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Characterizing dispersal patterns in a threatened seabird with limited genetic structure

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Abstract

Genetic assignment methods provide an appealing approach for characterizing dispersal patterns on ecological time scales, but require sufficient genetic differentiation to accurately identify migrants and a large enough sample size of migrants to, for example, compare dispersal between sexes or age classes. We demonstrate that assignment methods can be rigorously used to characterize dispersal patterns in a marbled murrelet (*Brachyramphus marmoratus*) population from central California that numbers approximately 600 individuals and is only moderately differentiated ($F_{ST} \sim 0.03$) from larger populations to the north. We used coalescent simulations to select a significance level that resulted in a low and approximately equal expected number of type I and II errors and then used this significance level to identify a population of origin for 589 individuals genotyped at 13 microsatellite loci. The proportion of migrants in central California was greatest during winter when 83% of individuals were classified as migrants compared to lower proportions during the breeding (6%) and post-breeding (8%) seasons. Dispersal was also biased toward young and female individuals, as is typical in birds. Migrants were rarely members of parent-offspring pairs, suggesting that they contributed few young to the central California population. A greater number of migrants than expected under equilibrium conditions, a lack of individuals with mixed ancestry, and a small number of potential source populations (two), likely allowed us to use assignment methods to rigorously characterize dispersal patterns for a population that was larger and less differentiated than typically thought required for the identification of migrants.

Keywords: age-biased dispersal, assignment methods, *Brachyramphus marmoratus*, marbled murrelet, microsatellites, migrants, sex-biased dispersal

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Introduction

Genetic assignment methods use multi-locus genetic data to determine the population membership of individuals and provide a means for characterizing the dispersal of individuals among populations on ecological time scales (Manel *et al.* 2005). This approach involves assigning individuals to candidate source populations based on their genotype likelihoods (Paetkau *et al.* 1995; Rannala & Mountain 1997). Confidence

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associated with individual assignments can be assessed by comparing estimated likelihoods to the distribution of expected likelihoods for resident individuals derived from simulation analyses (Cornuet *et al.* 1999; Paetkau *et al.* 2004). Individuals can also be 'excluded' from the population from which they were sampled if their genotype was less likely than a subjectively determined significance level (α). Thus an individual whose genotype likely originated from a different population than the one in which it was sampled can be defined as a migrant, and is indicative of dispersal (defined as the movement of an individual from its original population to a new population). In some cases, assignment methods have provided an accurate means for identifying migrant individuals (Berry *et al.* 2004) and for testing ecological hypotheses related to dispersal, such as whether dispersal is sex- or age-biased (Favre *et al.* 1997; Mossman & Waser 1999).

Statistically rigorous assignments depend on the degree of genetic divergence among putative source populations, where error rates are expected to be lowest in strongly differentiated populations which presumably exchange few migrants (Cornuet *et al.* 1999; Paetkau *et al.* 2004; Waples & Gaggiotti 2006). However, even moderately differentiated populations exchange few migrants per generation under genetic drift-migration equilibrium, and only small numbers of migrants are expected to be available for sampling in such populations. This problem is particularly acute for large populations because the level of divergence is determined by the effective number of migrants, and large populations are expected to contain proportionately fewer migrants for a given level of genetic divergence. The aforementioned issues are magnified when the objective is to compare dispersal behaviour among groups of individuals (e.g. sexes or age classes) because of the need for adequate sample sizes in each group. Accordingly, assignment methods are most appropriate for characterizing dispersal patterns in small populations. Moreover, the extent to which natural populations exchange a sufficient number of migrants but maintain enough genetic population structure to rigorously employ assignment methods is an area of active research (Paetkau *et al.* 2004).

In this study, we used assignment methods to characterize dispersal patterns in the marbled murrelet (*Brachyramphus marmoratus*), a small diving seabird in the family Alcidae, that nests in old-growth forests along the Pacific coast of North America. Harvesting of the murrelet's commercially-valuable nesting habitat throughout its range has resulted in a number of geographically isolated populations and was the primary reason the murrelet was listed as a threatened species under the U.S. Endangered Species Act. In particular, the central California population at the southern periphery of the murrelet's range is now isolated from the next closest significant population (in northern California) by several hundred kilometers with little nesting habitat and few murrelets occurring in the intervening area (Raphael 2006).

Murrelets are monogamous with breeding seasons that can range from as early as April to as late as October, depending on latitude. Individuals undergo a flightless, pre-basic molt after breeding, with peak molting periods occurring in August, September, and October (Carter & Stein 1995; Peery *et al.* 2008b). Post-breeding dispersal can occur either before or after the pre-basic molt, and often involves movements on the order of several hundred kilometers based on radiotelemetry, at-sea surveys, and anecdotal banding information (Agler *et al.* 1998; Beauchamp *et al.* 1999; Peery *et al.* 2008b; Hébért & Golightly 2009). Indirect measures of dispersal using genetic and demographic analyses suggest that central California may represent a sink population sustained by immigration from northern populations (Peery *et al.* 2006, 2008a), but more direct methods of quantifying dispersal into this population are needed.

Characterizing dispersal patterns using assignment methods is impractical throughout most of the murrelet's range because populations from northern California to central Alaska (northern populations) have little to no genetic structure (Friesen *et al.* 2005; Piatt *et al.* 2007). However, the central California population is genetically distinct from the northern populations which may make it possible to employ assignment methods to identify migrants in this region. Still, the utility of assignments tests for central California is questionable because the level of divergence between central California and northern populations ($F_{ST} \sim 0.03$; Friesen *et al.* 2005; Piatt *et al.* 2007) is less than what is generally accepted for accurate identification of migrants (Paetkau *et al.* 2004). Moreover, the number of migrants available for sampling in the central California population, which averaged 572 individuals from 1999 to 2003 (range = 487–641), is expected to be small under drift-migration equilibrium conditions. Therefore, our objectives were to evaluate the feasibility of using assignment methods to identify migrants and test for seasonal-, age-, and sex-biases in dispersal for this population. Addressing the latter objective increases our understanding of murrelet life history, provides managers with needed information on seasonal changes in distribution and movements, and increases our understanding of the level of connectivity among murrelet populations. We demonstrate that under non-equilibrium conditions, assignment methods can be used to characterize dispersal patterns in

reasonably large and only moderately differentiated populations.

Methods

Sampling

Blood or tissue samples from 589 marbled murrelets were collected from southeast Alaska to central California between 1997 and 2007 (Fig. 1). We sampled 306 murrelets from five locations in the northern populations including southeast Alaska, British Columbia, Washington, Oregon, and northern California, and sampled 271 murrelets in central California from April to October (rectangular symbols in Fig. 1), when most birds remain near nesting areas (Peery *et al.* 2008b). We sampled an additional 12 murrelets in California from November through March to assess seasonal changes in dispersal patterns (oval symbols in Fig. 1); no samples were collected in northern populations during this period. Blood samples were collected from live birds (n = 562) captured at night from an inflatable vessel using a night-lighting/dip-netting technique (Whitworth *et al.* 1997). Liver or muscle tissue samples (n = 24) were opportunistically collected from dead murrelets recovered from beaches, and foot 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 Extraction Kit (Qiagen) following the manufacturer's protocol for animal blood or tissue. Foot tissue samples were soaked in 95% ethanol for 24 h before DNA extraction to remove chemical inhibitors which could interfere with subsequent reactions. DNA was extracted from foot tissue using a modified phenol/chloroform extraction (Sambrook *et al.* 1989). DNA from birds captured in central California was sent to Zoogen for genetic sex determination.

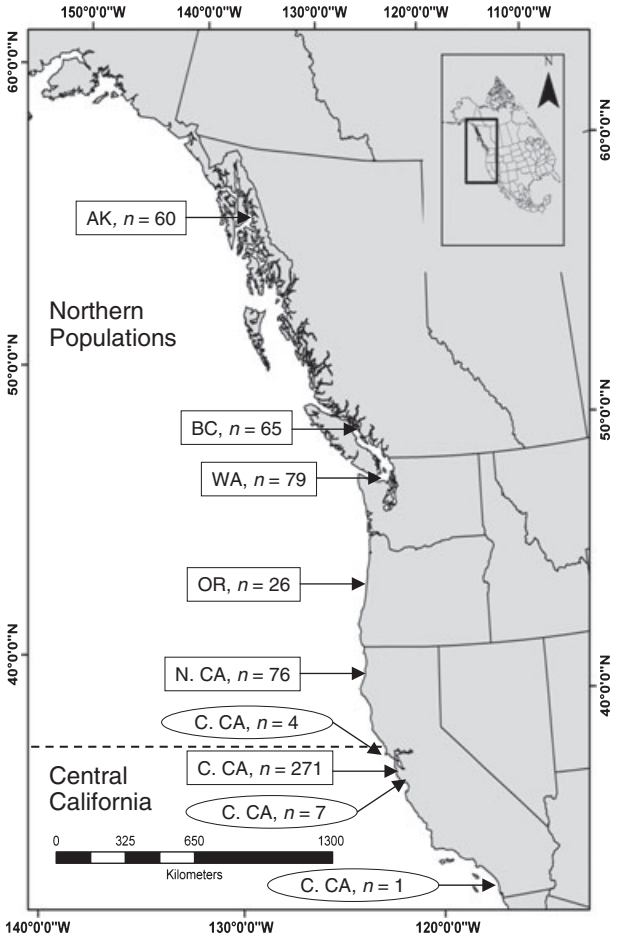

Fig. 1 Map of the Pacific Northwest depicting sampling locations for marbled murrelets (*Brachyramphus marmoratus*) collected in Alaska (AK), British Columbia (BC), Washington (WA), Oregon (OR), northern California (N. CA), and central California (C. CA) from 1997 to 2007. The number of individuals sampled for each population (n) is given. Rectangles outlining sample sizes represent individuals sampled in the breeding and post-breeding seasons (April–July and August–October, respectively), and ovals represent individuals sampled in the winter (November–March).

Laboratory methods

Thirteen tetranucleotide microsatellite markers (ACCT555, GACA456, TATC371, AGGT503, GGAT313, CCAT301, GGAT368, CCAT443, TATC356, GATA365, GATA439, TGAA523, GATA553) developed by Rew *et al.* (2006) were amplified for birds from the northern populations using polymerase chain reaction (PCR). Birds from central California were genotyped using the same 13 microsatellite makers as part of a previous study (Peery *et al.* 2008a). The forward or reverse primer for each microsatellite was labelled with a fluorescent dye (FAM, HEX, PET, or NED; Applied Biosystems) for subsequent electrophoresis and scoring. PCRs were carried out according to the methods described by Peery *et al.* (2008a). Microsatellites were run with LIZ 500 size standard on an ABI3730 sequencer and scored using GeneMapper software (Applied Biosystems).

Characterizing genetic population structure

We estimated observed and expected heterozygosity and tested for deviations from Hardy–Weinberg equilibrium for each locus in each population using exact tests in program Arlequin (Excoffier *et al.* 2006). Deviations from linkage equilibrium were tested for all pairs of loci in program GDA, also using exact tests (Lewis & Zaykin 2001). Pair-wise estimates of genetic distance

between populations were calculated using Wright's (1931) F_{ST}, and 95% confidence levels were calculated using a bootstrapping procedure in program GDA. *P*-values for F_{ST} estimates were calculated using the normal distribution (Zar 1999). The number of genetically distinct populations (K) was estimated using the method of Evanno *et al.* (2005) from simulations run in program Structure v. 2.2 (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.

Identifying migrants and assessing the accuracy of assignments

Migrant individuals were identified using exclusion methods implemented in GENECLASS2 (Piry *et al.* 2004) with Bayesian estimation methods (Rannala & Mountain 1997). We used L_{home}/L_{max} as the criterion to exclude individuals as residents from the population they were sampled (i.e. classify individuals as migrants), where L_{home} was the likelihood of an individual originating from the population it was sampled in, and L_{max} was the likelihood of an individual originating in its most likely population of origin. The probability of an individual originating from the population in which it was captured was calculated by comparing the criterion for the individual to a distribution of criteria generated by Monte Carlo re-sampling of 1000 multi-locus genotypes (Paetkau *et al.* 2004). Individuals with a probability less than the significance (α) level determined by simulations (see below) were excluded from the population they were sampled in and classified as migrants.

The probability of committing type I (falsely classifying a resident as a migrant) and type II (falsely classifying a migrant as a resident) errors depends on a subjectively chosen α level used to determine the statistical significance of the probability of an individual's genotype originating from the population in which it was captured. As α is increased, type I errors are expected to increase, and type II errors are expected to decrease. Therefore, α can be adjusted to minimize the expected number of type I or type II errors, or it can be optimized to make the number of type I and type II errors equal. We attempted to identify an α-value which accurately estimated the number of migrants present in each population and assigned individual birds as residents or migrants with confidence. To do so, we used coalescent simulations to calculate the expected number of type I and type II errors at different α levels. First, 10 sets of multilocus genotypes representing individual birds were generated for two populations in program SIMCOAL (Excoffier *et al.* 2000), with sample sizes approximately equal to the number of individuals sampled in central California and the northern populations ($n = 257$ and 329, respectively). Next, twenty genotypes from the northern populations were moved into the central California population to simulate movements among populations. Exclusions were then performed for the simulated murrelet populations in program GENECLASS2 with the same parameters used to analyze the empirical data. Last, we calculated the number of type I and type II errors at different significance levels ranging from 0.002 to 0.1 for the simulated central California population.

When simulating genotypes, we assumed that microsatellites evolved according to a stepwise mutation model and mutated at a rate of 10^{-5} mutations per locus per generation. Also, we assumed that, 12 generations in the past (approximately 100 years, assuming a generation time of 8 years for marbled murrelets; Peery *et al.* 2010), a small population of $N_e = 100$, representing central California, split from a much larger historic and equilibrium population of $N_e = 367\,500$, representing the northern populations, and that the two populations were unconnected by gene flow ($m = 0$) following the split. This demographic history reflects estimated changes in effective population size and genetic structure among marbled murrelet populations from the genetic analysis of historic and modern samples (Peery *et al.* 2010).

Characterizing dispersal patterns in marbled murrelets

To assess seasonal changes in dispersal patterns, we compared the proportion of migrants detected in central California among breeding, post-breeding, and winter seasons. We defined the 'breeding season' as April through July which encompasses the peak incubation and chick-provisioning period in central California (Peery *et al.* 2008b). We considered August through October to be the 'post-breeding season' because most juveniles fledge and adult murrelets begin their flightless molt during this period. We treated November to March as the 'winter season' because murrelets do not need to attend nest sites, have typically completed molt, and are regularly observed dispersing long distances from nesting areas in central California (Peery *et al.* 2008b).

We determined if dispersal propensity was related to breeding status by comparing the proportion of migrants between murrelets with and without a brood patch present. Brood patches are used to incubate eggs and brood young (McFarlane-Tranquilla *et al.* 2003) and were used as an indicator of breeding status because it was not logistically possible to assess whether all sampled individuals actually initiated nesting. We excluded birds captured during the post-breeding and winter

seasons from this analysis because the re-feathering of brood patches likely occurs soon after brooding is complete.

We tested for sex- and age-biased dispersal in central California by comparing the proportion of male and female migrants and the proportion of migrants in different age classes, respectively. For the age-class comparison, we classified murrelets in central California as hatch-year (0-year old), second-year (1-year old), and after-second-year (≥2-years old) based on plumage characteristics (Beissinger & Peery 2007; Carter & Stein 1995). Discriminating between second- and after-second-year individuals was only possible in central California in 2002 and 2003; in all other years individuals were classified as either hatch-year or after-hatch-year (≥1-year old) birds. The sample size of the younger age classes was small because of low reproductive success in this population (Peery *et al.* 2004, 2007), so hatch-year (classified in 1997–2003) and second-year (classified in 2002–2003) individuals were pooled for comparison with after-second-year (classified in 2002–2003) and after-hatch-year (classified in 1997–2001) murrelets. Assuming that age structure was similar between murrelets sampled in 1997–2001 and 2002–2003 (when 6 of 45 sampled murrelets were second-year individuals), approximately 13% of murrelets sampled in 1997–2001 were second-year individuals. However, the presence of these second-year individuals in the older age class would have yielded a conservative test of the hypothesis that dispersal is biased towards young birds.

Finally, we compared the reproductive contribution of resident and migrant murrelets to the central California population by comparing the number of resident and migrant individuals that had a parent or an offspring present in this population. Pairs of individuals that shared an allele at all loci were considered to be related as parent-offspring pairs. For this analysis, we excluded birds sampled during the winter season and used an additional three microsatellite loci genotyped by Peery *et al.* (2008a; TATC453, GATA464, and GATA465). Simulation analyses indicated that the number of false parent-offspring pairs expected with these 16 microsatellites was low (<10% of all matches were expected to involve individuals not related as parents and offspring) for central California, even in the presence of full siblings (Peery *et al.* 2008a). All statistical comparisons between groups (e.g. males vs. females) were conducted using chi-square tests corrected with a Yates correction factor (Zar 1999).

Results

Mean observed heterozygosity (0.764–0.843) and mean expected heterozygosity (0.779–0.816) across loci were very similar in the six regions (Table 1). Of the thirteen loci tested for each of the six regions (78 locus by population combinations), only four loci deviated from expectations under Hardy–Weinberg equilibrium after conducting a sequential Bonferroni correction for multiple comparisons (Tables 1 and S1). Similarly, for all populations, few (18 of 468) pairwise combinations of loci showed significant linkage disequilibrium after applying a sequential Bonferroni correction.

Table 1 Expected and observed mean heterozygosity across 13 microsatellite loci for six marbled murrelet (*Brachyramphus marmoratus*) populations

Population	Mean observed heterozygosity	Mean expected heterozygosity
Southeast Alaska	0.808	0.813
British Columbia	0.804	0.812
Washington	0.816	0.807
Oregon	0.839	0.816
Northern California	0.843	0.811
Central California	0.764	0.779
All populations	0.812	0.806

Two genetic populations were identified using program Structure ($K = 2$). The first population largely included murrelets sampled from the northern populations and the second largely included birds from the central California population (Fig. 2). F_{ST} values for pairs of marbled murrelet populations ranged from 0 to 0.038 (Table 2), with a global F_{ST} of 0.025 (95% CL: 0.018–0.032). Pairwise comparisons between each of the northern populations and central California had statistically greater genetic differentiation (mean = 0.034, SD = 0.002; Table 2) than pairwise comparisons between individual northern populations (mean = .005, SD = 0.003; Table 2). Two comparisons within the northern populations had F_{ST} estimates that were

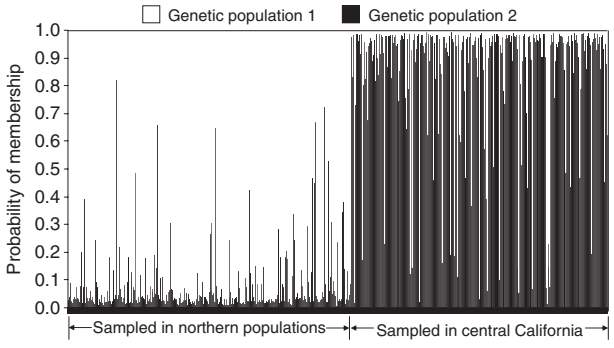

Fig. 2 Population assignment probabilities for marbled murrelets (*Brachyramphus marmoratus*) sampled from southeast Alaska to central California generated by Structure. Birds were assigned to two distinct genetic populations, shown in black and white.

Table 2 Pairwise F_{ST} estimates, with 95% CL in parentheses, based on 13 microsatellite loci (lower diagonal) and *P*-values for F_{ST} estimates, with approximate distance (in km) between sampling locations in parentheses, (upper diagonal) for six marbled murrelet (*Brachyramphus marmoratus*) populations

	Southeast Alaska	British Columbia	Washington	Oregon	Northern California	Central California
Southeast Alaska		0.115 (1147)	0.361 (1291)	0.082 (1631)	**0.001** (2033)	**<0.001** (2474)
British Columbia	0.002 (−0.001–0.006)		0.136 (149)	0.028 (533)	0.039 (958)	**<0.001** (1378)
Washington	0.001 (−0.002–0.003)	0.001 (−0.001–0.003)		0.049 (390)	**<0.001** (815)	**0.001** (1231)
Oregon	0.006 (−0.001–0.015)	0.003 (0.001–0.006)	0.007 (0.001–0.015)		0.201 (426)	**<0.001** (851)
Northern California	0.007 (0.003–0.012)	0.006 (0.001–0.013)	0.008 (0.004–0.013)	0.004 (−0.002–0.013)		**<0.001** (442)
Central California	0.033 (0.021–0.046)	0.032 (0.022–0.043)	0.038 (0.022–0.055)	0.034 (0.024–0.045)	0.032 (0.025–0.040)	

Statistically significant *P*-values, using $\alpha = 0.05$ with a sequential Bonferroni correction, are in bold.

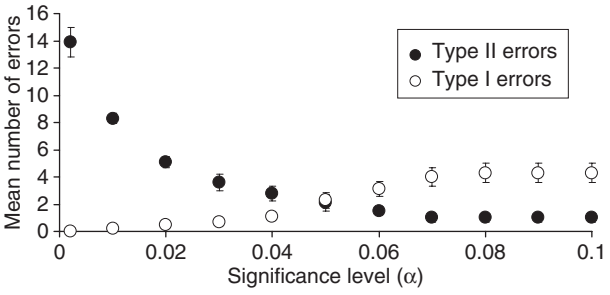

Fig. 3 Mean number of type I (open circles) and type II (solid circles) errors in population assignments made in GENECLASS2 for 10 simulated populations ($n = 277$ birds per population) of marbled murrelets (*Brachyramphus marmoratus*).

statistically significant. However, F_{ST} estimates between northern populations were considerably lower than those involving central California and we therefore did not attempt to identify migrants among the northern populations.

The expected number of type I errors increased and type II errors decreased for central California with increasing α-values, according to exclusions conducted for simulated populations (Fig. 3). An α-value of 0.05 yielded a low and approximately equal number of type I (2.3) and type II (2.1) errors (Fig. 3). Thus, an α-value of 0.05 seemed reasonable for exclusions intended to identify migrants and quantify dispersal for murrelets in central California, even though others have recommended using more stringent significance (α) levels (Paetkau *et al*. 2004).

Using this significance level, a greater proportion of murrelets sampled in central California between April and October were classified as migrants (0.07; 19 of 271) than were murrelets sampled in the northern populations during the same time period (<0.01; 2 of 306; $\chi^2_{0.05,\ 1} = 16.3$; $P < 0.001$). Because of the small number of migrants in the northern populations, we only conducted analyses of dispersal patterns for murrelets sampled in central California.

The proportion of migrants in central California during the winter season (0.83, 10 of 12) was significantly greater than during the breeding and post-breeding seasons collectively ($\chi^2_{0.05,\ 1} = 38.54$; $P < 0.001$). The latter were pooled because the proportion of migrants was not significantly different (breeding season = 0.06, 6 of 101; post-breeding season = 0.08, 13 of 169; $\chi^2_{0.05,\ 1} = 0.30$; $P = 0.582$; Fig. 4a.). Five murrelets were sampled during the winter in at-sea areas not in immediate proximity to nesting habitat. Four of these birds, sampled 40 km north of San Francisco Bay, were assigned to the northern populations even though they were sampled closer to breeding habitat in central California (100 km) than in northern California (approximately 300 km; Fig. 5). A single juvenile murrelet recovered in San Diego, California, approximately 500 and 900 km south of breeding habitat in central and northern California, respectively, was assigned to the northern populations as well. In addition, a greater proportion of females were classified as migrants (0.14, 18 of 127) than males (0.06, 9 of 152; $\chi^2_{0.05,\ 1} = 5.42$; $P = 0.020$; Fig. 4b). A significantly greater proportion of young birds (0.45, 5 of 11) were classified as migrants than were older birds (0.08, 22 of 260; $\chi^2_{0.05,\ 1} = 16.10$; $P < 0.001$; Fig. 4c), but the proportion of migrants did not differ statistically between birds with (0.04, 2 of 56) and without a brood patch (0.09, 3 of 33; $\chi^2_{0.05,\ 1} = 0.38$; $P = 0.538$; Fig. 4d). Finally, a significantly lower proportion of murrelets involved in parent-offspring pairs were classified as migrants (0.02, 2 of 116) than murrelets that were not a member of parent-offspring pairs (0.11, 17 of 154; $\chi^2_{0.05,\ 1} = 8.78$, $P = 0.003$; Fig. 4e). Based on individuals

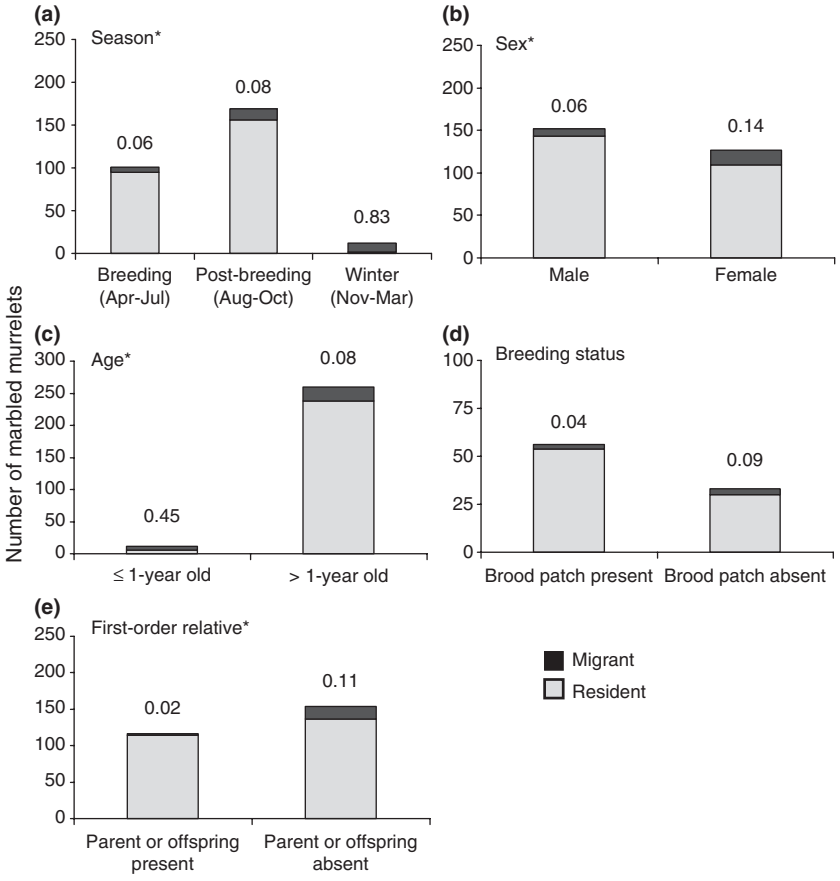

Fig. 4 The number of marbled murrelets (*Brachyramphus marmoratus*), captured in central California, assigned as migrants (black) and residents (grey) by (a) season, (b) sex, (c) age class [the ≤1-year age class includes hatch- (from 1997–2003) and second-year (from 2002–2003) birds, and the >1-year age class includes after-hatch- (from 1997–2001) and after-second-year (from 2002–2003) birds], (d) breeding status [assessed by presence or absence of a brood patch], and (e) whether the individual had a parent or offspring present in the sample. 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 according to chi square tests are indicated by an asterisk.

sampled in the breeding and post-breeding seasons, the proportion of migrants ranged from 0.02 in 1999 to 0.12 in 2002, and according to linear regression analysis, increased significantly by 1.4% per year from 1997 to 2003 ($F_{1,5} = 2.87$, $P = 0.039$, $R^2 = 0.61$; Fig. 6).

Discussion

Consistent with previous genetic studies of marbled murrelets (Friesen *et al.* 2005; Piatt *et al.* 2007), we detected a moderate amount of genetic population structure between central California and northern populations (mean $F_{ST} = 0.034$, SD = 0.002), and very little to no genetic structure among northern populations. Only a small number of individuals were expected to be of migrant origin in central California based on the estimated level of divergence. Assuming that this population was in drift-migration equilibrium, and using $F_{ST} = 1/(1 + 4N_em)$ with an effective population size of 155 (Peery *et al.* 2010), approximately seven effective migrants (N_em) were expected to enter into the central California population per generation. However, given that 7% of murrelets captured in central California between April and October were identified as migrants, an estimated 40 migrants (0.07×572) occurred in the population. This population was clearly not in drift-migration equilibrium and contained an excess of migrants. Moreover, a greater than expected number of migrants allowed us to sample enough migrant individuals to make meaningful comparisons between groups of individuals (e.g. sexes and age classes). Below we show that this excess was likely due to the presence of migrants that did not contribute offspring to the population, including young birds, seasonal migrants, and migrants whose breeding attempts were unsuccessful.

Accuracy of assignments

Coalescent simulations indicated that we were able to detect migrants with reasonable confidence, even though genetic structure was less than what is generally accepted for the rigorous application of assignment methods. Specifically, exclusions conducted using simulated populations predicted approximately two type I and two type II errors in central California when $\alpha = 0.05$. The low type I error rate predicted by simulated data was supported by the detection of only two

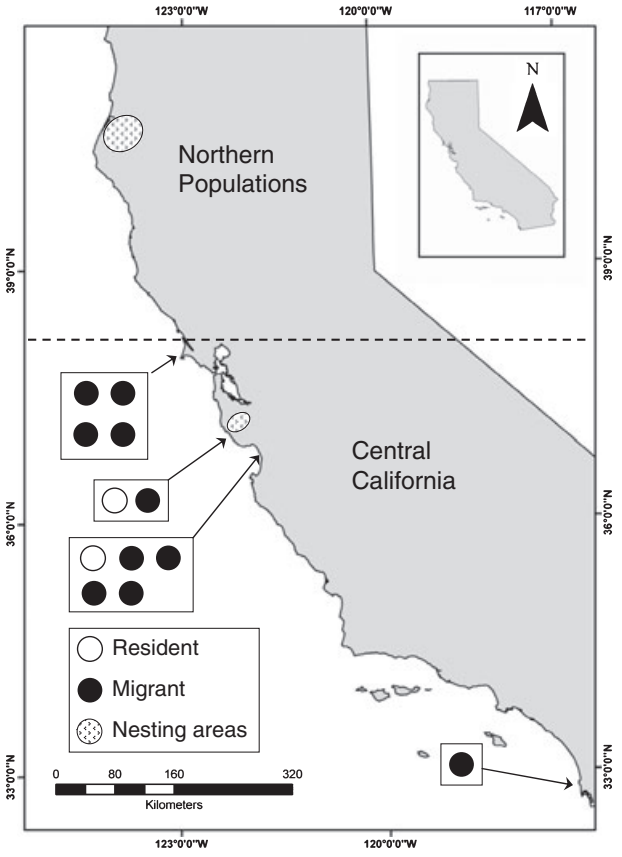

Fig. 5 Locations of migrant (solid circles) and resident (open circles) marbled murrelets (*Brachyramphus marmoratus*), in relation to nesting areas (shaded ovals), sampled in California during the winter season (November to March). Each circle represents an individual bird, with arrows indicating the locations where birds were sampled.

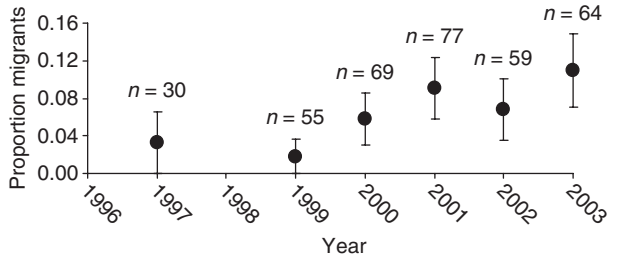

Fig. 6 Proportion of migrant marbled murrelets (*Brachyramphus marmoratus*), identified by genetic population assignments, observed in central California from 1997 and 1999–2003. Sample sizes for each year are shown above each proportion.

central California migrants in the northern populations. These two migrants were most likely type I errors because the northern population is approximately three orders of magnitude greater in size than the central California population (Peery *et al.* 2006; Raphael 2006; Piatt *et al.* 2007), and the probability of sampling migrants from central California in the northern populations was extremely low. Indeed, even if 50 migrants were present in the northern populations totaling 250 000 individuals, the probability of sampling two migrants with a sample size of 306 individuals was <1%. [Note that the current estimate of population size in the northern populations is less than the long-term effective population size estimated from the variance in repeat number (367 500) likely because of a large decline in murrelets in Alaska over the past few years (Piatt *et al.* 2007)]. Thus, the type I error rate for the northern populations can also be estimated by dividing the number of likely type I errors (two) by the total number of sampled individuals (306), or 0.007. A type I error rate of this magnitude would translate to 2.0 type I errors in central California (given a sample size of 283), which is similar to the number of errors predicted by the simulated data (2.3). Moreover, the estimated proportion of migrants in central California was probably reasonably unbiased because the expected number of type I and II errors were approximately equal.

Estimates of type I error rates from simulated datasets and the number of individuals classified as migrants in northern populations were well below the expected error rate of 0.05. F_1 individuals (the offspring of a migrant and a resident) are the most likely source of type I errors because half of their genes are of migrant origin, even though they are considered residents of the population from which they were sampled (Paetkau *et al.* 2004). But few, if any, F_1 individuals were likely present in central California because migrants appeared to produce very few offspring in the region based on the low number of migrants that were members of a parent-offspring pair. Thus, the presence of few individuals of mixed ancestry in the central California population likely resulted in a lower than expected number of type I errors. In addition, Paetkau *et al.* (2004) estimated type I error rates assuming that 10 populations exchanged migrants and thus assignment to any one of nine populations would lead to a type I error. In contrast, we only assigned individual murrelets to one of two potential source populations and only a single population could yield a type I error.

Our estimates of statistical power to detect migrants from simulated datasets were also optimistic relative to previous studies. For example, Paetkau *et al.* (2004) predicted that power to identify migrants was always ≤0.5 for 5–20 loci when F_{ST} <0.040 [Fig. 6 in Paetkau *et al.* (2004)], whereas we estimated power (calculated from simulations as the number of correctly assigned migrants divided by the total number of migrants) to be ~0.90 with 13 loci when F_{ST} = 0.034. One significant difference between our study and previous studies was the

large sample size of genotyped individuals (283 in central California and 306 in the northern populations) compared to previous simulation studies [e.g. 50 individuals per population in Paetkau *et al.* (2004)]. Moreover, our choice of a significance level ($\alpha = 0.05$) was considerably more liberal than the significance level ($\alpha = 0.002$) that Paetkau *et al.* (2004) used to assess the effect of population differentiation on power of assignments, and power can increase by a factor of four when α is increased from 0.002 to 0.05 (Paetkau *et al.* 2004; Fig. 3). We suspect that the absence of individuals with mixed ancestry allowed us to use a relatively liberal significance (α) level without appreciably increasing the number of type I errors, which in turn resulted in an increased power to detect migrants in central California in spite of the moderate population structure observed between central California and the northern populations.

Our results indicate that an understanding of demographic history and the extent to which dispersal among populations results in gene flow and influences genetic divergence is required to estimate the rate of type I and II errors for population assignments. Similar information will not be available for many less studied species and the relatively low error rates estimated here cannot necessarily be generalized. However, an excess of migrants and non-equilibrium conditions could certainly occur for species displaced by habitat loss or expanding in range. Moreover, the parent-offspring approach provides a convenient method for assessing the reproductive contribution of migrant individuals without necessarily requiring the long-term monitoring of individual breeding histories.

Dispersal patterns in marbled murrelets

The proportion of migrants in central California was more than 10 times greater during the winter (0.83), when birds were no longer constrained to attend nest sites and had completed their flightless molt than during the breeding and post-breeding seasons (0.06 and 0.08 respectively; Fig. 4a). These results support previous telemetry, banding, and survey-based studies which indicate that murrelets generally remain adjacent to nesting areas during the breeding season, but tend to make longer-distance (>100 km) movements away from nesting habitats after the breeding season (Agler *et al.* 1998; Beauchamp *et al.* 1999; Peery *et al.* 2008b). No murrelets out of a sample of 102 individuals radio-marked in northern California were detected dispersing into central California (Hébért & Golightly 2009), but murrelets were only tracked until August, before most individuals make long-distance dispersal movements (Peery *et al.* 2008b). Though most wintering murrelets sampled in central California were migrants, we suspect that a relatively small proportion of the combined northern populations winters in central California because the northern populations number in the hundreds of thousands (Piatt *et al.* 2007), and murrelet abundance does not appear to increase dramatically in central California during the winter (Henkel, 2004; Peery *et al.* 2008b). However, the northern California population is relatively small (numbering ~5000 individuals), and being the most likely source of dispersers based on proximity, could certainly be impacted by anthropogenic factors in central California such as oil spills during the winter.

Under the assumption that northern California was the source of migrants detected in central California, the minimum dispersal distances we observed ranged from approximately 300 to 900 km across individuals (Fig. 5). The larger of these distances is similar to maximum dispersal distances observed in murrelets radio-marked in northern California (724 km; Hébért & Golightly 2009), but was almost three times greater than distances recorded for murrelets radio-marked in central California (318 km; Peery *et al.* 2008b). Of course, dispersal distance could be much greater than the minimum estimates presented here if migrants in central California dispersed from regions north of northern California.

Dispersal in birds is generally female-biased (Greenwood 1980; Clarke *et al.* 1997), but our study is among the first to demonstrate female-biased dispersal in a seabird (but see also Ainley *et al.* 1990; Pietz & Parmelee 1994). Female-biased dispersal may have evolved as a mechanism to avoid inbreeding and competition for resources and mates (Perrin & Mazalov 2000). Our results also indicate that dispersal among murrelet populations is biased towards young birds, a pattern that is consistent with greater natal than breeding dispersal distances and stronger breeding than natal site fidelity observed in seabirds (Frederiksen & Petersen 2000). A noteworthy example involves a second-year murrelet that was assigned to the northern populations and recovered in San Diego (southern California), approximately 500 km south of the typical non-breeding distribution for this species and at least 900 km south of the closest of the northern populations (Fig. 5). Divoky & Horton (1995) suggested that natal dispersal may be especially high for marbled murrelets because (1) their non-breeding distribution is large and exposes birds to prospective breeding areas, (2) murrelets can assess potential breeding habitat by visiting nesting areas year round (Naslund 1993), and (3) the pre-breeding stage is long enough [2–5 years; Beissinger (1995)] for birds to disperse and assess breeding areas before recruitment.

The composition of the central California marbled murrelet population appears to be a mixture of three

categories of individuals: residents, migrants that have recruited into the resident breeding population, and temporary migrants from the northern populations. At least some migrants attempt to breed in central California, because telemetry data for a single radio-tagged migrant indicated that this bird attempted to nest in central California, but was unsuccessful (Peery *et al.* 2004). Still other migrants are likely to be temporary visitors because, on average, resident murrelets were recaptured in central California over longer time periods than migrants (LAH unpublished data). The relative proportion of recruiting and temporary migrants is difficult to assess and would require long-term radio-tracking of a large number of migrants, even though >100 murrelets were radio-tagged in previous studies (Peery *et al.* 2004, 2008b).

The annual increase in the proportion of migrants in central California may have been due to ongoing loss of nesting habitat in the northern populations that caused murrelets to disperse and prospect for new breeding sites (Divoky & Horton 1995). Indeed, 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 northern California from 1994 to 2004. Some northern populations are also experiencing high rates of nest failure due to nest predation (Raphael *et al.* 2002), and individuals with repeated nest failures may disperse to new habitats. To the extent that habitat loss and nest predation continue in northern populations, the number of migrants entering central California may continue to increase. Understanding the effects of the dispersal of individuals with limited recruitment into the population is critical for designing conservation plans and interpreting results from murrelet monitoring programs [see Peery *et al.* (2010) for a detailed discussion of this subject].

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Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Observed heterozygosity, expected heterozygosity, and *P*-values associated with exact tests for deviation from expected heterozygosity under Hardy–Weinberg equilibrium. Statistically significant tests, using $\alpha = 0.05$, after applying a sequential Bonferroni correction for multiple comparisons are in bold.

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