

CHARACTERIZING SOURCE-SINK DYNAMICS WITH GENETIC PARENTAGE ASSIGNMENTS

M. ZACHARIAH PEERY,^{1,2,3,6} STEVEN R. BEISSINGER,¹ ROGER F. HOUSE,⁴ MARTINE BERUBE^{1,5} LAURIE A. HALL,³
ANNA SELLAS,¹ AND PER J. PALSBJERG^{1,5}

¹*Department of Environmental Science, Policy and Management, 137 Mulford Hall, University of California, Berkeley, California 94720-3114 USA*

²*Museum of Vertebrate Zoology, 3101 Valley Life Sciences Building, University of California, Berkeley, California 94720-3160 USA*

³*Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, California 95039 USA*

⁴*12655 Fiori Lane, Sebastopol, California 95472 USA*

⁵*Department of Genetics, Microbiology and Toxicology, Stockholm University, SE-106 91, Stockholm, Sweden*

Abstract. Source-sink dynamics have been suggested to characterize the population structure of many species, but the prevalence of source-sink systems in nature is uncertain because of inherent challenges in estimating migration rates among populations. Migration rates are often difficult to estimate directly with demographic methods, and indirect genetic methods are subject to a variety of assumptions that are difficult to meet or to apply to evolutionary timescales. Furthermore, such methods cannot be rigorously applied to high-gene-flow species. Here, we employ genetic parentage assignments in conjunction with demographic simulations to infer the level of immigration into a putative sink population. We use individual-based demographic models to estimate expected distributions of parent-offspring dyads under competing *sink* and *closed-population* models. By comparing the actual number of parent-offspring dyads (identified from multilocus genetic profiles) in a random sample of individuals taken from a population to expectations under these two contrasting demographic models, it is possible to estimate the rate of immigration and test hypotheses related to the role of immigration on population processes on an ecological timescale. The difference in the expected number of parent-offspring dyads between the two population models was greatest when immigration into the sink population was high, indicating that unlike traditional population genetic inference models, the highest degree of statistical power is achieved for the approach presented here when migration rates are high. We used the proposed genetic parentage approach to demonstrate that a threatened population of Marbled Murrelets (*Brachyramphus marmoratus*) appears to be supplemented by a low level of immigration (~2-6% annually) from other populations.

Key words: *Brachyramphus marmoratus*; *demography*; *immigration*; *Marbled Murrelets*; *microsatellites*; *parentage assignments*; *parent-offspring dyads*; *source-sink dynamics*.

INTRODUCTION

The dynamics of spatially structured populations depend fundamentally on the amount of migration among populations. Populations connected by low rates of migration are more independent demographically than populations exchanging greater numbers of individuals. A variety of frameworks exist for characterizing spatially structured populations, but source-sink theory has become a leading paradigm over the past two decades (Pulliam 1988, Thomas and Kunin 1999). In this framework, source populations are self-supporting populations in high-quality habitats that produce a surplus of individuals that emigrate to other populations (Runge et al. 2006). Sink populations are incapable of maintaining viable population sizes without immigra-

tion of individuals from source populations, presumably because they occur in lower-quality habitats (Pulliam 1988, Thomas and Kunin 1999). As loss and fragmentation of natural habitats continue, understanding the nature and direction of migration among populations becomes increasingly important to guide reserve design and prioritize conservation resources.

Although source-sink dynamics have been suggested to characterize the population structure of many species, such dynamics have rarely been demonstrated convincingly. Identifying source and sink populations requires population-specific estimates of birth and survival rates as well as directional migration rates among populations (Diffendorfer 1998, Johnson 2004, Peery et al. 2006a, Runge et al. 2006). While birth and survival rates can often be measured in the field, estimating immigration and emigration rates with traditional mark-recapture methods is inherently difficult for most species (MacDonald and Johnson 2001). An alternative, indirect demographic approach is to estimate and compare rates

Manuscript received 11 December 2007; revised 11 January 2008; accepted 28 January 2008. Corresponding Editor: R. Greenberg.

⁶ E-mail: zpeery@nature.berkeley.edu

of population growth with immigration (e.g., using time series of population counts) and without immigration (e.g., using stage-based matrix models parameterized only with birth and survival rates) to determine if populations are self-sustaining in the absence of immigration (Kruzer and Huntley 2003, Peery et al. 2006a). This approach, however, requires the comparison of population growth rates estimated from very different methods, each of which is sensitive to the violation of a variety of different assumptions.

Population genetic methods have been widely employed to infer migration rates from the distribution of genetic diversity within and among populations. All other factors being equal, populations exchanging few individuals should be more genetically differentiated than populations exchanging greater numbers of individuals. Population genetic approaches include inferring the effective number of migrants per generation from estimates of Wright's F_{ST} (Wright 1969, Slatkin 1995) or from likelihood methods using a coalescent framework (e.g., Beerli and Felsenstein 2001, Nielsen and Wakeley 2001). However, these methods are based on relatively simplistic demographic models (e.g., that assume genetic-drift equilibrium), yield imprecise estimates when migration rates are high, and, perhaps more importantly, estimate migration on an evolutionary, rather than an ecological timescale (Waples 1988, Bossart and Powell 1998, Whitlock and McCauley 1999, Pearse and Crandall 2004).

Another approach involves estimating the probability of a sampled individual's multilocus genotype originating from each population in a set of potential source populations (Rannala and Mountain 1997, Waser and Strobeck 1998, Cornuet et al. 1999, Pritchard et al. 2000). Wilson and Rannala (2003) extended this approach to estimate migration rates from the migrants and their descendants detected in the genotyped samples. Assignment of individuals to source populations is appealing because estimation is conducted on an ecological timescale, and relaxes assumptions such as genetic drift-migration equilibrium. However, population assignments will generally yield imprecise estimates of migration for undifferentiated or weakly differentiated populations, such as when migration rates are high enough to affect local population dynamics (Wilson and Rannala 2003, Waples and Gaggiotti 2006, Faubet et al. 2007; but see Berry et al. 2004).

Using genetic parentage assignments to estimate immigration and identify sink populations

Palsboll (1999) proposed that migration rates could be quantified with genetic parentage assignments because the number of parent-offspring dyads in a population with overlapping generations is a function of the degree of immigration from other populations vs. the level of self-recruitment, all other factors being equal. Few parent-offspring dyads should be present in populations with a high proportion of recruitment due to immigra-

tion from other populations. In contrast, proportionately more parent-offspring dyads should be present in closed and self-sustaining populations. Parent-offspring dyads can be identified with a high level of certainty provided that a sufficient number of hypervariable genetic loci such as microsatellites are analyzed (Blouin 1996, Palsboll 1999). Telfer et al. (2003) and Waser et al. (2006) recently used genetic parentage assignments to estimate natal dispersal rates and distances for small mammals, but the extent to which distribution of close relatives can be used to quantify the impact of migration on population dynamics has not been evaluated.

In principle, it should be possible to estimate the *expected* distribution of parent-offspring dyads in a random sample of individuals collected from a single population given that population dynamics can be described by an appropriate demographic model. Doing so requires, at minimum, a reasonable understanding of the life history of the species and estimates of relevant population parameters such as abundance and age-specific vital rates. A given hypothesis may then be rejected if the observed number of parent-offspring dyads falls outside the expected distribution of dyads predicted by the hypothesized population model. Such an approach circumvents many of the caveats of the aforementioned genetic methods by allowing inferences under relatively complex population models, relaxing assumptions such as drift-migration equilibrium, and characterizing migration on an ecological rather than an evolutionary timescale (Palsboll 1999). Moreover, a parentage assignment approach for characterizing the effects of migration on local population dynamics only requires that a given individual be sampled in a single population (Palsboll 1999).

In this study, we evaluated the feasibility of estimating immigration and identifying sink populations with genetic parentage assignments. We define a sink population as a population that would decline or go extinct in the absence of immigration. Ours differs in part from previous definitions based on criteria that deaths must exceed births and immigration must exceed emigration (Pulliam 1988). According to our definition, immigration does not necessarily have to be greater than emigration, and a sink population could, for example, exchange an equal number of individuals with other populations, as occurs in "balanced dispersal" systems (McPeck and Holt 1992). However, ours is a commonly employed definition (Thomas and Kunin 1999, Kruzer and Huntley 2003, Holt and Gomulkiewicz 2004), and is often the only practical way to define a sink due to the difficulty of tracking emigrants and estimating emigration rates in open populations (Peery et al. 2006a). Moreover, for many conservation applications, it may not be imperative to distinguish between death and emigration, because the loss of an individual due to either process is just that—a loss to the population.

To characterize the role of immigration on local population dynamics, we developed a stochastic, indi-

vidual-based population model to estimate the expected number of parent-offspring dyads contained in a population or a random sample taken from a population under competing models of population dynamics (PARSIM v1.0; see Appendix and Supplement). We used the model to evaluate how the number of parent-offspring dyads is affected by the demographic characteristics of the population of interest, and to estimate statistical power to detect a sink population. We also determined how many microsatellite loci are required to discern parent-offspring dyads from unrelated individuals and full-sibling dyads unambiguously.

As an example, we apply the genetic parentage approach to test the hypothesis that populations of a threatened seabird, the Marbled Murrelet (*Brachyramphus marmoratus*), can be described by a source-sink model. The Marbled Murrelet lays a single egg in nests located primarily in coastal old-growth forests (Nelson 1997, Baker et al. 2006). Harvesting of old-growth forests is believed to have greatly reduced Marbled Murrelet populations, but other threats include oil spills, gillnetting, declines in prey availability, and increases in nest predators (Peery et al. 2004b, 2006a, Becker and Beissinger 2006, Becker et al. 2007). The central California population contains ~660 individuals (95% CL: 550, 800 individuals) (Peery et al. 2004a, 2006a, 2008), is located at the southern periphery of the species' range, and is isolated from the nearest significant population to the north by several hundred kilometers. This population has been hypothesized to be a sink population that is supplemented by individuals immigrating from larger populations to the north, since local abundance appears to be stable even though birth rates are very low, and because estimates of per capita immigration rates are high (~0.16 annually) based on indirect demographic assessments (Peery et al. 2006a, 2007, Beissinger and Peery 2007).

We adopted a hypothesis-testing framework for characterizing the role of immigration on the central California Marbled Murrelet population, where we defined the *closed-population model* as the null hypothesis (i.e., a demographically closed population that is self-sustaining in the absence of immigration) and the *sink population model* as the alternate hypothesis (i.e., a population that would decline or go extinct in the absence of immigration from other populations). If the number of parent-offspring dyads in a random sample of individuals taken from the population is significantly less than expected based on the closed-population model, we infer that the population is sustained by immigration from other populations.

METHODS

Sensitivity of the number of parent-offspring dyads in a population to demography

We used PARSIM to evaluate how the number of parent-offspring dyads in a population is affected by the demographic characteristics of the population using

Marbled Murrelets as a test case. We parameterized population models with annual, age-specific survival, birth, immigration, and emigration rates that spanned likely values for this species. We conducted four sets of model simulations, in each set manipulating one of the four demographic parameters incrementally while holding the other three parameters constant to determine the effect of each parameter independently. A description of parameter values used is provided in the "Sensitivity analysis" column of Table 1. When modeling the effect of birth rates on the number of parent-offspring dyads in a population we explored two scenarios, one in which the probability of producing an offspring was identical for all mated pairs above the age of first breeding (three years), and one in which expected birth rates varied among pairs (i.e., reproductive skew existed among pairs). For the immigration and emigration parameter sets, we compared two different models for the age structure of migrants to assess how age differences in these processes affected the number of parent-offspring dyads in a population. In the first model, all age classes immigrated or emigrated equally; in the second model, only juveniles (0 year olds) emigrated (all immigrants were one year old when they entered the population).

To make results comparable across simulations with different values for a given demographic rate, ending population sizes must be similar across simulations because more parent-offspring dyads will be present in larger populations. To keep ending population size (i.e., at year 25) reasonably similar among simulations, we manipulated initial population size so that the population size at year 25 fell between 650 and 670 individuals for all simulated parameter values (mean = 660 individuals). For example, a simulation with no emigration had a smaller initial population size than a simulation with the emigration rate set to 0.10. Simulations with different parameter values therefore had different mean population growth rates, but in our experience, population size is the critical parameter that needs to be held constant for comparisons (and estimated well for hypothesis testing), not population growth rate.

For each combination of parameters, we conducted 500 model runs in which the population was projected forward in time for 25 years, because the expected number of parent-offspring dyads generally reaches a plateau within this period (Appendix: Fig. A1). We tabulated the number of individuals and the number of parent-offspring dyads present in the population at the last time step of each model run.

Statistical power to detect a sink population with genetic parentage assignments

The utility of the genetic parentage approach for characterizing migration among populations depends on the level of statistical power that can be achieved to reject the null hypothesis of a closed population. In theory, power should increase as the number of sampled

TABLE 1. Demographic parameters used to estimate the expected number of parent-offspring dyads with 500 model simulations in PARSIM for three different analyses.

Parameter	Sensitivity analysis	Power analysis	Marbled Murrelet sink test
Adult survival rate	0.82, 0.84, 0.86, 0.88 , 0.90, 0.92, 0.94	0.88	0.88
SD for adult survival among simulations	0	0.06	0.06
Juvenile survival	70% of adult survival	0.62	0.62
SD for juvenile survival among simulations	0	0.06	0.06
Birth rate	0.1, 0.25, 0.40, 0.55 , 0.70, 0.85	NA	NA
SD for birth rate among pairs	0 , 0.20	0	0
Immigration rate	0 , 0.02, 0.04, 0.06, 0.08, 0.10	NA	NA
Immigration: birth†	NA	0:0.55, 0.04:0.37, 0.08:0.23, 0.12:0.12, 0.16:0.08	0:0.55, 0.01:0.50, 0.02:0.46, 0.03:0.42, 0.04:0.39, 0.05:0.33, 0.06:0.28, 0.07:0.27
Age classes of immigrants	juveniles only, equal among ages	equal among age classes	juveniles only
Emigration rate	0 , 0.02, 0.04, 0.06, 0.08, 0.10	0	0
Age class of emigrants	juveniles only, equal among ages	NA	NA
Sex ratio	even	even	even
Starting population size	variable so that ending $N = 650-670$	730, 7300	730, 1000
Mean ending population size (range)	660 (650-670)	660 (550-800), 6600 (5500-8000)	660 (550-800), 790-810 (800)
Number of sampled individuals	entire population	50-500 (by increments of 50)	271
Years sampled at end of simulation	1	1	7
Years simulated	25	25	25

Notes: Parameters in boldface type for the "Sensitivity Analysis" indicate default values used when another parameter was manipulated. NA = not applicable.

† The combination of immigration and birth rates used when modeling an approximately stable population over the 25-year modeling period. The immigration rate precedes the colon, and the birth rate follows the colon, so that, for example, 0.04:0.37 indicates that the annual immigration rate was 0.04 and the probability of a pair above the age of first breeding producing an offspring in a given year is 0.37.

individuals increases and as a greater proportion of the population is sampled. Power is likely affected by the proportion of the population that is sampled, because fewer parent-offspring dyads should be detected in a large population than in a small population for a given number of sampled individuals. Power should also increase as the sink population becomes increasingly dependent on immigration from source populations, because relatively few parent-offspring dyads should occur in sink populations receiving large numbers of immigrants compared to expectations under a closed-population model.

To evaluate the effect of the degree of immigration vs. local recruitment on power to detect a sink population, we estimated the expected number of parent-offspring dyads in samples of various sizes taken from populations experiencing annual per capita immigration rates of 0, 0.04, 0.08, 0.12, and 0.16, where zero immigration represented the null hypothesis of a closed population. Birth rates were adjusted so that the expected population growth rate was approximately zero in all cases (see "Power analysis" column in Table 1 for a complete

description of parameters used in these models). Power to detect a population sink was estimated by determining the proportion of sink-model runs that had fewer parent-offspring dyads than 95% of the closed-model runs (i.e., a critical value of 0.05). Hypothesis tests were one-tailed because the alternate hypothesis of interest was that fewer parent-offspring dyads occur in a sink than a stable population and, in theory, it is not possible to detect more dyads than occur in a closed population.

An important consideration for estimating distributions of the expected number of parent-offspring dyads involves taking into account uncertainty in demographic estimates used to parameterize population models. We incorporated this uncertainty by allowing ending population sizes and mean demographic rates that were not varied incrementally (as birth and immigration rates were) to vary stochastically across model runs. Specifically, we accounted for uncertainty in field-based estimates of survival by allowing survival rates to vary randomly around their respective means with a standard deviation of 0.06 (Peery et al. 2006b). To account for uncertainty in population size, we considered all model

runs with ending population sizes between 550 and 800 individuals for simulations with an expected ending population size of 660 individuals (Peery et al. 2006a). Similarly, we considered all model runs with ending population sizes between 5500 and 8000 individuals for simulations with an expected ending population size of 6600 individuals. Although simulated populations could grow or decline within these bounds, the expected population growth rate was stable.

Identifying parent-offspring dyads with genetic parentage exclusions

Parent-offspring dyads can be identified with a low level of uncertainty given that a sufficient number of polymorphic, Mendelian-inherited loci such as microsatellites are genotyped for each sampled individual, because parents and their offspring share at least one allele at all loci (barring the presence of null-alleles, allelic dropout, genotyping errors, or novel mutations). Any dyad of individuals not sharing at least one allele at one or more loci can be excluded as a potential parent-offspring dyad, unless allele sharing was the result of genotyping error. However, reliable identification of parent-offspring dyads requires that sufficient loci are sampled so that unrelated pairs of individuals do not share an allele at all loci purely by chance; the more loci sampled, the lower the probability of a "false positive." The level of polymorphism at 30 microsatellite loci developed for Marbled Murrelets by Rew et al. (2006) was used to estimate the number of loci required to identify parent-offspring dyads with low uncertainty among a sample of 300 individuals. In doing so, we assume the level of polymorphism detected in 15 individuals genotyped by Rew et al. (2006) was characteristic of the amount of genetic variation found in the entire population.

We estimated the probability of excluding a pair of unrelated individuals as a potential parent-offspring dyad (exclusion probability or P_E) by randomly bootstrapping alleles from the Marbled Murrelet genotype data in Rew et al. (2006). We generated six multilocus genotype data sets each containing 10000 pairs of unrelated individuals, where the number of loci in the six data sets ranged from 5 to 30, by increments of five. The least variable loci (i.e., highest probability of identity [Paetkau et al. 1995]) were always excluded so that, for example, the data set with 15 loci included only the 15 most variable loci. P_E was estimated as the proportion of the 10000 pairs that did not share at least one allele at all loci. We also estimated the expected number of false positives in a sample of 300 individual murrelets by multiplying $1 - P_E$ by 44850 (the number of pairwise comparisons among 300 individuals).

In the above simulations, all individuals were generated under the assumption that they were all unrelated. However, related individuals, particularly full siblings, have a higher probability of sharing at least one allele at all loci than unrelated individuals, and thus have a

greater probability of being incorrectly identified as a parent-offspring dyad. If significant numbers of full siblings are present in the sample, the simulations described above will yield overly optimistic estimates of the number of loci required to exclude pairs of individuals not related as parents and offspring. To assess the effect of full sibling dyads on the number of false positives, we estimated P_E for a pair of siblings by generating 10 000 pairs of sibling genotypes. For each full sibling dyad, we first randomly generated two parental genotypes from the original genotype data using the bootstrapping procedure just described. Genotypes for the two full siblings were then generated by randomly sampling one allele from each parent at each locus. We then estimated the expected number of false positives in a sample of 300 individuals (taken from a population of 660) that contained 62 full-sibling dyads (the expected number in a sample of 300 murrelets assuming a closed population; see the following section) by adding the product of the sibling P_E multiplied by 62 to the product of the unrelated P_E multiplied by 44 788 (the total number of pairwise comparisons between unrelated individuals). As with the simulations for unrelated individuals, these calculations were repeated for 5-30 locus genotypes, by increments of five loci.

Estimating immigration and testing the sink population hypothesis/or Marbled Murrelets

To test the sink hypothesis for Marbled Murrelets in central California, we captured and blood-sampled 271 individuals of all ages for subsequent genetic analysis over a seven-year period, 1997-2003. These individuals represent a subset of individuals used by Peery et al. (2006a, b) to demonstrate that central California was a sink population using demographic methods. Sampled murrelets were genotyped at 16 of the most polymorphic, tetra-nucleotide microsatellite loci (Table 2) developed by Rew et al. (2006) according to methods described therein. Parameters used to estimate expected frequency distributions for the number of parent-offspring dyads under both closed- and sink population models with varying levels of immigration are provided in the "Marbled Murrelet sink test" column in Table 1. In a first set of simulations, we considered only model runs with ending population sizes between 550 and 800 individuals (mean = 660 individuals) to account for uncertainty in population size (Peery et al. 2006a). In a second set of simulations, we only considered model runs with ending population sizes between 790 and 810 individuals (mean = 800 individuals), which reflects the approximate upper 95% CL for the estimated population size in the region, to provide a conservative test of the sink hypothesis. For both sets of simulations, we sampled individuals across the last 7 years of the 25 projected years to reflect the temporal distribution of field sampling.

Robust comparisons of expected and observed numbers of parent-offspring dyads assumes that null

TABLE 2. Sixteen microsatellite loci (Rew et al. 2006) genotyped for 271 Marbled Murrelets in central California, USA.

Locus	<i>n</i>	<i>K</i>	<i>H_o</i>	<i>H_e</i>	<i>P</i>
ACCT555	271	13	0.839	0.867	0.028
AGGT503	271	7	0.463	0.472	0.316
CCAT301	271	7	0.799	0.793	0.650
CCAT443	271	12	0.777	0.765	0.752
GACA456	271	4	0.702	0.707	0.390
GATA365	271	8	0.791	0.781	0.704
GATA439	271	11	0.842	0.825	0.844
GATA464†	148	6	0.493	0.561	0.011
GATA465†	148	23	0.892	0.902	0.320
GATA553	271	11	0.744	0.767	0.104
GGAT313‡	271	5	0.643	0.744	<0.001
GGAT368	271	21	0.876	0.909	0.011
TATC356	271	13	0.835	0.833	0.507
TATC371	271	14	0.835	0.849	0.145
TATC453	271	23	0.883	0.882	0.551
TGAA523	271	9	0.769	0.791	0.098

Notes: Variables are defined as follows: *K* = number of alleles; *n* = number of individuals; *H_o* = observed heterozygosity; *H_e* = expected heterozygosity; and *P* = probability that *H_o* < *H_e*. Boldface type indicates tests that were significant after applying Bonferroni's sequential correction (Holm 1979).

† Sex-linked, only males considered.

‡ Only three dyads that were excluded as potential parent-offspring dyads with GGAT313 had individuals that were not heterozygous at this locus, indicating that the effects of null alleles and allelic dropout were small.

alleles, allelic dropout, and laboratory/genotyping errors did not appreciably bias the observed number of dyads (Dakin and Avise 2004). Therefore, ~50% of the samples were re-extracted and reamplified at 10 loci to identify and correct errors. Then a subsample of 24 individuals was re-extracted and polymerase chain reactions were re-run for 10 loci to estimate genotyping error rates. We then evaluated the potential effects of errors on the estimated number of parent-offspring dyads by randomly generating errors in the 271 multi-locus genotypes, where the probability of mistyping a given allele at a given locus was set to 0.01, 0.02, and 0.03 in three separate analyses. For each level of genotyping error, we randomly generated 500 sets of 271 genotypes with bootstrapping and estimated the mean number of parent-offspring dyads across data sets for comparison with the actual number of parent-offspring dyads identified.

RESULTS

Effect of demography on the number of parent-offspring dyads

Based on simulation analyses, there were 704 parent-offspring dyads (mean, with 95% CL: 663, 745 dyads) in a closed, stable population numbering 660 individuals. Our sensitivity analysis indicated that the number of parent-offspring dyads declined when immigration increased for both the juvenile-only and age-constant models (Fig. 1a). The rate of decline in the number of parent-offspring dyads was slightly greater when only juveniles immigrated than when all age classes immigrated equally. Similarly, the number of parent-offspring dyads declined as emigration increased, and the

rate of decline was greater when only juveniles emigrated (Fig. 1b). The number of parent-offspring dyads increased rapidly with increasing birth rates, but the rate of increase declined at high birth rates (Fig. 1c). The number of parent-offspring pairs was identical when reproductive skew was incorporated in the model, compared to when all pairs had an equal probability of producing an offspring (results not presented in Fig. 1c because of the complete overlap of symbols). The number of parent-offspring dyads also increased with annual survival, but the effect was much less pronounced and the increase did not plateau at high survival rates (Fig. 1d). Thus, our simulations confirmed that fewer parent-offspring dyads are present in open populations (e.g., a sink population) compared to closed populations, as might be expected.

Sample size and statistical power to detect sink populations

The number of parent-offspring dyads detected in a sample of individuals taken from a population increases with sample size and decreases with population size (Fig. 2), such that significantly greater sample sizes are required to sample a similar number of dyads in large compared to small populations (Fig. 2). The mean expected number of parent-offspring dyads in a sample of 100 individuals taken from a population was greater under the closed model than the sink population model, and the difference increased with the rate of immigration into the population (Fig. 3). Thus, statistical power to reject the null hypothesis of a closed population (i.e., to detect a sink population) increased as both the immigration rate and the sample size of genotyped individuals increased (Fig. 4a). For a population of 660

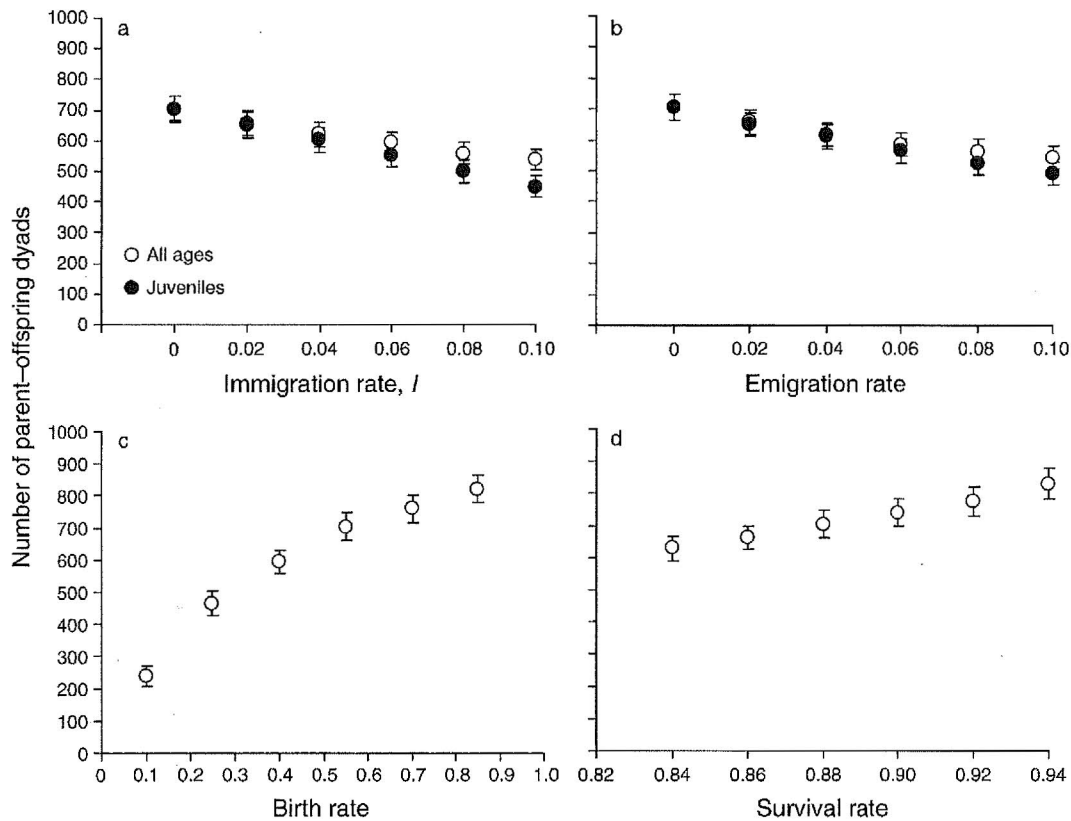


FIG. 1. Expected number of parent-offspring dyads in a population as a function of (a) immigration, (b) emigration, (c) birth, and (d) survival rates, based on 500 simulations in PARSIM. Other parameters used to estimate the expected number of parent-offspring dyads are given in the "Sensitivity Analysis" column in Table 1. Values are means with 95% CI.

individuals, power to reject the null hypothesis when the immigration rate equaled 0.04 was low with smaller sample sizes; to achieve a power of 80%, ~300 individuals (corresponding to 45% of the population) needed to be sampled. However, at higher immigration rates (0.08-0.12), power to reject the null hypothesis was >80% with sample sizes as low as 100 individuals. Statistical power approached 1.0 when 150 individuals were sampled from a population of 660 at these immigration rates. However, for a population of 6600 individuals experiencing an annual immigration rate of 0.08, power to reject the null hypothesis was zero until

150 individuals were sampled, indicating that power was sensitive to the proportion of the population sampled in addition to the absolute sample size. Three hundred individuals needed to be sampled to achieve a power >80% (Fig. 4b) in such a large population.

Identifying parent-offspring dyads with microsatellites

P_E for unrelated dyads was 0.986 when five loci were sampled (i.e., a 1.4% chance of incorrectly considering a dyad of unrelated individuals as a parent-offspring dyad). P_E was positively correlated with the number of loci and was >0.999 for 30 loci (Fig. 5a). Even though

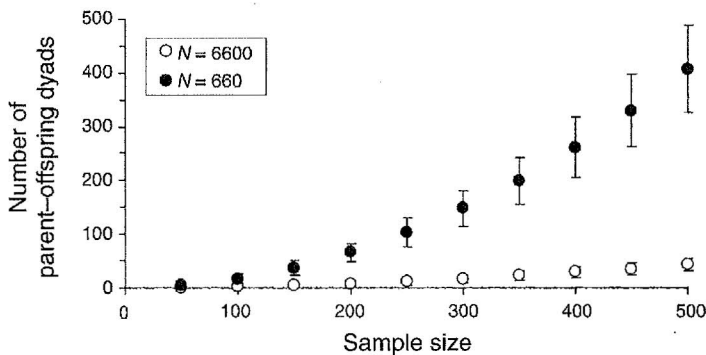


FIG. 2. Expected number of parent-offspring dyads in a sample of individuals taken from closed populations of 6600 and 660 individuals, as a function of sample size. Other parameters used to estimate the expected number of parent-offspring dyads are given in the "Power analysis" column in Table 1. Values are means with 95% CI.

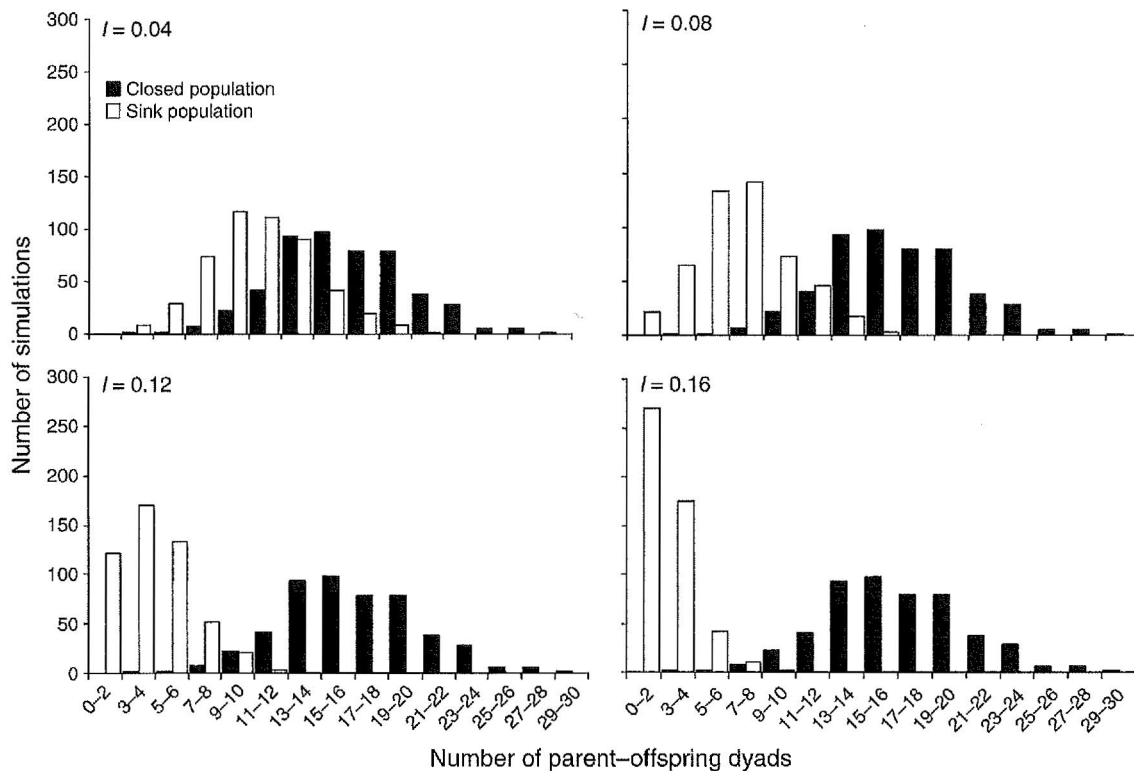


FIG. 3. Expected number of parent-offspring dyads in a sample of 100 individuals taken from a sink vs. a closed population of 660 individuals under varying levels of immigration (I), based on 500 simulations in PARSIM. Other parameters used to estimate the expected number of parent-offspring dyads are given in the “Power analysis” column in Table 1.

the probability of erroneously identifying a dyad of unrelated individuals as a parent-offspring dyad was low when five loci were sampled, the expected number of false positives in a sample of 300 individuals was high (614) due to the large number of possible pairwise comparisons (in this case 44 850). However, the expected number of false positives declined rapidly as the number of loci increased and was estimated to be less than one dyad when 20 loci were sampled (Fig. 5b).

P_E for full-sibling dyads was much lower than for dyads of unrelated individuals (0.540 for five loci). The probability increased as more loci were sampled and appeared to approach an asymptote around 0.896 at 20 loci, reaching 0.933 at 30 loci (Fig. 5a). Estimating the number of false positives depends on this probability as well as the number of sibling dyads in the sample. The number of sibling dyads increases with sample size, is greater in closed populations than populations experiencing immigration, and unlike the number of parent-offspring dyads, is slightly greater when skew in reproductive success exists among mated pairs, based on simulations in PARSIM (Table 3). For example, there were 62 sibling pairs in a sample of 300 individuals taken from a closed population of 660 when all pairs had an equal probability of producing young, and 67 sibling pairs when the standard deviation in the probability of producing an offspring was set to 0.20

(Table 3). There were 28 expected false positives due to the presence of 62 full siblings in a sample of 300 individuals when five loci were sampled, resulting in a total of 642 false positives. The total expected number of false positives declined to 7 (6 from full-sibling dyads) at 20 loci, where a point of diminishing returns was reached; sampling 30 loci only reduced the expected number of false positives to 5 (Fig. 5b).

Testing the sink population hypothesis for Marbled Murrelets

Seventy-seven pairs of individuals in our sample of 271 murrelets shared at least one allele at all loci and were treated as potential parent-offspring dyads. Based on the level of polymorphism detected at the 16 micro satellite loci, we estimated that six false positives occurred between unrelated individuals (in 36542 dyads), and one false positive occurred due to the presence of an estimated 43 full-sibling pairs, resulting in a total estimate of seven false positives. After subtracting the expected number of false positives from the number of potential parent-offspring dyads detected in our sample (77), we estimated that we sampled 70 true parent-offspring dyads.

An estimated 70 dyads was well below the lower 95% CL for the expected number of parent-offspring dyads in a sample of 271 individuals under the closed-

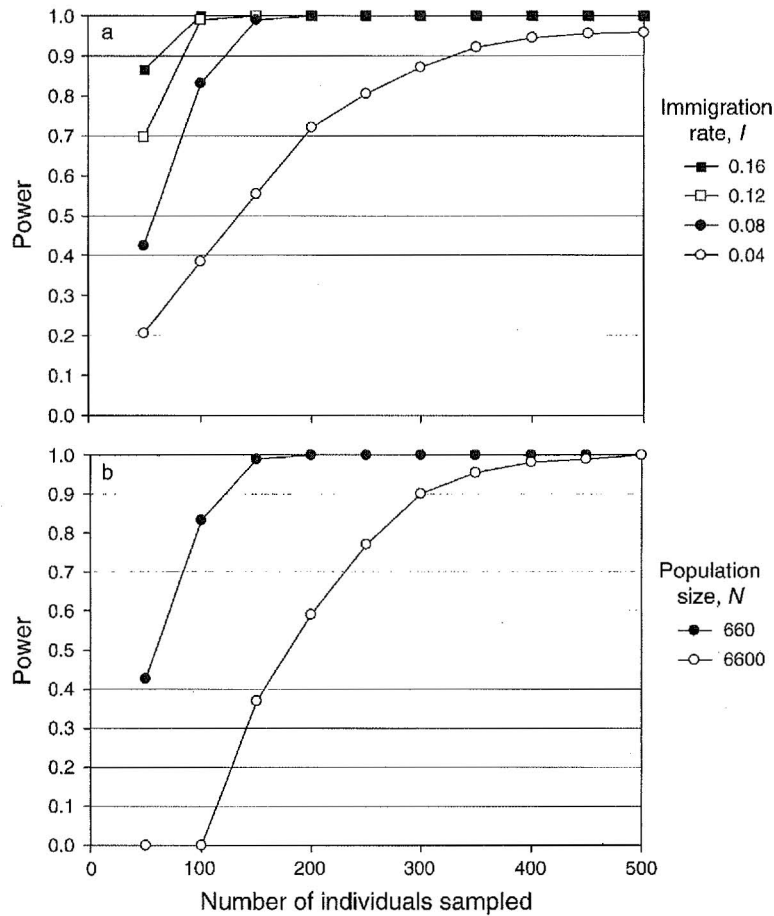


FIG. 4. Effect of sample size (number of individuals) on power to detect a sink population with genetic parentage assignments (a) at four different annual per capita immigration rates for a population of 660 individuals and (b) when annual per capita immigration rates were 0.08 and population size was 660 and 6600 individuals. Other parameters used to estimate the expected number of parent-offspring dyads are given in the "Power analysis" column in Table 1.

population model (mean = 116 dyads, 95% CI = 94-140 dyads) (Fig. 6), resulting in the rejection of the null hypothesis of no immigration (i.e., support for the sink-population hypothesis). The estimated number of parent-offspring dyads fell within the 95% CL for sink populations characterized by 4, 5, and 6% annual immigration, but did not fall within the 95% CL for populations with <4% or >6% annual immigration (Fig. 6). Accordingly, our results suggest that some immigration occurs, most likely at the rate of 4-6% per year, given a population size of 550 to 800 individuals.

The expected number of parent-offspring dyads in a sample of a given size is lower for large populations (Fig. 2), and the incorrect rejection of the null hypothesis could have occurred if the population was larger than estimated. Therefore, we estimated the expected number of parent-offspring dyads for a population of 800 individuals, which represents the upper 95% CL for the murrelet population in central California (Peery et al. 2006a). The lower 95% CL for number of parent-offspring dyads expected for a closed population

decreased when the population was assumed to number 800 individuals and tests of the sink hypothesis became more conservative (Fig. 6). However, we detected fewer parent-offspring dyads (70) than the lower 95% CL estimated (78) for a closed population of 800 individuals (Fig. 6). The estimated number of parent-offspring dyads fell within the 95% CL for sink populations characterized by 2, 3, 4, and 5% annual immigration, but did not fall within the 95% CL for populations with <2% or >5% annual immigration (Fig. 6). Thus, if the population abundance was as high as 800, the appropriate conclusion would be that immigration occurs at a rate between 2% and 5% per year.

The 24 individuals we used to assess of the consistency of genotyping had identical genotypes in the original and test samples, indicating that allelic dropout and laboratory/allele-calling errors were low [<1 error/(24 samples \times 10 loci) = 0.4%]. A previous accuracy assessment in our laboratory yielded an error rate of 0.1% per locus for humpback whales based on comparisons of microsatellite genotypes and identity

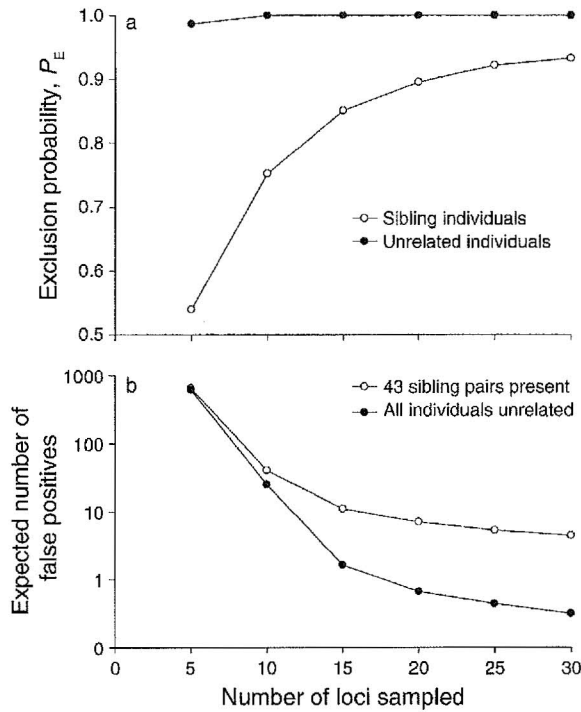


FIG. 5. (a) Probability of excluding a pair of individuals as a parent-offspring dyad as a function of the number of microsatellite loci sampled and (b) the expected number of false positives in a sample of 300 individuals.

determined with fluke photographs (Palsboll et al. 1997). Null alleles were probably not a significant source of error, because, with the exception of GGAT313, all loci conformed to Hardy-Wienberg equilibrium expectations after applying Bonferonni's corrections for multiple comparisons (Holm 1979; Table 2). Three dyads were excluded as potential parent-offspring dyads with only BmaGGA T313 and involved homozygous individuals. These dyads could have been related as parent and offspring, but this number is small compared to the difference in the number of dyads detected and the expected number of dyads under a closed-population model (Fig. 6). Based on simulation analyses, genotype errors reduced the number of parent-offspring dyads from 77 to 65, 54, and 45 assuming 1, 2, and 3% error

rates per locus, respectively. Although no large, multi-locus data set such as ours is likely to be completely free of genotype errors, we consider our error rate near or below the lower limit of the simulated range, and believe that tests of the sink hypothesis and estimates of immigration were reasonably robust to errors in genotypes.

DISCUSSION

We have demonstrated that the expected number of parent-offspring dyads present in a population is a function of the demographic characteristics of the population, and is greatest in populations that do not exchange individuals with other populations. Thus, hypotheses regarding the magnitude of migration can be tested by estimating the number of parent-offspring dyads contained in a random sample of individuals using genetic methods and comparing the observed number of dyads to the expected number of dyads under competing models of population dynamics. Because the parentage approach is based on identifying parents and their offspring, it quantifies migration that occurred only during recent generations in contrast to an evolutionary mean, as is the case with most estimates based upon more traditional population genetic methods. Moreover, unlike traditional population genetic methods, statistical power to detect a sink population with parentage assignments increases with the level of immigration (all other factors being equal). The estimated migration rate (2-6% per annum) for Marbled Murrelets in this study translates to $\sim 26-79$ effective migrants per generation, assuming an effective population size to census population size ratio of 0.25 and a generation time of 8 years (M. Z. Peery, unpublished data). Estimating this level of migration with traditional genetic methods would likely be problematic, requiring that a prohibitively large number of loci be sampled. Thus, genetic identification of parentage promises to provide a valuable tool for characterizing levels of connectivity among populations on contemporary time-scales, even when migration is high. The combined use of traditional demographic and genetic estimators with the spatiotemporal distribution of close relatives identified by genetic analyses could result in more compre-

TABLE 3. Number of parent-offspring and full-sibling dyads (mean, with 95% CL in parentheses) in a sample of n individuals taken from a population of 660 individuals as estimated with simulations in program PARSIM.

N	Annual per capita immigration = 0				Annual per capita immigration = 0.08			
	Full-sibling dyads		Parent-offspring dyads		Full-sibling dyads		Parent-offspring dyads	
	No skew	Skew	No skew	Skew	No skew	Skew	No skew	Skew
100	7 (1, 12)	7 (2, 13)	17 (9, 24)	16 (9, 24)	1 (0, 3)	2 (0, 4)	8 (2, 13)	8 (2, 18)
300	62 (42, 82)	67 (46, 88)	148 (128, 168)	148 (128, 168)	11 (4, 18)	14 (5, 23)	70 (53, 86)	70 (51, 89)
500	172 (140, 203)	183 (147, 220)	408 (376, 441)	409 (378, 441)	31 (19, 43)	42 (25, 58)	194 (167, 221)	197 (166, 228)

Notes: The number of parent-offspring and sibling pairs was estimated assuming zero vs. 0.08 annual per capita immigration and assuming skew and no skew in reproductive success among mated pairs. The standard deviation in the probability of a pair producing an offspring was set to 0.20 when estimating the number of parent-offspring and sibling pairs in the presence of reproductive skew (mean = 0.55). See "Power analysis" column in Table 1 for a complete list of parameters.

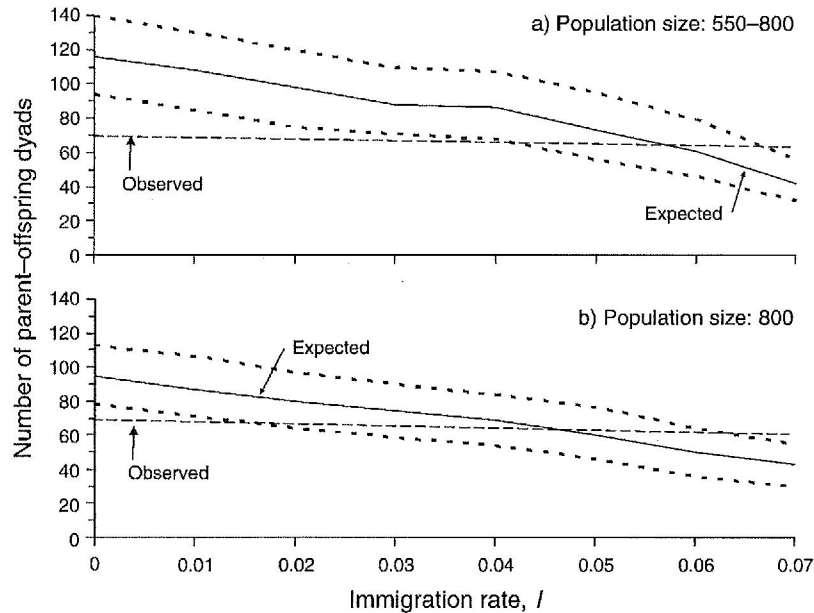


FIG. 6. Expected mean (solid line) with 95% CI (thick dashed lines) and observed (thin dashed line) number of parent-offspring dyads in the central California Marbled Murrelet population in a sample of 271 individuals as a function of immigration. Population size of 550–800 individuals indicates that ending population sizes for simulations implemented in PARSIM were allowed to vary between 550 and 800 to reflect uncertainty in actual population size. Population size of 800 indicates that only simulated populations with an ending size of 800 (790–810 to reduce computation times) were used to estimate the expected number of parent-offspring dyads. Other parameters used to estimate the expected number of parent-offspring dyads are given in the “Marbled Murrelet sink test” column in Table 1.

hensive insight into the dynamics of many structured populations.

Model assumptions and uncertainty

Characterizing migration with genetic parentage assignments assumes that appropriate population models are used to estimate expected frequency distributions of the number of parent-offspring dyads. Constructing such models requires estimates of population size, age-specific vital rates, and a basic understanding of the life history of the species of interest. If population models do not adequately reflect population dynamics, statistical tests based on the number of parent-offspring dyads in the population may be misleading. For example, if population size is underestimated, fewer parent-offspring dyads will likely be sampled from the population than expected, and the probability of rejecting a true null hypothesis of a closed population is greater than the critical value.

In practice, robust estimates for all required population parameters may not be available. However, uncertainty can be taken into account when constructing competing population models and estimating expected numbers of parent-offspring dyads in a couple of different ways. First, sampling error associated with estimated demographic rates and population size can be taken into account by allowing rates and population size to vary stochastically among model runs according to estimated sampling variances (Appendix). Second,

uncertainties in, for example, the age structure of immigrants and emigrants, can be taken into account by using the expected frequency distribution of parent-offspring dyads that yields the most conservative test of the closed-population hypothesis. For Marbled Murrelets, it would be more appropriate (and yield a more conservative test) to estimate the expected number of parent-offspring dyads assuming that only juveniles emigrated, because the number of parent-offspring dyads with this model was lower than when emigration was constant among ages.

Drawing robust inferences requires that parents and their offspring be sampled randomly. Biased estimates could result in a number of ways, including, for example, the preferential sampling of breeders, which would result in an overestimation of the number of parent-offspring dyads and an underestimation of immigration. The parentage approach also assumes that the sampling of offspring is independent of the sampling of their parents. For species with extended parental care, investigators may be more likely to sample recently born juveniles when the parent is also sampled. The lack of independence will result in more parent-offspring dyads present in the sample than predicted by an appropriate population model, and could reduce the probability of rejecting a false null hypothesis of a closed population, unless the sampling design is incorporated in the estimation of the null distribution for the number of parent-offspring dyads. A potential means of circum-

venting such biases is to limit sampling to nonjuvenile age classes or to exclude juveniles captured with their parents from analyses.

Sample size considerations

We have shown that high statistical power (>80%) to distinguish among population models may be achieved with the genetic parentage approach, but doing so may require genotyping a large number of individuals at many loci and sampling a significant proportion of the population of interest. For the population models considered here, ~250 out of a population of 660 individuals needed to be sampled to reliably detect 4% annual immigration rates, and 100 individuals to detect >8% annual immigration rates. Increased sampling will be necessary for larger populations because the probability of sampling both members of a parent-offspring dyad is reduced. For example, power to detect a sink population with 660 individuals characterized by 8% annual per capita immigration with a sample of 100 individuals was 84%, but 250-300 individuals needed to be sampled from a population of 6600 to achieve similar levels of statistical power.

Approximately 15-20 micro satellite loci were needed to identify parent-offspring dyads with sufficiently low error rates given the level of polymorphism in our example, a number of loci greater than that used in many studies of genetic population structure. Even with 15-20 loci, we expected that ~ 10 dyads from a sample of 300 individuals would share at least one allele at all loci purely by chance and be incorrectly classified as parent-offspring dyads. However, this number is relatively small compared to the difference in the expected number of parent-offspring dyads between a sink population experiencing a 16% immigration rate (a mean of 23 dyads; 95% CL: 13,34 dyads) and a closed population (a mean of 147 dyads; 95% CL: 120, 176 dyads). The estimated number of false positives can be subtracted from the number of dyads identified with genetic assignments to take into account the effect of false positives on hypothesis tests. Doing so requires an estimate of the number of sibling pairs in the sample" which is affected to a certain extent by the level of reproductive skew. We suspect that the significant sampling effort required for the effective use of parentage assignments will often be worthwhile, particularly when threatened or harvested species are involved, high migration rates have homogenized population structure, or contemporary migration rates are of interest.

Incorporating effects of emigration on the number of parent-offspring dyads

Like immigration, emigration results in a deficit in the number of parent-offspring dyads relative to expectations under a closed-population model (Fig. 1). How inference is made regarding the relative importance of immigration and emigration depends in a subtle way on

how survival is estimated for the population of interest and used to estimate the expected number of parent-offspring dyads under the null hypothesis of a closed population. Typically, estimates of survival rates from, for example, mark-recapture studies, represent "local" survival rates (i.e., the probability of surviving and remaining in the population), and can be expressed as the "true" survival rate minus the emigration rate (Nichols et al. 2000). Therefore, when local survival rates are used to estimate the expected number of parent-offspring dyads in a population, the effect of emigration is incorporated implicitly. In such cases, it will only be possible to test hypotheses germane to the role of immigration on populations with genetic parentage assignments; the rate of emigrants leaving the population is unknown and emigration is not testable.

If estimates of true survival rates are used to estimate the expected number of dyads, hypotheses relevant to the combined roles of immigration and emigration can be tested. However, the relative importance of the two processes will not be distinguishable because immigration and emigration have similar effects on the number of parent-offspring dyads in a population (Fig. 1). Thus, a significant deficit from the number of parent-offspring dyads expected in a demographically closed population would indicate that immigration and/or emigration are occurring and that the population is demographically open, but provide no insight into the direction of migration. An a priori expectation regarding the direction of migration based on, for example, habitat quality or population size (e.g., small populations in low-quality habitats may be more likely to receive immigrants than produce emigrants), would facilitate the interpretation of significant results in this case.

Implications for the dynamics and genetic structure of Marbled Murrelet populations

Our genetic parentage analysis indicated that (1) fewer parent-offspring dyads were present in the central California Marbled Murrelet population than expected if no immigration occurred, and (2) the number of parent-offspring dyads in our sample was consistent with a per capita immigration rate of 2-5% or 4-6% per year, depending on assumptions regarding population size. Thus, our results support the hypothesis that murrelets in central California represent a sink population, as suggested by earlier demographic work (Peery et al. 2006a). However, the annual migration rate was considerably lower than estimated by Peery (16% per year [2006a]) and we detected a significant number of parent-offspring dyads (70 in a sample of 271), suggesting that local reproduction composes a greater proportion of total recruitment than previously assumed.

The immigration rate detected with the parentage approach here needs to be reconciled with the significant genetic structure detected between the central California

population and larger Marbled Murrelet populations to the north (Friesen et al. 2005, Piatt et al. 2007). One possibility is that the genetic parentage approach and previous demographic analyses estimate the migration of individuals, whereas indirect genetic methods characterize the movement of genes into a population. Population structure could persist despite movement of individuals among populations if immigrants are selected against or do not permanently recruit into the population. Radio-marked murrelets regularly disperse several hundred kilometers to the north and to the south from breeding habitat in central California (Peery et al. 2008). Some of these birds are recaptured back in central California in subsequent years, suggesting that long-distance movements represent temporary, postbreeding dispersal movements (M. Z. Peery, unpublished data). Movements by individuals among genetically differentiated populations have been reported in Great Frigatebirds (*Fregata minor*; Dearborn et al. 2003) as well as grand skinks (*Oligosoma grande*; Berry et al. 2004). Regardless, the relatively low immigration we estimated (2-6%) compared to our previous demographic work suggests that immigration may be too low to maintain a stable population indefinitely, given that the death rate far exceeds the birth rate (Peery et al. 2006a, Beissinger and Peery 2007). This is especially true if immigration represents temporary dispersal that only masks local population declines and does not augment the breeding population. Thus, it would be unwise to assume that the population will persist in the absence of measures taken to increase local reproductive success and survival rates.

Future directions

Our application involved a single population, but the genetic parentage approach could be adapted to detect migration between pairs of populations based on the number of parent-offspring dyads split between populations. High migration rates will result in a relatively large number of split parent-offspring dyads, whereas low migration rates will generate fewer split dyads (Palsboll 1999). However, additional information, such as the age of dispersal and the relative ages of individuals in split parent-offspring dyads, will be needed to identify the dispersing individual and determine the direction of the dispersal event in applications involving multiple populations (Telfer et al. 2003). Other possible developments for the parentage approach could involve incorporating information from more distantly related dyads (e.g., half and full siblings [Palsboll 1999]), and the development of analytical estimators for the expected number of parent-offspring dyads.

ACKNOWLEDGMENTS

This research was funded by the Pacific Lumber Company, the University of California at Berkeley, Moss Landing Marine Laboratories, a Budweiser Conservation Scholarship to M. Z. Peery, the U.S. Fish and Wildlife Service (Sacramento and Arcata Field Offices), the Washington Department of Fish and Wildlife, the American Museum of Natural History, the

California Department of Fish and Game, the Oiled Wildlife Care Network (U.C. Davis), and the U.S. Coast Guard. We appreciate helpful comments on earlier drafts of this paper by R. Waples, M. Raphael, S. Courtney, and an anonymous reviewer. We also thank J. Baldwin for invaluable modeling and statistical advice. Finally, we are grateful to C. Moritz, J. Geller, and L. Smith for providing access to the molecular laboratory facilities at the Museum of Vertebrate Zoology at U.C. Berkeley and Moss Landing Marine Laboratories.

LITERATURE CITED

- Baker, L. M., M. Z. Peery, S. R. Beissinger, E. E. Burkett, S. W. Singer, and D. L. Suddjian. 2006. Nesting habitat characteristics of Marbled Murrelets in central California redwood forests. *Journal of Wildlife Management* 70:939-946.
- Becker, B. R., and S. R. Beissinger. 2006. Centennial decline in the trophic level of an endangered seabird after fisheries collapse. *Conservation Biology* 20:470-479.
- Becker, B. R., M. Z. Peery, and S. R. Beissinger. 2007. Ocean climate and prey availability affect the trophic level and reproductive success of the Marbled Murrelet, an endangered seabird. *Marine Ecology Progress Series* 329:267-279.
- Beerli, P., and J. Felsenstein. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in *n* subpopulations by using a coalescent approach. *Proceedings of the National Academy of Sciences (USA)* 98:4563-4568.
- Beissinger, S. R., and M. Z. Peery. 2007. Reconstructing the historical demography of an endangered seabird. *Ecology* 88:296-305.
- Berry, O., M. D. Toucher, and S. D. Sarre. 2004. Can assignment tests measure dispersal? *Molecular Ecology* 13:551-561.
- Blouin, M. S., M. Parsons, V. La Caille, and S. Lotz. 1996. Use of microsatellite loci to classify individuals by relatedness. *Molecular Ecology* 5:393-401.
- Bossart, J. L., and D. P. Powell. 1998. Genetic estimates of population structure and gene flow: limitations, lessons, and new directions. *Trends in Ecology and Evolution* 13:202-206.
- 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.
- Dakin, E. E., and J. C. Avise. 2004. Microsatellite null alleles in parentage analysis. *Heredity* 93:504-509.
- Dearborn, D. C., A. D. Anders, E. A. Schreiber, R. M. M. Adams, and U. Muellers. 2003. Inter-island movements and population differentiation in a pelagic seabird. *Molecular Ecology* 12:2835-2843.
- Diffendorfer, J. E. 1998. Testing models of source-sink dynamics and balanced dispersal. *Oikos* 81:417-433.
- 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.
- Friesen, V. J., T. P. Birt, J. F. Piatt, R. T. Golightly, S. H. Newman, P. N. Hebert, B. C. Congdon, and G. Gissing. 2005. Population genetic structure and conservation of marbled murrelets (*Brachyramphus marmoratus*). *Conservation Genetics* 6:607-614.
- Holm, S. 1979. A simple sequential rejective multiple test procedure. *Scandinavian Journal of Statistics* 6:65-70.
- Holt, R. D., and R. Gomulkiewicz. 2004. Conservation implications of niche conservatism and evolution in heterogeneous environments. Pages 244-264 in R. Ferriere, U. Dieckmann, and D. Couvet, editors. *Evolutionary conservation biology*. Cambridge University Press, Cambridge, UK.
- Johnson, D. M. 2004. Source-sink dynamics in a temporally heterogeneous environment. *Ecology* 85:2037-2045.

- Kruzel, M. P., and N. J. Huntly. 2003. Habitat-specific demography: evidence for source-sink population structure in a mammal, the pika. *Oecologia* 134:343-349.
- MacDonald, D. W., and D. P. Johnson. 2001. Dispersal in theory and practice: consequences for conservation biology. Pages 358-372 in J. Clobert, E. Danchi, A. A. Dhondt, and J. D. Nichols, editors. *Dispersal*. Oxford University Press, Oxford, UK.
- McPeck, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* 140:1010-1027.
- Nelson, S. K. 1997. Marbled Murrelet. Pages 1-25 in F. Poole and A. Gill, editors. *Birds of North America*, No. 276. Academy of Natural Sciences of Philadelphia and the American Ornithologists' Union, Washington, D.C., USA.
- Nichols, J. D., J. E. Hines, J.-D. Lebreton, and R. Pradel. 2000. Estimation of contributions of a reverse-time capture-recapture approach. *Ecology* 81:3362-3376.
- Nielsen, R., and J. Wakeley. 2001. Distinguishing migration from isolation: a Markov chain Monte Carlo approach. *Genetics* 158:885-896.
- Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4:347-354.
- Palsbell, P. J. 1999. Genetic tagging: contemporary molecular ecology. *Biological Journal of the Linnean Society* 68:3-22.
- Palsbell, P. J., et al. 1997. Genetic tagging of humpback whales. *Nature* 388:767-769.
- Pearse, D. E., and K. A. Crandall. 2004. Beyond F_{ST} : analysis of population genetic data for conservation. *Conservation Genetics* 5:585-602.
- 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., B. H. Becker, and S. R. Beissinger. 2007. Age ratios as estimators of productivity: testing assumptions on a threatened seabird, the Marbled Murrelet (*Brachyramphus marmoratus*). *Auk* 124:224-240.
- 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 radio-tagging. *Journal of Wildlife Management* 70:78-88.
- 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. 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. Henkel, S. H. Newman, B. H. Becker, J. T. Harvey, C. Thompson, and S. R. Beissinger. 2008. Effects of rapid flight-feather molt on post-breeding dispersal in a pursuit-diving seabird. *Auk* 125:113-123.
- Piatt, J. F., K. J. 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 Open-File Report 2006-1387.
- Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155:945-959.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- Rannala, B., and J. L. Mountain. 1997. Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences (USA)* 94:9197-9201.
- Rew, M. B., M. Z. Peery, S. R. Beissinger, M. Berube, J. D. Lozier, E. M. Rubidge, and P. J. Palsbell. 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.
- Runge, J. P., M. C. Runge, and J. D. Nichols. 2006. The role of local population within a landscape context: defining and classifying sources and sinks. *American Naturalist* 167:925-938.
- Slatkin, M. 1995. A measure of population subdivision based on microsatellite allele frequencies. *Genetics* 139:457-462.
- Telfer, S., S. B. Pierny, J. D. Dallas, W. A. Stewart, F. Marshall, J. L. Gow, and X. Lambin. 2003. Parentage assignment detects frequent and large-scale dispersal in water voles. *Molecular Ecology* 12:1939-1949.
- Thomas, C. D., and W. E. Kunin. 1999. The spatial structure of populations. *Journal of Animal Ecology* 68:647-657.
- Waples, R. S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *Journal of Heredity* 89:438-450.
- Waples, R., and O. Gaggiotti. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology* 15:1419-1439.
- Waser, P. M., J. D. Busch, C. R. McCormick, and J. A. DeWoody. 2006. Parentage analysis detects cryptic precapture dispersal in a philopatric rodent. *Molecular Ecology* 15:1929-1937.
- Waser, P. M., and C. Strobeck. 1998. Genetic signatures of interpopulation dispersal. *Trends in Ecology and Evolution* 13:43-44.
- Whitlock, M. C., and D. E. McCauley. 1999. Indirect measures of gene flow and migration: F_{ST} not equal to $1/(4Nm+1)$. *Heredity* 82:117-125.
- Wilson, G. A., and B. Rannala. 2003. Bayesian inference of recent migration rates using multi locus genotypes. *Genetics* 163:1177-1191.
- Wright, S. 1969. *The theory of gene frequencies*. University of Chicago Press, Chicago, Illinois, USA.

APPENDIX

Description of PARSIM v1.0, a program that simulates the expected number of close relatives in a population under different population models (*Ecological Archives* E089-155-A1).

SUPPLEMENT

Executable file for running population models in PARSIM v1.0 (*Ecological Archives* E089-155-S1).