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# Increasing the Accuracy of Productivity and Survival Estimates in Assessing Landbird Population Status

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**Abstract:** *The conservation of species with declining populations requires information on population demography and identification of factors that limit population growth. For landbird species, an understanding of large-scale population declines often requires assessment of local population processes, including the production of offspring, the survival of those offspring, and adult survival. Population growth has been modeled for several species of landbirds to date, and these studies have provided important information on relationships between population status and population-limiting factors. Several recent studies have illuminated field methods and analytical techniques that can aid in increasing the accuracy of productivity and survival estimates for population models. We reviewed these methods and recommend their implementation, including quantification of the season-long productivity of individuals, collection of empirical data on juvenile survival during the postfledging and overwintering periods, and incorporation of adult breeding dispersal into annual adult survival estimates. Such methods will allow for more accurate assessment of population status and provide a better understanding of the factors on which to focus our conservation efforts.*

**Key Words:** adult survival, demography, juvenile survival, landbird, Mayfield estimate, nest success, population models, productivity

Incremento en la Precisión de Estimaciones de Productividad y Supervivencia en la Evaluación del Estatus de Poblaciones de Aves Terrestres

**Resumen:** *La conservación de especies con poblaciones en declinación requiere de información sobre su demografía y la identificación de factores que limitan el crecimiento poblacional. Para especies de aves terrestres, el entendimiento de declinaciones poblacionales a gran escala a menudo requiere de la evaluación de procesos poblacionales locales, incluyendo la producción de descendencia, la supervivencia de esa progenie y la supervivencia de adultos. A la fecha, se ha modelado el crecimiento poblacional de varias especies de aves terrestres, y esos estudios han proporcionado información importante de las relaciones entre estatus de la población y factores que limitan a la población. Varios estudios recientes han clarificado métodos de campo y técnicas analíticas que pueden ayudar a incrementar la precisión de estimaciones de productividad y supervivencia en modelos poblacionales. Revisamos estos métodos y recomendamos su aplicación, incluyendo la cuantificación de la productividad estacional de individuos, la recolecta de datos empíricos de supervivencia de juveniles durante los períodos de postemplumaje e invierno y la incorporación de dispersión reproductiva de adultos en estimaciones de supervivencia anual de adultos. Tales métodos permitirán una evaluación más precisa del estatus de la población y proporcionarán un mejor entendimiento de los factores a enfocar en nuestros esfuerzos de conservación.*

**Palabras Clave:** ave terrestre, demografía, estimación de Mayfield, éxito de anidación, modelos poblacionales, productividad, supervivencia de adultos, supervivencia de juveniles

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## Introduction

Knowledge of population demography and the factors limiting population growth is critical in conserving species that exhibit declining population trends. Among North American landbird species, more than 30% of long-distance migrants, 35% of short-distance migrants, and 20% of permanent resident species have declined significantly over the past 35 years (Sauer et al. 2003). With landbird species declining to this extent, identification of the factors that limit populations is imperative to taking effective conservation action, and identification of these factors requires an understanding of the life-history stages at which populations are being most severely limited. Nest predation, avian brood parasitism, and food availability affect population productivity (Rodenhouse & Holmes 1992; Robinson et al. 1995; Arcese et al. 1996; Donovan et al. 1997; Woodworth 1999; Weidinger 2002; Smith & Moore 2003), and food availability and predation affect adult and juvenile survival (Conway et al. 1995; Sherry & Holmes 1996; Anders et al. 1997; Sillett et al. 2000; Sillett & Holmes 2002). Although each of these factors can potentially limit landbird populations, identification of the avian demographic stages that contribute the most to local population decline is necessary to focus conservation efforts most efficiently and effectively.

To identify which landbird populations are declining, quantify rates of decline, and assess which life-history stages are most vulnerable to population-limiting factors, researchers have used a variety of population models, including age- or stage-based matrix models (e.g., Woodworth 1999; Saether & Bakke 2000), demographic simulation models (e.g., Stacey & Taper 1992), dynamic stochastic models (e.g., Powell et al. 1999), spatially explicit models (e.g., Pulliam et al. 1992; With & King 2001), and population source/sink models (e.g., Trine 1998; Porneluzi & Faaborg 1999; Fauth 2001). Although these models differ in the specific suite of parameters used, all incorporate estimates of population productivity, juvenile survival, and adult survival. Population models have been and continue to be extremely important in determining population dynamics and the factors that limit population growth. Furthermore, recent models of landbird population dynamics have shown sensitivity to small changes in estimates of productivity and survival (Porneluzi & Faaborg 1999; Powell et al. 1999; Woodworth 1999). For this reason, empirical, population-specific data on productivity, adult survival, and juvenile survival are critical for accurately estimating rates of population change. Several recent studies have illuminated ways in which we can improve our data collection and analytical methods to increase the accuracy of estimates of landbird productivity and survival. We reviewed methods currently used to estimate these population parameters and recommend implementation of methods that will increase the accuracy of population models, thus allowing us to bet-

ter assess the status and conservation needs of landbird populations.

## Estimating Productivity

To obtain estimates of productivity (the number of female offspring produced per female within a breeding season in a population), most researchers have collected empirical data on nesting success from a sample of nests within a population. In many studies, these data alone were used to calculate productivity; that is, productivity is assumed to equal the mean number of female offspring fledged from the sample of nests monitored (assuming a 1:1 sex ratio of nestlings). However, many factors other than nest success influence the final number of young ultimately produced per season. Some involve inherent differences in species' life-history traits, such as clutch size, whether or not a species will attempt multiple broods, and total length of the breeding season (i.e., time available to re-nest after failed nesting attempts) (Martin 1995). These factors can also vary among populations and between years within populations.

To take into account the effects of re-nesting and multiple brooding, some researchers have combined nesting-success data with estimates of number of nesting attempts and number of broods fledged per season to calculate productivity:

$$\beta = (n) (1 - [1 - m]^a), \quad (1)$$

where  $\beta$  is the number of female offspring produced per female within a breeding season,  $n$  is the number of female offspring fledged per successful nest,  $m$  is the Mayfield estimate of overall nesting success (Mayfield 1961, 1975; Johnson 1979), and  $a$  is the mean number of nesting attempts per female per season. This analytical method likely increases the accuracy of productivity estimates; however, most studies lack empirical data on the number of nesting attempts and the frequency of multiple brooding within study populations, such that this method may still provide inaccurate estimates of productivity for use in population modeling (Murray 2000; Thompson et al. 2001; Underwood & Roth 2002).

Recent studies provide examples of problems in using nesting-success data alone (or with nonempirical estimates of the number of nesting attempts) to estimate population productivity. Data collected on a population of Golden-cheeked Warblers (*Dendroica chrysoparia*) provided a Mayfield estimate of nesting success (Mayfield 1961, 1975; Johnson 1979) of 0.14 ( $n = 27$  nests; Anders 2000). However, data on the season-long productivity of color-marked individuals ( $n = 156$  territories) of the same population, based on surveying territories for fledglings, indicated that 87.8% of pairs fledged young, yielding a population productivity estimate of 1.45 (1.65 female offspring fledged per successful nest  $\times$  0.878; Anders 2000).

To illustrate the implications of these different estimates for assessment of population status, if one uses an annual adult survival estimate of 0.65 and a juvenile survival estimate of 0.30, a productivity estimate of 1.45 leads to a calculation of  $\lambda$  (the finite rate of population change) of 1.09, which means that the population is increasing. In contrast, if productivity is estimated based on nesting success alone, even under the assumption that pairs undertake three nesting attempts per season, productivity would be estimated at only 0.60 (using Eq. 1). If one uses the same adult and juvenile survival estimates, this estimate of productivity leads to a  $\lambda$  of 0.83, which means that the population is declining.

In a second example, Underwood and Roth (2002), with data from a marked population of Wood Thrushes (*Hylocichla mustelina*) studied from 1974 to 1995, concluded that estimates of season-long productivity are only weakly correlated with annual nesting success, with only half of the variation in annual productivity being explained by nesting success ( $r^2 = 0.53$ ). In a similar analysis, DeCecco et al. (2000) found a weak relationship ( $r^2 = 0.56$ ) between Mayfield estimates of nest success and estimates of season-long productivity for Red-eyed Vireos (*Vireo olivaceus*), Blue-headed Vireos (*Vireo solitarius alticola*), Wood Thrushes, and Worm-eating Warblers (*Helmintheros vermivorus*). The discrepancy between nest success and season-long productivity was attributed to differences in breeding-season length, re-nesting frequency, and the production of multiple broods. These examples demonstrate that many factors other than nest success ultimately contribute to the number of young produced per year. Furthermore, these factors vary among species and likely between populations and within populations over time. Despite this increased realization and suggestions by researchers that nesting-success estimates are not accurate surrogates for estimates of season-long productivity (Holmes et al. 1992; Pease & Grzybowski 1995; Trine 1998; Powell et al. 1999; Murray 2000; Underwood & Roth 2002), a review by Thompson et al. (2001) found a decrease from 1987 through 1997 in the proportion of published articles in which re-nesting and multiple brooding were accounted for when population productivity was estimated.

The primary reason for the use of nesting success as a surrogate for season-long productivity is the perception that individually marking birds and monitoring the production of young throughout the breeding season is difficult and time-consuming. For species in which nests are difficult to find or access, however, trapping and color-banding or radio-marking adults and surveying territories for the presence of fledglings can be far less time-consuming than locating and monitoring nests (fledge families are often more easily located than are nests in many species because fledglings beg loudly and adults give alarm calls or chips in the presence of perceived threats). For example, Porneluzi and Faaborg (1999)

trapped, color banded, and monitored the season-long productivity of 147 male Ovenbirds (*Seiurus aurocapillus*) over the course of four breeding seasons. During this same time, only 66 nests were located and monitored to determine nesting success and brood size. The Mayfield estimate of nesting success based on this sample, under the assumption of a second nesting attempt following nest failure, provided a productivity estimate of 1.05 female offspring per adult female. In contrast, productivity based on surveying for the presence of fledglings with marked adults was 1.47 female offspring per adult female (Porneluzi & Faaborg 1999). In this example, as in the example of Golden-cheeked Warblers described above, nests of the study species are relatively difficult to find, and those that are located and monitored may not represent a random sample of nest fates within the population (nests located by humans may also be likely to be located by nest predators or brood parasites, or the act of searching for and monitoring nests may alter the frequency of nest predation or brood parasitism). The time and effort needed to locate nests may thus be better spent trapping and color-marking adults such that alternative methods of estimating productivity (which may ultimately be more accurate) can be used.

Even for species in which nests are relatively easy to find, the color-marking and monitoring of individual birds on relatively small study sites, or subsets of individuals on larger study sites, may provide more accurate data on population productivity than would a study in which nests are sampled from larger study sites but for which no information is known on the number of nesting attempts or number of broods successfully produced per season. For example, Trine (1998) monitored the season-long productivity of color-banded Wood Thrushes on approximately 30 territories each breeding season in Illinois. Through the monitoring of marked individuals, Trine (1998) documented successful double brooding by 24% of breeding pairs, accounting for 30% of the overall productivity of the population. In a second example, Fauth (2001) located and monitored nests of unmarked Wood Thrushes on a greater number of territories on larger study sites. In addition to carrying out traditional nest monitoring, however, he color banded 17 female Wood Thrushes across his study sites to obtain empirical data on the mean number of nesting attempts per individual per season. This additional monitoring of marked birds allowed for a more accurate estimate of season-long productivity throughout the population (Fauth 2001). Because productivity is defined as the number of offspring produced per pair within a breeding season, the most accurate estimates of productivity are based on the monitoring of individually marked birds to actually count the number of fledglings that are produced through the course of a breeding season. Although increased time and effort (for some species) or smaller sample sizes may be involved in collecting empirical data on the season-long productivity of individuals,

such work is logistically feasible (e.g., Roth & Johnson 1993; Holmes et al. 1996; Trine 1998; Porneluzi & Faaborg 1999; Anders 2000; Fauth 2001).

For some species in some studies, the marking and monitoring of individual birds to assess reproductive output through the course of the breeding season may remain prohibitively time-consuming or difficult. In such studies, population productivity may still be estimated more accurately than is possible with data on nesting success alone. A model constructed by Pease and Grzybowski (1995) enables researchers to estimate season-long productivity based on nesting success, frequency of reneating and multibrooding, length of nesting season, and reneating interval, among other population parameters. This model also gauges the relative influence of nest predation and brood parasitism on season-long productivity. Woodworth (1999) used the Pease and Grzybowski model to quantify the effects of nest predation and brood parasitism on the season-long productivity of Puerto Rican Vireos (*Vireo latimeri*). She then used the modeled estimates of season-long productivity to predict  $\lambda$  under the presence and absence of nest predators and brood parasites (Woodworth 1999). DeCecco et al. (2000) used the Pease and Grzybowski model to compare season-long productivity among species with differing breeding-season lengths, predation and parasitism rates, and propensity to double brood. Finally, Marshall et al. (2002) used this model to estimate the season-long productivity of Red-eyed Vireos to assess the effects of experimentally reduced prey abundance (following *Bacillus thuringiensis* treatment of gypsy moths [*Lymantria dispar*]) on forest songbird ecology. Use of the Pease and Grzybowski model enabled Marshall et al. (2002) to conclude that a delay in the onset of breeding caused by decreased caterpillar abundance had the potential to reduce Red-eyed Vireo population productivity by 0.15 to 0.25 offspring per female per year.

A second model to estimate season-long productivity, constructed by Powell et al. (1999), allows productivity to be estimated based on nesting success, season length, reneating interval, juvenile-care interval, and the survival rate of adults and juveniles through the breeding season. Although estimates of adult breeding-season survival are currently uncommon (but see Powell et al. 2000; Sillett & Holmes 2002), the increasing use of radiotelemetry to study the movements, habitat use, and survival of migrant birds during the breeding and postbreeding periods (e.g., Anders et al. 1997; Vega Rivera et al. 1998, 1999; Powell et al. 2000; Norris & Stutchbury 2001; Yackel Adams et al. 2001) will allow researchers to incorporate survival data into productivity models such as that of Powell et al. (1999). The use of models to estimate season-long productivity requires empirical population- or species-specific information beyond that provided by nesting-success data, and it requires quantitative methods beyond those used to analyze nesting-success data. Although the collection

of empirical data on season-long productivity, or on the parameters used to model season-long productivity, may be logistically challenging, the collection of such data is essential in accurately assessing population status.

## Estimating Juvenile Survival

A second population parameter that may be logistically difficult to obtain but which is critical to the understanding of population dynamics is juvenile survival. In many landbird species, natal dispersal is spatially extensive (Greenwood & Harvey 1982; Payne 1991; Paradis et al. 1998), such that individuals marked on natal territories generally cannot be located the following year to obtain mark and resight data for survival analyses. In addition, radio transmitters that are small enough for most species of landbirds currently have a maximum battery life of only a few months. For these reasons, estimates of juvenile survival through the first year are impossible to obtain empirically and, as a result, researchers have calculated values of juvenile survival for use in population modeling based on various assumptions. One method used to calculate juvenile survival is to divide adult mortality by the average number of offspring fledged (Ricklefs 1973). An implicit assumption of this method is that the population is producing young at replacement levels, contradicting the use of these estimates in models whose goals are to assess the growth rates of populations. Others have borrowed either from Greenberg's (1980) assumption that juvenile survival is half that of adult survival or Temple and Cary's (1988) calculation that juvenile survival equals 0.31.

Although a lack of natal-site fidelity often makes it impossible to obtain empirical data on juvenile survival through the first year, one can increase the accuracy of juvenile survival estimates by collecting empirical data on survival from the time of fledging through dispersal from the natal area. In addition to the feasibility of collecting these data, some evidence indicates that the highest periods of juvenile mortality may occur during the first several weeks after fledging. Data on juvenile survival collected through the use of radiotelemetry during the period between fledging and fall migration have yielded survival estimates of 0.42 for Wood Thrushes in Missouri through 8 weeks postfledging (Anders et al. 1997) and 0.75 for Wood Thrushes in Georgia through 14 weeks postfledging (Powell et al. 2000). Additional studies have reported survival rates of 0.32 for Yellow-eyed Juncos (*Junco phaeonotus*) through 3 weeks postfledging (Sullivan 1989), 0.37 for Lark Buntings (*Calamospiza melanocorys*) through 3 weeks postfledging (Yackel Adams et al. 2001), 0.39 for Yellow-breasted Chats (*Icteria virens*) through 8 weeks postfledging, 0.60 for Gray Catbirds (*Dumetella carolinensis*) through 12 weeks postfledging (Maxted 2001),

and 0.71 and 0.28 through 8 weeks postfledging within a population of Swainson's Thrushes (*Catbarus ustulatus*) in consecutive years (J. D. White, unpublished data).

Because empirical juvenile survival estimates as low as 0.28 and 0.39 have been obtained through just the first 2 months after fledging for migratory species, it is likely that annual juvenile survival differs considerably from the estimate of 0.31 used in many population models. Because empirical data now indicate that large differences in postfledging juvenile survival exist between populations (and between years within populations) and because population models are quite sensitive to estimates of juvenile survival (Porneluzi & Faaborg 1999; Powell et al. 1999; Woodworth 1999), additional empirical data are needed from other populations on juvenile survival during the postfledging, dispersal period.

In addition to the feasibility of collecting data on juvenile survival during the postfledging period, it is possible to collect empirical data on the overwinter survival of juvenile birds. Marra and Holmes (2001) collected data on the overwinter site persistence (a potential indicator of survival) of first-year male and female American Redstarts (*Setophaga ruticilla*) in Jamaica from October through March based on mark-and-resight data. These data indicated lower site persistence for first-year versus after-first-year females during the overwintering period and differences in the overwinter persistence of first-year birds in different habitat types (Marra & Holmes 2001). In a second example, Latta and Faaborg (2002) quantified the overwinter site persistence of first-year and after-first-year Cape May Warblers (*Dendroica tigrina*) in three different habitat types in the Dominican Republic. Like Marra and Holmes (2001), they found that site persistence was significantly lower for first-year versus after-first-year birds, and that overwinter site persistence varied between habitat types (Latta & Faaborg 2002).

In a final example, Sillett and Holmes (2002) estimated the survival of first-year Black-throated Blue Warblers (*Dendroica caerulescens*) in a single habitat type in Jamaica from October through March based on mark-and-resight data (unlike Marra & Holmes [2001] and Latta & Faaborg [2002], they found no differences in the overwinter persistence of first-year versus after-first-year birds). Sillett and Holmes (2002) then combined these empirical survival data with modeled estimates of survival during migration to estimate juvenile survival through the first year (excluding mortality during the postfledging, pre-migration period). Such mark-and-resight studies of juveniles during the overwinter period may be logistically feasible for several other landbird species, particularly those that exhibit delayed plumage maturation, differences in juvenile and adult rectrix shape, and/or incomplete skull ossification into the winter of the first year. Addition of empirical data on overwinter survival to those data being collected on juvenile survival during the postfledging period will greatly increase our knowledge of the survival of

juvenile birds through the first year. Until additional empirical data are available on juvenile survival, the use of a range of values for this parameter in population models is more appropriate than the use of a single value such as 0.31.

## Estimating Adult Survival

A final key area of uncertainty in avian population models concerns estimation of adult survival rates. Annual adult survival probability for many landbirds is commonly estimated by resighting or recapturing marked individuals over multiple years on one or several study plots. Whether or not a marked bird is resighted in subsequent years is a function of three components: (1) survival probability (Did the bird survive the period?), (2) emigration probability (Did the bird return to the study plot, given that it survived the period?), and (3) detection probability (Is the marked bird resighted, given that it survived the period and returned to the study plot?). Although empirical data can be collected on return rates of marked adults from one breeding season to the next or one wintering period to the next, true survival, permanent emigration, and detection probabilities are all confounded in this measurement. Because the parameter of interest is "true survival probability" when the growth rate of a population is determined, detection probabilities and permanent emigration should be estimated separately so as not to confound the parameter of interest.

Detection probabilities can be readily estimated with open population models (Lebreton et al. 1992), given sufficient data (generally 3 years of mark-and-resight data). Lebreton et al. (1992) and Martin et al. (1995) demonstrated that detection probabilities are typically <1.0 (marked birds that are present on the study plots are "missed" or not resighted) and can vary across years, habitats, observers, species, and/or sexes in most field studies of landbirds. Software programs are now available to estimate detection probabilities based on mark-and-resight data (e.g., Reboulet et al. 1999; White & Burnham 1999), and many researchers have used these analyses to estimate detection probabilities within their study systems (e.g., Murphy 1996; Horak & Lebreton 1998; Powell et al. 2000; Sandercock et al. 2000; Bayne & Hobson 2002; Cilimburg et al. 2002; Marshall et al. 2002; Moller & Szep 2002; Sillett & Holmes 2002). The inclusion of detection probabilities has greatly increased the accuracy of survival estimation; however, the resultant parameter (generally referred to as "apparent survival probability") remains a compound parameter that confounds true survival with permanent emigration (Lebreton et al. 1992). If the objective of a study is to compare demographic rates among different treatments, management options, habitats, or other factors, apparent survival probability is a meaningful parameter because it reflects the multiple ways in which

the population may be affected by the factor in question (birds may survive at lower rates as a result of a treatment or may move away from a treated area, for example). Hypotheses regarding the effects of a particular treatment can still be tested as long as it is recognized that the response variable includes both mortality and permanent emigration from the study area (Marshall et al. 2000).

The determination of population growth rate, however, and the examination of questions involving aspects of life-history theory, such as sex-specific survival or the costs of reproduction, require that true survival be estimated. If apparent survival estimates are used in these cases (i.e., as estimates of true survival), it must be assumed or demonstrated that permanent emigration does not occur. If permanent emigration does occur, then, by definition, apparent survival will underestimate true survival by some unknown amount.

For example, Cilimburg et al. (2002) found that permanent emigration of Yellow Warblers (*Dendroica pe-techia*) off of their study sites is common (30% of resighted birds were found off of their original study site in 1 year of the study), and that estimated survival probabilities increase by 0.07–0.23 with the inclusion of these dispersed birds. In a second study, between-year shifts in breeding territories of Prothonotary Warblers (*Protonotaria citrea*) could have resulted in underestimates of true survival of 0.17 for males and 0.19 for females had these movements not been detected by researchers (M. R. M., unpublished data). Underestimates of survival would have been greater for females than for males because of the more frequent and longer movements of females (a pattern expected given a female bias in between-year breeding dispersal; Clark et al. 1997). Illustrating the potential effects of these different estimates on the assessment of population status, if one calculates  $\lambda$  for this Prothonotary Warbler population with the empirical estimate of apparent female survival of 0.39, an empirical mean productivity estimate of 1.82, and an assumed juvenile survival estimate of 0.30 (M. R. M., L. A. Wood, and R. J. Cooper, unpublished data),  $\lambda$  is 0.94, meaning that the population is considered to be declining. In contrast, if one calculates  $\lambda$  based on an estimate of female survival that incorporates emigration (survival = 0.57), with the same estimates of productivity and juvenile survival,  $\lambda$  is 1.12, meaning that the population is considered to be increasing. Lastly, Sillett and Holmes (2002), recognizing this phenomenon, argue that differences in the survival rates of male and female Black-throated Blue Warblers in their study were likely due to differential movements off of the study plots and not to differences in true survival.

None of these studies were designed to quantify the probability of permanent emigration, yet all clearly indicate that differences in study-plot size, location of marked birds relative to study-plot edges, and the tendency of some surviving marked birds to move to different territories between years result in some unknown level of

permanent emigration from the study sites. Differences in apparent survival rates among species and sexes are likely to be the result of differences in emigration rates and differences in true survival, thus confounding inferences regarding differences in true survival probabilities.

It is not surprising that we have been unable to separate mortality from permanent emigration, given the inherent difficulties in detecting and quantifying bird movements (particularly movements of migratory birds between breeding seasons) and the lack of information on why adult birds exhibit breeding dispersal (Koenig et al. 1996; Murphy 1996; Haas 1998; Walters 2000; Hoover 2003). There are, however, situations and data types that currently allow for estimation of true survival probabilities. For example, models combining the use of capture-and-recapture and band-recovery data (Brownie et al. 1985) are commonly used for estimation of true survival in harvested populations. In addition, multistate capture-and-recapture models (Nichols et al. 1993), in which capture-and-recapture and resighting data are collected at a number of isolated breeding sites, can sometimes allow estimation of true survival and movement rates (Spender et al. 1995). For now, however, it is likely that these data are unavailable, inappropriate, or logistically impractical in most site-specific demographic landbird studies attempting to determine the growth rate of a local population.

Alternatively, different approaches to study design and analysis may result in apparent survival estimates that are closer to true survival and may be more practical in landbird field studies. Marshall et al. (2005) investigated via simulation two study designs involving a core area where all marking of birds takes place and a surrounding resight-only area where marked birds are resighted. They demonstrated that as the resighting area became progressively larger and more “emigrants” were resighted, apparent survival estimates began to approximate true survival rates. Given observed interannual movements of birds, however, it was likely to be logistically impractical to resight birds on sufficiently large resight-only areas to minimize bias. Therefore, they used the same study-area design but analyzed the data with subsets of three progressively larger resight-only areas. The data subsets provided four estimates of apparent survival that asymptotically approached true survival. This study design and analytical approach are likely to be logistically feasible in field settings, yield estimates of survival unbiased by incomplete breeding-site fidelity (Marshall et al. 2005), and can provide estimates of survival that can be used in population growth models.

## Conclusions

Accurate estimates of productivity, juvenile survival, and adult survival are critical in assessing the status of landbird

populations. In estimating productivity for use in population models, it is essential that factors other than nest success be incorporated to better reflect the multiple ways in which this parameter can vary. Season-long productivity of marked individuals, including the number of young fledged per nest and the number of broods successfully fledged per female, will provide the most accurate estimates of population productivity but may not always be logistically practical. Some level of marking individuals to estimate these parameters seems warranted, however, especially because marking is often a component of other study objectives.

In parameterizing juvenile survival for population models, we encourage the collection of empirical data on survival during the postfledging and overwintering periods for species in which this is logistically feasible. Until such data are available, we recommend the use of a range of values in parameterizing juvenile survival, rather than the use of a single, constant value such as 0.31.

Finally, in estimating annual adult survival, we encourage researchers to estimate detection probabilities with software for open population models. Because adult survival estimates are confounded by permanent emigration of individuals from study areas, we also encourage the development and use of study designs and analyses that incorporate the effect of permanent emigration on survival estimates, either by minimizing this effect or by directly estimating emigration probabilities.

Although many studies of landbird survival have focused on annual survival rates measured on the breeding grounds, these same approaches can be used to investigate annual survival from the wintering grounds and to study within-season survival during the breeding and wintering periods, portions of the annual cycle for which little survival data have been collected for most species. Because annual survival of adults and juveniles is potentially affected by events on both the breeding and wintering grounds, further advances in researchers' attempts to link breeding and wintering populations (Webster et al. 2002) are also extremely important.

In general, studies in which empirical data have been collected on productivity, juvenile survival, or adult survival indicate that values for these parameters can vary between landscapes, species, and years within single populations. For this reason, and because population models have shown sensitivity to small changes in the values of productivity and survival, we recommend the collection of empirical, population-specific data in estimating these parameters. We recommend avoidance of constant, single-value estimates in population models, particularly when these estimates are not based on empirical data, and instead encourage the use of models in which variability around parameter estimates can be incorporated.

Overall, the modeling of landbird population growth has begun to provide important information on factors that limit these species. However, efforts to improve our

estimates of productivity, juvenile survival, and adult survival will lead to more accurate assessments of population status. This greater accuracy will allow us to more quickly identify the factors limiting avian populations and thus will provide a better understanding of the factors on which to focus our conservation efforts.

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