Demographic Assessment of a Marbled Murrelet Population from Capture-Recapture Data

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Abstract: *Population size is a fundamental variable of interest in most conservation programs, as are the demographic processes underlying variation in numbers. The Marbled Murrelet (*Brachyramphus marmoratus*) is a seabird nesting in coastal old-growth forest in North America and is at the heart of a controversy concerning forest management. Despite the urgent need for a careful assessment of the demographic state of populations, the species is so secretive that its life history is poorly known and reliable estimates of the required vital rates are rare or missing. Here we present the first survival estimates obtained through capture-recapture data from a population in British Columbia, Canada. This population is in a site that has been heavily logged in the last 50 years and continues to be logged. Survival estimates (0.8289 and 0.9289 based on different samples corresponding to two capture techniques) fell within the range specified for small alcids, indicating that neither mortality nor emigration out of the study area is particularly high in the population. We used capture-recapture data to estimate the realized population growth rate (λ) from 1991 to 2000. $\hat{\lambda}$ was < 1 (0.9851), but the confidence interval was large and included 1 (stationary population). This estimate was obtained using part of the data (the sample with the higher survival rate) to meet the assumptions of the analytical approach. This lambda value might not reflect the growth rate of the overall population but may be specific to the segment of the population that successfully bred. The hypothetical value of λ corresponding to a survival probability of 0.8289 was 0.8593, which suggests that the population may be declining if the local survival rate based on the combined samples is closer to the true value. Because of our low recapture rates and poor precision of estimates, there is still uncertainty regarding the health of this population. Development of field techniques and achievement of higher detection probability should reduce uncertainty in future demographic studies of Marbled Murrelets and allow refined assessment of the conservation status of populations.*

Evaluación Demográfica de una Población de *Brachyrampus Marmoratus* con Datos de Captura-Recaptura

Resumen: *El tamaño poblacional es una variable de interés fundamental para la mayoría de los programas de conservación, así como lo son los procesos demográficos vinculados a cambios de esta variable.* Brachyramphus marmoratus *es una especie de ave marina que anida en bosques maduros costeros de Norte América y que se encuentra en medio de una controversia relacionada con el manejo forestal. A pesar de la urgente necesidad de una evaluación cuidadosa del estado demográfico de las poblaciones, la especie es tan secretiva que se conoce muy poco de su historia de vida y se carece de estimaciones confiables de sus tasas vitales requeridas o son escasas. Aquí presentamos las primeras estimaciones de sobrevivencia obtenidas de datos de captura-recaptura para una población en Columbia Británica, Canadá. Esta población se encuentra en un lugar que ha sido fuertemente talado en los últimos 50 años y que sigue siendo explotado. Las estimaciones de sobrevivencia (0.8289 y 0.9289, según muestras que corresponden a dos técnicas diferentes de captura) se ubicaron dentro del rango especificado para álcidos pequeños, lo que indica que tanto la mortal-*

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idad como la emigración del área de estudio no son especialmente altas para esta población. Utilizamos datos de captura-recaptura para estimar la tasa de crecimiento poblacional realizada (λ) de 1991 a 2000. $\hat{\lambda}$ fue < 1 (0.9851), pero el intervalo de confianza fue grande e incluyó 1 (población estacionaria). Se hizo esta estimación utilizando parte de los datos (la muestra con la mayor tasa de sobrevivencia) para cumplir con los supuestos del tratamiento analítico. Este valor de lambda puede no reflejar la tasa de crecimiento de la población en general pero puede ser específico para el segmento de la población que se reprodujo exitosamente. El valor hipotético de λ que corresponde a una probabilidad de sobrevivencia de 0.8289 fue 0.8593, lo que sugiere que la población puede estar declinando si la tasa de sobrevivencia local, basada en las muestras combinadas, se acerca más al valor real. Dado las bajas tasas de recaptura y la falta de precisión de las estimaciones, aún hay incertidumbre en cuanto a la salud de esta población. El desarrollo de técnicas de campo y una mayor probabilidad de detección reduciría esta incertidumbre en estudios demográficos futuros de Brachyramphus marmoratus y permitiría una evaluación más precisa del estado de conservación de las poblaciones.

Introduction

Population size is a fundamental variable of interest in most conservation programs. One of the main objectives of animal population surveys (Buckland et al. 1993) is to provide information on population trends. Detailed demographic studies are required to address the processes underlying temporal variation in numbers (Yoccoz et al. 1998). Accurate assessment of population trends and vital rates is particularly critical when populations might be threatened and when economic activities must be accounted for in management plans. To avoid controversy about the accuracy and robustness of the conclusions drawn, it is important to use robust approaches to estimating vital rates (Franklin et al. 2000).

The Marbled Murrelet (*Brachyramphus marmoratus*) is a seabird (alcid) found on the Pacific coast of North America. This species nests on large, moss-covered limbs of coastal old-growth trees and is at the heart of a controversy over forest management. Human development, deforestation, modification of the murrelet breeding habitat, and increased risk of mortality at sea associated with gill-net fishing and oil spills may pose threats to the persistence of populations. Despite the urgent need for a careful assessment of the demographic state of Marbled Murrelet populations (Cooke 1999), the species is so secretive that reliable estimates of the required vital rates are rare or missing (Ralph & Long 1995; Beissinger & Nur 1997; Boulanger et al. 1999). The most complete demographic studies have relied partly on allometric approaches and estimates of reproductive rates from different populations (Beissinger 1995; Beissinger & Nur 1997; Boulanger et al. 1999). This is the only possible approach in the absence of field data, but it is impossible to determine whether the combinations chosen are relevant. Parameter values from other species may differ substantially from those of the study population. From a management perspective, it is desirable to assess population growth based on data from the population(s) about which one wants to draw inferences. Here we report the first survival estimates based on data from a capture-recapture study conducted in British Columbia (Canada) from 1991 to 2000. The vital rates of any Marbled Murrelet population are difficult to estimate because nests are difficult to locate and birds are hard to capture. However, the development of two capture techniques allowed us to capture large numbers of birds during the breeding season.

As for many species of conservation concern (Heppell et al. 2000), only minimal demographic data are available with which to specify the life cycle of the Marbled Murrelet. Approximate matrix population models can be used to assess the responses of the population growth rate (λ) to perturbations (e.g., Heppell et al. 2000). Such models have been used for Marbled Murrelets to assess the asymptotic λ under various assumptions about vital rates, based on data from different populations and species (Beissinger 1995; Beissinger & Nur 1997; Boulanger et al. 1999). Even if our goal was not to "predict" what will happen to the population (e.g., Coulson et al. 2001; as opposed to "projection," Caswell 1989), refined assessment of λ would require better knowledge of the life-history of the species. Because many life-history traits remain unknown for our study population, we used an approach that does not rely on the same assumptions about vital rates. We used capture-recapture models to estimate the "realized growth rate" of the population from 1991 to 2000 (Pradel 1996; Nichols et al. 2000; Nichols & Hines 2002; Williams et al. 2002), as opposed to an asymptotic one. The former corresponds to the rate of change in local population size during the study period, whereas the latter corresponds to the rate of change that would be obtained if the conditions under which the vital rates have been estimated "were to be maintained indefinitely" (Caswell 1989, 2000*b*).

Modifications of the breeding and feeding habitats of the Marbled Murrelet may have several direct and indirect consequences for vital rates and the population growth rate. First, this population occurs in Desolation

Sound, a site that has been heavily logged in the last 50 years and continues to be logged. Deforestation and fragmentation of original habitats may directly influence reproduction. They may lead to a decrease in suitable habitat and number of potential nesting sites, which may translate into decreased breeding probability in adults and decreased recruitment of young breeders or of individuals that have previously bred elsewhere. They may also lead to increased probability of failure due, for example, to increased risk of predation (Huhta et al. 1998). Although the population growth rate of long-lived species is generally less sensitive to variation in fecundity parameters than in survival (Stearns 1992; Sæther & Bakke 2000), substantial decreases in productivity are still likely to have negative consequences for population growth rate.

Second, human activities at sea (gill-net fishing, oil spills) may lead to decreased survival. However, deterioration of the murrelet breeding habitat may also indirectly influence local survival. When assessed with data from a single location, survival corresponds to the product [1 − (true mortality)]*[1 − (permanent emigration)] (e.g., Spendelow et al. 1995). There is extensive evidence in the literature that breeding failure is associated with increased probability of dispersing (e.g., Danchin & Monnat 1992; Boulinier et al. 2002), a phenomenon that can be amplified through loss of attractiveness of the location if many neighbors established in this location also fail (Danchin et al. 1998; Doligez et al. 1999; Brown et al. 2000; Danchin et al. 2001). Deterioration of the quality of breeding habitat may lead to increased probability of permanent emigration out of the study area and, therefore, lower local survival. We compared our survival estimates to the range specified for small alcids and determined whether mortality or emigration out of the study area is particularly high in this population. Moreover, decreased attractiveness of a potential breeding location may lead to reduced recruitment or immigration into the population (Danchin et al. 1998; Doligez et al. 1999; Brown et al. 2000)—that is, a decrease in the "gain" components underlying variation in numbers. We sought to determine which vital rates—survival, recruitment, or immigration—made the greatest contribution to realized local population growth rate over the study period.

Methods

Data Collection

We collected data in Desolation Sound, British Columbia (lat. 50°05′N, long. 124°45′W), and Theodosia Inlet (lat. 50° 04′N, long. 124°42′W), a fjord adjoining Desolation Sound. The watersheds around this area have been heavily logged and are still being logged; forests correspond primarily to second-growth trees. Approximately 20% of the landmass in the study area corresponds to old-growth forest (F. Huettman, personal communication). Murrelets nest in the remnant patches of old-growth forest.

We marked individuals with a Canadian Wildlife Service/U.S. Fish and Wildlife Service metal band and collected data for two weeks in June in 1991 and 1993 and from May to August from 1994 to 2000. We captured birds by different methods in the two locations (Hull 2000). We used mist nets (Kaiser et al. 1995) in Theodosia Inlet from 1991 to 2000. The steep sides and narrow mouth of the inlet funnel murrelets through Theodosia Inlet as they fly between nesting areas in the nearby hills and marine feeding areas. We deployed nets every day (weather and tide conditions permitting) for about 3 hours around dusk and dawn. In addition, we captured birds on the water at night by "night-lighting" (Whitworth et al. 1997) in Desolation Sound from 1997 onward. Hereafter we refer to this sample as the "dip-net" sample.

Estimation of Survival

We used capture-recapture models to estimate survival (Pollock et al. 1990; Lebreton et al. 1992). Plumage criteria can be used to distinguish young of the year from older individuals. We excluded data from the former. Consequently, our survival estimates correspond to individuals aged 1 or more. The two locations were 6 km apart on average. We tried to use multistate models (Nichols & Kendall 1995) to test the hypothesis that survival probability varies with location, but the dip-net sample was inadequate to test the hypothesis formally. We decided to pool the samples to increase sample size.

We used data from 1499 individuals. Our most general model had time-specific probabilities of survival (ϕ) and recapture (p). We first assessed the fit of the general model using Release (Burnham et al. 1987). The components of this goodness-of-fit test provide insight into trap-dependence and the presence of transients. We specifically tested the hypothesis that the proportion of residents is <1 (Peach 1993; Pradel et al. 1997) with Tmsurviv (Hines 1996). Lastly, we investigated the influence of time on survival and recapture probabilities with Mark (White & Burnham 1999). Model selection was based on Akaike's information criterion (AIC) or a second-order AIC (AICc; Burnham & Anderson 1998). Because AIC (or AICc) values are interpretable on a relative scale only, we report weighted information criteria (Buckland et al. 1997; Burnham & Anderson 1998). We also determined whether there was evidence of overdispersion (Burnham & Anderson 1998) by using a bootstrap approach based on the model $\phi_t p_t$.

Estimation of Rate of Population Change

We used the mist-net sample (966 individuals released from 1991 to 2000) to estimate realized population growth rate (λ) based on the approach developed by Pradel (1996). We excluded the dip-net sample (begun in 1997) because changes in the size of the study area may bias estimation of λ (Franklin et al. 2000; Hines & Nichols 2002; Nichols & Hines 2002). The initial model included time-specific recapture and survival probabilities and time-specific λ *s*. We determined the relative contribution of survival and recruitment (of young and adult immigrants) to λ by fitting a model parameterized with seniority rates (η) to the same data (Nichols et al. 2000; Nichols & Hines 2002; Williams et al. 2002). We used Mark for this analysis. Model selection was based on AICc weights.

We computed the proportional change in survival that would lead to a population growth rate of 1 (Nichols et al. 2000) and the change in λ corresponding to a change α in survival ($\eta' = \alpha\hat{\eta}$). The population growth rate (λ') corresponding to the hypothetical survival value (η') is computed as follows if survival increases:

$$\lambda' = (1 + \alpha\hat{\eta})\hat{\lambda}. \tag{1}$$

The factor is $(1 - \alpha\hat{\eta})$ if survival decreases.

Results

Survival

We did not find evidence of lack of fit of the model with time-specific parameters (Release goodness-of-fit test); test 2 + test 3, $\chi^2 = 19.47$, df $= 21$, $p = 0.55$). When parameterized with survival, recapture, and a residency parameter (γ; Hines 1996), the models with largest AIC weights had a residency rate of 1, which supports the hypothesis that the proportion of transients is equal to zero (Table 1). This result suggests that the residency parameter was not needed to model the process that gave rise to the data. Consequently, we used model $\phi_t p_t$ as a starting point to determine the influence of time on rates of survival and recapture.

Table 1. Model selection results for models including a residency parameter of <1 versus models including residents only.*

Model	*Number of parameters*	*AIC*	*AIC weights*
$\phi.\ p_t\ \gamma = 1$	9	157.1	0.87
$\phi_t\ p_t\ \gamma = 1$	15	161.9	0.08
$\phi_t\ p_t\ \gamma.$	16	163.0	0.04
$\phi_t\ p_t\ \gamma_t$	22	171.2	0.00
$\phi.\ p.\ \gamma = 1$	2	191.9	0.00
$\phi.\ p.\ \gamma.$	3	193.3	0.00

**The first time interval was set equal to 2 years. AIC, Akaike's information criterion. Data from Marbled Murrelets in Desolation Sound, British Columbia, Canada.*

Table 2. Influence of time on survival and recapture probabilities in the Marbled Murrelet in Desolation Sound, British Columbia, Canada.*

Model	*Number of parameters*	*AICc*	*AICc weights*
$\phi.\,p_t$	8	1347.7	0.99
$\phi_t p_t$	15	1357.5	0.01
$\phi_t p.$	9	1366.4	0.00
$\phi.\,p.$	2	1385.4	0.00

**No individual previously released in 1991 was recaptured in 1993. Consequently,* p_{93} *was set equal to 0. The first time interval was set equal to 2 years. AICc, second-order Akaike's information criterion.*

There was little evidence of overdispersion ($\hat{c} = 1.11$; 500 simulations), so we proceeded, using AICc for determining the influence of time on probabilities of survival and recapture. As expected, results were similar to those obtained with Tmsurviv (Table 2). The model with the largest weight had time-specific recapture probability and constant survival. Although we did not find evidence of an effect of time on survival, our ability to detect such an effect was low. Many values were either close to boundaries or estimated imprecisely (Table 3). All the models with time-specific survival probability resulted in a large number of parameters that were not estimated. Consequently, we decided not to account for model uncertainty (Burnham & Anderson 1998) because standard errors of zero would prevent estimation of corrected variances. The survival estimate made under model $\phi_t\ p.$ was 0.8289 (95% confidence interval [CI]: 0.7162–0.9029; Table 3).

Realized Population Rate of Change

The model with the largest AICc weight had constant survival and λ and time-specific recapture probability (Table 4). As above, because many parameters were not estimated, our ability to detect time specificity was low.

Table 3. Estimates of survival and recapture probability in the Marbled Murrelet in Desolation Sound, British Columbia, Canada (model $\phi.\,p_t$, Table 2).*

Parameter	*Estimate*	*95% confidence interval*
ϕ	0.8289	0.7162 – 0.9029
p_{93}	Fixed	
p_{94}	0.0376	0.0052 – 0.2261
p_{95}	0.0547	0.0282 – 0.1033
p_{96}	0.0341	0.0180 – 0.0636
p_{97}	0.1337	0.0917 – 0.1907
p_{98}	0.0820	0.0558 – 0.1188
p_{99}	0.0565	0.0378 – 0.0836
p_{00}	0.0269	0.0160 – 0.0450

**No individual previously released in 1991 was recaptured in 1993. Consequently,* p_{93} *was set equal to 0. The first time interval was set equal to 2 years.*

Because of the large number of parameters not estimated in models accounting for time specificity, we did not account for model uncertainty. The estimated population growth rate was 0.9851 (95% CI: 0.8493–1.1426; Table 5), and the estimate of survival from mist-net data only was 0.9289 (95% CI: 0.6291 – 0.9901; Table 5). We used a model with time-specific recapture probability and constant seniority rate (Table 6) to assess the contribution of adult survival to λ. In the temporal symmetry framework (Pradel 1996; Nichols et al. 2000), the seniority rate (η) denotes the probability that a member of the population at sampling occasion $t + 1$ is a survivor from occasion t. The estimate of seniority probability was 0.9566 (95% CI: 0.9454–0.9657), indicating an unambiguous tendency of adult survival to be more important to population growth than recruitment ($\hat{\eta} > 0.50$; Nichols et al. 2000).

We used Eq. 1 to compute the proportional change in survival that would lead to a population growth rate of 1 (Nichols et al. 2000), based on the above estimates ($\hat{\lambda} = 0.9851$ and $\hat{\eta} = 0.9566$). The corresponding increase in λ was 1.51%. The proportional change in survival leading to such a change in λ was 1.58% (survival probability of 0.9717). A hypothetical 1% increase in survival ($\eta = 0.9661$) would lead to a population growth rate of 0.9945, and a 3% increase in survival ($\eta = 0.9845$) would lead to $\lambda' = 1.0134$. A 1%, 3%, 5%, 10%, and 15% decrease in survival ($\eta = 0.9470$, 0.9279, 0.9088, 0.8609, 0.8131, respectively) would lead to $\lambda' = 0.9757$, 0.9568, 0.9380, 0.8901, 0.8431, respectively. A 13.35% decrease in survival ($\eta = 0.8289$) was required to obtain a survival value corresponding to the survival estimate based on the combined samples (mist-net and dip-net sample). This led to a hypothetical value of $\lambda' = 0.8593$.

Table 5. Estimates of survival, population growth rate, and recapture probabilities in the Marbled Murrelet in Desolation Sound, British Columbia, Canada (model $\phi.\ p_t\ \lambda.$, Table 4).*

Parameter	*Estimate*	*95% confidence interval*
ϕ	0.9289	0.6291–0.9901
p_{91}	0.0058	0.0021–0.0153
p_{93}	0.0043	0.0019–0.0095
p_{94}	0.0519	0.0305–0.0868
p_{95}	0.0599	0.0386–0.0920
p_{96}	0.0323	0.0213 –0.0485
p_{97}	0.0655	0.0438–0.0967
p_{98}	0.0554	0.0348–0.0871
p_{99}	0.0154	0.0084–0.0281
p_{00}	0.0072	0.0033–0.0155
λ	0.9851	0.8493–1.1426

**The first time interval was set equal to 2 years.*

Table 4. Influence of time on survival, population growth rate, and recapture probability in the Marbled Murrelet in Desolation Sound, British Columbia, Canada.*

Model	*Number of parameters*	*AICc*	*AICc weights*
$\phi.\ p_t\ \lambda.$	11	4135.0	0.92
$\phi_t\ p_t\ \lambda.$	18	4141.6	0.04
$\phi.\ p_t\ \lambda_t$	18	4141.6	0.03
$\phi_t\ p.\ \lambda_t$	15	4149.9	0.00
$\phi_t\ p_t\ \lambda_t$	25	4182.1	0.00
$\phi.\ p.\ \lambda_t$	10	4153.7	0.00
$\phi_t\ p.\ \lambda.$	10	4702.1	0.00
$\phi.\ p.\ \lambda.$	3	4709.6	0.00

**The first time interval was set equal to 2 years. AICc, second-order Akaike's information criterion.*

Discussion

The survival estimates we reported for the Marbled Murrelet are the first values estimated from field data. The estimates used in previous studies have been obtained with allometric approaches; these are the only values we can use for comparison. According to Beissinger and Nur (1997), the adult survival rate (individuals aged 3 or older) is expected to fall between 0.85 and 0.90. We reported two estimates: 0.8289 (95% CI: 0.7162–0.9029) and 0.9289 (95% CI: 0.6291–0.9901). These estimates were imprecise. The latter was based on data collected in a consistent manner from 1991 to 2000, whereas the former corresponds to birds captured in the field in two locations 6 km apart by different methods (mist-nets and dip-nets) over different time periods ("night-lighting" started in 1997). If we consider the confidence intervals, our estimates are consistent with the range specified by Beissinger and Nur (1997), even though our sample includes an unknown proportion of 1- and 2-year-old individuals (excluded by Beissinger & Nur 1997). Our estimates also fall within the range specified by Hudson (1985) for adult auks. However, all the values previously reported for alcids have not been assessed by robust methods for estimating survival (i.e., incorporating detection probability), and the various values may not be comparable. Our estimates fall within the "usual range" for adult survival in long-lived seabird species (including alcids); this can be interpreted as evidence that neither mortality nor emigration out of the study area is alarm-

Table 6. Influence of time on seniority rate and recapture probability in the Marbled Murrelet in Desolation Sound, British Columbia, Canada.*

Model	*Number of parameters*	*AICc*	*AICc weights*
$\eta.\ p_t$	8	814.8	1.00
$\eta_t\ p_t$	16	824.28	0.00
$\eta_t\ p.$	9	821.21	0.00
$\eta.\ p.$	2	879.81	0.00

**The first time interval was set equal to 2 years. AICc, second-order Akaike's information criterion.*

ing in this population. This conclusion, however, should be assessed in the light of the large standard errors.

Because of the imprecision of our survival estimates, it is not possible to tell whether the two values based on the two samples are really different. It can be hypothesized that sampling and uncertainty linked to the estimation process entirely explain the apparent discrepancy between the two estimates, but several biological hypotheses can also be proposed to explain this discrepancy. The mist-net sample may include mostly active breeders flying from nesting areas to feeding areas, whereas the dip-net sample may be more heterogeneous in terms of breeding status and success. Breeding success may reflect individual quality (Coulson 1968; Curio 1983); under this hypothesis, successful breeders are expected to have a higher survival rate than others (Cam et al. 2002). Successful breeders may also exhibit higher site fidelity and therefore a higher rate of local survival (e.g., Boulinier et al. 1997). In addition, we started capturing 0- and 1-year-old birds only when night-lighting started in 1997 (Hull 2000). The average age of the individuals captured by the two approaches may be different. Younger individuals probably have lower survival rates (Curio 1983; Hudson 1985), which may help explain the lower survival rate in the combined sample. Lastly, the dip-net sample consisted of data collected at night and may include individuals present in the Desolation Sound staging and feeding area but not breeding in that area. As discussed below, our ability to detect transients was probably low, and it is possible that the lower survival rate corresponding to the combined sample reflects permanent emigration.

We used a capture-recapture model to estimate the realized population growth rate (Pradel 1996; Nichols et al. 2000) in individuals aged 1 or more. The estimated λ was close to 1 (0.9851). This suggests that this population is close to stationary or slightly declining. However, the 95% CI overlapped $\lambda = 1$ (95% CI: 0.8493–1.1426). Our data do not permit us to draw definitive conclusions about the dynamics of this population. Moreover, this analysis was based on the mist-net sample only, in which active, successful breeders with higher survival rates and a lower probability of emigrating out of the study area may be overrepresented. Consequently, our estimate of λ may be higher than the overall λ representative of the entire population. The hypothetical value of λ corresponding to a situation where survival is 0.8289 is $\lambda' = 0.8593$. That is, if the survival estimate corresponding to the combined samples is closer to the true local survival probability, than the hypothetical value of λ suggests that the population may be declining.

The realized population growth rate cannot be compared with asymptotic growth rates previously published: they are not interpreted in the same way (Nichols et al. 2000; Nichols & Hines 2002). First, the realized λ reflects the actual rate of change in population size from 1991 to 2000, whereas the λ from a projection matrix model is the population growth rate obtained in situations where the conditions under which the vital rates have been estimated to remain the same (Caswell 1989). The realized λ corresponds to a single realization of the dynamics of the population (Barker et al. 2002) and may not be indicative of the future behavior of the population (Nichols et al. 2000). On the other hand, the assumption that conditions remain the same indefinitely may not always be realistic. In addition, the models previously used for Marbled Murrelets did not account for temporal variation in vital rates. Such variation may result in substantial differences between realized and asymptotic growth rates (Nichols et al. 2000). Little is known about the influence of time on life-history traits in the Marbled Murrelet. We did not find evidence of temporal variation in survival, but our ability to detect it was probably low because of the low recapture rate.

Second, the underlying assumptions are different. Single-site matrices are asymmetric in terms of movement of individuals in and out of the study area (Nichols et al. 2000; Nichols & Hines 2002). They correctly account for the two “loss” components of the demography of local populations, mortality and emigration. Estimates of local survival used in matrix models incorporate emigration out of the study area, and asymptotic λs therefore account for mortality and emigration. However, these models account for only one “gain component”: fecundity. Changes in population size also depend on immigration (young recruits born elsewhere or adults that have previously bred elsewhere). In contrast, realized growth rates account for individual immigrants. Immigration can be incorporated in single-site matrices (e.g., Cooch et al. 2001) or multisite models (Lebreton 1996; Caswell 2000*a*), but the required parameters are not available for Marbled Murrelets. It is possible that the actual asymptotic λ is higher than the values previously reported (e.g., Franklin et al. 2000).

The interpretation of λ depends on whether the sample used is representative of a specific population (Barker et al. 2002). Eighty-four of the 207 individuals equipped with radio transmitters from 1998 to 2000 were classified as breeders in our study area (Bradley 2002). However, there isn’t sufficient information on the breeding status and nesting site of the individuals retained for analysis or on breeding and natal dispersal in the study area to assess whether our sample comes from one or more population(s) and is representative of a discrete “demographic unit.” Consequently, we do not make the assumptions that the study population is isolated or that our sample is representative of the entire local breeding population and of only one population. Moreover, studies of subdivided populations have provided evidence that population dynamics can vary over space and time (Hanski 1999; Franklin et al. 2000), and populations may persist within metapopulations even if local conditions are unfavorable (Hanski 2001; Macdonald & Johnson 2001). Generalizations based on a single location would be risky.

The difficulties encountered in the field in studies of Marbled Murrelets explain why no estimate of survival based on field data has been published and why the recapture probability is low in our study. Although large numbers were marked and released, most have never been recaptured. This is an unfavorable situation for estimation of survival probability (Barker 1997) or other parameters using capture-mark-recapture data, which results in low power to assess the presence of transients (Pradel et al. 1997), trap dependence (Pradel 1993), or the influence of time on survival and realized population growth rate. Low detection rates are likely to have led to the poor precision of estimates of survival and realized rate of local population growth. Uncertainty in parameter estimates leads to the same type of difficulty when asymptotic λs are used to make inferences about population status. The standard error of λ depends on those of the vital rates in the matrix (Lande 1988; Caswell 1989). The influence of uncertainty in the entries of matrix population models previously built has not been thoroughly assessed for Marbled Murrelets.

Marbled Murrelets are secretive and difficult to capture. Investigators may detect only a small fraction of the individuals present and alive in study areas. It has long been known that sampling artifacts are likely to make it risky to use ad hoc approaches to estimation of vital rates (Clobert 1995). Robust inferences about many life-history parameters require use of telemetry or capture-recapture approaches (Williams et al. 2002). Our study shows that detection probability was low even though the field effort was high. The risk of drawing erroneous inferences increases when the probability of detecting individuals alive and present in the study area is low and when this parameter is ignored (Martin et al. 1995). Development of field techniques and achievement of higher recapture rates will therefore be critical to the success of future demographic studies of the Marbled Murrelet.

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