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LOCAL SURVIVAL OF ADULT AND JUVENILE MARBLED MURRELETS AND THEIR IMPORTANCE FOR ESTIMATING REPRODUCTIVE SUCCESS

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Abstract. Juvenile ratios estimated using numbers of hatch year (HY) and after-hatch-year (AHY) Marbled Murrelets (*Brachyramphus marmoratus*) counted concurrently during at-sea surveys have been used to estimate fecundity in this species. These ''concurrent'' juvenile ratios assume that HY birds remain in an area, and are likely biased because they do not account for potential differences in emigration rate of HY and AHY birds. We studied the emigration rates of adult and juvenile Marbled Murrelets marked with radio-transmitters. Juveniles had a high emigration rate compared to adults. The weekly local survival rate (ϕ) of newly radio-tagged HY birds was 27%. AHY local survival was 95% during incubation and early chick rearing, suggesting a resident population during the breeding season. We calculated juvenile ratios from 1996–1998 using (1) HY counts corrected for emigration and mean AHY counts around the breeding season peak, and (2) HY and AHY counts from concurrent at-sea surveys. The average ''corrected'' juvenile ratio (0.13 ± 0.05 SE) was higher than the ''concurrent'' juvenile ratio (0.04 ± 0.02 SE) but lower than estimates of fecundity from nest monitoring (0.18–0.22). Low juvenile ratios from at-sea surveys could result either from an unknown proportion of nonbreeding birds in the population, or, more likely, from differences in the at-sea distribution of AHY and HY birds. Fluctuation in the timing of the peak number of AHY birds across years might result in an uncorrectable bias in the counts. Because of biases and potential problems, caution is needed when interpreting juvenile ratios from at-sea surveys.

Key words: Alcidae, Brachyramphus marmoratus, *British Columbia, juvenile ratio, local survival, Marbled Murrelet, radio-telemetry, seabird.*

Supervivencia Local de *Brachyramphus marmoratus* Adultos y Juveniles y su Importancia para Estimar Éxito Reproductivo

Resumen. Utilizamos los cocientes entre individuos juveniles (nacidos en un año) y adultos (nacidos en años anteriores) de *Brachyramphus marmoratus*, censados simultáneamente durante conteos en el mar, para estimar la fecundidad de esta especie. Estos cocientes ''simultáneos'' de individuos asumen que los juveniles permanecen en una misma área, y podrían estar sesgados ya que no toman en cuenta diferencias en las tasas de migración de juveniles y adultos. Estudiamos las tasas de emigración de individuos juveniles y adultos de *B. marmoratus* marcados con radio-transmisores. Los juveniles tuvieron una tasa alta de emigración comparada con los adultos. La tasa de supervivencia local semanal (ϕ) para juveniles fue del 27%. La tasa de supervivencia local para adultos durante la incubación e inicio de la cría de polluelos fue del 95%, sugiriendo que se trata de una población residente durante la estación reproductiva. Calculamos el cociente entre juveniles y adultos para 1996–1998 utilizando (1) conteos de juveniles corregidos por emigración y promedio de adultos contados durante el pico de la estación reproductiva, y (2) juveniles y adultos contados simultáneamente durante los censos. El cociente ''corregido'' promedio entre juveniles a adultos (0.13 ± 0.05 EE) fue mayor que el cociente ''simultáneo'' (0.04 ± 0.02 EE) pero menor que las estimaciones de fecundidad obtenidas por medio del monitoreo de nidos (0.18–0.22). Los bajos cocientes obtenidos de conteos en el mar podrían explicarse por la presencia de una proporción desconocida de aves no-reproductivas en la población, o, más probablemente, por diferencias existentes en la distribución de juveniles y adultos en el mar. Fluctuaciones anuales en la sincronización del período pico de la estación reproductiva

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podrían introducir error a los conteos de adultos. Debido a estos sesgos y problemas potenciales, es importante interpretar con cautela los cocientes entre juveniles y adultos obtenidos de conteos en el mar.

INTRODUCTION

The conservation of Marbled Murrelet (*Brachyramphus marmoratus*) populations is a concern over most of the species' range, including Oregon, Washington, and British Columbia, where the species has been designated threatened (Rodway 1990, Rodway et al. 1992, U.S. Fish and Wildlife Service 1992) and California, where the species is listed as endangered (U.S. Fish and Wildlife Service 1997). All changes in population size result from changes in vital rates (births, deaths, emigration, or immigration; Caswell 1989). Conservation measures are usually more effective and reliable with knowledge of the demography of a population, especially the vital rates (Caughley 1994). Although none of these rates are known with any certainty for any

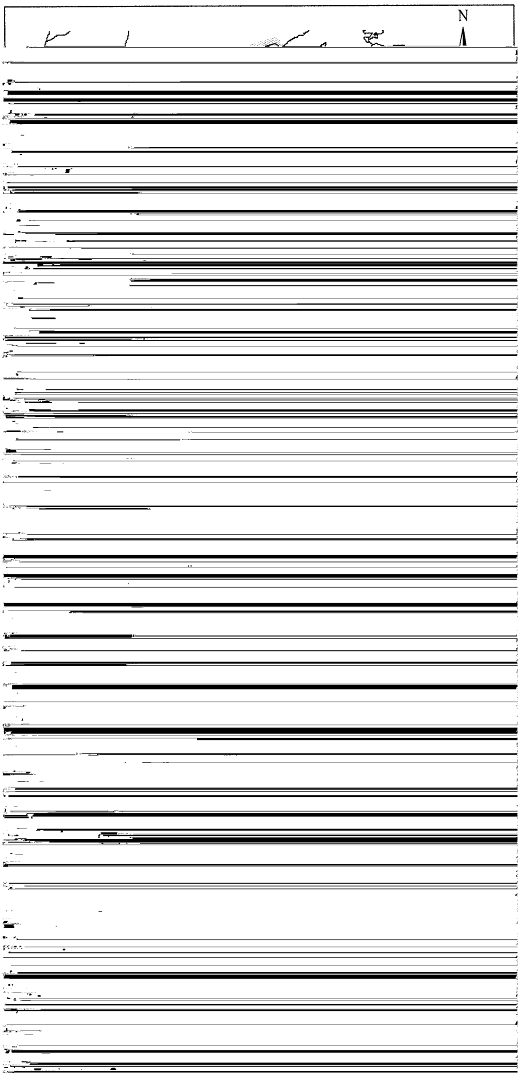

FIGURE 1. Study area (shaded) in Desolation Sound, British Columbia.

ber changed in 1998. At-sea surveys were replicated 24 times in 1996, 23 times in 1997, and 17 times in 1998 at average intervals of 4, 4, and 6 days respectively (range 1–12) between May and mid-August. Surveys were cancelled during rain or wind-wave conditions beyond 2 on the Beaufort scale. At-sea surveys ended after mid-August when HY birds could not be accurately differentiated from AHY birds as a result of AHY birds molting into basic plumage (Carter and Stein 1995). Surveys were estimated to cover 76% of the fledging period in Desolation Sound (Lougheed et al. 2002).

ESTIMATION OF JUVENILE MOVEMENT

We defined ''local survival'' as the probability of a bird staying alive and remaining in the survey area. To estimate the daily rate of juvenile local survival, radio-transmitters were attached to 16 recently fledged Marbled Murrelets captured by nightlighting (Whitworth et al. 1997) in the survey area from 10 July to 10 August 1998. Identification of HY birds during capture was based on plumage characteristics, egg-tooth presence, and weight (Carter and Stein 1995), although the exact age in days at first capture was unknown. Radio-transmitters were ATS Model 394 (Advanced Telemetry Systems, Isanti, Minnesota), weighing 2.0 g and with a battery life of 45 days. Transmitters were attached on each bird's back, between the scapulars, using epoxy glue (Bird Adhesive, Titan Corporation, Washington) and fiberglass insect screen. The birds were tracked during daylight from a 5.2-m Boston Whaler using a 4-element directional antenna mounted 3 m above the waterline, coupled with an ATS R4000 programmable receiver. Monitoring of the radio-tagged birds was done by boat at seven fixed at-sea locations within the survey area, 22 times from 11 July to 13 August (every 1.5 days on average, range 1–4 days). Movement of juveniles out of the survey area was confirmed by sporadic boat telemetry at 3 stations outside the survey area and by aerial telemetry over a wider area using a fixed-wing Cessna 172 airplane. Aerial telemetry was done on 10 August and 19 August following the coastline from Vancouver to Desolation Sound and the northern portion of the Strait of Georgia.

Program MARK (White 1999) was used to estimate the daily local survival of radio-tagged HY birds, using standard Cormack-Jolly-Seber open population models. We examined several models with different assumptions about the constancy of survival rate and recapture rate (detection) between intervals, and discriminated between models using Akaike's Information Criterion (AIC) as described in Lebreton et al. (1992). We tested whether survival rate (ϕ) and recapture rate (P) varied over time with likelihood ratio tests (LRT, Cooch and White 1999) by (1) comparing the fit of the time-dependent model of survival [$\phi(t)P(.)$] with that of the model with constant survival [$\phi(.)P(.)$], and (2) comparing the fit of the model with time dependent recapture [$\phi(.)\ P(t)$] with that of the model with constant recapture [$\phi(.)P(.)$]. We used $1 - \phi$ as an estimate of the daily rate of permanent emigration (which included mortality and radio loss, as well as true emigration). Residence time (R) was estimated as $1/-\ln(\phi)$ (White 1999). We estimated the weekly local survival rate of HY birds (ϕ^7) to allow comparison with that of AHY birds.

CORRECTED JUVENILE COUNTS

Each at-sea HY count was adjusted for juvenile turnover rate using the correction $J_n = J_o - (J_p \times \phi^d)$, where J_n = the number of ''new'' juveniles in the observed sample from the present at-sea survey, J_o = the number of juveniles observed on the present at-sea survey, J_p = the number of juveniles observed on the previous survey, ϕ^d = the daily probability of a juvenile staying in the survey area (local survival), and d = the number of days between the present survey and the previous survey. This correction estimates the number of ''new'' HY birds counted during a survey by calculating the number of HY birds seen on the present survey that are likely to have been seen on a previous survey, and subtracting that number from the total count. We estimated the cumulative number of HY birds for the season by summing J_n

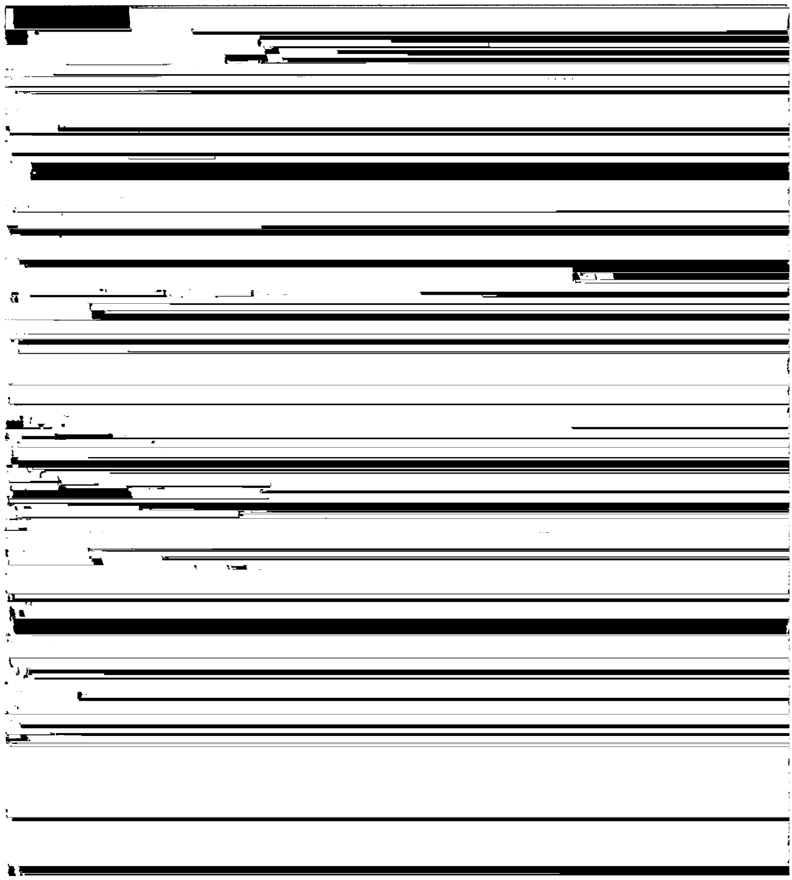

FIGURE 2. Capture and detection locations for 16 hatch-year (HY) Marbled Murrelets marked with radio-transmitters in Desolation Sound, British Columbia. Capture was within the survey area, but many radio-tagged HY birds were subsequently detected outside it, where these birds would not have been sighted during at-sea surveys.

the local adult population because of the weekly emigration rate of adults.

We also calculated ‘‘concurrent’’ juvenile ratios using the common technique of dividing the number of HY birds by the number of AHY birds counted concurrently during surveys at sea conducted throughout the fledging period. We calculated the mean juvenile concurrent ratio for all surveys done from the first observation of a HY bird at sea to the end of the survey period each year.

RESULTS

LOCAL SURVIVAL

Twelve of the 16 juveniles were detected by telemetry in the survey area on at least one occasion after capture; nine of these were not detected in the vicinity of Desolation Sound once they left the survey area. Two other juveniles were never detected in the survey area, but were detected on one occasion each outside the survey area, one by boat telemetry and the other by aerial telemetry. Two juveniles were never detected after tagging and release. Aerial telemetry detected three birds on 10 August, one in the survey area and two outside it, and three on 19 August all in the vicinity of Desolation Sound, but outside the survey area. Capture and sighting locations are shown in Figure 2. No juveniles with radios were detected in any other area of the Strait of Georgia.

The daily local survival rate of juveniles in the survey area (ϕ

TABLE 1. Fit of survival models to detection data for hatch-year and after-hatch-year Marbled Murrelets in Desolation Sound, British Columbia. For both age groups, the most parsimonious model (with the lowest AIC) is the reduced model with constant survival (ϕ) and recapture (*P*) rates, ϕ(·)*P*(·).

Age group	Model	AIC	ΔAIC	No. of parameters	Model deviance
Hatch year	ϕ(·)*P*(·)				
	ϕ(*t*)*P*(·)				
	ϕ(·)*P*(*t*)				
	ϕ(*t*)*P*(				

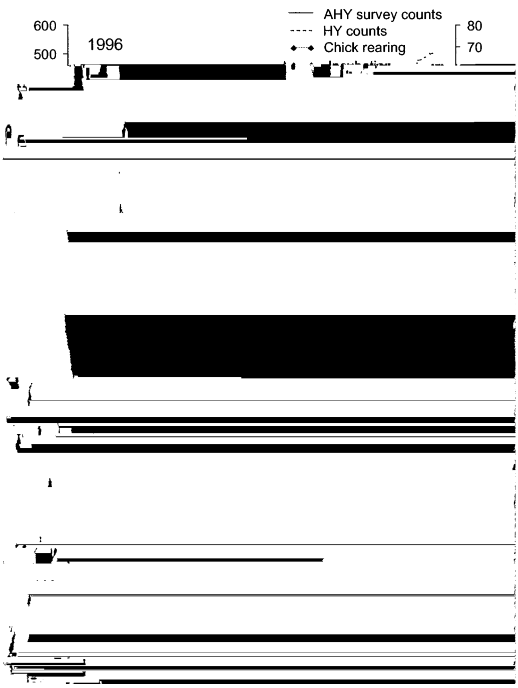

FIGURE 3. After-hatch-year (AHY) and cumulative uncorrected hatch-year (HY) Marbled Murrelet counts during at-sea surveys. Incubation and chick-rearing periods are shown for each year.

The mean concurrent juvenile ratio was 0.04 ± 0.02, ranging from 0.02–0.08 (Table 2).

DISCUSSION

This study provides the first estimates of the emigration rates of HY and AHY Marbled Murrelets during the breeding season. HY birds had a high emigration rate compared to AHY birds. Juveniles do not accumulate in the same areas adults do, and because it is logistically difficult to cover large areas of water, emigration of HY birds must be accounted for prior to the calculation of the juvenile ratio in our study area. It appears, however, that there are other factors affecting juvenile ratios. Although AHY birds were residents, unpredictable variation in breeding success could lead to variation in at-sea counts. This may make year-to-year variation in juvenile ratios difficult to interpret. Although our estimates are unique to Desolation Sound, this study highlights the importance of understanding local movements of Marbled Murrelets at sea.

Emigration of AHY birds from the survey area was low during incubation and early chick rearing (high weekly local survival, about 95%), confirming that birds using the area of Desolation Sound during the breeding season are residents, rather than transients. The weekly 5% adult emigration rate is possibly related to nesting failure. We could not estimate local survival of AHY birds after chick rearing because most of the radio-transmitters had either fallen off or curs in the San Juan Islands starting in late July (M. G. Raphael, pers. comm.). There was no evidence of juveniles moving to nursery areas in the vicinity of Desolation Sound as reported for Alaska (Kuletz and Piatt 1999). Although there is no evidence of mortality of marked juveniles or radio loss during the study, either are possible and cannot be ruled out. Both mortality and radio loss would lead to an overestimate of the emigration rate, and consequently, an overestimate of the number of juveniles.

The 1996–1998 average juvenile ratio (corrected for movement) was 0.13, about 3 times the ratio obtained from concurrent counts (0.04). Reported juvenile ratios from British Columbia, Washington, Oregon, and California range between 0.004 and 0.04 (Beissinger 1995), and are similar to the ratios estimated from concurrent counts in this study. In Alaska, where the ratios were calculated using breeding-season AHY counts, the reported ratios ranged between 0.02 and 0.11 (Kuletz and Kendall 1998), similar to our corrected juvenile ratios. Because the ratios were calculated with different methods, location and calculation method are confounded. These ratios cannot be compared directly.

Year-to-year variation in fecundity is common in alcids (Ainley and Boekelheide 1990) and this is another confounding factor. We found a substantial amount of annual variation in juvenile ratio (CV = 70%) for the three years of the study. Since we extrapolated information on relative movements from 1998 only, it is possible that relative movements were different in 1997, and this could explain some of the observed variation in the estimated counts of juveniles.

Despite that the average corrected juvenile ratio from Desolation Sound was higher than those reported for other areas, it is low compared to independent estimates of fecundity obtained by radio-telemetry from the same population, which suggest that fecundity should be in the range of 0.18–0.22 female fledglings per breeding female (LWL, unpubl. data). Corrected juvenile ratios were also lower than nest success in the area, estimated by tree climbing (0.33, Manley 1999); however, these two measures are not directly comparable because nest success will always be higher than fecundity. There are two possible explanations for low juvenile ratios from at-sea surveys. The first one is an unexpectedly high proportion of nonbreeding birds in the survey counts: because both adult and subadult AHY birds have the same plumage characteristics (Carter and Stein 1995, Strong et al. 1995), subadult AHY birds cannot be identified during at-sea surveys. Therefore, a high proportion of subadult AHY birds in the survey area would cause juvenile ratios to be underestimated. The second explanation for low juvenile rafor long-term monitoring, even if magnitude of the index were disregarded.

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