CHARACTERIZING DISPERSAL PATTERNS OF MARBLED MURRELETS

(*BRACHYRAMPHUS MARMORATUS*) WITH GENETIC

POPULATION ASSIGNMENTS

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ABSTRACT

Characterizing dispersal patterns of Marbled Murrelets (*Brachyramphus marmoratus*)
with genetic population assignments

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Seabirds present an interesting challenge for quantifying and understanding
dispersal because they are highly mobile but often exhibit natal site fidelity when
breeding (Frederiksen and Petersen 2000, Steiner and Gaston 2005, Milot et al. 2008). I
quantified movement and examined dispersal patterns of an elusive and threatened
seabird, the Marbled Murrelet (*Brachyramphus marmoratus*) with genetic population
assignments using thirteen microsatellite loci. Two genetically distinct populations of
Marbled Murrelets were identified: one included birds from southern Alaska to northern
California and the other included birds from central California. Pair-wise comparisons of
Fst values for central California had the greatest genetic differentiation (0.034 ± 0.001),
whereas all other pair-wise comparisons had low Fst values (0.005 ± 0.001). I identified
twenty-nine migrant birds from the northern populations in central California. A greater
proportion of migrants was observed in central California during winter (November to
March) than during breeding (April to July) and post-breeding (August to October)
seasons. The number of female migrants ($n = 18$) was significantly greater than the
number of male migrants ($n = 9$), implying that dispersal in Marbled Murrelets was sex-
biased. In addition, migrant birds had shorter residence times in central California than
birds that were classified as residents, and a low proportion of migrants (0.02) had a first-
order relative in central California. My results indicated that birds from the northern
populations dispersed into central California but did not permanently recruit to the central
California population. These migrants would increase competition with resident birds for

resources without contributing to the reproductive output of the central California

population and would be counted and included in population estimates potentially

obscuring the detection of a population decline in the central California Marbled Murrelet

population.

ACKNOWLEDGMENTS

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INTRODUCTION

Understanding how populations are connected via dispersal is fundamental to the studies of population biology, foraging ecology, and conservation. Seabirds present an interesting challenge for quantifying and understanding dispersal. Most are highly mobile and capable of long distance movements, however, seabirds often exhibit natal site fidelity (Frederiksen and Petersen 2000, Steiner and Gaston 2005, Milot et al. 2008), that may limit gene flow among populations (Friesen et al. 2007). The complexity of studying dispersal in seabirds has lead some researchers to use a combination of direct measurements from tracking information and indirect measurements from genetic data to better understand inter-population movements (Burg et al. 2003, Dearborn et al. 2003, Milot et al. 2008).

Dispersal can be measured directly by mark-recapture techniques or tracking of radio-tagged individuals, or indirectly using genetic data. Direct techniques are useful for estimating emigration and immigration rates used in demographic models. However, measuring dispersal directly can be costly and logistically difficult. When using mark-recapture techniques, with large populations, recapture rates may be too low causing inaccurate assessment of dispersal. Radio-tracking of individuals is difficult because of the limited duration of radio-tag attachment. Also, it can be costly to track radio-tagged individuals over large geographic scales, especially for highly mobile organisms, such as seabirds. Given these issues, long distance dispersal often is undetected in populations (Koenig et al. 1996). Furthermore, direct measurements of dispersal may not be indicative of gene flow among populations, because dispersers may not reproduce in the populations they have entered. Alternatively, genetic data can be used to indirectly

measure dispersal and gene flow independently. Pair-wise genetic distances, such as Fst, can be used to assess gene flow among populations (Paetkau et al. 1995, Dearborn et al. 2003, Friesen et al. 2005, Milot et al. 2008), and dispersal can be quantified using a parentage approach (Peery et al. 2008a) or assignment testing (Paetkau et al. 1995, Berry et al. 2004).

Population assignment tests are useful for quantifying movement of individuals and describing dispersal patterns by estimating real-time migration rates and identifying individual migrants in a population. Previous researchers using population assignments have estimated accuracy and power of assignment methods from simulated data sets (Cornuet et al. 1999, Paetkau et al. 2004, Faubet et al. 2007) or quantified rates of movement among populations (Paetkau et al. 1995, Berry et al. 2004). Assignment methods also can be used for characterizing patterns in dispersal, such as testing for sex-biased dispersal (Paetkau et al. 1995, Favre et al. 1997, Mossman and Waser 1999). Few researchers have used assignment tests, however, to conduct a comprehensive analysis of dispersal patterns by examining differences in the number of migrants among seasons, age classes, and breeders and non-breeders.

In this study, I quantified the movement of individuals and examined dispersal patterns using genetic population assignments of an elusive and threatened seabird, the Marbled Murrelet (*Brachyramphus marmoratus*). The Marbled Murrelet is a small, diving seabird that forages in the near-shore marine environment and lays a single egg in a nest in old-growth forests along the Pacific coast of North America. This species ranges from southern Alaska to central California. The central California region has the smallest estimated population size of 660 (95% CL: 550-800) birds and is projected to

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decrease by 9.5% per year in the absence of immigration from northern populations (Peery et al. 2004b, Peery et al. 2006a). However, limited gene flow between central California and the northern populations of Marbled Murrelets (Friesen et al. 2005, Piatt et al. 2007) indicates that recruitment into central California from the northern populations is not occurring.

Understanding dispersal in Marbled Murrelets has proven difficult because of their elusive breeding behavior. Marbled Murrelets nest high in the trees of coastal old-growth forests, making it difficult to capture and track breeding birds. Due to their secretive nature, most of the information about movements of Marbled Murrelets comes from radio-tracking of birds captured at sea (Lougheed et al. 2002, McFarlane Tranquilla et al. 2003, Peery et al. 2004a, Peery et al. 2004b, Peery et al. 2006b, Peery et al. 2008b), or anecdotal evidence from re-captures of banded birds (Beauchamp et al. 1999). Many researchers have observed seasonal shifts in Marbled Murrelet distributions throughout their range, although in some regions only a portion of the population appears to disperse (Nashlund 1993, Strong et al. 1995, Agler et al. 1998, Beauchamp et al. 1999, Peery et al. 2008b). In central California, most birds remain adjacent to nesting areas during the breeding and post-breeding seasons, and disperse away from nesting areas after molting. A number of previous studies have examined dispersal of resident birds away from nesting areas, but few studies have examined the movement of individuals among Marbled Murrelet populations.

Characterizing the movement of birds with genetic population assignment tests would increase our understanding of dispersal among Marbled Murrelet populations. Here, I used population assignment testing to first estimate the number of migrant birds

in the central California population of Marbled Murrelets and then characterize dispersal patterns in Marbled Murrelets by comparing the number of migrant birds captured in central California among: 1) seasons; 2) sexes; 3) age classes; 4) birds with and without a brood patch; and 5) birds with and without a first-order relative in the population. In addition, I compared the residence times of migrant and resident birds in central California and examined the effect of migrant birds on population estimates for the central California population of Marbled Murrelets. I expected that a greater proportion of migrants would be present during winter (November through March) than breeding (April through July) and post-breeding (August through October) seasons, because birds do not need to attend nest sites during winter. As observed in other bird species (Greenwood 1980, Clarke et al. 1997), I expected a greater proportion of migrants would be female and juvenile birds than males and adults. Genetic data from previous studies suggests that migrant birds from the northern populations are not recruiting to central California, therefore I expected birds with a brood patch and birds with a first-order relative in central California would be less likely to be migrants than birds without a brood patch or birds without a first-order relative in central California. In addition, I expected that resident birds would have a greater residence time in central California than migrant birds.

METHODS

Blood or tissue samples from 588 Marbled Murrelets were collected from southeast Alaska to central California between 1997 and 2007 (Fig. 1). Most samples were collected during the breeding season ($n = 381$), however, some samples were collected in central California during post-breeding ($n = 195$) and winter ($n = 12$) seasons to assess differences in dispersal among seasons. Blood samples were collected from live birds ($n = 561$) captured at night from an inflatable vessel using a night-lighting/dip-netting technique (Whitworth et al. 1997). Liver, muscle, or foot tissue samples ($n = 24$) were collected from dead beach-cast birds, and toe skin tissue samples ($n = 3$) were collected from museum specimens. DNA was extracted from 20 µl of blood or 25 mg of tissue using a DNeasy Tissue Extraction Kit (Qiagen, Valencia, CA) following the manufacturer's protocol for animal tissues. The toe skin samples were soaked in 95% ethanol for 24 hours before DNA extraction. DNA was extracted from the toe skin using a modified phenol/chloroform extraction (Sambrook et al. 1989). DNA from birds captured in central California was sent to Zoogen (Davis, CA) for sex determination.

Thirteen microsatellite markers (BmaACCT555, BmaGACA456, BmaTATC371, BmaAGGT503, BmaGGAT313, BmaCCAT301, BmaGGAT368, BmaCCAT443, BmaTATC356, GATA365, BmaGATA439, BmaTGAA523, BmaGATA553), developed by Rew et al. (2006), were amplified for all birds using polymerase chain reaction (PCR). An additional three microsatellite markers (BmaGATA464, BmaGATA465, BmaTATC453; Rew et al., 2006) were amplified for birds captured in central California. These additional loci were used to determine the number of first-order relatives for each bird captured in central California (Peery et al. 2008a). Peery et al. (2008a) demonstrated

that first-order relatives can be identified using 16 microsatellite markers with less than 10% error. The forward or reverse primer for each microsatellite was labeled with a fluorescent dye (FAM, HEX, PET, or NED; Applied Biosystems, Foster City, CA) for subsequent electrophoresis and scoring. PCRs were conducted in a GeneAmp 9700 thermalcycler (Applied Biosystems, Foster City, CA), using Qiagen's Core PCR kit, under the following conditions: approximately 10 ng of genomic DNA in a 10 µL reaction composed of 1 µL of 10x buffer, 0.2 mM of each dNTP, 0.25 U *Taq* DNA polymerase, 0.5 µM of reverse primer, and 0.5 µM of forward primer. Cycling profiles for all markers except BmaGGAT313 were composed of: 1) a 3 minute initial denaturing step at 94°C; 2) 24-40 cycles of a 30 second denaturing step at 94°C, a 30 second annealing step at 59-62°C, and a 30 second extension step at 72°C; and 3) a 10 minute final extension step at 72 °C. Cycling for BmaGGAT313 was composed of: 1) a 3 minute initial denaturing step at 94°C; 2) 19-22 cycles of a 30 second denaturing step at 94°C, a 30 second annealing step at 59°C, and a 30 second extension step at 72°C; 3) 7-10 cycles of a 30 second denaturing step at 94°C, a 30 second annealing step at 53°C, and a 30 second extension step at 72°C; and 4) a 10 minute final extension step at 72 °C. Microsatellites were run with LIZ 500 size standard on an ABI3730 sequencer (Applied Biosystems, Foster City, CA) and scored using GENEMAPPER (Applied Biosystems, Foster City, CA).

ARLEQUIN (Schneider et al. 2000) was used to calculate observed and expected heterozygosities to test for Hardy-Weinberg equilibrium, and linkage disequilibrium was tested in GDA (Lewis and Zaykin 2001). Pair-wise comparisons of genetic distance among populations were calculated using Wright's (1931) Fst in GDA (Lewis and Zaykin

2001). Confidence intervals (95% CI) for each pair-wise comparison were calculated in GDA (Lewis and Zaykin 2001) by bootstrapping with 1000 replicates.

The number of genetically distinct populations was calculated with STRUCTURE v. 2.2 software, a model-based clustering method that uses a Marchov-chain Monte Carlo algorithm to first estimate allele frequencies for each genetically distinct population and then estimate the population of origin for each individual (Pritchard et al. 2000). Data was analyzed in STRUCTURE (Pritchard et al. 2000) using the admixture model for K = 1-6, with a burn in of 30,000 iterations followed by a simulation of 50,000 iterations. The number of distinct populations (K) was identified as the K value with the greatest probability (Pritchard et al. 2000).

Migrant birds in central California were identified using population assignments. Populations assignments were calculated in GENECLASS2 (Piry et al. 2004) using the Bayesian method of Rannala and Mountain (1997), which calculates the probability of a genotype occurring in a population based on the observed allele frequencies for that population. This method was used because it performed better than other assignment methods in a simulation study by Cornuet et al. (1999). Likelihood estimates were calculated in GENECLASS2 as L_{home}/L_{max} (Paetkau et al. 2004), and alpha values were estimated for each bird, from 1000 simulations, using the Monte Carlo re-sampling method of Paetkau et al. (2004). Birds that had a less than 5% probability ($\alpha < 0.05$) of being a resident of the population they were captured in were identified as migrants.

I assessed the accuracy of population assignments for birds captured in central California in several ways. First, I plotted the negative log likelihood of an individual originating from central California against the negative log likelihood of the same

individual originating from the northern population. In addition, ten datasets, created in

SERIAL SIMCOAL (Excoffier et al. 2000) using coalescence simulations (see Peery et

al. in prep, for simulation methods), were used to generate microsatellite genotypes for a

simulated population of Marbled Murrelets, composed of a central California population

(n = 257) and a northern population (n = 329). Twenty birds from the northern

population were moved into the central California population to simulate migration.

Population assignments for each simulated dataset were made in GENECLASS2

following the parameters used in the empirical data analysis. I then estimated the mean

number of α and β errors in the population assignments from the simulated central

California populations by calculating the number of residents incorrectly assigned as

migrants (α errors) and the number of migrants incorrectly assigned as residents (β

errors).

Differences in dispersal were assessed among seasons (breeding, post-breeding,

and winter), sexes, age classes (≤ 2 years old and > 2 years old), breeding status (birds

with and without a brood patch), and relatives (birds with and without a first-order

relative in the population). The breeding season included April through July, because in

central California, Marbled Murrelet breeding and nest attendance occurs primarily

between April and July (U.S. Fish and Wildlife Service 1997). I considered August

through October the post-breeding season. This is consistent with a study by Peery et al.

(2008b), which determined that Marbled Murrelets in central California typically remain

adjacent to nesting areas while undergoing a pre-basic molt from August to October. I

included November to March as winter, because Marbled Murrelets in central California

typically have completed their molt and are capable of dispersing from nesting areas

during this time period (Peery et al. 2008b). Marbled Murrelets were aged using plumage. Hatch year birds have unique plumage which differentiates them from older birds, and second year birds can be identified by white under-wing coverts, which are present until they molt at the end of the breeding season (August) in their second year. The breeding status of Marbled Murrelets in central California was assessed using the presence or absence of a brood patch. Brood patch information is easily obtained from captured birds, therefore, it was used as a proxy for breeding. It is difficult to confirm breeding in Marbled Murrelets due to their secretive nesting behavior. I also determined the number of first-order relatives for each Marbled Murrelet captured in central California. First-order relatives were identified as birds who shared at least one allele at each locus (Peery et al. 2008a). A likelihood ratio chi-square analysis was used to test for significant differences in dispersal among seasons, sexes, age classes, breeding status, and relatives. Data from birds captured during the post-breeding and winter seasons were excluded from chi-square tests comparing breeding status, and data from birds captured during winter were excluded from chi-square tests comparing first-order relatives. Chi-square analyses with small samples sizes were corrected with a Yates correction factor (Zar 1999).

I used a bootstrapping program, with 1000 iterations, in RESAMPLING STATS (Appendix A) to compare the observed number of male and female Marbled Murrelets captured in central California to an expected distribution of male and female birds assuming a 1:1 sex ratio. I drew randomly, without replacement, 328 individuals from a population of 660 Marbled Murrelets (Peery et al. 2004b, Peery et al. 2006a) with a hypothetical 1:1 sex ratio. I tested for a male-biased sex ratio, because female-biased

dispersal, which is common in birds (Greenwood 1980, Clarke et al. 1997), can lead to male-biased sex ratios in small, isolated populations (Dale 2001). To examine whether a male-bias was present in the central California population of Marbled Murrelets, I compared the observed number of males captured in central California to the distribution for the expected number of males based on a 1:1 sex ratio ($\alpha = 0.05$).

I calculated the mean number of captures and mean residence times for Marbled Murrelets captured in central California between 1997 and 2003 from capture information and compared the number of captures and residence times between birds classified as residents and migrants. I defined residence time as the number of years an individual was observed in the population. Capture data used for the number of captures and residence time calculations were collected from 340 Marbled Murrelets captured in central California, however, only 278 of these individuals were genotyped for population assignments.

I also calculated the annual percentage of migrants observed in central California for 1997 and 1999 to 2003. Information about the number of migrant birds captured in central California during 1998 was not available because birds captured in 1998 were not genotyped. To examine the effect of migrant birds on population estimates for central California Marbled Murrelets, I compared the trend in annual percentage of migrants observed in central California to the trend in Marbled Murrelet population estimates for central California made by Peery et al. (2006a). I also plotted a projected population decline of 9.5% per year (Peery et al. 2006a) assuming an initial population size of 487 individuals in 1999, as predicted by Peery et al. (2006a).

RESULTS

Mean expected heterozygosity for all populations was 81% and ranged from 48% to 95% (Table 1). The mean observed heterozygosity for all populations was 81% and ranged from 43% to 100% (Table 1). Of the thirteen loci tested for each of the six regions sampled, only two loci deviated from Hardy-Weinberg expectations after applying a Bonferroni correction (Table 1). No pair-wise combinations of loci showed significant linkage disequilibrium following a Bonferroni correction.

Two distinct genetic populations (K) were identified using STRUCTURE ($P_{(K=2)}$ >99.99; Fig. 2). The first population included Marbled Murrelets from southeast Alaska to northern California (hereafter referred to as the northern population), and the second included birds from central California (hereafter referred to as the central California population). Fst values for Marbled Murrelets were 0 to 0.038 with a global Fst of 0.025 (95% CI: 0.018-0.032; Table 2). The pair-wise comparisons involving central California had the greatest genetic differentiation (0.034 ± 0.001; Table 2). All other pair-wise comparisons had low Fst values (0.005 ± 0.001; Table 2).

A study by Cornuet et al. (1999) estimated a 25% error rate when assigning individuals to populations with an Fst of 0.08 using 10 microsatellites. In this study, the average Fst from pair-wise comparisons between central California and the northern population was 0.034 (± 0.001). To assess error in my population assignments, I plotted the negative log likelihood of an individual originating from central California against the negative log likelihood of the same individual originating from the northern population (Fig. 3). This plot allowed me to assess the separation between individuals assigned to the northern population and individuals assigned to central California. Ten of the twenty-

five individuals identified as migrants in central California had negative log likelihood values that were relatively equal for central California and the northern population (i.e. the difference between the likelihood values was less than one, and they were distributed in close proximity to the 1:1 line; Fig. 3). Therefore, it is likely that a proportion of birds identified as migrants in central California were actually residents (α errors) and a proportion of birds identified as residents in central California were actually migrants (β errors). Paetkau et al. (2004) recommended using a stringent alpha value of 0.002 to reduce errors in assigning individuals to their population of origin. However, it is not uncommon to use more liberal alpha values for statistical analyses involving species of conservation concern. Marbled Murrelets are listed as threatened throughout most of their range, so due to the management implications of this analysis I chose to use a less stringent alpha value ($\alpha = 0.05$) than that suggested by Paetkau et al. (2004). Using simulated data I estimated the mean number of α errors in population assignments for central California at an alpha value of 0.05 was 2.30 ($\pm$ 0.58), and the mean number of β errors was 2.10 ($\pm$ 0.60; Fig. 4). Choosing an alpha value of 0.05 was optimal given that the mean number of α and β errors were approximately equal at that alpha value (Fig. 4). Therefore it appears that an alpha value of 0.05 is an appropriate choice for population assignments of Marbled Murrelets.

Of the 588 Marbled Murrelets captured from southeast Alaska to central California, 304 were identified as residents of the northern population, two were identified as migrants in the northern population, 253 were identified as residents of central California, and twenty-nine were identified as migrants in the central California population. It is likely that the two birds identified as migrants in the northern population

were actually residents (α errors). Based on my simulations, approximately two α errors were expected at an alpha value of 0.05 (Fig. 4). In addition, the two birds assigned as migrants in the northern population had negative log likelihood values that were approximately equal for both the northern and central California populations (Fig. 3), so it is possible that the assignments for these two birds were not accurate. The number of migrant birds observed during the breeding and post-breeding seasons were not significantly different ($\chi^2_{0.05, 1} = 0.303$; $p = 0.582$), therefore, these seasons were pooled and compared with the number of migrants observed during winter. The number of migrant birds observed in central California during winter was significantly greater than the number of migrants observed during the breeding and post-breeding seasons ($\chi^2_{0.05, 1} = 38.542$; $p < 0.001$). A greater proportion of birds captured during winter (0.83) were classified as migrants, whereas a smaller proportion of birds captured during the breeding (0.06) and post-breeding (0.08) seasons were classified as migrants (Fig. 5a). The number of migrant birds in central California also was significantly different between sexes. A greater proportion of females (0.14) were classified as migrants than males (0.06; $\chi^2_{0.05, 1} = 5.416$; $p = 0.020$; Fig. 5b). In addition, the proportion of individuals with a first-order relative in central California that were classified as migrants (0.02) was less than the proportion of individuals without a first-order relative in the population that were classified as migrants (0.11; $\chi^2_{0.05, 1} = 7.409$; $p = 0.006$; Fig. 5c). The number of migrant birds in central California was not statistically significant between age classes ($\chi^2_{0.05, 1} = 2.211$, $p = 0.137$), however a large proportion (0.45) of juvenile birds (≤ 2 years old) were classified as migrants, and a smaller proportion (0.18) of adult birds (> 2 years old) were classified as migrants (Fig. 5d). Last, the number of migrants was not statistically

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significant between birds with and without a brood patch ($\chi^2_{0.05, 1} = 0.379$; $p = 0.538$),

although, as expected, the proportion of birds with a brood patch that were classified as

migrants (0.04) was less than the proportion of birds without a brood patch that were

classified as migrants (0.09; Fig. 5e).

One hundred fifty-one female and 177 male Marbled Murrelets were captured in

central California. The number of male Marbled Murrelets captured in central California

was greater than 95% of the values from the distribution of the expected number of male

birds generated with RESAMPLING STATS, assuming a 1:1 sex ratio (Fig. 6).

Therefore, the sex ratio for the central California population of Marbled Murrelets

appears to be male biased.

Marbled Murrelets identified as residents of central California were captured an

average of 1.25 (95% CI: 1.20-1.30) times, and birds identified as migrants were captured

an average of 1.16 (95% CI: 1.02-1.30) times. Eighty-four recaptures of Marbled

Murrelets, classified as residents of central California, occurred between 1997 and 2003.

Birds were recaptured in different years between one and four times. Two hundred

thirty-one birds classified as residents had a residence time of one to two years, and

twenty-nine migrants had a residence time of one to two years. Twenty-two resident

birds had a residence time greater than two years but no migrants had a residence time

greater than two years. Thirteen Marbled Murrelets had residence times of greater than

or equal to four years. Only eleven of these birds were genotyped, but all eleven were

classified as central California residents, and seven of these birds had a first-order relative

in the central California population.

The average annual percentage of migrant birds in central California was 7.06%

and ranged from 2.44% in 1999 to 10.53% in 2002 (Table 3). I observed an increasing

trend in the percentage of migrants per year ($F = 9.656$; $p = 0.036$; $b = 0.013$, $r^2 = 0.707$).

From 1997 to 2003, the number of migrants in central California increased by

approximately 1.3% per year (Fig. 7).

DISCUSSION

Genetic Structure

I identified two distinct genetic populations, the first included birds from southeast Alaska to northern California and the second included birds from central California. Moderate population genetic structure was present between central California and the northern population ($Fst = 0.034 \pm 0.001$). This moderate population differentiation allowed me to assign birds to either central California or the northern population with relatively few α (2.30 ± 0.58) and β (2.10 ± 0.60) errors. All other pair-wise comparisons had low Fst estimates (0.005 ± 0.001), indicating that there was minimal genetic structure among subpopulations from southeast Alaska to northern California. Although a few pair-wise comparisons involving areas in the northern population had Fst values greater than zero, these Fst values were too low to be biologically significant and indicate that gene flow most likely occurred frequently among the subpopulations in the north. Because these subpopulations lack genetic structure, it is not possible to perform population assignments for birds from the northern population. The genetic structure observed in this study was consistent with previous genetic studies by Friesen et al. (2005) and Piatt et al. (2007) which identified significant population genetic structure between central California and the populations to the north.

Dispersal Patterns in Marbled Murrelets

The proportion of migrants observed in central California during winter (0.83) was greater than the proportion of migrants observed during the breeding (0.06) and post-breeding seasons (0.08; Fig. 5a), indicating that either birds from the northern population dispersed into central California in greater numbers during winter than other seasons or

that a greater number of central California residents emigrated from the study area during the winter. I was unable to differentiate whether the high proportion of migrants observed in central California during winter was due to immigration of a greater number of migrants from the northern populations or emigration of a greater number of central California residents because the sample size for winter was small ($n = 12$). Only two of the twelve birds sampled during winter were classified as central California residents (Fig. 8). A study by Peery et al. (2008b) indicated that most Marbled Murrelets in central California dispersed southward during winter to Monterey Bay and the San Luis Obispo area. My results, in conjunction with the tracking study by Peery et al. (2008b), indicated that during winter some central California residents dispersed southward and were replaced by birds dispersing into central California from the northern population.

I identified migrants from the northern population in central California between Pt. Reyes and Coronado, California from November to March indicating that Marbled Murrelets can disperse > 900 km from their breeding areas during winter (Fig 8). This distance is approximately twice that of those reported for related alcid species such as the Common Murre (420 km; Halley and Harris 1992) and the Atlantic Puffin (450 km; Harris and Wanless 1991). Peery et al. (2008b) reported several long-distance dispersal events (mean = 256 ± 43 km) made by Marbled Murrelets from central California during the post-breeding season, and Beauchamp et al. (1999) observed a female that dispersed 220 km during the non-breeding season from British Columbia to Washington. Seabirds are more likely to disperse long distances during winter because they are not committed to a nest site. Birds may disperse between breeding seasons in search of suitable prey resources or more protected wintering habitat. Also, it is possible that Marbled Murrelets

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dispersing during the non-breeding season are assessing prospective nesting habitat in new areas (Divoky and Horton 1995). This idea is supported by the observation of Marbled Murrelets flying inland to nesting habitats during the non-breeding season (Nashlund 1993)

I demonstrated that dispersal in Marbled Murrelets is female-biased. No previous studies have detected female-biased dispersal in Marbled Murrelets, although Beauchamp et al. (1999) reported a female bird that dispersed 220 km from British Columbia to Washington. Peery et al. (2008b) did not observe a female bias in dispersal (six of twelve long-distance dispersers were male and six were female). However, the Peery et al. (2008b) study had a limited sample size ($n = 12$) and examined dispersal *from* central California, whereas my study examined dispersal *into* central California. It is commonly accepted that dispersal in birds is female-biased, but few researchers have examined sex-biased dispersal in seabirds. Female-biased dispersal has been observed in some marine and shorebird species including Killdeer (Lenington and Mace 1975), Piping Plovers (Wilcox 1959), and South Polar Skuas (Ainley et al. 1990, Pietz and Parmelee 1994). Although female-biased dispersal may be beneficial for species to avoid inbreeding (Greenwood 1980, Perrin and Mazalov 2000) and minimize competition for resources (Greenwood 1980) and mates (Perrin and Mazalov 2000), it can decrease the number of breeding females and may lead to male-biased sex ratios in populations (Dale 2001). In fact, I detected a male-biased sex ratio in the central California Marbled Murrelet population from capture data. Vanderkist et al. (1999) observed a male bias in captures using floating mist nets for Marbled Murrelets off British Columbia. However, the capture rates for males and females in central California using a night-lighting/dip-netting

technique were not significantly different (Peery et al. 2006b). Therefore, the male bias in my sample is most likely due to a male-biased sex ratio in the central California Marbled Murrelet population rather than a capture bias. Populations with biased sex ratios experience stronger genetic drift and have lower productivity, because of the high number of unpaired individuals (Dale 2001). Such effects could be especially detrimental and possibly cause local extirpation in small, isolated populations such as the central California murrelet population (Dale 2001).

My results also indicate that dispersal in Marbled Murrelets may be juvenile-biased. Although there is little direct evidence of juvenile-biased dispersal in Marbled Murrelets, I observed a second-year bird in Coronado, California approximately 500 km south of the typical non-breeding distribution for this species. Juvenile-biased dispersal has been observed in other species of alcids. For example, Black Guillemot natal dispersal is much greater than dispersal to new breeding sites by established breeders (Frederiksen and Petersen 2000). Moreover, the recent increase in new colony formation and growth rate observed in some alcids on the west coast of North America has been attributed to immigration and indicates that natal dispersal is probably common in this family (Divoky and Horton 1995). Divoky and Horton (1995) suggested that natal dispersal may be especially high for Marbled Murrelets for several reasons. First, the non-breeding distribution of this species is relatively large (Piatt et al. 2007) and exposes birds to prospective breeding areas. Second, Marbled Murrelets can assess potential breeding habitat by visiting nesting areas year round (Nashlund 1993). In fact, Peery et al. (2004a) observed non-nesting birds that flew inland to visit nesting habitat during the breeding season even without active nests. Third, the pre-breeding stage in Marbled

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Murrelets (2-5 years; Beissinger 1995) is long enough for birds to disperse and assess

breeding areas before recruitment. Last, prospecting behavior may be selected for in

Marbled Murrelets because the potential breeding habitat for this species is extensive and

distributed in a wide band along the coast, making the search for nesting areas difficult.

Metapopulation Dynamics

I detected significant genetic structure between central California and the northern

population of Marbled Murrelets, indicative of limited gene flow between these groups.

However, a genetic study by Peery et al. (2008a) estimated an annual migration rate of 2-

6% from the northern population into central California using a parentage approach.

Peery et al. (2008a) suggested that this migration rate should provide adequate gene flow

to homogenize population genetic structure, unless migrants are selected against or are

making temporary movements and are not attempting to breed in central California. I

found that a small proportion of migrants had a first-order relative in central California

(Fig. 5c) and that migrant birds had shorter residence times in central California than

birds that were classified as residents. In other words, migrant birds spent less time in

central California than resident birds, and they were less likely to have a parent or

offspring in the population. These results support the hypothesis by Peery et al. (2008a)

that dispersal of Marbled Murrelets into central California does not result in permanent

recruitment. However, there is insufficient data to determine if migrants are not

permanently recruiting to central California because they are selected against or because

they are making temporary movements and are not attempting to breed in central

California.

Migrant birds from the northern population may affect population estimates for central California. Migrant birds would be counted during at-sea surveys and included in population estimates for central California, potentially obscuring the detection of population declines. Furthermore, variability in the percentage of migrants observed in central California each year (Fig. 7) would increase the variability in population estimates making it difficult to statistically detect a population decline. The demographic parameters for Marbled Murrelets in central California indicate the population would decline at a rate of 9.5% annually in the absence of immigration (Peery et al., 2006a; Peery et al., 2006b; Fig 7), and I detected an increasing trend of 1.3% per year in the percentage of migrants observed in central California (Fig 7). This increasing trend in the percentage of migrants would confound the trend in annual population estimates making it difficult to detect a decline in the central California population of Marbled Murrelets (Fig. 7).

The percentage of migrants in central California may be increasing due to an increase in nest failures from predation or an increase in habitat loss and fragmentation in the northern populations (Divoky and Horton 1995, Raphael 2006). Raphael (2006) observed a 2% loss of Marbled Murrelet nesting habitat from federal lands and a 12% loss of nesting habitat from nonfederal lands in Washington, Oregon, and California. This decrease in available nesting habitat may displace Marbled Murrelets in the northern population and force them to disperse to new nesting areas. Migrants in central California may be prospecting for new nesting habitat, but if they do not recruit to the central California population, they would increase competition with residents for prey resources without contributing to the reproductive output of the central California

murrelet population. This could be especially detrimental to the central California population in years when low food availability limits reproduction (Peery et al. 2004b).

Conservation Implications

My results indicate that Marbled Murrelets can disperse great distances, and may frequently make movements between the northern population and central California. I observed the greatest proportion of migrants in central California during winter. Migrants also were present in central California during the breeding and post-breeding seasons, indicating that Marbled Murrelets move between populations year round. Therefore, at any time of year, the birds present in a habitat may be composed of residents and migrants. It is important to consider this mixed composition of residents and migrants when making management decisions such as oil spill mitigation. Mortality from oil spills presents a major threat to Marbled Murrelet populations, especially in California where population declines have reduced the number of birds to less than 5,000 (McShane et al., 2004). Most often, oil spill mitigation efforts are concentrated on the habitats closest to the spill site. However, my data indicate that Marbled Murrelets affected by an oil spill in California may originate from two distinct genetic stocks. Therefore, a more effective mitigation strategy may be to partition restoration efforts among habitats throughout the state regardless of the spill location. This strategy would be especially beneficial for the central California population of Marbled Murrelets given its small population size (660, 95% CL: 550-800) and the projected decline for this population (Peery et al. 2006a).

These results also have important implications for management of the central California population of Marbled Murrelets. Population estimates for this population

have been previously overestimated because the estimates did not account for migrants in central California. An average of 7.06% per year of the Marbled Murrelets captured in central California were identified as migrants (Table 3), and the percentage of migrants observed in central California increased by 1.3% per year (Fig. 7). Migrant birds from the northern population are not permanently recruiting to central California. However, it remains unclear if migrants are not recruiting because they are selected against or because they are making temporary movements and are not attempting to breed. Additional data about the breeding status and success of migrant birds in central California could provide the information necessary to explain why migrants are not permanently recruiting to central California. Whatever the cause, if migrant birds from the northern population do not permanently recruit to central California they would be competing with resident birds for resources, such as prey and nest sites, without contributing offspring to the central California population. Disentangling the effect of migration from population estimate trends for the central California Marbled Murrelet population, and understanding the effect of resource competition between migrants and residents in central California has been challenging. Therefore, it is important to recognize both the confounding effect migration on population estimates for Marbled Murrelets in central California, and the negative impact of resource competition between migrants and residents when making management decisions for the already threatened central California Marbled Murrelet population.

LITERATUTRE CITED

Agler, B. A., S. J. Kendall, and D. B. Irons. 1998. Abundance and distribution of marbled and Kittlitz's murrelets in southcentral and southeast Alaska. Condor **100**:254-265.

Ainley, D. G., C. A. Ribic, and R. C. Wood. 1990. A demographic study of the south polar skua Catharacta maccormicki at Cape Crozier. Journal of Animal Ecology. Vol. 59:no. 1.

Beauchamp, W. D., F. Cooke, C. Lougheed, L. W. Lougheed, C. J. Ralph, and S. Courtney. 1999. Seasonal movements of Marbled Murrelets: Evidence from banded birds. Condor **101**:671-674.

Beissinger, S. R. 1995. Population trends of the Marbled Murrelet projected from demographic analyses. Page 420 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the Marbled Murrelet. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA.

Berry, O., M. D. Tocher, and S. D. Sarre. 2004. Can assignment tests measure dispersal? Molecular Ecology **13**:551-561.

Burg, T. M., J. Lomax, R. Almond, M. d. L. Brooke, and W. Amos. 2003. Unraveling dispersal patterns in an expanding population of a highly mobile seabird, the Northern Fulmar (*Fulmaris glacialis*). Proceedings of the Royal Society of London, series B **270**:979-984.

Clarke, A. L., B. E. Saether, and E. Roskaft. 1997. Sex biases in avian dispersal: A reappraisal. Oikos **79**:429-438.

Cornuet, J.-M., S. Piry, G. Luikart, A. Estoup, and M. Solignac. 1999. New methods employing multilocus genotypes to select or exclude populations as origins of individuals. Genetics **153**:1989-2000.

Dale, S. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. Oikos **92**:344-356.

Dearborn, D. C., A. C. Anders, E. A. Schreiber, R. M. M. Adams, and U. G. Mueller. 2003. Inter-island movements and population differentiation in a pelagic seabird. Molecular Ecology **12**:2835-2843.

Divoky, G. J. and M. Horton. 1995. Breeding and natal dispersal, nest habitat loss and implications for Marbled Murrelet populations. Page 420 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the Marbled Murrelet. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA.

Excoffier, L., J. Novembre, and S. Schneider. 2000. SIMCOAL: a general coalescent program for the simulation of molecular data in interconnected populations with arbitrary demography. Journal of Heredity **91**:506-509.

Faubet, P., R. S. Waples, and O. E. Gaggiotti. 2007. Evaluating the performance of a multilocus Bayesian method for the estimation of migration rates. Molecular Ecology **16**:1149-1166.

Favre, L., F. Balloux, J. Goudet, and N. Perrin. 1997. Female-biased dispersal in the monogamous mammal *Crocidura russula*: evidence from field and microsatellite patterns. Proceedings of the Royal Society of London, series B **269**:127-132.

Frederiksen, M. and A. Petersen. 2000. The importance of natal dispersal in a colonial seabird, the Black Guillemot, *Cepphus grylle*. Ibis **142**:48-57.

Friesen, V. L., T. P. Birt, J. F. Piatt, R. T. Golightly, S. H. Newman, P. N. Herbert, B. C. Congdon, and G. Gissing. 2005. Population genetic structure and conservation of Marbled Murrelets (*Brachyramphus marmoratus*). Conservation Genetics. **6**:607-614.

Friesen, V. L., T. M. Burg, and K. D. McCoy. 2007. Mechanisms of population differentiation in seabirds. Molecular Ecology **16**:1765-1785.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour. **28**:1140-1162.

Halley, D. J. and M. P. Harris. 1992. Intercolony movement and behavior of immature guillemots *Uria aalge*. Ibis **135**:264-270.

Harris, M. P. and S. Wanless. 1991. Population studies and conservation of Puffins *Fratercula arctica*. Pages 230-248 *in* C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, editors. Bird population studies: relevance to conservation and management. Oxford University Press, New York, NY.

Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology and Evolution **11**:514-517.

Lenington, S. and T. Mace. 1975. Mate fidelity and nesting site tenacity in the Killdeer. The Auk **92**:149-151.

Lewis, P. O. and D. Zaykin. 2001. Genetic data analysis: computer program for the analysis of allelic data. Version 1.0 (d16c). Page Free program distributed by the authors over the internet.

Lougheed, C., L. W. Lougheed, F. Cooke, and S. Boyd. 2002. Local survival of adult and juvenile Marbled Murrelets and their importance for estimating reproductive success. Condor **104**:309-318.

McFarlane Tranquilla, L., P. Yen, R. Bradley, B. Vanderkist, D. Lank, N. Parker, M. Drever, L. Lougheed, G. Kaiser, and T. Williams. 2003. Do two murrelets make a pair? Breeding status and behavior of Marbled Murrelet pairs captured at sea. Wilson Bulletin **115**:374-381.

McShane, C., T. Hamer, H. Carter, G. Swartzman, V. Friesen, D. Ainley, R. Tressler, K. Nelson, A. Burger, L. Spear, T. Mohagen, R. Martin, L. Henkel, K. Prindle, C. Strong, and J. Keany. 2004. Evaluation report for the 5-year status review of the Marbled Murrelet in Washington, Oregon, and California. . U.S. Fish and Wildlife Service, Region 1, Seattle, WA.

Milot, E., H. Weimerskirch, and L. Bernatchez. 2008. The seabird paradox: dispersal, genetic structure and population dynamics in a highly mobile, but pholopatric albatross species. Molecular Ecology **17**:1658-1673.

Mossman, C. A. and P. M. Waser. 1999. Genetic detection of sex-biased dispersal. Molecular Ecology **8**:1063-1067.

Nashlund, N. L. 1993. Why do Marbled Murrelets attend old-growth forest nesting areas year-round? Auk **110**:594-602.

Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology [MOL. ECOL.]. Vol. 4:no. 3.

Paetkau, D., R. Slade, M. Burden, and A. Estoup. 2004. Genetic assignment methods for the direct, real-time estimation of migration rate: A simulation-based exploration of accuracy and power. Molecular Ecology **13**:55-65.

Peery, M. Z., B. H. Becker, and S. R. Beissinger. 2006a. Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. Ecological Applications **16**:1516-1528.

Peery, M. Z., S. R. Beissinger, E. Burkett, and S. H. Newman. 2006b. Local survival of Marbled Murrelets in Central California: Roles of oceanographic processes, sex, and radiotagging. Journal of Wildlife Management **70**:78-88.

Peery, M. Z., S. R. Beissinger, R. H. House, M. Berube, L. A. Hall, A. Sellas, and P. J. Palsboll. 2008a. Characterizing source-sink dynamics with genetic parentage assignments. Ecology **89**:2746-2759.

Peery, M. Z., S. R. Beissinger, S. H. Newman, B. H. Becker, E. Burkett, and T. D. Williams. 2004a. Individual and temporal variation in inland flight behavior of Marbled Murrelets: Implications for population monitoring. Condor **106**:344-353.

Peery, M. Z., S. R. Beissinger, S. H. Newman, E. B. Burkett, and T. D. Williams. 2004b. Applying the declining population paradigm: Diagnosing causes of poor reproduction in the Marbled Murrelet. Conservation Biology **18**:1088-1098.

Peery, M. Z., L. A. Hall, A. Sellas, S. R. Beissinger, C. Moritz, M. Berube, M. G. Raphael, S. K. Nelson, R. T. Golightly, L. McFarlane Tranquilla, S. H. Newman, and P. J. Palsboll. in prep. Crytpic extinction in Marbled Murrelets. Science.

Peery, M. Z., L. A. Henkel, S. H. Newman, B. H. Becker, J. T. Harvey, C. W. Thompson, and S. R. Beissinger. 2008b. Effect of rapid flight-feather molt on post-breeding dispersal in a threatened alcid. Auk **25**:113-123.

Perrin, N. and V. Mazalov. 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. American Naturalist **155**:116-127.

Piatt, J. F., J. K. Kuletz, A. E. Burger, S. A. Hatch, V. L. Friesen, T. P. Birt, M. L. Arimitsu, G. S. Drew, A. M. A. Harding, and K. S. Bixler. 2007. Status review of the Marbled Murrelet (*Brachyramphus marmoratus*) in Alaska and British Columbia. . U.S. Geological Survey.

Pietz, P. J. and D. F. Parmelee. 1994. Survival, site and mate fidelity in south polar skuas Catharacta maccormicki at Anvers Island, Antarctica. Ibis. Vol. 136:no. 1.

Piry, S., A. Alapetite, J. M. Cornuet, D. Paetkau, L. Baudouin, and A. Estoup. 2004. GENECLASS2: A software for genetic assignment and first-generation migrant detection. Journal of Heredity **95**:536-539.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics **155**:945-959.

Rannala, B. and J. L. Mountain. 1997. Detecting immigration by using multilocus genotypes. Proceedings of the National Academy of Sciences of the United States of America **94**:9197-9201.

Raphael, M. G. 2006. Conservation of the Marbled Murrelet under the Northwest Forest Plan. Conservation Biology **20**:297-305.

Rew, M. B., M. Z. Peery, S. R. Beissinger, M. Berube, J. D. Lozier, E. M. Rubidge, and P. J. Palsboll. 2006. Cloning and characterization of 29 tetranucleotide and two dinucleotide polymorphic microsatellite loci from the endangered Marbled Murrelet (*Brachyramphus marmoratus*). Molecular Ecology Notes **6**:241-244.

Sambrook, J., E. F. Fritsch, and T. Maniatis. 1989. Molecular cloning: a laboratory manual. 2nd edition. CSHL Press, Woodbury, NY.

Schneider, S., D. Roessli, and L. Excoffier. 2000. Arlequin ver. 2.000: a software for population genetic data analysis., Genetics and Biometry Laboratory, University of Geneva, Switzerland.

Steiner, U. K. and A. J. Gaston. 2005. Reproductive consequences of natal dispersal in a highly philopatric seabird. Behavioral Ecology **16**:634-639.

Strong, C. S., B. S. Kiett, W. R. McIver, C. J. Palmer, and I. Gaffeney. 1995. Distribution and population estimates of Marbled Murrelets at sea in Oregon during the summers of 1992 and 1993. Page 420 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the Marbled Murrelet. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA.

Vanderkist, B. A., X.-H. Xue, R. Griffiths, K. Martin, W. Beauchamp, and T. D. Williams. 1999. Evidence of male-bias in capture samples of Marbled Murrelets from genetic studies in British Columbia. Condor **101**:398-402.

Whitworth, D. L., J. Y. Takekawa, H. R. Carter, and W. R. McIver. 1997. Night-lighting as an at-sea capture technique for Xantus' Murrlelets in the Southern California Bight. Colonial Waterbirds **20**:525-531.

Wilcox, L. R. 1959. A twenty year banding study of the the Piping Plover. The Auk **76**:129-152.

Wright, S. 1931. Evolution in Mendelian populations. Genetics **16**:97-159.

Zar, J. H. 1999. Biostatistical analysis. 4th edition. Prentice-Hall Inc., Upper Saddle River, New Jersey.

Table 1. Expected and observed mean heterozygosities for Marbled Murrelets (*Brachyramphus marmoratus*) from different regions. Microsatellite loci which differed significantly (p< 0.05) from Hardy-Weinberg equilibrium are listed for each region.

Population	Mean Observed Heterozygosity	Mean Expected Heterzygosity	Loci with significant p-values
Alaska	0.8077	0.8132	
British Columbia	0.8038	0.8122	TATC371
Washington	0.8156	0.8074	
Oregon	0.8391	0.8156	
Northern California	0.8427	0.8114	
Central California	0.7641	0.7789	GGAT313

Table 2. Wright's Fst values (lower diagonal) and 95% confidence intervals (upper diagonal) from pair-wise comparisons for populations of Marbled Murrelets (*Brachyramphus marmoratus*) from Alaska (AK), British Columbia (BC), Washington (WA), Oregon (OR), northern California (NCA), and central California (CCA). Sample sizes (*n*) are listed to the left of each population.

n		AK	BC	WA	OR	NCA	CCA
60	AK		-0.001-0.006	-0.002-0.003	-0.001-0.015	0.003-0.012	0.021-0.046
65	BC	0.002279		-0.001-0.003	0.001-0.006	0.001-0.013	0.022-0.043
79	WA	0.000461	0.001077		0.001-0.015	0.004-0.013	0.022-0.055
26	OR	0.006220	0.002960	0.006857		-0.002-0.013	0.024-0.045
76	NCA	0.007307	0.006163	0.008228	0.003892		0.025-0.040
282	CCA	0.032522	0.031938	0.037519	0.034072	0.031971	

Table 3. Percentage of migrant Marbled Murrelets (*Brachyramphus marmoratus*) observed in central California from 1997-2003. Samples from 1998 were not genotyped.

Year	Residents	Migrants	Total	% Migrants
1997	21	1	22	4.55
1999	40	1	41	2.44
2000	62	4	66	6.06
2001	56	6	62	9.68
2002	34	4	38	10.53
2003	40	4	44	9.09
Mean				**7.06**
SD				**3.21**
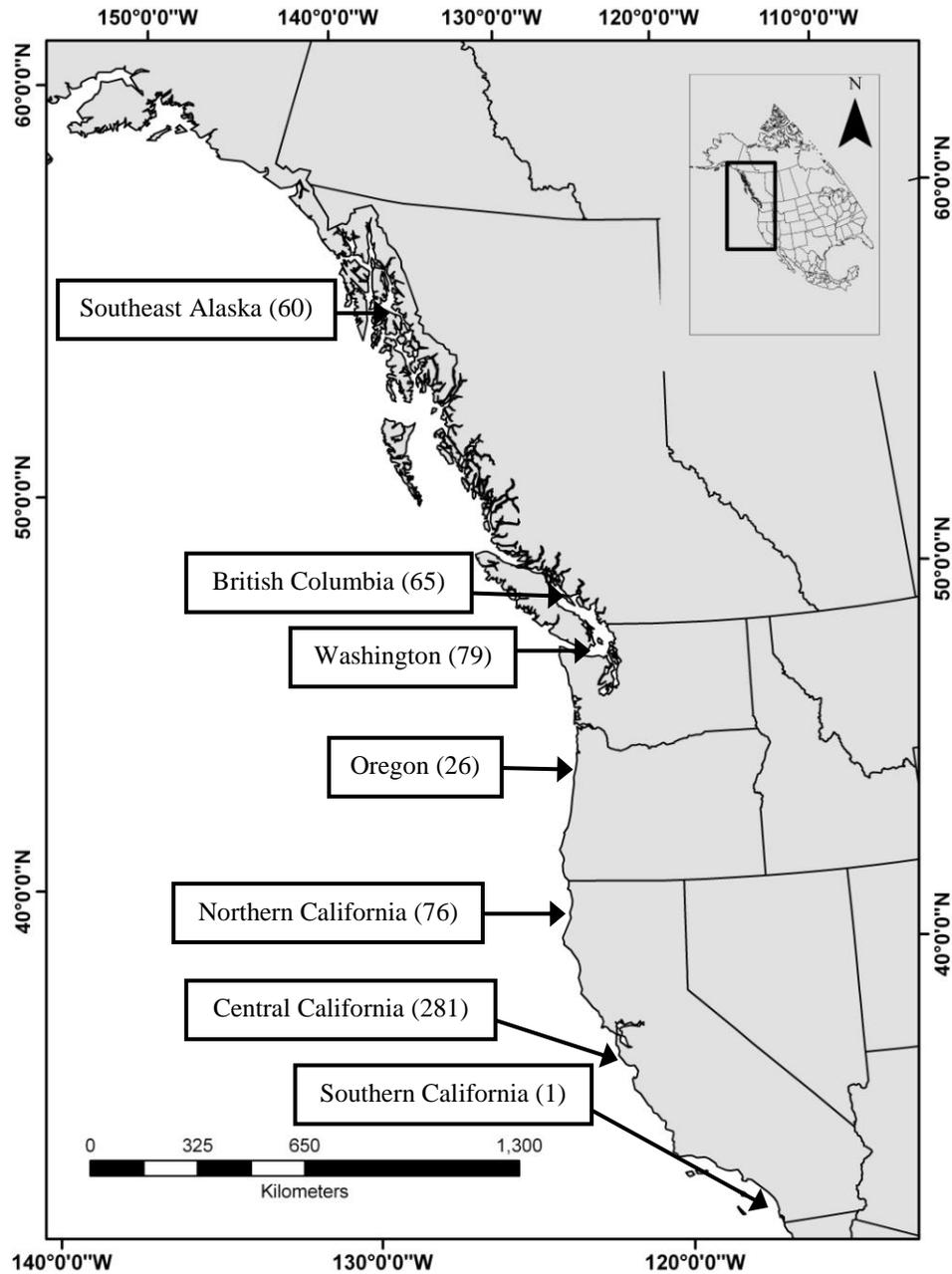
Figure 1. Map of the Pacific northwest showing collection locations of Marbled Murrelet (*Brachyramphus marmoratus*) genetic samples collected between 1997 and 2007. Arrows point to approximate sampling locations with sample sizes for each location indicated in parentheses.
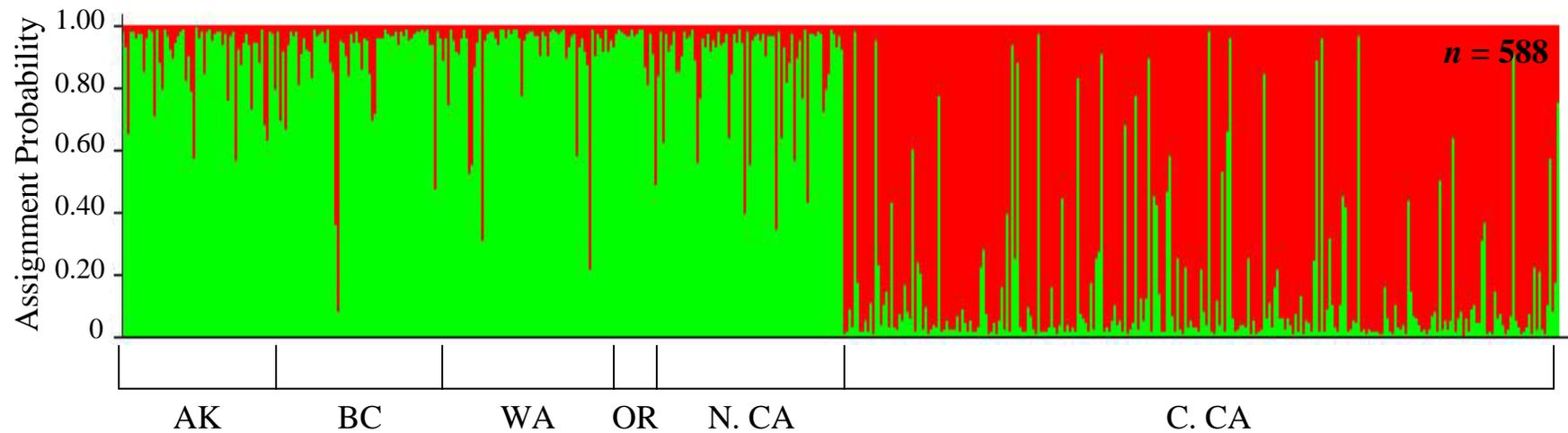
Figure. 2. Population assignment probabilities for Marbled Murrelets (*Brachyramphus marmoratus*) captured from southern Alaska to central California from the program STRUCTURE. Capture locations are listed on the x-axis. Birds were assigned to two distinct genetic populations (shown in green and red).
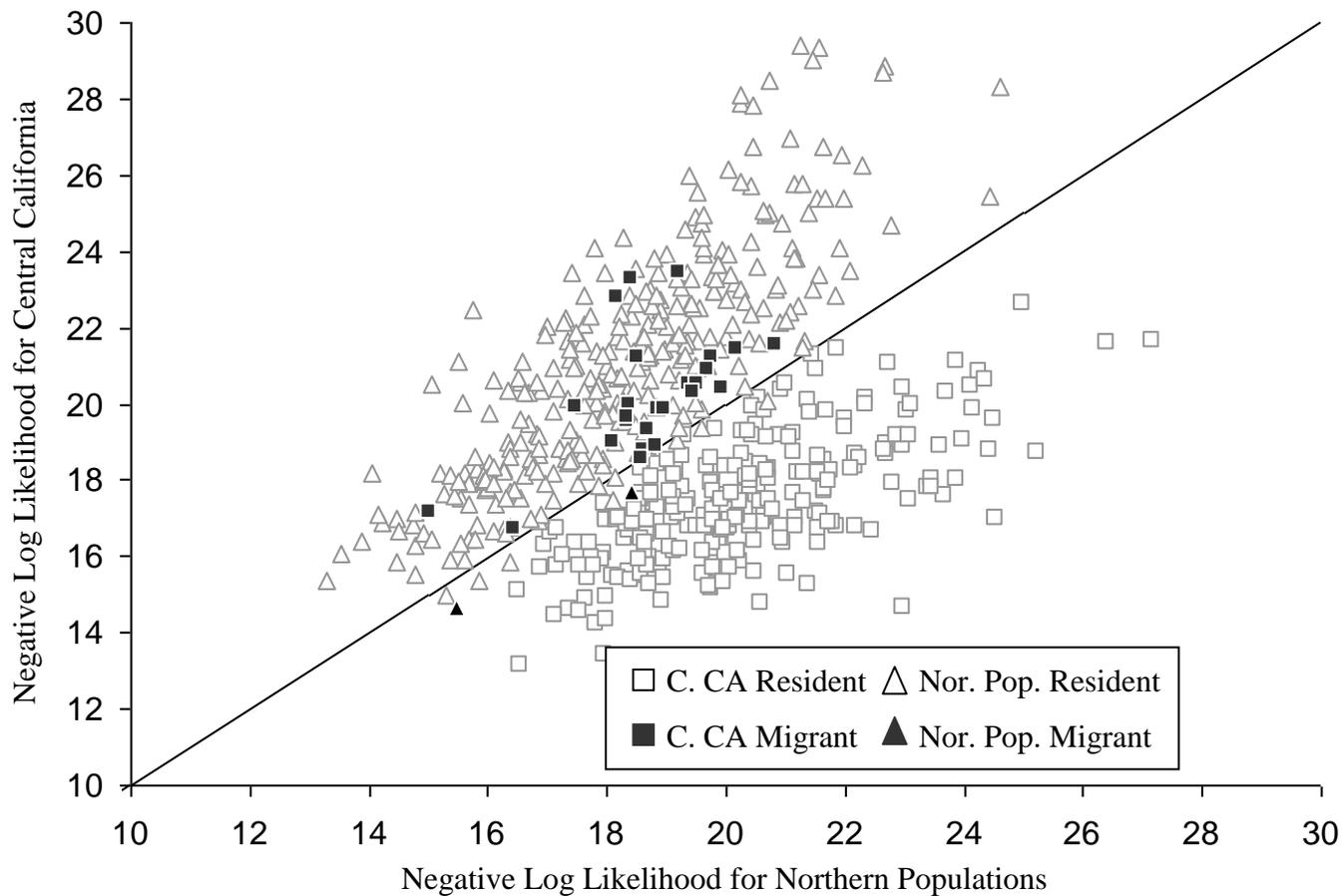
Figure. 3. Negative log likelihood values for population assignments from Marbled Murrelets (*Brachyramphus marmoratus*) captured in central California (C. CA) or a population north of central California (Nor. Pop.). The central California residents (open squares) are separated from the northern population residents (open triangles) by a 1:1 line. Birds identified as migrants (shaded squares or triangles) were captured in one population, but are distributed in a cluster with the other population.
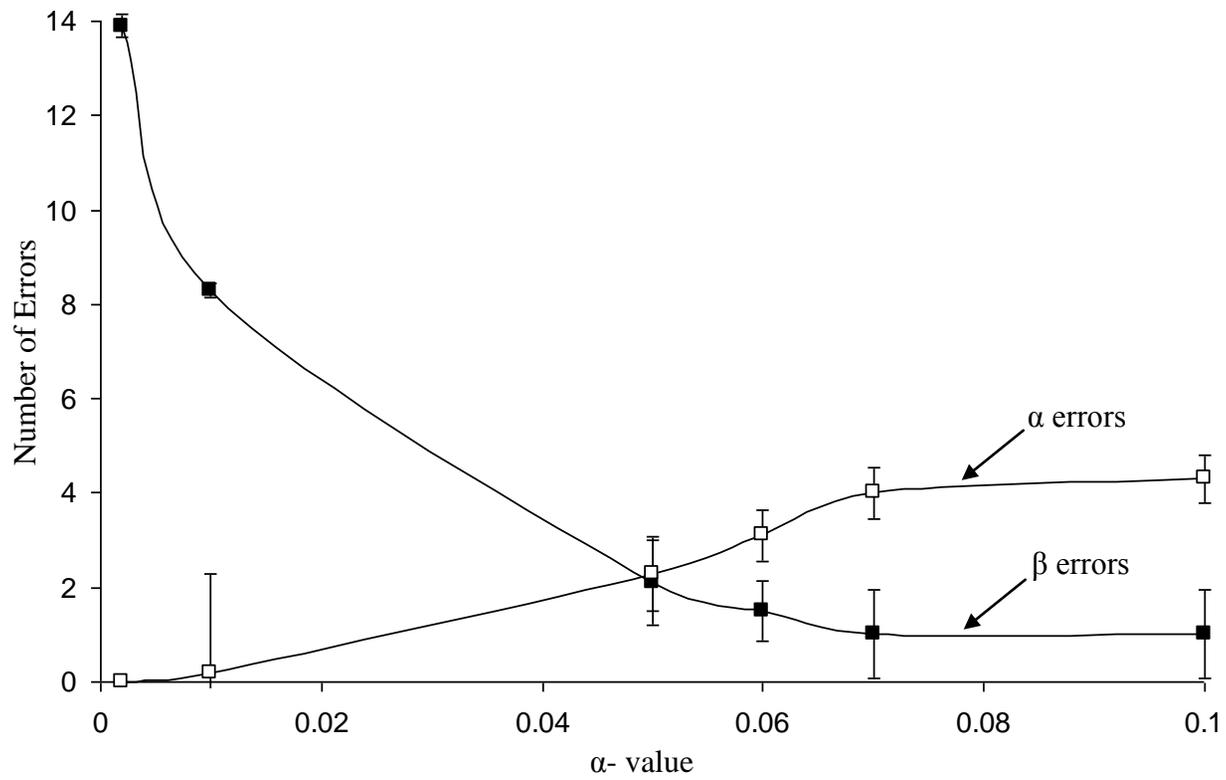
Figure 4. Mean number of α (open squares) and β (solid squares) errors in population assignments made in GENECLASS2 for simulated populations of Marbled Murrelets.
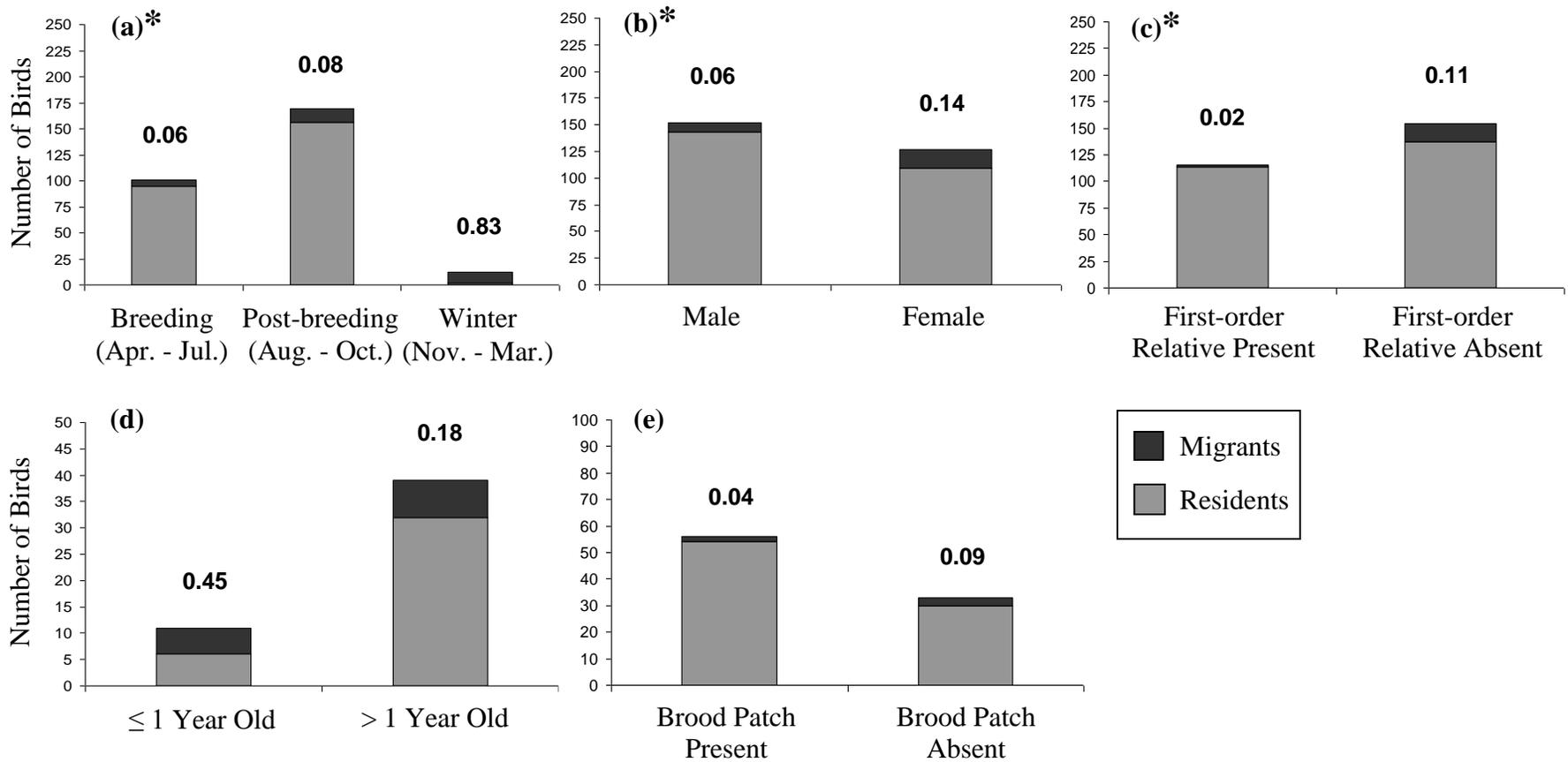
Figure 5. The number of Marbled Murrelets (*Brachyramphus marmoratus*) assigned as migrants (black) and residents (gray) from different (a) seasons, (b) sexes, (c) relative statuses, (d) age classes, and (e) breeding statuses. Numbers above each bar represent the proportion of migrants present in the group. Groups with a statistically significant difference in the number of residents and migrants are indicated by an asterisk.
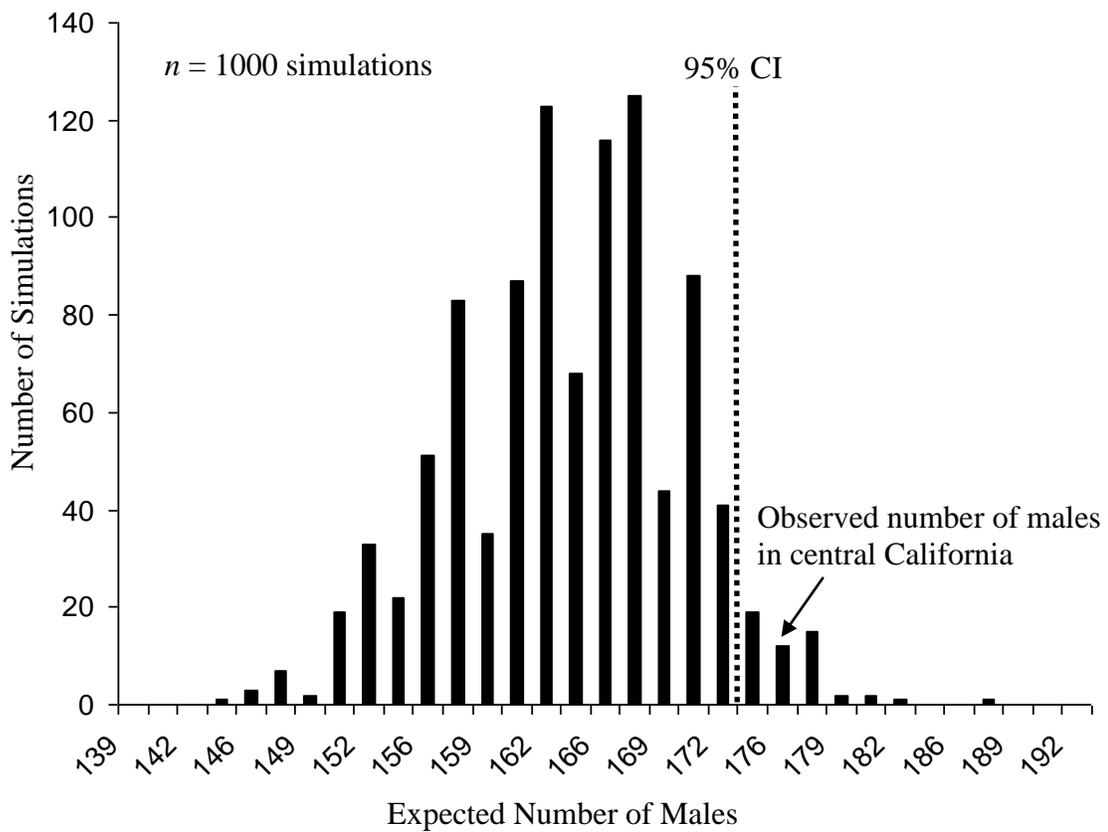
Figure 6. Expected distribution for the number of male Marbled Murrelets (*Brachyramphus marmoratus*) generated by RESAMPLING STATS assuming a 1:1 sex ratio. The upper 95% confidence interval is shown as a dashed line, and the observed number of males captured in central California is depicted by an asterisk.
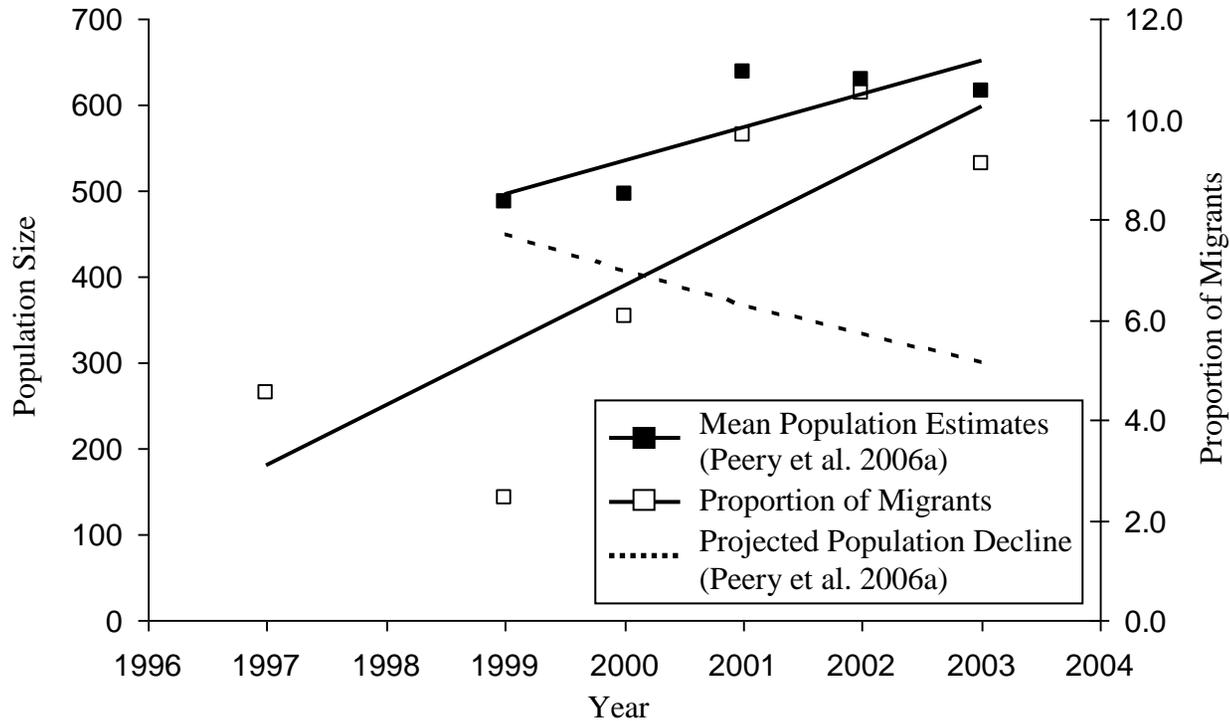
Figure 7. Mean population size estimates (solid diamonds) and trend (solid line) for Marbled Murrelets (*Brachyramphus marmoratus*) in central California from at-sea surveys for 1999 to 2003 (Peery et al. 2006a) plotted with a 9.5 % projected annual decline (dashed line) for the central California population (Peery et al. 2006a), and the proportion of migrant birds (open diamonds) and trend (solid line) observed in central California from 1999 to 2003.
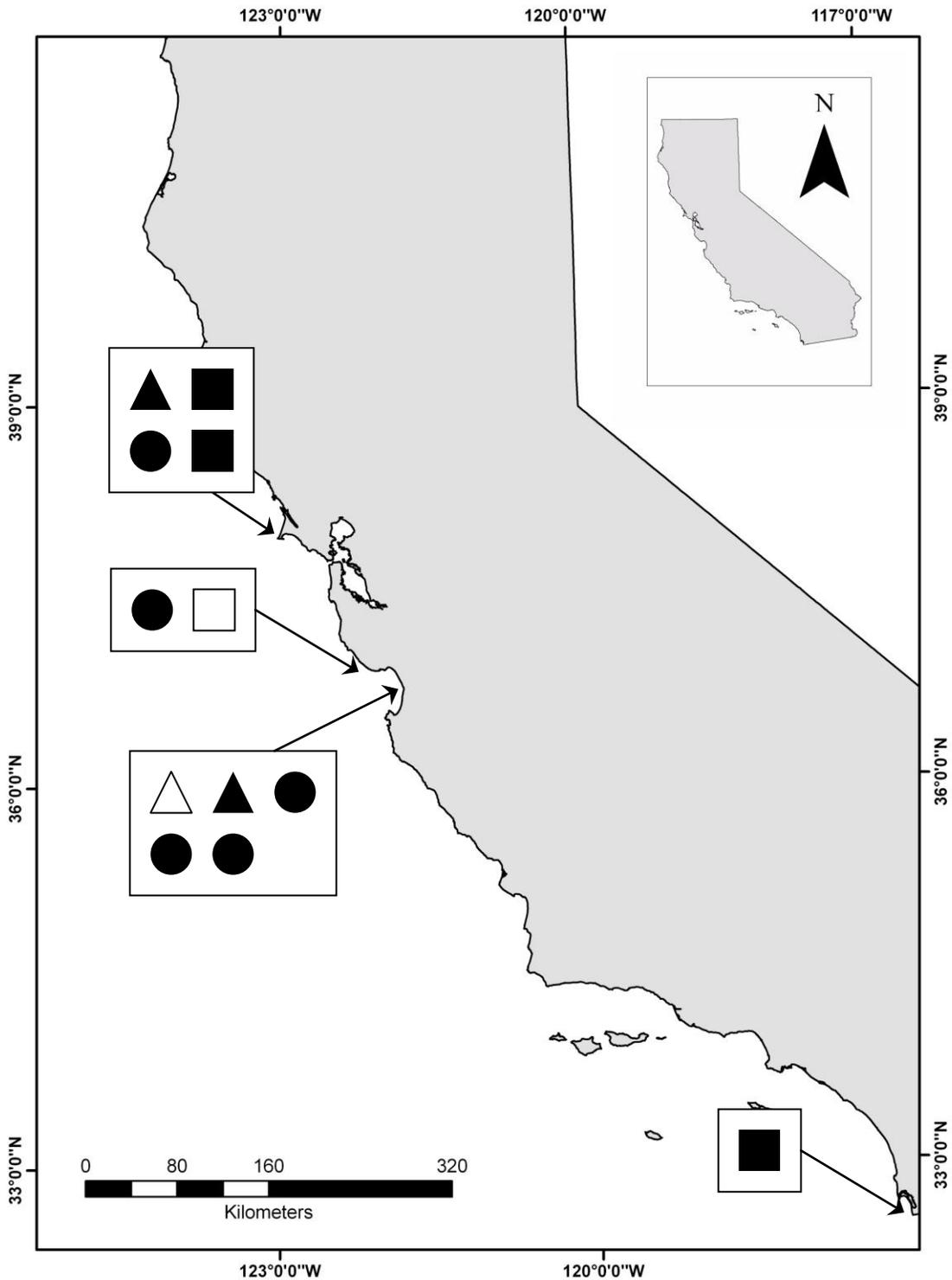
Figure 8. Map of central California showing migrants (black) and residents (white) for Marbled Murrelets (*Brachyramphus marmoratus*) collected from the winter season (November to March). Male birds are depicted as squares, females are depicted as circles, and birds of unknown sex are depicted as triangles.

APPENDIX A

SEX-RATIO RESAMPLING TEST

set 330 1 m

set 330 0 f

concat m f pop

repeat 1000

shuffle pop popsh

take popsh 1,328 samp

sum samp sampsum

score sampsum hist

end

histogram hist