <https://doi.org/10.1111/ele.13573>
- Whitaker, D. M., P. D. Taylor, and I. G. Warkentin. 2008. Survival of adult songbirds in boreal forest landscapes fragmented by clearcuts and natural openings. *Avian Conservation and Ecology - Écologie et conservation des oiseaux* 3(1):5. <https://doi.org/10.5751/ACE-00223-030105>
- White, G. C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. *Journal of Wildlife Management* 47:716-728. <https://doi.org/10.2307/3808607>
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: S120-S139. <https://doi.org/10.1080/00063659909477239>
- Wilson, S., J. F. Saracco, R. Krikun, D. T. T. Flockhart, C. M. Godwin, and K. R. Foster. 2018. Drivers of demographic decline across the annual cycle of a threatened migratory bird. *Scientific Reports* 8:7316. <https://doi.org/10.1038/s41598-018-25633-z>
- Wolfe, J. D., P. C. Stouffer, and G. F. Seeholzer. 2014. Variation in tropical bird survival across longitude and guilds: a case study from the Amazon. *Oikos* 123:964-970. <https://doi.org/10.1111/oik.00849>