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COMBINING DEMOGRAPHIC AND COUNT-BASED APPROACHES TO IDENTIFY SOURCE–SINK DYNAMICS OF A THREATENED SEABIRD

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Abstract. Identifying source–sink dynamics is of fundamental importance for conservation but is often limited by an inability to determine how immigration and emigration influence population processes. We demonstrate two ways to assess the role of immigration on population processes without directly observing individuals dispersing from one population to another and apply these methods to a population of Marbled Murrelets (*Brachyramphus marmoratus*) in California (USA). In the first method, the rate of immigration (i) is estimated by subtracting local recruitment (recruitment from within the population due to reproduction) estimated with demographic data from total recruitment (f; recruitment from within the population plus recruitment from other populations) estimated using temporal symmetry mark–recapture models developed by R. Pradel. The second method compares population growth rates estimated with temporal symmetry models ($\hat{\lambda}_{TS}$) and/or population growth rates estimated from counts of individuals over multiple sampling periods ($\hat{\lambda}_C$) with growth estimates from a stage-structured projection matrix model ($\hat{\lambda}_M$). Both $\hat{\lambda}_{TS}$ and $\hat{\lambda}_C$ incorporate all demographic processes affecting population change (birth, death, immigration, and emigration), whereas matrix models are usually constructed without incorporating immigration. Thus, if $\hat{\lambda}_{TS}$ and $\hat{\lambda}_C$ are ≥ 1 and $\hat{\lambda}_M < 1$, the population is sustained by immigration and is considered to be a sink. Using the first method, recruitment estimated with temporal symmetry models was high ($\hat{f} = 0.182$, SE $= 0.058$), the mean adult birth rate, as estimated using the ratio of juveniles to ≥ 1 year old individuals (observed during ship-based surveys) was low ($\hat{\bar{b}}_A = 0.039$, SE $= 0.014$), and immigration was 0.160 (SE $= 0.057$). Using the second method, murrelet numbers in central California were stable ($\hat{\lambda}_C = 1.058$, SE $= 0.047$; $\hat{\lambda}_{TS} = 1.064$, SE $= 0.033$), but were projected to decline 9.5% annually in the absence of immigration ($\hat{\lambda}_M = 0.905$, SE $= 0.053$). Our results suggest that Marbled Murrelets in central California represent a sink population that is stable but would decline in the absence of immigration from larger populations to the north. However, the extent to which modeled immigration is due to permanent recruitment or temporarily dispersing individuals that simply mask population declines is uncertain.

Key words: Brachyramphus marmoratus; *central California; demography; emigration; immigration; Marbled Murrelets; mark–recapture; rate of population change; source–sink theory.*

INTRODUCTION

It has long been known that heterogeneity in habitat quality affects behavior and life history decisions (e.g., Fretwell and Lucas 1970, Charnov 1976), but its impact on population dynamics was recognized more recently. Although there are several models and conceptual frameworks for describing the dynamics of spatially structured populations (McPeek and Holt 1992, Doncaster et al. 1997, Hanski 1999, Morris and Diffendorfer 2004), a dominant paradigm is the source–sink perspective (Pulliam 1988, 1996, Pulliam and Danielson 1991). Sources are self-supporting populations producing surplus individuals that emigrate to sink populations, which are not self-sustaining. Without an influx of individuals from source populations (i.e., a rescue effect; Brown and Kodric-Brown 1977), sink populations become extirpated (Thomas and Kunin 1999). As destruction, fragmentation, and degradation of natural habitats continue, the identification of source–sink dynamics becomes increasingly important. Maintaining source populations may be required for the persistence of sink populations, but sinks may make important contributions to metapopulation size and persistence (Howe et al. 1991, Roy et al. 2005). Intense interest in the source–sink concept over the past two decades for both theoretical and applied purposes has led to alternative formalizations of Pulliam's (1988) original model (e.g., Pulliam and Danielson 1991, Danielson 1991, Kawecki 1995, Holt 1997, Thomas and Kunin 1999, Holt et al. 2003). In nature, source–sink dynamics

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have often been inferred (e.g., Foppen et al. 2000, Vierling 2000, Duguay et al. 2001, Wing et al. 2003), but have rarely been demonstrated (Diffendorfer 1998, Johnson 2004).

Rigorous identification of source–sink dynamics requires detailed information on population- or patch-specific estimates of fitness (natality and survival rates) as well as rates of movement among populations. Although rates of reproduction and survival are often feasible to estimate, estimating immigration and emigration rates by marking individuals in the population of origin and recapturing them in a destination population is inherently difficult for most natural populations (MacDonald and Johnson 2001). As a result, demographic studies of source–sink systems frequently present little or no movement data (Diffendorfer 1998). Dispersal rates can be estimated using genetic analyses (Rousset 2001), but interpreting estimates of gene flow on an ecological time scale is problematic because they reflect average movement rates over evolutionary time and often disagree substantially with contemporary estimates from tagging studies (Hastings and Harrison 1994, Slatkin 1994, Koenig et al. 1996, Palsbøll 1999). An alternative and more feasible approach is to estimate λ (the geometric rate of population growth) with and without immigration (Pulliam 1996, Kruzer and Huntley 2003). Source populations are stable or grow ($\lambda \geq 1$) in the absence of immigrants and are net exporters of individuals, whereas sink populations require immigrants for $\lambda \geq 1$ (Thomas and Kunin 1999). We use these definitions for sources and sinks throughout this paper.

In this paper, we demonstrate two ways to identify sink populations and to assess the role of immigration on population processes without directly observing individuals dispersing from one population to another. In the first approach, mark–recapture models developed by Pradel (1996) to estimate the rate of population change and total recruitment are combined with estimates of local recruitment to measure the rate of immigration. The second approach develops inference about the impact of immigration on population dynamics from the combined use of different estimators of population growth.

To illustrate these approaches, we first note that the rate of population change from year t to $t+1$ (λ_t) can be expressed as

$$\lambda_t = \frac{N_{t+1}}{N_t} = \phi_{t(\mathrm{SA})} + b_t\phi_{t(\mathrm{J})} + i_t$$

where N_t is the population size in year t, $\phi_{t(\mathrm{SA})}$ is the joint local survival probability of subadults and adults from year t to $t+1$, b_t is the number of juveniles produced per subadult and adult in the population in year t, $\phi_{t(\mathrm{J})}$ is the survival probability of juveniles from year t to $t+1$, and i_t is the immigration rate for year t (i.e., the number of new individuals from other populations entering the population in year $t+1$ per individual in the population in year t). The sum of the $b_t\phi_{t(\mathrm{J})}$ and i_t terms equals total recruitment at time t (f_t; the number of new individuals entering the population in year $t+1$ per individual in the population in year t) due to both local recruitment (surviving young produced in the population) and immigration from other populations.

Immigration rates can be estimated by calculating the difference between estimates of total recruitment (f_t) derived from temporal symmetry mark–recapture models developed by Pradel (1996) and estimates of local recruitment derived from other demographic data. The temporal symmetry modeling approach is a useful tool for estimating population trends and understanding population processes, although relatively few studies have used the approach to address questions in population ecology and conservation biology (Nichols et al. 2000, Dreitz et al. 2002, Sandercock and Beissinger 2002, Cam et al. 2003, Franklin et al. 2004). This class of models applies the original Cormack-Jolly-Seber (CJS; Cormack 1964, Jolly 1965, Seber 1965) mark–recapture models for open populations to the capture data viewed simultaneously in a forwards and backwards manner (Nichols and Hines 2002, Williams et al. 2002). When data are viewed in a forward manner, the parameter of interest is annual local survival (ϕ_t; the probability that an individual in the population in year t will survive and remain in the population in year $t+1$); when viewed backwards, the parameter of interest becomes the seniority probability (γ_t; the probability that an individual did not enter the population between years t and $t-1$). Moreover, alternative parameterizations of temporal symmetry models allow for the estimation of time-specific rates of population change λ_t because

$$\lambda_t = \frac{\phi_t}{\gamma_{t+1}}$$

and for the estimation of total recruitment f_t because

$$f_t = \lambda_t - \phi_t$$

(Franklin 2001, Williams et al. 2002). Because total recruitment includes local recruitment and immigration from other populations, the immigration rate in year t can be estimated using

$$i_t = f_t - b_t\phi_{t(\mathrm{J})}.$$

An assumption of this equation is that locally produced recruits enter the population at one year of age. If recruitment occurs later at later stage in life, for example at the age of first breeding, the survival term will need to be raised to a higher power. The approach presented here is conceptually similar to Pollock's Robust Design used by Nichols and Pollock (1990) to decompose total recruitment into its component processes, in that recruitment originating from within-population birth processes is subtracted from total recruitment to estimate immigration. However, our approach does

TABLE 1. Comparison of three approaches used to estimate the rate of population change.

	Approach for estimating rate of population change, λ		
Characteristic	Temporal symmetry	Population counts	Deterministic projection matrices
Model type	mark–recapture	regression of population sizes or indices, or mean of N_{t+1}/N_t's	(st)age-based matrix
Estimated parameters	rate of population change, local survival, total recruitment	rate of population change	rate of population change, stable age distribution, reproductive values, elasticities, net reproductive rate, generation time, etc.
Data required	encounter histories	time series of population sizes or indices	(st)age-specific survival and birth rates
Demographic processes incorporated	birth, death, emigration, immigration	birth, death, emigration, immigration	birth, death, and emigration†
Rate of population change	realized	realized	asymptotic and projected
Major model assumptions	constant study area boundaries, equal capture probabilities between marked and unmarked individuals	unbiased population estimates, time invariant detection probabilities for population indices	unbiased demographic estimates, time-invariant parameters/stable age distribution, (st)age-structure adequately defined

† Immigration can be incorporated into projection matrices but is usually ignored due to the difficulty associated with estimating immigration for natural populations.

not require multiple secondary sampling periods that assume demographic closure within each primary sampling period.

The second approach uses similar logic, but develops inference about the impact of immigration on population dynamics from the combined use of different estimators of population growth (Table 1). Population growth rates from temporal symmetry models ($\hat{\lambda}_{TS}$) and/or from counts of individuals estimated over multiple sampling periods ($\hat{\lambda}_C$) are compared with estimates from a deterministic projection matrix model ($\hat{\lambda}_M$; Caswell 2001). Both the temporal symmetry models and count-based approaches incorporate all demographic processes affecting population change (i.e., birth, death, immigration, and emigration), constitute estimates of the realized rate of population growth, and should theoretically provide similar estimates of growth (Table 1). In contrast, projection matrices are typically parameterized with age- or stage-specific estimates of birth and local survival rates (Caswell 2001), are usually constructed without incorporating immigration, and provide model-based estimates of the projected, asymptotic rate of population change in the absence of immigration. Thus, $\hat{\lambda}_{TS}$, $\hat{\lambda}_C$, and $\hat{\lambda}_M$ should all be equal when a population receives no immigrants, and $\hat{\lambda}_{TS}$ and $\hat{\lambda}_C$ should never be less than $\hat{\lambda}_M$ because negative immigration is not possible. If the difference between $\hat{\lambda}_{TS}$ and/or $\hat{\lambda}_C$ and $\hat{\lambda}_M$ is significant, it provides an estimate of the immigration rate, assuming that vital rates are measured with precision. It is not possible to estimate emigration by comparing λ estimates because emigration and mortality are confounded for all approaches.

Comparing λ estimates from these three approaches provides insight into population dynamics and the

TABLE 2. Interpreting estimates of rates of population change (λ) in terms of the dynamics of a single population.

Population model outcomes			Description of population dynamics		
λ_C or λ_{TS}	λ_M	λ_C (or λ_{TS}) $-$ λ_M	Population trend	Immigration → 0	Population status
<1	<1	$=0$	declining	no change	declining
<1	<1	>0	declining	faster decline	declining sink
≥1	<1	>0	stable or increasing	decline	sink
$=1$	$=1$	$=0$	stable	no change	closed or source
>1	>1	$=0$	increasing	no change	closed or source
>1	$=1$	>0	increasing	stabilize	open and potential source
>1	>1	>0	increasing	slower increase	open and potential source

Notes: Here, λ_C is the rate of population change based upon a times series of population size estimates or indices, λ_{TS} is the rate of population change based on temporal symmetry mark–recapture models, and λ_M is the rate of population change estimated with a projection matrix model parameterized only with estimates of local survival and birth rates. λ_C and λ_{TS} should be similar because both are estimates of the true rate of population change, but may differ from λ_M which does not include immigration processes.

demographic consequences of movements among populations (Table 2). A population where $\hat{\lambda}_{\mathrm{TS}}$ and/or $\hat{\lambda}_{\mathrm{C}}$ are equal to $\hat{\lambda}_{\mathrm{M}}$ and all estimates are <1 is considered to be a declining population that does not receive immigrants (Table 2, row 1). If $\hat{\lambda}_{\mathrm{TS}}$ and/or $\hat{\lambda}_{\mathrm{C}}$ are greater than $\hat{\lambda}_{\mathrm{M}}$ and $\hat{\lambda}_{\mathrm{M}}$ is <1, the population receives immigrants, would decline in the absence of immigration, and is considered a sink that is either in decline or being sustained by the rescue effect (Table 2, rows 2–3). A population where $\hat{\lambda}_{\mathrm{TS}}$ and/or $\hat{\lambda}_{\mathrm{C}}$ are equal to $\hat{\lambda}_{\mathrm{M}}$ and all estimates are ≥ 1 is self-sustaining and does not receive immigrants (Table 2, rows 4–5). Such a population is either closed or a source, depending on whether it produces emigrants that sustain other populations. A population where $\hat{\lambda}_{\mathrm{TS}}$ and/or $\hat{\lambda}_{\mathrm{C}}$ are greater than $\hat{\lambda}_{\mathrm{M}}$, and where $\hat{\lambda}_{\mathrm{M}}$ is ≥ 1 (Table 2, rows 6–7) is stable or increasing but is not a sink, because it is self-supporting. Such a population is considered a potential source population depending on whether emigration occurs.

We use these techniques to identify a sink population of Marbled Murrelets (*Brachyramphus marmoratus*) in central California, USA. The Marbled Murrelet is a federally threatened seabird found in the Pacific Northwest, Canada, and Alaska. It lays a single egg in nests located primarily in coastal old-growth forests (Nelson 1997, USFWS 1997). Extensive harvesting of old-growth forests is believed to have greatly reduced Marbled Murrelet populations, but other threats include oil spills, gillnetting, declines in prey availability, and increases in nest predator populations (Carter and Erickson 1992, USFWS 1997, Becker and Bessinger 2006, Peery et al. 2004*b*, *in press b*). Its maritime foraging habitats and secretive behavior at nest sites have made the murrelet an extremely challenging species to study, and its ecology and demography remain poorly understood. The central California population is the smallest murrelet population, is located at the southern end of the murrelet's range, and is isolated from the nearest population to the north by several hundred kilometers (Ralph et al. 1995). This population nests in old-growth forests in the Santa Cruz Mountains, primarily in state and county reserves. During the breeding season, the population is distributed primarily between Half Moon Bay (San Mateo County) and Santa Cruz (Santa Cruz County), but individuals disperse up to several hundred kilometers to the north and south in the fall (M. Z. Peery, *unpublished data*).

METHODS

Estimating the rate of population change and immigration with temporal symmetry models

Estimating the rate of population change.—To estimate λ_{TS}, we captured 331 subadult and adult (≥ 1 year old) murrelets at night using a 2.5-m salmon dip net for seven years from April to October 1997–2003 from an inflatable vessel in areas with relatively high murrelet densities (Whitworth et al. 1997; Peery et al., *in press b*). From 1997 to 1999, we captured birds exclusively in Año Nuevo Bay, but we expanded capture areas to include Half Moon Bay and areas offshore of Pescadero Point, Pigeon Point, and Santa Cruz in 2000–2003. Upon capture, murrelets were marked with a uniquely numbered stainless steel U.S. Fish and Wildlife Service band and a subset of ≥ 1 year old individuals ($n = 122$) were radio-marked (Peery et al. 2004*a*, *b*, *in press b*). Recaptured murrelets were identified by their band number.

We estimated λ_{TS} using the λ parameterization of temporal symmetry models in Program MARK (White and Burnham 1999). First, we assessed the goodness of fit for the global model (model ϕ_t, p_t, λ_t), where p is recapture probability, using program RELEASE (Burnham et al. 1987). We then constructed several candidate models that included various combinations of time structure for these three parameters. Parameters that varied by year were denoted λ_t, ϕ_t, and p_t, whereas parameters that were constant over years were denoted $\lambda.$, $\phi.$, and $p.$. Recapture probabilities were allowed to differ between 1997–1998 and 1999–2003 because time devoted to capturing birds increased during the latter years of the study (denoted p_{effort}). An assumption for the unbiased estimation of λ_{TS} is that study area boundaries do not increase and that new individuals are not made available for capture artificially (Franklin 2001, Hines and Nichols 2002). Study area boundaries increased in 2000 to include areas other than Año Nuevo, potentially biasing λ. Therefore, we also considered models in which λ was allowed to differ between 1998–2000 and 2001–2003 (denoted λ_{area}), and only made inference to λ estimates in 2001–2003. Competing models were ranked according to how well they were supported by the capture data using $\mathrm{AIC_c}$ and $\mathrm{AIC_c}$ weights (Burnham and Anderson 2002). We initially ranked eight models containing all possible combinations of constant and year-specific λ, ϕ, and p parameters. All models containing a ϕ_t term were poorly supported ($\mathrm{AIC_c}$ weights < 0.001) and no further models with time-varying survival terms were explored, resulting in a total of 13 competing models.

We were unable to incorporate the potential effect of radio-tagging on survival or population growth when estimating λ_{TS} because the use of individual covariates is not supported with the temporal symmetry approach (G. C. White, *personal communication*). To offset any effects of radio-tagging on the estimation of survival and λ_{TS}, we used the estimate of Peery et al. (*in press b*) of annual local survival for murrelets that were not radio-marked (0.882, SE = 0.058) and adjusted λ_{TS} by adding the difference between this survival estimate and the survival estimate from temporal symmetry modeling based on both radio-marked and non-radio-marked birds.

Another assumption for the unbiased estimation of λ_{TS} is that individuals do not permanently become "trap shy" or λ will be biased high (Seber 1982, White et al.

1982, Hines and Nichols 2002). To test this assumption, we determined whether capture success (the proportion of individuals seen that were captured) declined over the study period. We used a general linear model with season (pre- vs. post-breeding, i.e., April–June vs. July–October) and year (treated as a linear effect) as independent variables. We conducted a second test of the trap-shy assumption by comparing the mean time (in minutes) required to catch unbanded and previously banded birds; we used a t test for 48 birds for which capture times were recorded.

Estimating the rate of immigration.—We estimated the rate of immigration using estimates of f_t, $\phi_{t(\mathrm{J})}$, and b_t as described previously. We estimated $\widehat{\mathrm{var}}(\hat{i}_t)$ using a bootstrapping procedure by generating 500 values of f_t, b_t, and $\phi_{t(\mathrm{J})}$ from their point estimates and associated sampling variances, and calculating $\hat{i}_t$ for each set. We modeled and estimated f_t using the f_t-parameterization of the temporal symmetry model in Program MARK with the banding data described previously. Insufficient numbers of juveniles were captured to estimate their survival directly, so we used three different values of juvenile survival: (1) 0.510, as estimated for juvenile Marbled Murrelets in Desolation Sound, British Columbia, Canada (Parker et al. 2003); (2) 0.617 (SE = 0.058), assuming that juvenile survival was 70% of subadult and adult survival, following Beissinger (1995) and Beissinger and Nur (1997); and (3) 0.882 (SE = 0.058), assuming that juvenile survival was equal to subadult and adult survival. We considered the first value to be a minimum estimate because it was estimated using radiotelemetry during the first few weeks after fledging when mortality is likely to be highest (Parker et al. 2003). The second estimate was based on the relationship between juvenile and adult survival for the Common Murre (*Uria aalge*), the most closely related species for which juvenile survival has been estimated. The third value represents a maximum estimate because it is highly unlikely that juveniles survive at a greater rate than more experienced, older birds.

We estimated the mean birth rate ($\bar{b}_t$), defined as the mean number of juvenile murrelets produced per subadult and adult, from 1997 to 2003, based on the ratio of juvenile to subadult and adult individuals observed during at-sea surveys conducted in the breeding season from 1997 to 2003 (Peery et al. 2004*a, b*). Although juvenile ratios have been questioned as estimators of reproductive success for Marbled Murrelets (Kuletz and Piatt 1999, Lougheed et al. 2002), estimates of birth rates from juvenile ratios agree well with estimates derived from the reproductive histories of radio-marked individuals, murrelets rarely emigrate from our survey area prior to the cessation of surveys, and juveniles are not spatially segregated from after-hatch-year individuals in central California (Peery et al. 2004*a*, *in press a*). At-sea surveys were conducted along transects placed (1) parallel to and 400 m from shore from 1997 to 2000, and (2) in a zigzag manner that ranged from 200 to 2500 m from shore from 1999 to 2003 (Becker and Beissinger 2003, Peery et al. 2004*a, b*). Surveys were conducted from 10 July, when at least 35% of young were expected to have fledged, to 23 August, when 75% of young had fledged and adults had become indistinguishable from juveniles as they molted into their basic plumage (Carter and Stein 1995, Peery et al. 2004*a*; *in press a*). Because some juveniles were expected to have fledged after the survey was conducted and not be counted (Hamer and Nelson 1995), we estimated the cumulative proportion of young expected to have fledged as a function of date, based on 47 known fledging events in California (Hamer and Nelson 1995; T. Hamer, *unpublished data*). We used linear regression following Beissinger and Nur (1997) and Peery et al. (2004*a*). This regression model was then used to correct the number of juveniles observed ($H_{\mathrm{o}(i)}$) during survey i for the proportion of young that had not yet fledged with the following equation:

$$H_{\mathrm{c}(i)} = H_{\mathrm{o}(i)}\left(\frac{1}{-1.5433 + 0.0098(\mathrm{DATE}_i)}\right)$$

where ($H_{\mathrm{c}(i)}$) was the date-corrected number of juveniles and DATE_i was the Julian date for survey i. We estimated the mean (corrected) juvenile ratio in year t ($\hat{\bar{R}}_t$), which is equivalent to $\hat{\bar{b}}_t$, using the following equation:

$$(\hat{\bar{R}}_t) = \frac{\sum_1^n H_{\mathrm{c}(i)}}{\sum_1^n A_i}$$

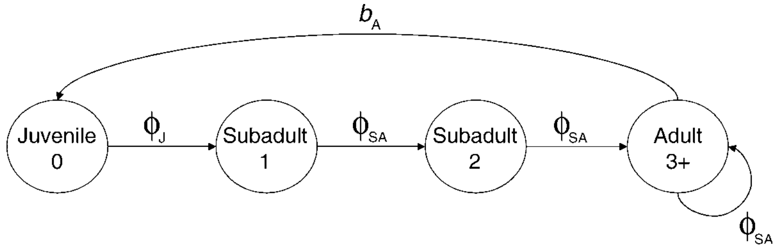
where A_i was the number of subadult and adult birds ($\geq$1 year old) observed for survey i, respectively, and n was the number of surveys conducted in year t (Levy and Lemeshow 1991). The variance for $\hat{\bar{R}}_t$, $\widehat{\mathrm{var}}(\hat{R}_t)$, was estimated as

$$\widehat{\mathrm{var}}(\hat{R}_t) = \frac{1}{n}\left\{\frac{\widehat{\mathrm{var}}\left[\hat{H}_{\mathrm{c}(t)}\right]}{\hat{\bar{A}}_t^2} + \frac{\hat{\bar{H}}_{\mathrm{c}(t)}^2\widehat{\mathrm{var}}\left(\hat{A}_t\right)}{\hat{\bar{A}}_t^4} - \frac{2\hat{\bar{H}}_t\widehat{\mathrm{cov}}\left[\hat{H}_{\mathrm{c}(t)}, \hat{A}_t\right]}{\hat{\bar{A}}_t^3}\right\}$$

where $\hat{\bar{H}}_{\mathrm{c}(t)}$ and $\hat{\bar{A}}_t$ were the mean of $H_{\mathrm{c}(i)}$ and A_i in year t, respectively, $\widehat{\mathrm{var}}[\hat{H}_{\mathrm{c}(t)}]$ was the variance in $H_{\mathrm{c}(i)}$ in year t, $\widehat{\mathrm{var}}(\hat{A}_t)$ was the variance of A_i in year t, and $\widehat{\mathrm{cov}}(\hat{A}_t, \hat{H}_t)$ was the covariance in year t (van Kempen and van Vliet 2000). We estimated the mean juvenile ratio for the entire study period ($\hat{\bar{R}}$) by averaging annual estimates, and $\widehat{\mathrm{var}}(\hat{\bar{R}})$ was estimated as

$$\widehat{\mathrm{var}}(\hat{\bar{R}}) = \frac{\sum_1^n \widehat{\mathrm{var}}(\hat{R}_t)}{n}$$

where n was the number of years in which surveys were conducted (Thompson et al. 1998).



$$\begin{pmatrix} 0 & 0 & \phi_{SA}b_A & \phi_{SA}b_A \\ \phi_J & 0 & 0 & 0 \\ 0 & \phi_{SA} & 0 & 0 \\ 0 & 0 & \phi_{SA} & \phi_{SA} \end{pmatrix}$$

FIG. 1. Four-stage-class, post-breeding projection matrix model and associated life-cycle diagram used to estimate the population growth rate (λ_M) for Marbled Murrelets in central California, USA, where ϕ_J was juvenile survival, ϕ_{SA} was the joint subadult and adult survival rate, and b_A was the number of juveniles produced per adult.

Estimating the rate of population change with counts of individuals

To estimate λ_C, we estimated the population size of Marbled Murrelets (N_t) in central California from 1999 to 2003 using visual, ship-based at-sea surveys along a line transect and distance sampling techniques (Becker et al. 1997, Buckland et al. 2001). The Appendix provides a detailed description of the survey and modeling techniques used to estimate N. We estimated λ_C in year t using

$$\hat{\lambda}_{C(t)} = \frac{\hat{N}_{t+1}}{\hat{N}_t}$$

where $\hat{N}_t$ was the population size in year t. We estimated the geometric mean λ_C from 1999 to 2003 using

$$\hat{\bar{\lambda}}_C = \left(\Pi\ \hat{\lambda}_{C(t)}\right)^{1/N}$$

following Morris and Doak (2002), where N was the number of years λ was estimated (here, $N = 4$). To estimate $\widehat{\mathrm{var}}(\hat{\bar{\lambda}}_C)$, a bootstrapping procedure was used to randomly generate five consecutive population sizes from the point estimates of N_t and associated sampling variances. We then estimated $\hat{\bar{\lambda}}_C$ from simulated estimates of N_t, repeated this procedure 500 times, and used the distribution of $\hat{\bar{\lambda}}_C$'s to estimate var($\hat{\bar{\lambda}}_C$).

Estimating the rate of population change with a projection matrix model

We used a four-stage-class, post-breeding projection matrix model developed by Beissinger (1995) and Beissinger and Nur (1997), parameterized with stage-specific birth and local survival rates, to estimate λ_M (Caswell 2001). The stage classes were juveniles (0 years old), 1-year-old subadults, 2-year-old subadults, and adults ($\geq$3 years old), where only adults were able to breed (Fig. 1). We used a common estimated mean survival rate of 0.882 (SE = 0.058) for subadults and adults because these stages were not distinguishable in the field. This estimate was derived by Peery et al. (*in press b*), using only birds that were not radio-marked. Because we were not able to capture a sufficient number of juveniles to estimate survival directly, we parameterized the matrix model with the three estimates of juvenile survival discussed earlier, spanning the likely minimum and maximum values.

We parameterized the matrix model with the mean adult birth rate ($\hat{\bar{b}}_A$). We used the matrix model to iteratively estimate $\bar{b}_A$ by determining the birth rate that resulted in a stable age distribution that matched $\hat{\bar{R}}$ estimated from at-sea surveys (Beissinger 1995, Beissinger and Nur 1997). We estimated 95% confidence limits (and standard errors) for $\hat{\bar{b}}_A$ by determining the birth rates that resulted in the upper and lower 95% limits of $\hat{\bar{R}}$. We estimated the sampling variance for the rate of population change (var($\hat{\lambda}_M$)) using the delta method (Seber 1982, Oehlert 1992, Alvarez-Buylla and Slatkin 1994). We explored uncertainty in model structure by also estimating λ_M with the age of first breeding set to 2 years and 4 years for each of the three juvenile survival rates (De Santo and Nelson 1995).

Deterministic projection matrices use mean demographic rates to project the population forward in time, which assumes that survival and birth rates change little over time and that the population is characterized by a stable age distribution (Caswell 2001:30). However, the assumptions of time-invariant parameters and a stable stage distribution are not critical for estimating λ if inference is restricted to projecting what the population would do if demographic parameters remained as they have been during the study period (rather than forecasting what the population will do; Caswell 2001:30). Moreover, even if survival and birth rates vary over time, λ approximates an average estimate

TABLE 3. $\mathrm{AIC_c}$ scores for the 10 best temporal symmetry mark–recapture models estimating local survival (ϕ), recapture probability (p), and rate of population change (λ) based on 331 Marbled Murrelets captured from 1997 to 2003 in central California, USA.

Model	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	w	K
$\phi.$, p_{effort}, $\lambda.$	1885.03	0	0.644	4
$\phi.$, p_{effort}, λ_{area}	1887.05	2.01	0.236	5
$\phi.$, $p.$, λ_{area}	1890.19	5.16	0.049	4
$\phi.$, p_t, $\lambda.$	1891.69	6.65	0.023	9
$\phi.$, p_{effort}, λ_t	1892.42	7.40	0.016	9
$\phi.$, p_t, λ_{area}	1892.95	7.92	0.012	10
$\phi.$, $p.$, λ_t	1893.39	8.35	0.010	8
$\phi.$, $p.$, $\lambda.$	1894.18	9.14	0.007	3
$\phi.$, p_t, λ_t	1897.56	12.53	0.001	13
ϕ_t, p_t, $\lambda.$	1897.70	12.67	0.001	13

Notes: $\Delta\mathrm{AIC_c}$ scores represent the difference between the $\mathrm{AIC_c}$ score of the model in question and the highest ranked model (Burnham and Anderson 2002). $\mathrm{AIC_c}$ weights (w) provide an estimate of the relative likelihood of each model and sum to 1.0 (Burnham and Anderson 2002). Three models with $w < 0.001$ are not presented. K is the number of parameters in the model.

during the years when the rates were estimated (Franklin et al. 1996).

Testing for population stability and comparing λ estimates

We tested if $\lambda = 1$ for all three approaches using two-tailed Z tests:

$$Z = (\hat{\lambda} - 1)/\mathrm{SE}(\hat{\lambda})$$

following Franklin et al. (1996). We compared λ_{TS} and λ_{C} to λ_{M} with one-tailed Z tests for two samples using the following equation:

$$Z = (\hat{\lambda}_i - \hat{\lambda}_{\mathrm{M}})/\mathrm{SE}(\hat{\lambda}_i - \hat{\lambda}_{\mathrm{M}})$$

where $\hat{\lambda}_i$ represented either $\hat{\lambda}_{\mathrm{TS}}$ or $\hat{\lambda}_{\mathrm{C}}$, and $\mathrm{SE}(\hat{\lambda}_i - \hat{\lambda}_{\mathrm{M}})$ was the standard error of the difference between $\hat{\lambda}_i$ and $\hat{\lambda}_{\mathrm{M}}$. We used a one-tailed test because, in theory, it is not possible for the growth rate estimate from the matrix model to exceed the estimate from either counts of individuals or the mark–recapture method (Table 2). We tested for a difference between $\hat{\lambda}_{\mathrm{TS}}$ and $\hat{\lambda}_{\mathrm{C}}$ with a two-sided Z test.

RESULTS

Estimating the rate of population change and immigration with temporal symmetry models

Estimating the rate of population change.—The global model (model ϕ_t, p_t, λ_t) fit the capture data adequately using program RELEASE (for Test 2, $\chi^2 = 8.00$, df $= 7$, $P = 0.33$; for Test 3, $\chi^2 = 8.22$, df $= 9$, $P = 0.51$). Based on $\mathrm{AIC_c}$ scores, model $\phi.$, p_{effort}, $\lambda.$ best explained the capture data, indicating that survival was constant over time, recapture probabilities differed between 1997–1998 and 1999–2003, and population growth was constant over time (Table 3). This model was almost three times more likely than the next best model ($\phi.$, p_{effort}, λ_{area}), which indicated that population growth increased when the study area was expanded and was about 13 times more likely than the third best model ($\phi.$, $p.$, λ_{area}) (Table 3). Based on model $\phi.$, p_{effort}, $\lambda.$, we estimated that $\hat{\phi} = 0.843$ (SE $= 0.055$); $\hat{p} = 0.088$ (SE $= 0.019$) in 1997–1998 and $\hat{p} = 0.152$ (SE $= 0.026$) in 1999–2003; and $\hat{\lambda}_{\mathrm{TS}} = 1.025$ (SE $= 0.033$). After adjusting $\hat{\lambda}_{\mathrm{TS}}$ for the effect of radio transmitters (by adding the difference in survival between non-radio-marked individuals and all individuals; 0.039), $\hat{\lambda}_{\mathrm{TS}} = 1.064$ (SE $= 0.033$); $\hat{\lambda}_{\mathrm{TS}}$ was close to being significantly greater than 1.0 ($Z = 1.94$, $P = 0.05$). However, Z was overestimated in this test because sampling variance for the radio transmitter effect was unknown and not included, although it was probably small due to the relatively small magnitude of the effect.

Murrelets did not become trap shy during the study. There was no decline in capture success over the study period ($F_{1,5} = 3.59$, $P = 0.12$). Likewise, there was no difference ($t_{1,35} = 0.80$, $P = 0.43$) between the time required to catch unbanded (2.33 ± 2.32 min; mean ± SE, $n = 36$ birds) and previously captured individuals (1.75 ± 1.60 min, $n = 12$ birds). Thus, there was little evidence suggesting that $\hat{\lambda}$ was biased high due to trap response.

It is also highly unlikely that expanding our study area boundaries in 2000 affected our λ estimate. First, 403 of 416 (97%) captures occurred within the original study area boundaries due to high densities of birds in Año Nuevo Bay. Second, radiotelemetry data indicated that there was little or no difference in the identity of birds within the original study area boundaries and the expanded boundaries because murrelets regularly travel between the two areas (M. Z. Peery, *unpublished data*). Third, there was more support for temporal symmetry models *without* an area effect for λ than there was for models with an area effect (Table 3). Even for the best model containing an area effect, there was very little difference between growth estimates for the pre- and post-expansion periods ($\hat{\lambda}. = 1.043$ and 1.069), and this small difference was swamped by sampling error. Fourth, although all data from 1997 to 2003 were included in the analysis, inference was made only for the rate of population change in years *after* the study area was expanded. Thus, increasing the pool of available individuals should not have affected the estimate of λ_{TS} that will be compared to estimates from at-sea counts and the projection matrix.

Estimating immigration.—We conducted a total of 56 at-sea surveys from 1997 to 2003, during which we observed 86 juveniles and 7366 subadults and adults to estimate b_t. Consistent with Peery et al. (2004*b*), $\hat{\bar{R}}$ was low (0.036, SE $= 0.011$), but ranged from 0.004 in 1998 to 0.064 in 2001. Consequently, $\hat{\bar{b}}_{\mathrm{A}}$ was also low (0.039 juveniles produced per adult, SE $= 0.014$) and ranged from 0.003 in 1998 to 0.075 in 2001 (Fig. 2).

Modeling f with program MARK yielded $\mathrm{AIC_c}$ values identical to those from the modeling of λ (Table 3) because the λ- and f-parameterizations are equivalent ($\lambda_t = f_t + \phi_t$). Based on the best recruitment model, $\phi.$,

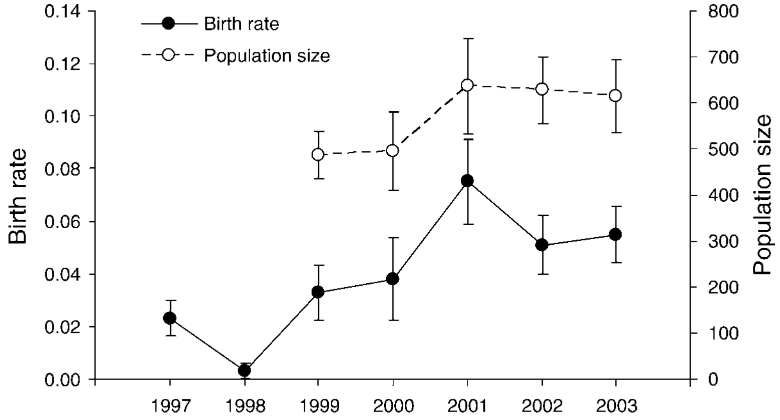


FIG. 2. Estimates (mean ± SE) of birth rates ($\hat{\bar{b}}_t$) and population sizes for Marbled Murrelets in central California estimated using at-sea surveys from 1997 to 2003.

p_{effort}, $f.$, $\hat{f} = 0.182$ (SE = 0.058) and was considerably greater than the birth rate. Because $\hat{f}$ from this model was constant among years and we had no estimate of annual variation in juvenile survival, we used a constant recruitment rate, mean birth rate, and constant juvenile survival rate to estimate a single, mean immigration rate for the study period. For the three estimates of juvenile survival, 0.510, 0.617, and 0.882, we estimated that $\hat{\bar{i}} = 0.163$ (95% CL = 0.051, 0.276), $\hat{\bar{i}} = 0.160$ (95% CL = 0.048, 0.272), and $\hat{\bar{i}} = 0.154$ (95% CL = 0.037, 0.271), respectively. Because these three immigration estimates were very similar, accurate estimates of juvenile survival were not required. Moreover, the lower confidence limits for all three immigration estimates were greater than zero, suggesting that significant immigration occurred.

Estimating the rate of population change with counts of individuals

Population size ranged from 487 to 641 (Appendix) and appeared to increase by about 100 birds between 2000 and 2001 (Fig. 2), although the 95% confidence limits for population size overlapped. Based on these estimates of population size, $\hat{\lambda}_C = 1.058$ (SE = 0.047) and was not significantly different from 1 ($Z = 1.23$, $P = 0.22$), indicating that the population was stable between 1999 and 2003. No difference existed between $\hat{\lambda}_C$ and $\hat{\lambda}_{TS}$ ($Z = 0.10$, $P = 0.91$).

TABLE 4. Point estimates of λ_M for Marbled Murrelets using a projection matrix model assuming three different ages of first breeding and estimates of juvenile survival.

	Age of first breeding (yr)		
Juvenile survival	2	3	4
0.510†	0.902	0.902	0.901
0.617‡	0.905	0.905	0.905
0.882§	0.915	0.914	0.913

† From radio-marked individuals in British Columbia, Canada (Parker et al. 2003).

‡ Juvenile survival set to 70% of subadult and adult survival (Beissinger 1995, Beissinger and Nur 1997).

§ Juvenile survival equal to subadult and adult survival.

Estimating the rate of population change with a projection matrix model

Using the projection matrix (Fig. 1), $\hat{\lambda}_M = 0.905$ (SE = 0.053) using $\hat{\bar{b}}_A = 0.039$ (SE = 0.014), $\hat{\phi}_{SA} = 0.882$ (SE = 0.058), $\hat{\phi}_J = 0.617$ (SE = 0.058), and an age of first breeding of 3 years. This estimate was almost significantly less than 1.0 ($Z = 1.79$, $P = 0.07$) and suggested that, in the absence of immigration, the population would decline by 9.5% per year. Moreover, $\hat{\lambda}_M$ was significantly less than $\hat{\lambda}_C$ and $\hat{\lambda}_{TS}$ ($Z = 2.16$, $P = 0.02$ and $Z = 2.55$, $P = 0.01$, respectively). Adjusting the age of first breeding to 2 and 4 years of age and using alternative estimates of juvenile survival had little effect on $\hat{\lambda}_M$, and the population was projected to decline under all scenarios in the absence of immigration (Table 4).

DISCUSSION

Our results suggest that Marbled Murrelets in central California represent a sink population that is being augmented by individuals immigrating from larger populations to the north. Too few juveniles were born locally and recruited into the population to compensate for losses due to death and emigration. Although the matrix model projected the population to decline rapidly (9.5% per year) in the absence of immigration, numbers did not decline, as indicated by at-sea counts and temporal symmetry mark–recapture models (Fig. 3). We suggest that differences in λ estimates occurred because the temporal symmetry and at-sea survey approaches incorporated immigration as well as birth, death, and emigration processes, but the matrix model did not include immigration. The fact that recruitment, as estimated with temporal symmetry models, was high (0.182; SE = 0.058) despite a very low birth rate (0.039; SE = 0.014) further supports the immigration and population sink hypothesis. Although estimates of λ from counts of individuals cannot be decomposed into the

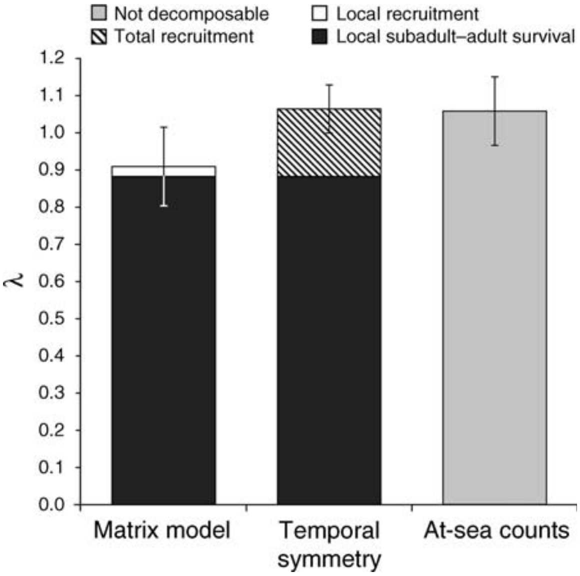


FIG. 3. Estimates (mean and 95% CI) of the population growth rate, λ, from 1997 to 2003 for Marbled Murrelets in central California Different estimates were based on a projection matrix model, temporal symmetry mark–recapture models, and at-sea counts. Shadings depict parameter estimates involved in estimating λ and provide an indication of the relative contribution of each demographic process to the population growth rate. Local recruitment equals the birth rate multiplied by the rate of juvenile survival.

component processes that affect population growth, they provided complementary information that increased our confidence in λ estimates from temporal symmetry models. It was encouraging, and yielded strong inference, that these two methods that incorporated the same demographic processes yielded such similar estimates for population growth even though they were based on entirely different and independent types of information.

Prior to this study, little was known about the interdependence of murrelet populations, although the sink hypothesis for the central California population was previously suggested by Divoky and Horton (1995), based on the population's small size and the degraded state of nesting habitat in the region. Source–sink dynamics for Marbled Murrelet populations appear to conflict with the strong breeding fidelity observed in other alcid species (Birkhead 1977, Ashcroft 1979, Gaston 1992). However, an unknown number of breeding murrelets are displaced by the logging of their nesting habitat and may need to range far in search of available habitat because they do not appear to pack into remaining nesting habitat after logging (Burger 2001, Raphael et al. 2002). Moreover, one of 98 Marbled Murrelets radio-marked during the breeding season in central California was detected moving >300 km north to at-sea areas used by the murrelet population in northern California (M. Z. Peery, *unpublished data*; E. Burkett, *unpublished data*), indicating that individuals originating from one population could be counted or marked in another breeding population. Although it is not known whether this individual permanently recruited into the northern California population or returned to the central California population, such movements could theoretically result in differences between $\hat{\lambda}_C$ or $\hat{\lambda}_{TS}$ and $\hat{\lambda}_M$. Genetic analyses suggest that murrelets in central California are distinct from northerly populations (Friesen et al. 2005), but F_{st} and related parameters of differentiation are relatively low for adjacent populations (0.03–0.07) and not all populations have been characterized. Frequent movements can occur among breeding populations of seabirds without homogenizing genetic population structure if interbreeding is limited or immigrants are selected against (Dearborn et al. 2003). Further support for the potential interdependence of Marbled Murrelet populations includes the following: (1) long-distance intercolony dispersal events by both juvenile and breeding alcids have been reported (Gaston 1990, Harris and Wanless 1991, Halley and Harris 1992); (2) the recent establishment of several new alcid colonies in western North America can only be explained by dispersal of individuals from other colonies (Divoky and Horton 1995); and (3) there is an increasing realization that natal dispersal by alcids has an important impact on the dynamics of alcid populations (Frederiksen and Petersen 2000).

It is unlikely that permanent emigration by adults was a significant demographic process for murrelets in central California. Local survival was so high (0.882) that few losses could be attributed to emigration, even if mortality was low. Although a radio-marked Marbled Murrelet was detected moving from central to northern California during the breeding season, it is unknown if this individual returned to central California in the following breeding season. Moreover, the mean adult birth rate (0.039) was so low that few juveniles were produced to emigrate to other populations, although we cannot exclude that possibility. Even in the unlikely event that all individuals that died or left the population ($1 - \phi = 0.118$) did emigrate to other populations, the central California population would still receive a net input of individuals because the immigration rate was estimated to be 0.160.

Source–sink dynamics for murrelet populations would have important conservation implications because sink populations depend critically on the continued persistence of source populations. Management plans in regions where populations are still relatively large should consider potential impacts beyond local populations. Nevertheless, only ~90–100 immigrants per year would need to enter the central California population to produce the level of immigration that we estimated (an immigration rate of 0.16 for 600 individuals in the population). This number represents a small fraction of the range-wide population size (947 500) of Marbled Murrelets (McShane et al. 2004), suggesting that a low emigration rate from northerly populations could sustain murrelets in central California.

Inferring population dynamics from comparisons of λ estimates

Commonly used estimators of λ do not treat population processes equally and differences in these estimates can be used to gain insight into population dynamics. Specifically, $\hat{\lambda}_C$ and $\hat{\lambda}_{TS}$ are estimates of the realized rate of change in population size and include immigration, whereas $\hat{\lambda}_M$ provides an estimate of the asymptotic and projected rate of population change in the absence of immigration (Table 1). Thus, tests of the hypotheses that λ_C and/or $\lambda_{TS} \geq 1$, and that $\lambda_M \geq 1$ pose different questions. The first hypothesis asks if the number of individuals in the population is stable or increasing. The second hypothesis can be phrased in two equivalent ways. (1) Is the population projected to remain stable or increase in absence of immigration? (2) Does local recruitment compensate for deaths and emigration? Testing the hypothesis that $\hat{\lambda}_C$ and/or $\hat{\lambda}_p \geq \hat{\lambda}_M$ asks: "Does immigration into the population occur?" Using results from these three tests in the context of the scenarios in Table 2 provides information on the role of immigration in maintaining populations that cannot be obtained by estimating λ with a single approach. Testing these hypotheses not only provides insight into population dynamics, but also is likely to be feasible for many population studies where young and adults are both marked and counted. Nevertheless, comparing λ estimates does not separate death and emigration processes, so it can only identify *potential* source populations (Table 2).

The conservation literature is replete with examples where $\hat{\lambda}_M$ is treated as an estimate of the actual change in population size. However, $\hat{\lambda}_M$ will be an underestimate of the true rate of population change if immigration occurs, and populations projected to decline with matrix models may, in fact, be stable or increasing. Estimates of immigration can be incorporated into matrix models, in which case λ_M becomes more likely to predict the actual rate of population growth (Cooch et al. 2001, Sandercock and Beissinger 2002). Nevertheless, temporal symmetry models and counts of individuals estimate realized rates of change and may be more feasible because estimates of birth rates and survival for various life stages are not required (Table 1).

We estimated immigration by subtracting local recruitment (the product of the birth rate and juvenile survival) from total recruitment estimated using temporal symmetry models. Nichols and Pollock (1990) proposed a similar approach in which the number of surviving adults and juveniles was subtracted from the total number of adults in the population to estimate the number of immigrants. This framework uses closed population mark–recapture models to estimate the number of individuals in the young and adult age classes, and makes use of secondary sampling periods nested within primary sampling periods. Primary sampling periods are used to estimate age-specific survival rates with CJS mark–recapture models for open-population models. Our approach may be more feasible when it is difficult to capture individuals on several occasions within a short time span. Note that immigration can also be estimated by subtracting $\hat{\lambda}_M$ from $\hat{\lambda}_{TS}$ or $\hat{\lambda}_C$. The former will yield the same estimate of immigration as $i_t = f_t - b_t\phi_{t(J)}$, but subtracting $\hat{\lambda}_M$ from $\hat{\lambda}_C$ will be useful when it is not possible to estimate λ with temporal symmetry models. For Marbled Murrelets, this approach yielded an immigration estimate of 0.153, which was very similar to estimates derived from $i_t = f_t - b_t\phi_{t(J)}$. All of these methods estimate immigration and the effect of immigration on populations indirectly without observing marked or radio-tagged animals moving between populations. Therefore, a thorough evaluation of model assumptions, such as equal capture probabilities between unmarked and marked individuals for the temporal symmetry model, is required for robust inference (Table 1).

In this study, we defined a sink as a stable or increasing population that would decline in the absence of immigration (Table 2). Our definition differs, in part, from Pulliam's (1988) original definition for a sink, which also included the criteria that deaths must exceed births and immigration must exceed emigration. However, ours is a commonly employed definition (Pulliam 1996, Thomas and Kunin 1999, Kruzer and Huntley 2003, Holt and Gomulkiewicz 2004, Roy et al. 2005) and is often the only feasible way to define a sink, due to the difficulty of tracking emigrants and estimating emigration rates in open populations. It should be noted that, according to our definition, a sink population could: (1) provide more recruits for other populations than it received; or (2) exchange an equal number of individuals with other populations as occurs in "balanced dispersal" systems (McPeek and Holt 1992). Death and emigration will be confounded for most studies of natural populations, making Pulliam's definition and the balanced-dispersal concept of limited utility in conservation. In practice, defining a sink as any population that would decline in the absence of immigration may yield greater insight into population dynamics by generating testable hypotheses, for example, with the approaches presented here. Moreover, for many applications, such as estimating the population growth rate and understanding the role of immigration for Marbled Murrelets in central California, it may not be imperative to distinguish between death and emigration because the loss of an individual due to either process is just that: a loss to the population.

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APPENDIX

Estimated population size of Marbled Murrelets with distance sampling (*Ecological Archives* A016-051-A1).