

RECONSTRUCTING THE HISTORIC DEMOGRAPHY OF AN ENDANGERED SEABIRD

STEVEN R. BEISSINGER¹ AND M. ZACHARIAH PEERY²

*Department of Environmental Science, Policy and Management, 137 Mulford Hall, University of California,
Berkeley, California 94720-3114 USA*

Abstract. Reducing extinction risk for threatened species requires determining which demographic parameters are depressed and causing population declines. Museum collections may constitute a unique, underutilized resource for measuring demographic changes over long time periods using age-ratio analysis. We reconstruct the historic demography of a U.S. federally endangered seabird, the Marbled Murrelet (*Brachyramphus marmoratus*), from specimens collected ~100 years ago for comparison with predictions from comparative analyses and with results from contemporary field studies using both age-ratio analysis and conventional demographic estimators. Reproduction in the late 1800s and early 1900s matched predictions from comparative analysis, but was 8–9 times greater than contemporary estimates, whereas adult survival was unchanged. Historic reproductive rates would support stable populations, but contemporary levels should result in population declines. Contemporary demographic estimates derived from age-ratio analysis were similar to estimates from conventional estimators. Using museum specimens to reconstruct historic demography provides a unique approach to identify causes of decline and to set demographic benchmarks for recovery of endangered species that meet most assumptions of age-ratio analysis.

Key words: *age-ratio analyses; Brachyramphus marmoratus; demography; endangered species; historical demography; limiting factor; Marbled Murrelet; matrix population model; museum specimens; population growth.*

INTRODUCTION

As the number of species threatened with extinction continues to expand, conservation biologists and practitioners try to identify factors that cause species' declines and to develop management prescriptions for their recovery. The first step in this process is to confirm that the population has declined and to determine which demographic parameters are depressed (Caughley 1994, Peery et al. 2004). Although population declines often can be inferred from reduction in geographic range over time (Abbitt and Scott 2001), rates of survival and reproduction prior to anthropogenic impacts are rarely known because demography-based field research has only been conducted for a few decades and little impetus for ecological study exists prior to endangerment. As a result, it is often problematic to determine the cause of population declines and to set demographic targets for recovery.

Museum collections may constitute a unique, underutilized resource for measuring demographic changes over long time periods. Museum specimens have been used to document changes in geographic range (Parme-

san 1996, Shaffer et al. 1998, Pergams and Nyberg 2001, Graham et al. 2004, Suarez and Tsutsui 2004) or specific life history traits (Beissinger 1986, McGraw 2001) in response to habitat loss, climate change, and other environmental factors, and to yield DNA for analysis of changes in genetic diversity or estimation of effective population size (Paxinos et al. 2002, Leonard et al. 2005). Yet, demographic parameters, such as birth and death rates, can be estimated from museum specimens using age-ratio analysis or ratios of the number of individuals in different age classes, which has been done to examine geographic variation in survival (Snow 1956, Greenberg 1980, Ricklefs 1997, Rohwer 2004). If applied to specimens of threatened species with distinguishable age or stage classes that were collected prior to the onset of population declines, age-ratio analysis could provide novel baseline rates of reproduction and survival that could be used to reconstruct historical demography and to set demographic benchmarks for recovery.

Age-ratio analysis has fallen in and out of vogue in ecology (Hanson 1963, Caughley 1974, Anderson et al. 1981, Skalski et al. 2005) and recent applications have rekindled debate over the validity of demographic estimates derived from this approach because critical assumptions may be violated (Conn et al. 2005, Ricklefs and Rohwer 2005). Age ratios are often used as an index of reproduction in monitoring and management programs (Megrey 1989, McCullough et al. 1994, Flanders-

Manuscript received 24 May 2006; revised 21 July 2006; accepted 26 July 2006. Corresponding Editor: R. Greenberg.

¹ E-mail: beis@nature.berkeley.edu

² Present address: Moss Landing Marine Laboratories, 7544 Sandholdt Road, Moss Landing, California 95039 USA.

Wanner et al. 2004, Iverson et al. 2004, Skalski et al. 2005). Renewed interest in age-ratio analysis arose for estimating demographic rates that would otherwise have been infeasible due to the large geographic scale of analysis (Graves 1997, Ricklefs 1997, Rohwer 2004) or due to sampling logistics (Flanders-Wanner et al. 2004, Green 2004, Peery et al. 2007). Age-ratio analysis has been used instead of conventional estimators of fecundity (e.g., nest success) and survival (e.g., mark-recapture methods) when conventional estimates suffer from bias (Newton 1999, Ricklefs and Rohwer 2005). Age-ratio analysis assumes that ages can be reliably distinguished, populations are not fluctuating strongly, and immigration or emigration do not occur during the survey period (Ricklefs 1997, Udevitz and Ballachey 1998, Conn et al. 2005, Ricklefs and Rohwer 2005). Biased estimates from museum materials could also arise if collectors targeted or avoided a particular age class, if age classes differed in "collectibility," or if collections occurred in areas preferred or avoided by an age class (Domenech and Senar 1997, Ricklefs 1997, Rohwer 2004, Conn et al. 2005, Ricklefs and Rohwer 2005, Peery et al. 2007). Direct comparisons of demographic estimators developed from age-ratio analysis with conventional measures of fecundity and survival are notably lacking (Newton 1999, Green 2004, Bonenfant et al. 2005).

Here we reconstruct the historic demography of an endangered population of Marbled Murrelets (*Brachyramphus marmoratus*; family Alcidae) in central California, USA, using age-ratio analysis of museum specimens collected ~100 years ago, prior to large-scale population declines. We compare the results with (1) contemporary estimates to examine changes over the past century in birth, survival, and population growth rates; and with (2) estimates predicted from life history theory using comparative analyses and allometry (Calder 1984, Gaillard et al. 1989), which also provide predicted benchmarks for demographic rates under pre-decline conditions. Contemporary estimates of survival were derived from both age-ratio analysis of birds captured at sea and from mark-recapture studies (Peery et al. 2006b), which allows a direct comparison of survival estimates from the two methods. Contemporary estimates of reproduction were made using age ratios of birds surveyed at sea (Peery et al. 2006a, 2007) and from age ratios of birds captured for demographic studies. These were compared with each other and with direct estimates of reproductive success from telemetered birds (Peery et al. 2004). Finally, we evaluated the potential for bias that could arise from applying age-ratio analysis to murrelets.

METHODS

The Marbled Murrelet, a seabird, was among the last North American bird species to have their nests discovered because nests are usually located high in the canopy of coastal old-growth forests in the Pacific

Northwest (Ralph et al. 1995). Despite receiving little study until the past decade, murrelets are well represented in museum collections, with 170 specimens from central California in the California Academy of Sciences and the Museum of Vertebrate Zoology (University of California, Berkeley) (see Plate 1).

We sampled historic specimens collected from 1892 to 1922 to estimate rates of reproduction (hereafter, productivity) from the ratio (\hat{R}) of hatch-year (HY; 0-yr-old) to after-hatch-year (AHY; ≥ 1 -yr-old) birds, and survival (\hat{S}) from the number of second-year (SY, 1-yr-old) to after-second-year (ASY; ≥ 2 -yr-old) individuals.

Murrelet age class determination

Marbled Murrelets are sexually monomorphic in all plumages, but AHY murrelets have distinct alternate (breeding) and basic (winter) plumages (Carter and Stein 1995, Nelson 1997, Thompson et al. 2003) that can be distinguished readily at a distance or in the hand. HY murrelets (or juvenile individuals) have different plumage characteristics than AHY adults in breeding plumage (both SY and ASY) that can be readily identified from a boat before late August and in hand after late August. Discriminating between SY and ASY birds requires examination in the hand (Carter and Stein 1995, Nelson 1997, Thompson et al. 2003).

AHY murrelets undergo a prebasic molt from August to October; in basic plumage they have completely white breasts, sides of the head, and partial neck collars. Their backs are covered with blackish-brown back feathers and white scapulars. AHY murrelets molt into alternative plumage from March to April and appear much darker, as they have brown to brownish-black upperparts, rusty margins on the back feathers between the nape and rump, and reddish-brown scapulars. The chest, sides, flanks, and sides of the head to above the eye and neck are mottled brown, composed mostly of white feathers with broad brown margins.

HY murrelets appear on the water in June and are readily distinguished from AHYs in breeding plumage until the AHYs undergo prebasic molt in late August (Carter and Stein 1995, Nelson 1997, Thompson et al. 2003). HY murrelets resemble AHYs in their basic plumage because they both have white breast and neck feathers, but these feathers have blackish-brown tips on HY murrelets that can be identified by careful examination in hand. Recently fledged HY murrelets also have a conspicuous dark neck band on the upper breast formed by dark-margined feathers. Both the dark neck band and the blackish-brown-tipped breast feathers become white within 2–4 months following fledging. At this point, HY murrelets are generally indistinguishable from AHYs in basic plumage unless they are examined in the hand to determine the color of their underwing coverts (Carter and Stein 1995, Nelson 1997, Thompson et al. 2003). HYs have underwing coverts that contain a variable amount of white and retain these feathers until

their first prebasic molt in the following August, when they reach one year of age.

SY individuals are murrelets in year t that fledged in year $t - 1$ (i.e., 1-yr-old birds). They can be identified in their second calendar year by the presence of white underwing coverts until August, when they undergo their prebasic molt and lose these feathers (Lethaby 2000, Thompson et al. 2003). ASY (≥ 2 -yr-old) murrelets have completely dark brown underwing coverts.

Estimating R and S

Productivity was estimated at the end of the breeding season (August–October) both for historic specimens and for contemporary murrelets captured in dip nets from the total number of individuals in each age class (N_{HY} and N_{AHY}) during the sampling period as:

$$\hat{R} = N_{\text{HY}} / N_{\text{AHY}}.$$

Productivity (\hat{R}) represents the number of offspring produced per individual in the population. We use this measure rather than $N_{\text{HY}}/N_{\text{AHY}}$, because it is directly comparable with at-sea surveys, where ASY and SY individuals cannot be distinguished. Standard errors incorporating demographic variation, but not other forms of uncertainty, were estimated following Ricklefs (1997) as

$$\text{SE}(\hat{R}) = \left[(N_{\text{HY}} \times N_{\text{AHY}}) / (N_{\text{HY}} + N_{\text{AHY}})^3 \right]^{1/2}.$$

Historic specimens were collected from August through October, 1892–1922 (see Plate 1). Modern samples were restricted to those individuals captured during the same months in 2002 and 2003, after aging techniques had been developed to distinguish between SY and ASY birds in the hand.

We also estimated R for contemporary Marbled Murrelets based on HY:AHY ratios from at-sea surveys conducted between 10 July and 23 August from 1996 to 2003, when 34% to 75% of young were expected to have fledged (Peery et al. 2007). To adjust the sample to be equivalent to one collected at the end of the breeding season, the number of HY birds detected on a given survey was divided by the proportion of young expected to have fledged by the time of the survey to yield a date-corrected HY:AHY ratio. We estimated this proportion based on 47 known fledging events in California using linear regression analysis, with the cumulative proportion of young fledged as the dependent variable and Julian date (1 January is Julian day 1) as the independent variable (Beissinger 1995, Peery et al. 2007). Simulation analyses indicated that annual variation in the timing of breeding results in only small biases in HY:AHY ratios estimated in this manner (Peery et al. 2007).

We estimated the HY:AHY ratio from the date-corrected at-sea survey data in year t with the following equation:

$$\hat{R}_t = \frac{\sum_i^n H_i}{\sum_i^n A_i}$$

where H_i and A_i are the number of HY and AHY individuals for survey i , respectively, and n is the number of surveys conducted in year t (Levy and Lemeshow 1991, Peery et al. 2007). We estimated $\text{var}(\hat{R}_t)$ as

$$\hat{\text{var}}(\hat{R}_t) = \frac{1}{n} \left(\frac{\hat{\text{var}}(\hat{H}_t)}{\hat{A}_t^2} + \frac{\hat{H}_t^2 \hat{\text{var}}(\hat{A}_t)}{\hat{A}_t^4} - \frac{2\hat{H}_t \hat{\text{cov}}(\hat{H}_t, \hat{A}_t)}{\hat{A}_t^3} \right)$$

where $\hat{\text{var}}(\hat{H}_t)$ is the variance in the number of HYS observed in year t ; $\hat{\text{var}}(\hat{A}_t)$ is the variance in the number of AHYs observed in year t ; $\hat{\text{cov}}(\hat{H}_t, \hat{A}_t)$ is the covariance between the number of HY and AHYs observed in year t ; and \hat{H}_t and \hat{A}_t are the mean number of HYS and AHYs observed in year t , respectively (Levy and Lemeshow 1991, Peery et al. 2007). The mean HY:AHY ratio for all years (\hat{R}) was estimated by averaging unweighted annual estimates and $\hat{\text{var}}\hat{R}$ was estimated as

$$\hat{\text{var}}(\hat{R}) = \frac{\sum_i^n \hat{\text{var}}(\hat{R}_i)}{n}$$

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

AHY survival was estimated as $\hat{S} = N_{\text{ASY}} / (N_{\text{ASY}} + N_{\text{SY}})$, where N_{ASY} was the number of after-second-year individuals and N_{SY} was the number of second-year individuals (Ricklefs 1997). Standard errors incorporating demographic variation, but not other forms of uncertainty, were estimated as $\text{SE}(\hat{S}) = [(N_{\text{ASY}} \times N_{\text{SY}}) / (N_{\text{ASY}} + N_{\text{SY}})]^{1/2}$.

Comparative analysis

Comparative analyses using allometry and life history traits (Calder 1984, Gaillard et al. 1989) were conducted to derive benchmark HY:AHY ratios and survival rates for Marbled Murrelets for comparison with historic and contemporary estimates. The productivity index, R , should increase with clutch size and should decrease with body mass because body mass is negatively related to clutch size and positively related to age of first breeding (Calder 1984, Sæther 1988). On the other hand, survival, S , should decrease with clutch size and increase with body mass. HY:AHY ratios for 29 bird species estimated near the end of the breeding season (Appendices A and C), and adult survival rates for 12 species of Alcidae (Appendices B and C) were used in multiple regression analyses with body mass and clutch size as independent variables to derive predictive equations for R and S , respectively.

TABLE 1. Estimates of historic, predicted, and contemporary demographic rates (mean \pm SE, with n or 95% confidence intervals in parentheses) for Marbled Murrelets in central California, USA.

Demographic rate	Historic (1892–1922) age ratios of specimens	Predicted allometry†	Contemporary (1997–2003)	
			Surveys and mark–recapture	Age ratios of captured birds
HY:AHY ratio, R	0.297 ± 0.061 (48)	0.292 (29)	0.035 ± 0.011 (59)‡	0.032 ± 0.011 (257)
AHY survival, S	0.840 ± 0.073 (25)	0.835 (12)	0.882 ± 0.058 (331)§	0.905 ± 0.037 (63)
Population growth, $\lambda $	1.017 (CI: 0.900–1.138)	1.006	0.905 (CI: 0.801–1.009)	0.924 (CI: 0.854–0.997)

† Predicted from relationships in Fig. 1 and equations in the text for a bird with typical murrelet body mass (215 g) and clutch size (one egg).

‡ Estimated based on surveys identifying 4267 individual HY and AHY murrelets at sea from 1996 to 2003 (Peery et al. 2006a).

§ Estimated based on mark–recapture analysis of AHY murrelets captured at sea from 1997 to 2003 (Peery et al. 2006b).

|| See Appendix D for details on the stage-based matrix model used to estimate lambda.

Stage-based matrix model and analyses

We compared annual population growth rate (λ) for Marbled Murrelets in central California for historic (1892–1922) and contemporary (1997–2003) sampling periods using a four-stage, post-breeding matrix model (0-yr-olds, 1-yr-olds, 2-yr-olds, and ≥ 3 -yr-olds), where only adults were able to breed and age of first breeding was 3 years (Beissinger and Nur 1997, Caswell 2001, Peery et al. 2006a). Appendix D presents the life cycle diagram and matrices. We used a common survival rate for AHY age classes (1-, 2-, and ≥ 3 -yr-olds) because these stages were not distinguishable in the field until the final two years of marking. Survival transitions for AHY age classes were parameterized for the historic population using age ratios of museum specimens. For the contemporary period, a survival rate for AHY age classes was parameterized from analysis of mark–recapture histories of 331 individuals captured in central California, April–October, 1997–2003 (Peery et al. 2006b). Fecundities were derived from estimates of HY:AHY ratios (\hat{R}) by iteratively parameterizing the matrix with different values for fecundity until the stable age distribution yielded an R equal to the estimated ratio (Beissinger and Nur 1997, Caswell 2001, Peery et al. 2006a). We were not able to capture a sufficient number of HY birds to estimate juvenile survival directly, so we assumed that it was 70% of the survival rate estimated for AHY classes based on similar age relationships in other seabirds (Beissinger and Nur 1997, Nur and Sydeman 1999). Density dependence, which can affect the probability of becoming a breeder in colonial seabirds (Nur and Sydeman 1999), was not considered because there is little evidence to suggest that nest sites are limiting in central California (Peery et al. 2004) and adult breeders, nonbreeders, and juveniles share the same feeding areas. Growth rate estimates from matrix models are relatively insensitive to the survival value of age class 0 (Peery et al. 2006a). We estimated λ through matrix eigenanalysis (Caswell 2001) and estimated standard errors using the delta method (Oehlert 1992, Alvarez-Buylla and Slatkin 1994).

A life table response experiment (LTRE) was conducted to compare how each matrix element contributed

to differences in projected population trends between historic and contemporary murrelets (Caswell 2001). Matrices were constructed from the parameters in Table 1 as previously described, and are shown in Appendix D.

Analysis of bias in \hat{R} and \hat{S}

Bias produced from ageing mistakes, fluctuating populations, and specimen collecting methods was evaluated as follows. We evaluate the potential for bias from aging mistakes on \hat{R} using a formula derived by P. B. Conn:

$$B(\hat{R}) = \frac{R - R\theta^J + \theta^A}{1 - \theta^A + R\theta^J} - R$$

where R is the true ratio of HY/AHY in the population, θ^J is the probability of incorrectly aging a HY as an AHY, and θ^A is the probability of incorrectly aging an AHY as HY. We calculated the impact of aging errors on bias in estimates of adult survival [$B(\hat{S})$] from Conn et al. (2005):

$$\hat{B}(\hat{S}) = \theta^I - S(\theta^I + \theta^A)$$

where θ^I is the proportion of SY birds incorrectly aged as ASY, θ^A is the proportion of ASY birds incorrectly aged as SY, and S is the adult survival probability. From Ricklefs (1997), we estimated the bias in adult survival when $\lambda \neq 1$ as $B(\hat{S}) = S(1 - \lambda)/\lambda$. Finally, we examined the field notebooks and correspondences that accompany some specimens in museum collections to determine the goals and techniques used to obtain historic specimens.

RESULTS

Comparison of historic, predicted, and contemporary demography of Marbled Murrelets

Historical estimates of productivity derived from age-ratio analysis of museum specimens ($\hat{R} = 0.297$) closely matched predictions from comparative analyses (Table 1). Comparative analysis found that R was positively correlated with average clutch size (C) and negatively correlated with body mass (B) for 29 bird species (Fig. 1A, B). Both variables made significant, independent contributions to variation in R (clutch size partial r =

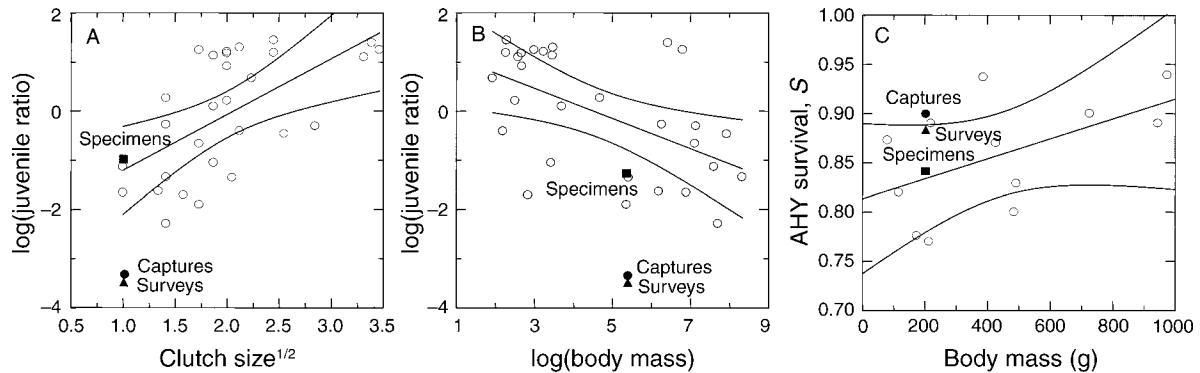


FIG. 1. Comparison of demography for historic and modern murrelets with predictions from life history theory. Allometric relationships of demography for comparison with Marbled Murrelet demographic estimates are derived from historic specimens, contemporary captures, and contemporary at-sea surveys and mark-recapture analyses of murrelets (solid squares, circles, and triangles, respectively). Regression lines and their 95% confidence intervals were calculated for species other than murrelets (open circles). A log-transformed index of productivity (R), based on HY:AHY ratios for 29 bird species, was regressed against (A) clutch size and (B) log-transformed body mass. (C) Regression of AHY survival vs. body mass for 12 species of alcids (open circles), in comparison with murrelets (solid symbols). Comparative data are available in Appendices A and B.

0.614 , $P = 0.001$; body mass partial $r = -0.556$, $P = 0.002$). When entered into a multiple regression model, they explained 56% of the variation in HY:AHY ratios: $\ln(R) = -0.255\ln(B) + 0.989C^{1/2} - 0.848$. For Marbled Murrelets, comparative analysis predicted $R = 0.292$ (Table 1). Similar results were obtained when we treated family as the sampling unit ($r^2 = 0.56$, $n = 17$ families, predicted $R = 0.263$), suggesting that our sample of bird species was well distributed among families and phylogenetic dependence did not appreciably bias predictions in the species-level analysis.

Reproduction was almost an order of magnitude lower in contemporary murrelet populations than in historic populations or than predicted rates from comparative analysis (Table 1, Fig. 1). \hat{R} estimated with museum specimens was 8.5 times greater than \hat{R} estimated from contemporary at-sea captures (0.035), which are equivalent to specimens in the sense that they represent samples of birds “collected” at sea, and 9.3 times greater than estimates from at-sea surveys (0.032). These differences were highly significant (for captures, $Z = 3.91$, $P < 0.01$; for surveys, $Z = 3.96$, $P < 0.01$). The upper 95% confidence interval of the contemporary juvenile ratio based on captures (0.057) and at-sea surveys (0.054) did not overlap the 90% prediction interval (Neter and Wasserman 1974) from comparative analyses (0.064–1.38) and barely overlapped the 95% prediction interval (0.048–1.80), indicating that reproduction in contemporary murrelets was much lower than expected based on their life history strategy.

AHY survival (Table 1) did not differ significantly ($Z = 0.86$, $P = 0.388$) between historic (0.840) and contemporary murrelets estimated from at-sea captures (0.905). Both estimates are very similar to an independent mark-recapture estimate of AHY survival (0.882) for this population (Peery et al. 2006b) and to survival rates predicted from comparative analyses (0.835; Fig.

1C). Adult survival rates of other Alcidae species increased marginally with body mass ($r = 0.53$, $P = 0.073$; $S = 0.00010B + 0.813$). Contemporary and historic survival estimates (0.835) were well inside the 95% prediction interval (0.714–0.957) of the predicted survival for an alcid of the murrelet’s mass.

We explored how differences in the historic and modern estimates of reproduction would affect projections of murrelet population dynamics (Table 1) using a stage-based matrix model (Appendix D). Historic levels of reproduction would have been sufficient to support a stable murrelet population in central California ($\lambda = 1.017$) and the historic estimate of λ was not significantly different from 1 ($Z = 0.27$; $P = 0.394$). Contemporary levels of reproduction should result in a projected population decline ($\lambda = 0.905$), and λ was marginally less than 1.0 ($Z = 1.79$; $P = 0.070$) when estimated using \hat{S} from mark-recapture analyses and \hat{R} from HY:AHY ratios from counts at sea (Table 1), the best measures of contemporary demography (Peery et al. 2006a). A life table response experiment (Caswell 2001) indicated that the contribution of reproduction was the overwhelming cause of differences in projected population trends between historic and contemporary murrelets (Fig. 2).

Comparison of age-ratio and conventional estimators of \hat{R} and \hat{S}

Demographic rates for contemporary Marbled Murrelets estimated from age-ratio analyses differed little from rates estimated using conventional methods (Table 1). Estimates of \hat{R} from HY:AHY ratios from counts at sea and from age-ratio analysis of dip net captures (0.032 and 0.035, respectively) differed little (Z test, both $P > 0.15$) from a directly comparable estimate of the number of HY produced per AHY (0.049) based on the product of the proportion of birds breeding (0.31) and nest success (0.16) derived from telemetry studies

(Peery et al. 2004). Likewise, AHY survival (0.882) estimated from mark–recapture methods (Peery et al. 2006b) did not differ ($Z = 0.334$, $P = 0.728$) from the estimate from age-ratio analysis of murrelets captured in dip nets (0.905).

Analysis of potential bias in \hat{R} and \hat{S}

We first examine the potential for bias in age-ratio estimates of \hat{R} and \hat{S} from errors in aging. Although no formal studies have been conducted, the criteria used to discriminate HY from AHY individuals appear to be 100% reliable during the months when they were identified (Carter and Stein 1995, Nelson 1997), so there should be little bias in \hat{R} produced from aging mistakes. Nevertheless, some observers may have mistakenly classified HYs as AHYs during at-sea surveys, which would result in an underestimate of contemporary HY:AHY ratios. Assuming that all adults were correctly identified and $\hat{R} = 0.29$ (the value both for historic specimens and predicted from allometry; Table 1), the rate of misclassifying juveniles as adults during both at-sea surveys and when captured would have to be extremely high (~0.85) for contemporary HY:AHY ratios to approach historic values. Errors in correctly assigning individuals to SY and ASY age classes may occur. Combining the results of Thompson et al. (2003) and Lethaby (2000), $\theta^I = 0.075$ and $\theta^A = 0.090$, based on a total of 106 juveniles and 176 adults of known age. These error rates are smaller than those evaluated by Conn et al. (2005). For typical alcid adult survival rates ranging from 0.8 to 0.9 (Appendix B, Table B1), $B(\hat{S})$ is modest (−0.06 to −0.08).

Bias in survival estimates from age ratios can occur if populations are declining or increasing. Because $\lambda \approx 1$ using \hat{R} for historic murrelets, $B(\hat{S})$ is very small for historic estimates of S (−0.01). For substantial bias to affect historic estimates of survival (i.e., $B(\hat{S}) > 0.1$), fluctuations in population growth rates would need to be $0.89 < \lambda > 1.15$, which are unlikely values for historic estimates of λ to assume. Moreover, λ reaches 1.15 only when AHY survival approaches 0.94 and all birds ≥ 3 years old reproduce successfully, and the maximum possible value that λ could achieve for a murrelet life history is only 1.3 (assuming that all individuals survive and reproduce at age ≥ 3 years). Only in the case of continued catastrophes would λ regularly be less than 0.89. If contemporary murrelet populations are declining at the rates predicted from matrix population models (Table 1), bias would be larger for ratios from contemporary capture samples $B(\hat{S}) = 0.07\text{--}0.09$.

Museum specimens were probably collected whenever murrelets were encountered. R. H. Beck was a prolific collector of museum skins in the early 1900s, and his field notes and correspondence with Leverett Mills Loomis, the Director of the California Academy of Science, are particularly enlightening about seabird collection goals and methods. The Academy's collection goal for seabirds was opportunistic. In a letter dated 13

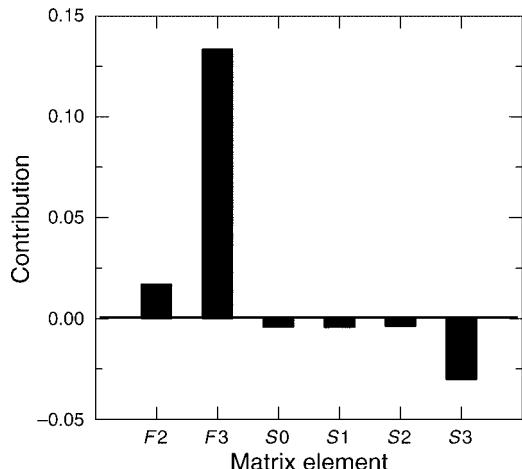


FIG. 2. Life table response experiment to evaluate the relative contributions of stage-specific fertility (F) and survival (S) matrix elements of various stage classes (0–3) to differences in rates of population growth (λ) between historic and contemporary murrelets in central California, USA. The size of the contribution of an element indicates its impact on the differences in growth between historic and contemporary populations. Positive contributions indicate better demographic performance under historic conditions. Stage classes are: 0 (juvenile), young-of-the-year birds; 1 (subadult 1), 1-yr-old or second-year (SY) birds; 2 (subadult 2), 2-yr-old birds; 3 (adult), birds ≥ 3 yr old. See Appendix D for the projection matrix and life cycle diagram.

September 1907, Loomis instructs Beck that the Academy wants “*all of the birds at Monterey and the Pacific Ocean, now and forever more*” and further encourages Beck to collect all the seabird specimens that he can, in an 11 October 1909 letter stating “*We have ten new empty zinc cases to house any sendings from Pacific Grove.*” Seabirds were collected with shotguns from small boats that were rowed up to 8 km out from shore. Marbled Murrelets primarily occur with 1–2 km of shore in Monterey Bay (Becker et al. 1997), and adults and juveniles do not differ in their offshore or onshore distribution (Peery et al. 2007). Thus, rowboats would have been an adequate, but challenging, method to sample both age classes. These rigors prompted Beck to request funds from the California Academy of Sciences to buy a motor for collecting, but Loomis replied: “*I hardly think it is worth while to buy a motor. There is plenty to do inshore when the weather is unfavorable for offshore work. It would take some years to really exhaust the vicinity of Point Pinos inshore....*”

DISCUSSION

Differences in historic and contemporary demography of Marbled Murrelets

Contemporary estimates of productivity in central California are almost an order of magnitude lower than those that Marbled Murrelets experienced in the late 19th and early 20th centuries, and HY:AHY ratios are well below the low levels expected of a bird that lays



PLATE 1. Marbled Murrelets (*Brachyramphus marmoratus*) in the Museum of Vertebrate Zoology collected about 100 years ago. Photo credit: S. R. Beissinger.

only one egg (Fig. 1A). Both historic ratios and comparative analysis suggest that conserving murrelets will require restoring reproductive performance to yield juvenile ratios of 0.2–0.3 (Fig. 1), a measurable benchmark for evaluating recovery. Environmental changes responsible for a decline in murrelet birth rates include increased nest predation by an expanding corvid population (Nelson and Hamer 1995, Peery et al. 2004) and diminished prey resources due to overfishing and climate change that have caused a decline in the trophic level of Marbled Murrelets feeding in California Current System (Becker and Beissinger 2006). Although annual variation in food appears to have less impact on adult survival than do other sources of mortality (Peery et al. 2006b), Becker and Beissinger (2006) suggested that reduced food resources may greatly affect egg production, which appears energetically costly to murrelets, because they lay a single egg weighing ~25% of their pre-breeding body mass. A large percentage (50–90%) of murrelets now forgo breeding annually in central California and may do so because they cannot find sufficient food resources (Peery et al. 2004). Life history theory suggests that long-lived seabirds like murrelets should reduce breeding efforts during years of low food availability rather than increase their chance of starvation (Stearns 1992). Factors such as logging of nesting habitat and mortality from gill nets and oil spills, which

contributed to the decline of the species, are unlikely to cause the chronically low levels of productivity observed. Most logging of old-growth redwood nesting habitat in central California occurred prior to 1950 (Evarts and Popper 2001). Although habitat loss should result in a permanent reduction of population size, it would only cause a temporary decrease in HY:AHY ratios because displaced breeders would have died long before contemporary sampling occurred.

The large difference that we found between contemporary and historic HY:AHY ratios and the lack of a difference between contemporary and historic survival rates were unlikely to be due to grossly violating assumptions of age-ratio analysis. The criteria used to identify HYs from AHYs appear to be reliable (Carter and Stein 1995, Nelson 1997) and huge levels of aging error by observers conducting at-sea surveys would be required to create the temporal differences in \hat{R} observed. Characteristics used to distinguish between SY and ASY individuals have low error rates, but this results in only a modest bias to \hat{S} . Moreover, we know of no reason why the rate of aging error would have differed between historic and contemporary sampling periods. Only large fluctuations in population growth rates, which seem unlikely to occur, would affect conclusions regarding no temporal change in AHY survival estimates. Little immigration or emigration

occurs during the months when age ratios were estimated (Peery et al. 2007).

Differences between contemporary and historic HY:AHY ratios were not likely to be the result of bias in the collection of museum specimens. Biased estimates of R and S from museum materials could arise if collectors targeted or avoided a particular age class, if age classes differed in "collectability," or if collections occurred in areas preferred or avoided by an age class. First, murrelet age classes in museums were unlikely to be sampled in a highly biased fashion. Catalogued field notes of collectors indicate that historic specimens are overwhelming composed of murrelets shot at sea from small rowboats near shore, a logistically challenging endeavor that motivated catholic and opportunistic collecting of seabirds. Collectors were unlikely to have targeted young murrelets, because historic juvenile ratios were still high in September and October (0.40) after HY and AHY plumages become indistinguishable. Second, differences in collectability were unlikely to result in high historic HY:AHY ratios because contemporary HY and AHY individuals were equally difficult to approach and capture at sea, as indicated by nearly identical estimates of R from captures and at-sea surveys (Table 1). Finally, contemporary HY and AHY murrelets are not distributed differently along-shore or off-shore in the Monterey Bay region where historic specimens were collected (Peery et al. 2007).

Historic reconstruction of demographic rates using age-ratio analysis

Reconstruction of historic demography using age-ratio analysis of museum specimens is a virtually unexplored approach to gain insight for recovering threatened species (Graham et al. 2004, Suarez and Tsutsui 2004). Although this approach is feasible only for species with identifiable age- or stage-related characters, extensive museum collections for a broad array of taxa are available, spanning time scales not amenable for study with conventional field techniques. Even the Marbled Murrelet, a species that was poorly studied until its placement on the U.S. Endangered Species List in 1992 prompted concerted research efforts, was sufficiently represented in collections to infer historic demographic rates. Museum collections may not only provide unique baseline demographic information prior to population declines, but also permit comparison of changes in population dynamics through time (Fig. 2). The power of this approach is magnified when combined with habitat, genetic, isotope, disease, or other studies of museum specimens (Rocque and Winker 2005, Winker 2005), and with contemporary field studies designed to test hypotheses concerning specific threats or limiting factors responsible for demographic change and causing elevated risk of extinction (Peery et al. 2004). For example, comparison of specimens to contemporary birds have shown not only historic changes in murrelet demography but also a

decline in its trophic level that occurred during the past 100 years by comparing stable isotopic signatures of the feathers of specimens to feathers from contemporary birds (Becker and Beissinger 2006).

Estimates of historic demographic rates depend on the validity of demographic estimates derived from age-ratio analysis. Survival estimation from age-ratio analysis is an indirect and imperfect measure, and its validity should be carefully evaluated (Conn et al. 2005, Ricklefs and Rohwer 2005). Our results suggest that age-ratio analyses and mark-recapture methods can yield very similar survival estimates (Table 1), at least for a species that met most assumptions of both methods (Peery et al. 2006b, 2007). Alternatively, the ratio of juveniles to adults (HY:AHY) can offer a direct way to estimate fecundity because it incorporates all components of productivity (Beissinger 1995, Newton 1999), such as the proportion of the population that breeds, the number of breeding attempts, clutch size, hatching success, and fledging success, if measured near the end of the breeding season. For Marbled Murrelets, fecundity estimation from HY:AHY ratios (Table 1) was very similar to an estimate derived from marked birds and nest studies (Peery et al. 2004). These comparisons support our application of age-ratio analysis to estimate demographic rates of historic Marbled Murrelets.

Rigorous reconstruction of historic demographic rates requires data from a variety of sources in addition to age ratios of museum specimens. First, comparative analysis provides a benchmark for interpreting both historic and contemporary demographic rates (Fig. 1). Like age-ratio analysis of museum specimens, the comparative analysis assumes that demographic estimates are derived from populations that are not increasing or decreasing rapidly. Large deviations from population stability add variation and decrease the strength of regression relationships in Fig. 1, but do not invalidate comparisons. The data provided in Appendix A can be used for comparison of reproductive rates for avian species, and similar databases could be built for other taxa. Second, contemporary field studies need to develop robust estimates of demographic rates that are directly comparable to age-ratio estimators and should test assumptions underlying age-ratio analyses (Peery et al. 2007). Confidence in the estimates derived from age-ratio analysis increases greatly when ancillary data are available to support model assumptions (Menkens and Boyce 1993). Third, the field notes of collectors should be examined to evaluate potential sources of bias in historic age ratios from collecting methods and motivations. In conclusion, the validity of demographic estimates derived from historic reconstruction depends on consilience of results from multiple sources.

ACKNOWLEDGMENTS

Suggestions by D. Biggert, P. Conn, P. Doherty, C. Moritz, M. Raphael, R. Ricklefs, B. Sandercock, and anonymous reviewers greatly improved this paper. N. Nur and Point Reyes Bird Observatory kindly provided unpublished data on juvenile

ratios for Appendix A. This work was supported by grants from the Big Creek Lumber Company, California Department of Fish and Game, California Department of Parks and Recreation, The David and Lucile Packard Foundation, Oiled Wildlife Care Network, Pacific Lumber Company, U.S. Fish and Wildlife Service, and the University of California-Berkeley.

LITERATURE CITED

- Abbitt, R. J. F., and J. M. Scott. 2001. Examining differences between recovered and declining endangered species. *Conservation Biology* 15:1274–1284.
- Alvarez-Buylla, E. R., and M. Slatkin. 1994. Finding confidence limits on population growth rates: three real examples revised. *Ecology* 75:255–260.
- Anderson, D. R., A. P. Wywialowski, and K. P. Burnham. 1981. Tests of the assumptions underlying life table methods for estimating parameters from cohort data. *Ecology* 62: 1121–1124.
- Becker, B. H., and S. R. Beissinger. 2006. Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conservation Biology* 20:470–480.
- Becker, B. H., S. R. Beissinger, and H. Carter. 1997. At-sea density monitoring of Marbled Murrelets in central California: methodological considerations. *Condor* 99:743–755.
- Beissinger, S. R. 1986. Demography, environmental uncertainty, and the evolution of mate desertion in the Snail Kite. *Ecology* 67:1445–1459.
- Beissinger, S. R. 1995. Population trends of the Marbled Murrelet projected from demographic analyses. Pages 385–393 in G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. *Ecology and conservation of the Marbled Murrelet*. USDA Forest Service General Technical Report PSW-GTR-152, Albany, California, USA.
- Beissinger, S. R., and N. Nur. 1997. Appendix B: Population trends of the Marbled Murrelet projected from demographic analysis. Pages B1–B35 in *Recovery Plan for the Marbled Murrelet (*Brachyramphus marmoratus*) in Washington, Oregon, and California*. U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- Bonenfant, C., J. M. Gaillard, F. Klein, and J. L. Hamann. 2005. Can we use the young:female ratio to infer ungulate population dynamics? An empirical test using red deer *Cervus elaphus* as a model. *Journal of Applied Ecology* 42:361–370.
- Calder, W. 1984. *Size, function and life history*. Harvard University Press, Cambridge, Massachusetts, USA.
- Carter, H. R., and J. L. Stein. 1995. Molts and plumages in the annual cycle of the Marbled Murrelet. Pages 99–112 in C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. *Ecology and conservation of the Marbled Murrelet*. USDA Forest Service General Technical Report PSW-GTR-152, Albany, California, USA.
- Caswell, H. 2001. *Matrix population models*. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Caughley, G. 1974. Interpretation of age ratios. *Journal of Wildlife Management* 38:557–562.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215–244.
- Conn, P. B., P. F. Doherty, and J. D. Nichols. 2005. Comparative demography of new world populations of thrushes (*Turdus* spp.): Comment. *Ecology* 86:2536–2541.
- Domenech, J., and J. C. Senar. 1997. Trapping methods can bias age ratio in samples of passerine populations. *Bird Study* 44:348–354.
- Evarts, J., and M. Popper. 2001. *Coast redwood a natural and cultural history*. Cachumas Press, Los Olivos, California, USA.
- Flanders-Wanner, B. L., G. C. White, and L. McDaniel. 2004. Validity of prairie grouse harvest-age ratios as production indices. *Journal of Wildlife Management* 68:1088–1094.
- Gaillard, J. M., D. Pontier, D. Allaine, J.-D. Lebreton, J. Trouvilliez, and J. Clobert. 1989. An analysis of demographic tactics in birds and mammals. *Oikos* 56:59–76.
- Graham, C. H., S. Ferrier, F. Huettman, C. Moritz, and A. T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology and Evolution* 19:497–503.
- Graves, G. R. 1997. Geographic clines of age ratios of Black-throated Blue Warblers (*Dendroica caerulea*). *Ecology* 78: 2524–2531.
- Green, R. E. 2004. A new method for estimating the adult survival rate of the Corncrake *Crex crex* and comparison with estimates from ring-recovery and ring-recapture data. *Ibis* 146:501–508.
- Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493–504 in A. Keast and E. S. Morton, editors. *Migrant birds in the neotropics: ecology, behavior, distribution and conservation*. Smithsonian Institute Press, Washington, D.C., USA.
- Hanson, W. R. 1963. Calculation of productivity, survival, and abundance of selected vertebrates from sex and age ratios. *Wildlife Monographs* 9:1–60.
- Iverson, A. S., B. D. Smith, and F. Cooke. 2004. Age and sex distributions of wintering surf scoters: implications for the use of age ratios as an index of recruitment. *Condor* 106:252–262.
- Leonard, J. A., C. Vila, and R. K. Wayne. 2005. Legacy lost: genetic variability and population size of extirpated US grey wolves (*Canis lupus*). *Molecular Ecology* 14:9–17.
- Lethaby, N. 2000. The identification of Long-billed Murrelet in alternate plumage. *Birding* 32:438–444.
- Levy, P. S., and S. Lemeshow. 1991. *Sampling of populations*. John Wiley, New York, New York, USA.
- McCullough, D. R., F. W. Weckerly, P. I. Garcia, and R. R. Evett. 1994. Sources of inaccuracy in black-tailed deer herd composition counts. *Journal of Wildlife Management* 58: 319–329.
- McGraw, J. B. 2001. Evidence for decline in stature of American ginseng plants from herbarium specimens. *Biological Conservation* 98:25–32.
- Megrey, B. A. 1989. Review and comparison of age-structured stock assessment models from theoretical and applied points of view. Pages 8–48 in E. F. Edwards and B. A. Megrey, editors. *American Fisheries Society Symposium* 6. American Fisheries Society, Bethesda, Maryland, USA.
- Menkens, G. E., and M. S. Boyce. 1993. Comments on the use of time-specific and cohort life tables. *Ecology* 74:2164–2168.
- Nelson, S. K. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). *Birds of North America* 276:1–32.
- Nelson, S. K., and T. E. Hamer. 1995. Nesting success and the effects of predation on Marbled Murrelets. Pages 89–98 in C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt, editors. *Ecology and Conservation of Marbled Murrelet*. USDA General Technical Report PSW-GTR-152, Albany, California, USA.
- Neter, J., and W. Wasserman. 1974. *Applied linear statistical models*. Richard D. Irwin, Georgetown, Ontario, Canada.
- Newton, I. 1999. An alternative approach to the measurement of seasonal trends in bird breeding success: a case study of the bullfinch *Pyrrhula pyrrhula*. *Journal of Animal Ecology* 68: 698–707.
- Nur, N., and W. J. Sydeman. 1999. Demographic processes and population dynamic models of seabirds. *Current Ornithology* 15:149–188.
- Oehlert, G. W. 1992. A note on the delta method. *American Statistician* 46:27–29.
- Parmesan, C. 1996. Climate and species' range. *Nature* 382: 765–766.
- Paxinos, E. E., H. F. James, S. L. Olson, J. D. Ballou, J. A. Leonard, and R. C. Fleischer. 2002. Prehistoric decline of genetic diversity in the nene. *Science* 296:1827.

- Peery, M. Z., B. H. Becker, and S. R. Beissinger. 2006a. Combining demographic and count-based approaches to identify source-sink dynamics: an example using an endangered seabird. *Ecological Applications* 16:1516–1528.
- Peery, M. Z., B. H. Becker, and S. R. Beissinger. 2007. Age ratios as estimators of productivity: testing assumptions on an endangered seabird, the Marbled Murrelet. *Auk* 124, *in press*.
- Peery, M. Z., S. R. Beissinger, E. B. Burkett, and S. H. Newman. 2006b. Local survival of Marbled Murrelets in central California: roles of oceanographic processes, sex, and radio-tagging. *Journal of Wildlife Management* 70:78–88.
- Peery, M. Z., S. R. Beissinger, S. H. Newman, E. B. Burkett, and T. D. Williams. 2004. Applying the declining population paradigm: diagnosing causes of poor reproduction in the marbled murrelet. *Conservation Biology* 18:1088–1098.
- Pergams, O. R. W., and D. Nyberg. 2001. Museum collections of mammals corroborate the exceptional decline of prairie habitat in the Chicago region. *Journal of Mammalogy* 82: 984–992.
- Ralph, C. J., G. L. Hunt, M. G. Raphael, and J. F. Piatt. 1995. Ecology and conservation of the Marbled Murrelet in North America: an overview. Pages 3–22 *in* C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt, editors. *Ecology and conservation of the Marbled Murrelet in North America*. USDA Forest Service General Technical Report PSW-GTR-152, Albany, California, USA.
- Ricklefs, R. E. 1997. Comparative demography of new world populations of thrushes (*Turdus* spp.). *Ecological Monographs* 67:23–43.
- Ricklefs, R. E., and S. Rohwer. 2005. Comparative demography of New World populations of thrushes (*Turdus* spp.): Reply. *Ecology* 86:2541–2544.
- Rocque, D. A., and K. Winker. 2005. Use of bird collections in contaminant and stable-isotope studies. *Auk* 122:990–994.
- Rohwer, S. 2004. Using age ratios to infer survival and despotic breeding dispersal in hybridizing warblers. *Ecology* 85:423–431.
- Sæther, B. E. 1988. Pattern of covariation between life-history traits of European birds. *Nature* 331:616–617.
- Shaffer, H. B., R. N. Fisher, and C. Davidson. 1998. The role of natural history collections in documenting species declines. *Trends in Ecology and Evolution* 13:27–30.
- Skalski, J. R., K. E. Ryding, and J. J. Millspaugh. 2005. *Wildlife demography: analysis of sex, age, and count data*. Elsevier Academic Press, Boston, Massachusetts, USA.
- Snow, D. W. 1956. The annual mortality of the blue tit in different parts of its range. *British Birds* 49:174–177.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, New York, New York, USA.
- Suarez, A. V., and N. D. Tsutsui. 2004. The value of museum collections for research and society. *BioScience* 54:66–74.
- Thompson, C. W., K. J. Pullen, R. E. Johnson, and E. B. Cummins. 2003. Specimen record of a Long-billed Murrelet from eastern Washington, with notes on plumage and morphometric differences between Long-billed and Marbled Murrelets. *Western Birds* 34:157–168.
- Thompson, W. L., G. C. White, and C. Gowan. 1998. *Monitoring vertebrate populations*. Academic Press, San Diego, California, USA.
- Udevitz, M. S., and B. E. Ballachey. 1998. Estimating survival rates with age-structure data. *Journal of Wildlife Management* 62:779–792.
- Winker, K. 2005. Bird collections: development and use of a scientific resource. *Auk* 122:966–971.

APPENDIX A

Ratio of hatch-year to after-hatch-year individuals (R) and life history traits for 29 bird species used in the comparative analysis (*Ecological Archives* E088-018-A1).

APPENDIX B

Survival estimates derived from mark-recapture analyses and life history traits of alcids used in comparative analysis (*Ecological Archives* E088-018-A2).

APPENDIX C

Literature cited for Appendices A and B (*Ecological Archives* E088-018-A3).

APPENDIX D

Life cycle diagram, Leslie matrix model, and parameterized historic and contemporary matrices used to estimate population growth rate (λ) and to conduct a life table response experiment (LTRE) for Marbled Murrelets in central California (*Ecological Archives* E088-018-A4).