

INFERRING BREEDING SUCCESS THROUGH RADIOTELEMETRY IN THE MARBLED MURRELET

RUSSELL W. BRADLEY,^{1,2} Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC, V5A 1S6, Canada

FRED COOKE, Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC, V5A 1S6, Canada

LYNN W. LOUGHEED, Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada

W. SEAN BOYD, Canadian Wildlife Service, RR1 5421 Robertson Road, Delta, BC V4K 3N2, Canada

Abstract: Demographic parameter estimates are essential for understanding population ecology and developing management plans for species of concern. We inferred measures of breeding success using radiotelemetry in the marbled murrelet (*Brachyramphus marmoratus*), a secretive, forest-nesting seabird, from 1998 to 2001 in Desolation Sound, British Columbia, Canada. Our estimates of mean annual nesting success and fecundity (0.19–0.23 female offspring/adult female/yr) are among the highest reported for the species. We suspect that our estimates are high compared to previous estimates in our study area (Manley 1999), primarily because of our higher success in areas inaccessible to ground-based human observers. We detail how behavior-based inferences of activity at different reproductive stages did not differ between confirmed nest sites and suspected nest sites that were physically inaccessible to us. We were able to accurately predict initiations of breeding and incubation success from the duration of adults' repeated daily shifts from the ocean to their inland nest sites. Chick-rearing success was accurately predicted by visitation rates of adults during provisioning. We discuss the assumptions and potential biases of our methods and their effects on our results. Our method may overestimate early breeding failure, but it likely provided unbiased fecundity estimates for our population. Accurately inferring breeding success through radiotelemetry is costly and labor-intensive. However, radiotelemetry could provide crucial demographic information once thought impossible to obtain for secretive breeding species.

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Population size and changes over time are fundamental variables of interest in most conservation programs. Detailed demographic studies are required to address the processes underlying temporal variation in population numbers (Yoccoz et al. 1998). From a management perspective, identification of the most relevant management actions should be based on the relative contribution of the vital rates to population growth, the ability of management actions to affect changes in the different vital rates, and the costs of such actions (Nichols et al. 2000, Nichols and Hines 2002). For practical reasons, implementing management plans and specifying objectives that focus on breeding habitat or breeding success are easier than using adult survival. For this reason, accurate assessment of breeding success is critical to most conservation programs.

Assessment of breeding success is relatively straightforward for many species. Investigators usually locate numerous breeding individuals

and identify breeding state and success by direct observation (Clutton-Brock et al. 1982, Cooke et al. 1995). However, some species cannot be studied in this way. These species may be too secretive, use breeding habitats inaccessible to humans, or be too sensitive to disturbance. Few studies have assessed reproductive status indirectly, using physiological (Vanderkist et al. 2000) or behavioral (Green et al. 1997) approaches.

Telemetry allows remote monitoring of free-ranging animals (White and Garrott 1990). Radio and satellite telemetry has permitted extensive study of habitat use (Aebischer et al. 1993, Ganey et al. 1998, Polovina et al. 2000), movement (Thompson et al. 1996, Hughes et al. 1998), survival (Bunck and Pollock 1993, Hellgren et al. 2000), and population estimation (Landa et al. 1998, Ries et al. 1998). However, few studies have used telemetry to estimate breeding success directly. Green et al. (1997) described timing of breeding, duration of breeding stages, and mortality rates of clutches and broods of the corn-crake (*Crex crex*) using radiotelemetry data.

Secretive, inaccessibly breeding species often have poorly understood reproductive ecology.

¹ Present address: Marine Ecology Division, PRBO Conservation Science, 4990 Shoreline Highway, Stinson Beach, CA 94970, USA.

² E-mail: rbradley@prbo.org

Management decisions concerning these species are therefore difficult due to uncertainty about the status of populations. Without such information, developing an unbiased understanding of population demographics is virtually impossible. For a threatened or endangered species, a conservation strategy developed without knowledge of breeding propensity and reproductive success might not fully address management needs (Ralph et al. 1995, Meretsky et al. 2000, Sutherland 2001).

We assessed breeding status and success of marbled murrelets indirectly based on presence and absence of radiomarked murrelets in marine (foraging) and forest (nesting) habitats. The marbled murrelet is a small Pacific seabird (family Alcidae) that is difficult to study because its nests are located in relatively inaccessible habitats, primarily in large trees in coastal old-growth forest (Nelson 1997). Concern for the marbled murrelet has grown in recent years due to suspected population declines over much of the species' range (nearshore waters of Alaska to central California). These suspected declines have been associated with loss and fragmentation of nesting habitats due to forestry (Nelson 1997). However, a lack of basic information on population and breeding biology for marbled murrelets has hampered our knowledge of the population status and development of management and conservation policies (Ralph et al. 1995). Previous assessments of marbled murrelet reproductive success often have been made from counts of juveniles at sea and the ratio of juveniles to adults (Beissinger 1995, Kuletz and Kendall 1998). However, these methods may be biased because they do not account for immigration or emigration rates of adults and juveniles. Further, behavioral differences between adults and juveniles may affect their detection (Beissinger 1995, Kuletz and Kendall 1998, Loughheed et al. 2002a).

Based on the knowledge that marbled murrelet's incubation shifts last 24 hr (Nelson 1997; F. Cooke, Simon Fraser University, unpublished data), we knew that individuals alternated between nest sites and marine foraging habitat daily during the incubation stage. If we detected a murrelet at its nest site on day i , we expected to find it on the ocean on day $i + 1$, and vice versa. We used patterns of presence and movements of radiomarked murrelets throughout their breeding cycle to ascertain reproductive status, hatching success, and fledging success. Our objectives were to assess marbled murrelet reproductive

success through radiotelemetry and estimate possible biases associated with this indirect approach.

STUDY AREA AND METHODS

Our study was conducted at Desolation Sound, British Columbia, Canada (50°05'N, 124°40'W; Fig. 1). The topography consists of islands, fjords, and steep-sided valleys rising above the tree line to approximately 2,500 m. The lower elevation forest is dominated by western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and Douglas fir (*Pseudotsuga menziesii*) with a transition to yellow cedar (*Chamaecyparis nootkatensis*) and mountain hemlock (*Tsuga mertensiana*) at higher elevations (Green and Klinka 1994).

Breeding Biology

In our study area, murrelets on the ocean prior to nesting included both breeders and non-breeders (Vanderkist et al. 2000). Murrelets feed in the ocean, primarily on Pacific sand lance (*Ammodytes hexapterus*; Carter and Sealy 1990, Loughheed 2000). Most murrelets start nesting in April and May (Loughheed et al. 2002b, McFarlane-Tranquilla 2001). They lay 1 egg and incubate for approximately 30 days. Males and females take equal 24-hr incubation shifts, switching duties at dawn (Sealy 1975; Nelson 1997; F. Cooke, Simon Fraser University, unpublished data). Unlike most alcids, breeding is asynchronous in murrelets (Loughheed et al. 2002b, Nelson 1997). If incubation fails, adults return to sea, but females may lay a replacement egg (McFarlane-Tranquilla et al. 2004).

During chick feeding, adults generally are absent from nest sites during the day and provision primarily at dawn, and to a lesser extent at dusk (Nelson 1997, Bradley et al. 2002). While some provisioning has been documented during the day (Nelson and Hamer 1995, Nelson and Peck 1995), we observed this on only a few occasions in hundreds of hours of automated monitoring of our study birds (R. Bradley, Simon Fraser University, unpublished data). Some nonbreeding murrelets visited inland sites, possibly prospecting for future nest sites (Nelson 1997, Bradley et al. 2002). Breeding murrelets in our study area often commuted long distances from foraging to nesting sites, sometimes traveling >100 km each way (Hull et al. 2001). Chick rearing lasts approximately 30 days (Bradley et al. 2002), but periods up to 40 days have been reported (Nelson 1997). At fledging, chicks fly to sea (Nelson 1997).

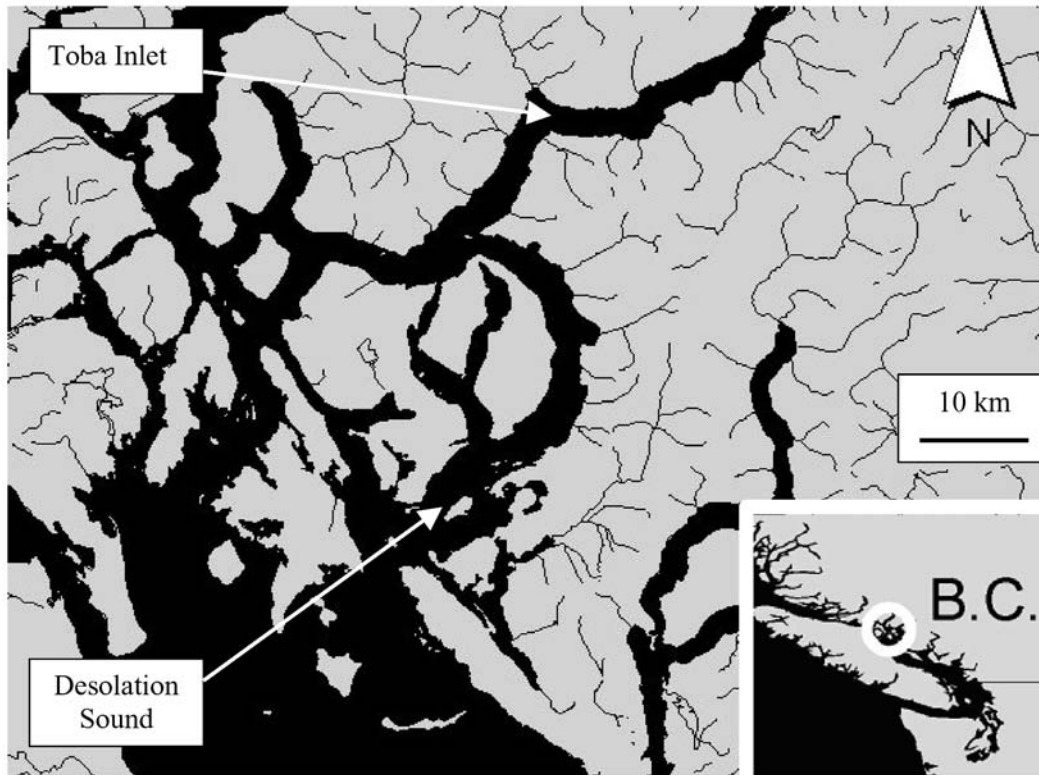


Fig. 1. Study site of Desolation Sound, British Columbia, Canada, with capture sites marked. Inset map of British Columbia (B.C.) shows study site in white circle.

Capture and Radiomarking of Murrelets

All analyses of methods were based on data from 190 adult marbled murrelets captured in Desolation Sound from April to early June 1998–2000 ($n = 40$ in 1998, 100 in 1999, and 50 in 2000) and 25 murrelets captured in 2000 in Toba Inlet ($50^{\circ}25'N$, $124^{\circ}37'W$), located approximately 35 km northwest of Desolation Sound (Fig. 1). For demographic analyses and comparisons of breeding success between ground-truthed accessible nests and inaccessible sites, we included additional data from 75 murrelets captured and radiomarked in Desolation Sound in April–June 2001. Murrelets were captured from small boats at night using a dip-netting technique (Whitworth et al. 1997, Vanderkist et al. 1999). We fitted murrelets with radiotransmitters attached to a subcutaneous anchor (Model 394 in 1998 and Model 386 in 1999–2001; Advanced Telemetry Systems, Isanti, Minnesota, USA) following methods of Newman et al. (1999). However, we used a small amount of epoxy (Bird Adhesive, Titan Corporation, Seattle, Washington, USA) to secure the radiotransmitter to body feathers, and

we did not anesthetize the murrelets. Model 394 radiotransmitters weighed 2.2 grams (approx 1% of adult mass) and had an insured life of 45 days; Model 386 radiotransmitters weighed 3.0 grams (approx 1.4% of adult mass) and had an insured life of 80 days. The actual radiotransmitter life-span often exceeded the insured lifespan. Most radiomarked murrelets were captured prior to breeding (McFarlane-Tranquilla et al. 2003), although 8% of known nesters had already begun incubation at the time of capture.

Aerial Radiotracking

After murrelets were radiomarked, we located each bird as often as possible until the radiotransmitter failed or fell off or the murrelet died or left the area. Marine and inland locations were determined by over 500 hr of helicopter radiotracking from early May until early August from 1998 to 2001 (see Hull et al. 2001 for methods in 1998). From 1999 to 2001, we used a Robinson 44 piston engine helicopter with H antennas mounted at 45° on brackets at the anterior ends of the helicopter struts for radiotracking.

We conducted 2 types of helicopter search flights. Water flights obtained general marine locations of individuals and determined whether radiomarked murrelets were present in a defined marine search area. These flights were an efficient way to obtain information on multiple murrelets that typically returned to marine feeding sites throughout a breeding season (F. Cooke, Simon Fraser University, unpublished data). Water flights were conducted daily for most of the breeding season and were reduced in frequency when all known nesting radiomarked murrelets were well advanced in chick rearing. We scanned the entire bank of possible frequencies at 2-sec intervals, and we removed a radio from the bank when the murrelet's location on the water was confirmed. Water flights ranged in altitude from 300 m in poor conditions to 1,500 m in good conditions. Field trials indicated that detection distance in good conditions was a minimum of 5 km. These water flights were supplemented by stationary telemetry from a mountain peak (elevation approx 1,280 m) using a handheld Yagi 3D antennae (Advanced Telemetry Systems, Isanti, Minnesota, USA) over stretches of ocean. This stationary telemetry could reliably detect signals up to 15 km away. Marine detections from the entire breeding season verified whether radiotransmitters of nesting murrelets continued to function properly and allowed us to accurately assess when chick-rearing murrelets were visiting their nests.

Nest-search flights searched inland for nesting sites of murrelets not present on the ocean. These flights ranged from 1,500 to 3,000 m in altitude, and detection distances in good weather exceeded 10 km. Nest-search flights were less efficient in detecting multiple birds because we located radiomarked murrelets nesting up to 54 km from their capture location (F. Cooke, Simon Fraser University, unpublished data). When we detected an inland signal, we determined the location of the signal to an area approximately 100 × 100 m in size. Where possible, ground-based telemetry was subsequently used to locate the nesting tree. However, some nests were inaccessible from the ground, being located in or adjacent to exceptionally steep terrain or too remote from suitable helicopter landing locations.

Land-based Radiotracking

To detect murrelets flying between nests and their feeding areas, we conducted ground-based radiotracking along likely inland travel routes,

often close to nest sites. In this way we could monitor adult nest visitation during chick rearing. Due to equipment and personnel restrictions and the breeding asynchrony of the murrelets, we could not monitor each nest at the end of chick rearing. Therefore, our monitoring activities lasted 2–15 days at each nest site and occurred between 10 days after estimated hatch and the end of chick rearing. We defined breeding success, estimated from regular daily visits to nest sites by radiomarked murrelets, as “mid-chick” rearing success. This was our best proxy of breeding success for all nest sites. Detailed methodology for this nest-site monitoring and its assumptions are described in Bradley et al. (2002). We assumed nest sites to be active and that parents were feeding chicks if radiomarked adults returned at least once every 48 hr throughout our monitoring period (Bradley et al. 2002).

To confirm the fate of nests, we climbed accessible nest trees after the breeding season (Hamer et al. 1994). Successful nests showed a pronounced fecal and down ring around the nest cup (Nelson 1997, Manley 1999). Nests assumed to have failed in chick rearing showed signs of hatch, egg shell fragments with albumen, and usually signs of chick activity: a small amount of feces or presence of a dead chick, but no large fecal ring and down. Nests that failed during incubation showed no murrelet feces or down, no evidence of hatch, and usually a depredated or unhatched egg.

Statistical Analyses

We analyzed our methods within a framework that started with nesting murrelets for which we had the most data and extrapolated backward to assess the certainty of our behavior-based inferences. Therefore, all radiomarked murrelets used in our analyses fell into 1 of 3 categories: (1) breeding murrelets for which we obtained good marine detection data, located the nest site from helicopter telemetry, conducted telemetry observations of nest visits during chick rearing, and climbed the tree to assess nesting success; (2) breeding murrelets with all the data from the first category except tree-climbing results; or (3) murrelets with marine detection data only. We excluded from analyses 8 murrelets that had <10 marine detections.

Initiation of Breeding.—We assessed behavioral data from radiomarked murrelets in the early stages of breeding to (1) infer breeding by murrelets and the initiation of incubation, (2) differ-

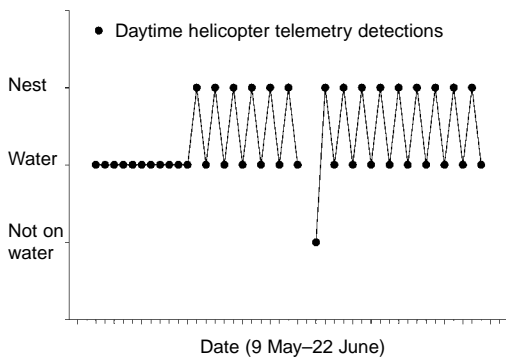


Fig. 2. Typical On-Off pattern (OP) for marbled murrelets during incubation (from 1999 Male 5.254). Unlike most murrelets, this individual nested close to our camp, so radiotelemetry detections of the murrelet on its nest were easy to obtain.

entiate breeders from nonbreeders, and (3) investigate bias in our methodology. We observed an attendance pattern in breeding murrelets associated with a 24-hr incubation shift. This pattern is a consecutive 2-day presence-absence pattern of detection on the ocean, referred to here as an “On-Off pattern” (OP; Fig. 2). The few birds whose nests were located close to our field camp, and whose nests could be monitored daily throughout incubation, showed the reverse 2-day presence-absence pattern of detection at their nest sites (Fig. 2). For each murrelet in our study, we calculated an OP value: the longest continuous period that this pattern of ocean detection was observed. For example, an OP value of 15 would correspond to a consecutive 30-day presence-absence pattern of a murrelet on the ocean, the approximate mean duration of incubation for the species. An OP value of 1 would indicate that an individual was detected during water flights every day and was absent from our ocean study area only once during daily aerial telemetry surveys. If OP duration was a reliable predictor of initiation of nesting and incubation success, then this behavioral variable could be used to infer breeding status and incubation success for nests that could not be ground-truthed.

We examined OP duration during incubation of murrelets with fledging success data from climbed trees, and thus unquestionable proof of nesting. We compared OP distribution with OP results from suspected breeding murrelets with inaccessible nests (Fisher’s 2-tailed exact test). Our goal was to determine whether both samples showed similar distributions of OP values. To address the differences in OP between breeders

and nonbreeders, we combined datasets of the 2 samples of breeding murrelets. We then compared this combined dataset to OP duration in suspected nonbreeding murrelets.

To assess potential bias in OP values from failing to detect murrelets on the ocean, we calculated our probability of detecting individuals in our marine survey area from 1999 and 2000 radiotracking data. We assumed that the only time murrelets were not in our survey area was when they were incubating. We also developed curves to illustrate the probability of detecting OP by chance under different detection-rate scenarios by simulating detection probabilities of 90, 75, and 50%. In addition, the day and coverage area of nest search flights affected our likelihood of finding a nest. In many bird species, nests that fail early are less likely to be located (Mayfield 1975). To quantify the length of time needed to locate nests, we developed a logistic curve (PROC GENMOD; SAS Institute 2001) to determine the probability of locating the nest based on the frequency distribution of the OP duration for breeders compared to suspected nonbreeders. We also investigated the degree that individuals were faithful to the OP and whether anomalous incubation shifts occurred.

Incubation Success.—We tested for statistical differences between the mean rank (Mann-Whitney Wilcoxon Test) and distribution (Fisher’s 2-tailed exact test) of OP for murrelets that hatched young and those that failed.

Chick-rearing Success.—We compared the mean dawn (AM), dusk (PM), and total visitation rates by adults at nest sites during the chick-rearing period for successful nests and those we assumed failed. Because preliminary analyses showed an equal sex ratio in both the total sample (24 females, 25 males) and subsamples partitioned by success category, we pooled data from both sexes. Preliminary analyses also showed no significant year effects so we pooled samples from all years. We made comparisons among the following 3 groups of chick-rearing murrelets (Mann-Whitney Wilcoxon tests): (1) confirmed successful: successfully fledged a chick, as confirmed by tree-climbing observations; (2) suspected successful: visited their nests regularly during chick rearing, as documented from radiotracking results, but had inaccessible nest sites; (3) suspected failed: had inaccessible nests and were assumed to have succeeded through incubation, but visited nest sites sporadically or not at all during chick rearing. We did not include nests that were con-

Table 1. Proportion of radiomarked marbled murrelets from Desolation Sound, British Columbia, Canada (1998–2001) reaching the successive stages of reproduction, with estimated standard errors and number of individuals.

Stage	Year			
	1998	1999	2000	2001
Breeding attempt ^a	0.70 ± 0.07 <i>n</i> = 33	0.55 ± 0.05 <i>n</i> = 62	0.56 ± 0.05 <i>n</i> = 50	0.79 ± 0.05 <i>n</i> = 50
Incubation ^b	0.69 ± 0.08 <i>n</i> = 23	0.94 ± 0.04 <i>n</i> = 34	0.778 ± 0.07 <i>n</i> = 28	0.97 ± 0.03 <i>n</i> = 31
Mid-chick	0.80 ± 0.09 <i>n</i> = 15	0.74 ± 0.07 <i>n</i> = 32	0.75 ± 0.08 <i>n</i> = 22	0.92 ± 0.05 <i>n</i> = 29
Fledging	0.75 ± 0.11 <i>n</i> = 4	0.33 ± 0.06 <i>n</i> = 20	0.87 ± 0.08 <i>n</i> = 15	0.64 ± 0.08 <i>n</i> = 24

^a The sample is likely to include both prebreeders and mature individuals skipping a breeding opportunity. The sample also excludes individuals of unknown breeding status.

^b For individuals to be included in this total, they must have attempted to breed. These are probabilities conditional on the fact that the individual reached the previous stage.

firmed failures in chick rearing in these analyses due to low sample size (*n* = 4).

Demographic Parameter Estimates

We reported the annual proportion of individuals in our sample that successfully reached the following reproductive stages: nesting attempt, incubation, mid-chick rearing, and fledging. Parameter estimates presented are from murrelets radiomarked at our primary capture site in Desolation Sound. We presented fledging data only from accessible nests. We incorporated data from 2001 in these demographic analyses, while we conducted all methodological analyses on 1998–2000 data. We defined breeding propensity as the proportion of radiomarked murrelets classified as initiating a nesting attempt, based on an OP value of 4 or 8 days of this pattern. This a priori estimate was a minimum because nests failing early in incubation might not achieve OP values sufficient to be classified as breeding. For the sample of murrelets detected initiating a nesting attempt, we used the Kaplan-Meier estimator (Kaplan and Meier 1958) to estimate success across intervals defined by the following events: (1) initiated nesting attempt, (2) eggs hatched, (3) reached the mid-chick stage, and (4) fledged. Nesting success is the probability that a pair that initiated a nesting attempt fledges a chick (events 2–4). Breeding success is the probability that an individual fledges a chick (events 1–4). We chose the Kaplan-Meier estimator because it allowed us to censor radiotransmitters that failed (White and Garrott 1990). We compared mid-chick-rearing success of nests that were accessible versus those

that were inaccessible to assess potential biases in reproductive success between the 2 site types.

Our measure of productivity was fecundity (i.e., the number of females produced per adult female per year; Caswell 2000). We calculated fecundity as

$$\frac{(\text{no. females fledging chicks})}{(\text{no. breeding females marked})/2},$$

adjusting for nonbreeders and assuming equal juvenile sex ratio at fledging. We assumed a sex ratio of 1:1 in adults, based on the findings of Vanderkist et al. (1999) for our capture method in our study area. We also calculated fecundity estimates based on mid-chick-rearing success for comparison because our inaccessible nest sites had no fledging data.

RESULTS

We collected >8,000 detections of marbled murrelets on the water and at, or traveling to, their inland breeding areas. Of the 207 radiomarked murrelets from 1998 to 2000 used in the methodological analyses, we located 84 at inland nest sites. We confirmed 25 of these breeders by tree climbing and found that all contained 1 active nest from that year. At all sites where a chick was fledged, we had detected the radiomarked adults visiting the nest regularly during the mid-chick rearing stage. We estimated fledging success only from nests in climbed trees. Fifty-nine murrelets with inaccessible nests were suspected nesters.

Demographic Parameter Estimates

Based on our Desolation Sound sample of radiomarked individuals, the average annual minimum breeding propensity, under our conservative criteria for recognizing nest initiation, was 0.65 (range = 0.55–0.79; Table 1). Due to concerns that these breeding propensity data were biased low due to certain aspects of our methods, we report a range of fecundities based on assumptions that 0.95 or 0.80 of adult murrelets in the sample were in fact breeders, which is consistent with a large survey of alcids by Hudson (1985).

Demographic analyses from our primary capture site in Desolation Sound showed relatively stable reproductive rates between 1998 and 2001 (Table 1). Mean incubation success was 86%, with reduced probability of success in each subsequent stage (mid-chick = 81%, fledging = 69%; Table 2). Based on radiotracking data, if we consider only murrelets that initiated a breeding attempt, nesting success from cumulative Kaplan-

Table 2. Estimated probability that breeding radiomarked marbled murrelets from Desolation Sound, British Columbia, Canada (1998–2001), reach the successive stages of reproduction ($n = 116$).

Stage	Probability of success at each stage		Cumulative probability (Kaplan-Meier estimates)	
	Estimate	95% CI	Estimate	95% CI
Incubation	0.86	0.79 to 0.92	0.86	0.79 to 0.92
Mid-chick	0.81	0.73 to 0.88	0.69	0.61 to 0.77
Fledging	0.69	0.63 to 0.75	0.48	0.41 to 0.55

Meier estimates was 0.48 (Table 2). Based on the assumption that 95% of adults breed, the overall breeding success was 0.46. With an assumed breeding proportion of 80%, breeding success was 0.38. The corresponding fecundity values were 0.23 and 0.19, respectively. Using the mid-chick-nesting success of 0.69 in the same approach, mid-chick fecundity values were 0.33 and 0.28. In each year of study, mid-chick success was higher at inaccessible sites versus accessible ones (Table 3), although pooled analyses showed this effect to be only marginally significant (Mann-Whitney Wilcoxon test; $W = 25$, $P = 0.057$).

Initiation of Breeding

We observed extended OPs associated with incubation for radiomarked murrelets with confirmed nest sites (Fig. 3). We detected no difference in the OP frequency distributions (Fisher's 2-tailed exact test; $P = 0.54$) or means between confirmed and suspected breeders (mean \pm SE confirmed = 12.24 ± 0.86 OPs, suspected = 11.10 ± 0.58 OPs; 2-tailed Mann-Whitney test; $P = 0.172$). The OP distribution of suspected nonbreeding murrelets showed most individuals with an OP value of 1, with very few nonbreeding murrelets having high OP values (Fig. 4). Conversely, the pooled sample of known and suspected breeders had many more individuals with higher OP values and no murrelets with an OP value of 1 (Fig. 4). The mean OP for pooled breeders of 11.73 (0.47 SE) was 6.5 times greater than the

Table 3. Proportion of ground-accessible and inaccessible nests of radiomarked marbled murrelets from Desolation Sound and Toba Inlet, British Columbia, Canada, that were successful to mid-chick rearing in each study year (1998–2001).

Year	% successful accessible nests	% successful inaccessible nests
1998	50.0 ($n = 10$)	63.6 ($n = 11$)
1999	40.0 ($n = 10$)	84.2 ($n = 19$)
2000	58.3 ($n = 12$)	75.0 ($n = 12$)
2001	65.4 ($n = 26$)	77.7 ($n = 9$)

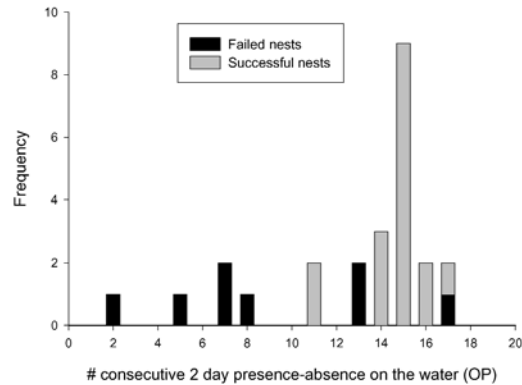


Fig. 3. Frequency of On-Off patterns (OP) of ocean attendance for failed and successful ground-truthed nests of radiomarked marbled murrelets during incubation from 1998 to 2000 ($n = 25$), Desolation Sound and Toba Inlet, British Columbia, Canada.

mean of presumed nonbreeders of 1.81 (0.22; 2-tailed Mann-Whitney test, $P < 0.001$).

We found no difference in our probability of detecting murrelets between years ($t = 1.37$, $P = 0.173$, $df = 161$). Mean probability of detecting murrelets on the ocean throughout the breeding season, assuming birds were only absent when incubating, was 0.65 (range = 0.14–1, SE = 0.03). Using theoretical detection probabilities of 90, 75, and 50%, we determined the likelihood of detecting false OP by chance due to missed marine detections when the murrelet was present in our study area (Fig. 5). Even at only 50% detection probability, the odds of observing the extended OP values we recorded by chance alone was virtually nil.

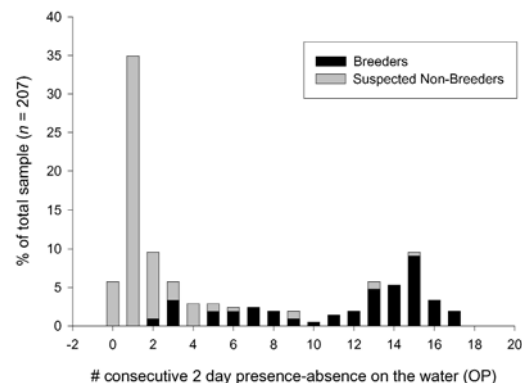


Fig. 4. Frequency of On-Off patterns (OP) of ocean attendance of breeding and suspected nonbreeding marbled murrelets from 1998 to 2000 in Desolation Sound and Toba Inlet, British Columbia, Canada, as percent of total sample of breeders and nonbreeders ($n = 207$).

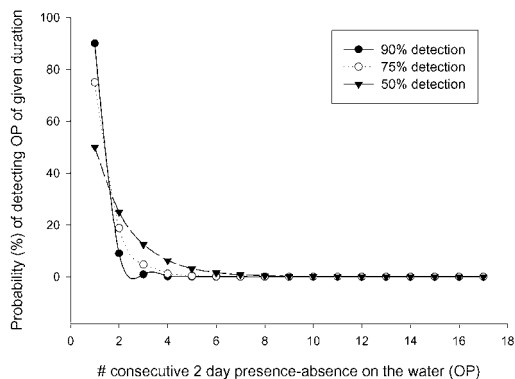


Fig. 5. Probability (%) of detecting On-Off patterns (OP) by chance, due to missed detections of marbled murrelets on the ocean, given detection probabilities of 90, 75, and 50%.

As expected, the probability of finding the nest of a breeding murrelet increased with OP duration, and a 95% confidence level corresponded to an OP of approximately 11.5 (23 days). The OP value was consistent throughout the incubation period for 87% of our breeding murrelets. The remaining 13% showed 1 skipped incubation shift in their 30-day cycle.

Incubation Success

For ground-truthed nest sites ($n = 25$), murrelets that failed in incubation had a significantly lower mean OP than successful incubators (mean \pm SE failed = 9.00 ± 1.74 , successful = 14.59 ± 0.374 ; 2-tailed Mann-Whitney U , $P = 0.005$; Fig. 3). The distribution of OP frequencies for these 2 groups was significantly different (Fisher's 2-tailed exact test; $P < 0.001$). The mean OP for murrelets that successfully completed incubation was approximately 15 (i.e., the OP value that would represent a 30-day incubation period). The 2 successful murrelets with OP values of 11 (22 days) both exhibited OP behavior immediately after capture, as soon as they were radiotracked.

Chick-rearing Success

During chick rearing, rates of visitation by radiomarked murrelets at confirmed successful nests did not differ from rates of visitation at suspected successful nest sites (Table 4). As expected, this pooled sample of confirmed and suspected nests showed significantly higher rates of nest visitation than suspected failed nests when comparing AM, PM, and total nest visits (Table 4). Of the 4 radiomarked murrelets that were confirmed to have failed during chick rearing, 2 actively

attended early in chick rearing but not in the late rearing period, 1 bird never attended, and 1 bird's radio signal disappeared.

DISCUSSION

Breeding Success Estimates

We presented the first estimates of reproductive parameters for a marbled murrelet population based on observations of individually radiomarked birds. A striking feature of our study is that nesting-success estimates are higher than or fall in the upper range of previously published values for the species (Hamer and Nelson 1995, Beissinger and Nur 1997, Kuletz and Piatt 1999). Several circumstances may explain this. Some estimates have been based on at-sea juvenile ratios (e.g., Beissinger and Nur 1997) that incorporate juvenile mortality after fledging and thus are likely to be lower than other estimates. These ratios also reflect both the proportion of juveniles observed at sea and differences in detection probabilities among age classes (Lebreton et al. 1992).

Our values of breeding propensity for marbled murrelets were low relative to studies of other seabirds (Aebischer and Wanless 1992, Chastel et al. 1995, Cam et al. 1998). Three probable reasons for this result are: (1) our sample included a few prebreeders that should not have been included in fecundity estimates, (2) capturing activities may have inhibited murrelets from breeding

Table 4. Mean nest visitation rates (detections/observation session) during chick rearing for radiomarked marbled murrelets from Desolation Sound and Toba Inlet, British Columbia, Canada (1998–2000). The following samples are reported: confirmed successful breeders (CS), with ground-truthed nests ($n = 11$); unconfirmed successful breeders (US), without ground-truthed nests ($n = 29$); all successful breeders (AS; confirmed and suspected, $n = 40$); and unconfirmed failed breeders (UF; $n = 9$). Rates for AM, PM, and all detections are reported. Standard errors for each sample are reported in parentheses. We also present the results of 2-tailed Mann Whitney tests comparing the groups.

	Detection class		
	All	AM	PM
Nest visitation rate			
CS	0.567 (0.067)	0.761 (0.072)	0.350 (0.092)
US	0.623 (0.043)	0.900 (0.062)	0.389 (0.067)
AS	0.608 (0.036)	0.862 (0.049)	0.378 (0.054)
UF	0.197 (0.082)	0.343 (0.131)	0.005 (0.005)
Mann Whitney 2-tailed tests			
CS – US	0.437	0.190	0.938
CS – UF	0.006	0.019	0.007
AS – UF	<0.001	0.005	0.001

in some cases (McFarlane-Tranquilla 2001), and, most likely, (3) our method had difficulty detecting early incubation failure. This uncertainty is the reason that we reported a range of fecundities based on assumptions that 0.95 or 0.80 of adult murrelets in the sample were in fact breeders, consistent with Hudson's (1985) review of alcid demography.

Marbled murrelets in our study area showed lower levels of interannual variability in reproductive success than seen in other alcids (Bertram et al. 2001). This may be because the inshore prey and ocean environments are not as variable for our study population in the Strait of Georgia, between southern Vancouver Island and the British Columbia mainland, as those found in adjacent continental shelf upwelling systems where most colonial alcids feed (Hobday and Boehlert 2001). Differences in abundance of Pacific sand lance have been shown between sites with varying oceanographic conditions (Robards et al. 2002); however little is known about interannual variation of inshore sand lance populations. Variation in forage fish populations remains an important area of research for coastal seabirds in the North Pacific Ocean that needs further study.

Marbled murrelet breeding-success estimates from other studies may be biased low. Breeding failure, which often occurs earlier in the breeding process, is easier to confirm than breeding success. Individuals that have not been confirmed as having failed cannot be considered as successful. Therefore, unknown cases may more likely be successful than failures. Furthermore, our results show that the probability of failure increases as breeders reach later reproductive stages. Our results show higher success during incubation than in previous studies, but our values are similar to other studies during the chick-rearing period (Hamer and Nelson 1995, Beissinger and Nur 1997). This might result from our nest-finding approach that may generate a more random sample in terms of nest location than samples from other studies, which depend mainly on nests sighted by observers from accessible locations. This idea is supported by our finding that nests located in sites inaccessible to human observers on the ground had higher mid-chick-breeding success than accessible sites (Table 3). Bradley (2002) detailed how the radio-marked murrelets in our study preferred to nest in more inaccessible habitats, with steeper slopes, and had higher breeding success at these sites.

Methodological Analyses

Using aerial radiotelemetry data from a large sample of murrelets and ground-truthed breeding-success data in a smaller sample of individuals, we showed that the behavior of murrelets at confirmed breeding sites did not differ from behavior at inaccessible suspected breeding sites. In addition, the behavior of successful breeders differed significantly from the behavior of failed breeders and nonbreeders. We detected a strong correlation between OP and incubation behavior. The observed duration of OP did not vary between confirmed and suspected breeders; however, murrelets that failed during incubation had OP values significantly lower than those of successful breeders. During chick rearing, both confirmed and suspected successful nest sites showed similar mean visitation rates that were, as expected, significantly higher than failed nests.

The 95% probability of locating the nest of a breeding murrelet was reached with only 25% of the bird's incubation period remaining. This low rate reflects the logistical difficulties of searching land area within, and sometimes beyond, 50 km of our capture location. This nest-detection issue may explain why some murrelets showed an extended OP but were not included in the confirmed breeder sample (Fig. 4). Locating nest sites is necessary for addressing questions about nesting habitat choice (F. Huettman and Y. Zharikov, Simon Fraser University, unpublished data). However, we believe that radiotelemetry is a useful tool for inferring key demographic parameters for the marbled murrelet, whose breeding behavior is difficult to observe. However, before we concluded that our results gave an accurate measure of breeding success, we examined our methodology for potential sources of bias.

Breeding Propensity and Initiation of Breeding

Detecting Early Breeding Failures.—One difficulty in using OP to assess the initiation of breeding is interpreting an OP that occurs for only a few days. A murrelet showing a very short OP might be a breeder that failed early in incubation. We have shown that locating the nest of a murrelet as soon as it begins breeding is quite difficult. Therefore, we may be underestimating the proportion of breeders in our population and overestimating nesting success due to our inability to detect early failures. This problem is common when evaluating nesting success (Mayfield 1975). However, these potential early failures misclassi-

fied as nonbreeders would not affect our estimates of fecundity, since the number of chicks fledged is unchanged.

On-Off Patterns Generated by Chance.—One possible alternative explanation for the OP patterns we observed is that the observed patterns might be due to random patterns in the data due to missed marine detections of murrelets on the ocean when they were actually present. In addition, murrelets might temporarily move outside the study area on certain days.

We may not have detected some murrelets in the marine survey area when they were actually present. Some radiotransmitters might periodically produce weak signals due to inherent qualities of that transmitter or the position of the antennae on the murrelet (e.g., Boyd et al. 2000). Submergence of the antennae, when murrelets dive to forage, stops transmission of the radio signal and might prevent detection. During water flights, we scanned numerous radiotransmitters ($n = 100$ in 1999, $n = 75$ in 2000). Because a complete scan of all radio frequencies would take 2.5–3 min on a 2-sec scan interval, a murrelet possibly could go undetected because the observer was scanning other frequencies. In areas of large concentrations of radiomarked murrelets, we attempted to make repeated searches to increase detection. Stationary land-based telemetry over areas of open water early in search flights also helped to increase marine detections by scanning each frequency slowly.

Because marbled murrelets have been observed to range over 100 km between marine and inland sites during the breeding season (Whitworth et al. 2000, Hull et al. 2001), birds may have temporarily foraged at marine sites outside our core search area during incubation. Therefore, some nesting murrelets that bred within our inland search area may have frequented marine areas outside our study area and would show OP values of short duration (Fig. 4). While marbled murrelets are marine birds, observations have been recorded of individuals loafing and foraging on inland lakes (Carter and Sealy 1986). However, we detected lake use by murrelets on only 3 occasions in over 100 hr of inland search flights over lakes (F. Cooke, Simon Fraser University, unpublished data); we therefore believe the effect of any lake use by murrelets on our OP data was minor.

Despite the potential bias of missed marine detections and temporary emigration on our marine detection data, we believe that these factors cannot explain the extended OP we observed as random events. For each breeding mur-

relet used in these analyses, we obtained up to 80 marine detections and saw strong site fidelity to our core marine survey areas (F. Cooke, Simon Fraser University, unpublished data). Multiple estimates of our detection probability of murrelets on the water, even overly conservative minimum estimates of 50%, would not randomly produce the OP durations we observed (Fig. 5). Thus, we conclude that our observed extended OP values are accurate indications of incubation behavior in marbled murrelets, and that our initial criterion of an OP value of 4 to indicate breeding likely is very conservative. Using a less-conservative criterion like an OP value of 2, the breeding propensity in our radiomarked murrelets would more closely resemble the values we used in our demographic modeling.

Confounding Effects on Classifying a Breeder through Radiotelemetry.—Certain attributes of a murrelet at capture may cause overestimation of nonbreeding in our study population through inferred radiotelemetry methods. McFarlane-Tranquilla (2001) used analyses of the egg precursor protein vitellogenin to show that some of the radiomarked females in our sample that did not breed, based on telemetry observations, were producing eggs at the time of capture. Therefore, while any capture or extremely early failure effect on breeding success appeared to be negligible for radiomarked murrelets that nested, estimates of proportions of nonbreeders in our population from radiotelemetry alone may have been biased high. Parameter adjustments are therefore necessary for demographic assessment of the population. The presence of prebreeders in our sample also might have overestimated our proportion of nonbreeders, but identification of 2-year, prebreeding murrelets in our sample (through plumage characters) suggests that their contribution to our study population was minor (F. Cooke, Simon Fraser University, unpublished data). Finally, capturing murrelets after they have already failed or when they are chick rearing (i.e., when they are absent from the nest during daytime nest search flights) could also inflate estimates of nonbreeding. However, the timing of our capture efforts appeared to complement the timing of egg production in our study population (McFarlane-Tranquilla et al. 2003).

Incubation Success

Temporal variation in initiation of breeding could affect our interpretation of results using OP duration as a measure of incubation success. The strongest behavioral inference in successful-

ly breeding murrelets appears to be an OP value of 15 (Fig. 4) relating to the approximately 30-day incubation period. However, this pattern would be observed only if radiotransmitter attachment and radiotracking began before the murrelet initiated nesting. Some confirmed breeding murrelets that successfully completed incubation showed OP values well below 15. In all of these cases, the OP began with the first telemetry observations. This suggests that these murrelets were already incubating at the time of radiotransmitter attachment.

We used 30 days as an estimate of incubation duration, but some variation is associated with this mean (Fig. 4). Because of this variation, as well as the logistical difficulties of starting telemetry observations of chick-rearing behavior immediately after hatch, differentiating between late incubation failure and early chick-rearing failure was difficult. Thus, results from murrelets whose radiotransmitters were attached later in the breeding season, and whose lay dates were likely prior to capture, must be carefully interpreted. Assuming that an observed OP value of 15 was necessary for successful incubation would lead to an overestimation of incubation failure.

Chick-rearing Success

Evaluating Mid-chick-rearing and Fledging Success.—Because successful nests showed higher rates of nest visitation than unsuccessful nests, we assumed that nest visitations corresponded to chick-feeding events. However, some murrelets may have been visiting their nest sites for reasons other than provisioning. These reasons might include visiting failed nest sites, prospecting for new nest sites, or defending territories (Naslund 1993, Nelson and Peck 1995, Bradley et al. 2002).

Results from radiotelemetry monitoring at nest sites and along flyways showed that murrelets with successful nests visited their breeding sites, presumably to feed chicks, more often than suspected failures. However, mid-chick-rearing success cannot be confused with fledging success. Tree-climbing data showed that nest visitation appeared to indicate that a nest site was active and a chick was being fed. With our limited resources to monitor nests, however, this telemetry observation is only valid at that time in chick rearing. A suspected, inaccessible nest could be identified as successful due to the presence of adults feeding young at day 20 of chick rearing, but that nest might still fail before the offspring fledges. Thus, mid-chick-rearing success is only a

proxy of fledging success. However, despite its shortcomings, the mid-chick measure has great utility by allowing success measures to be calculated for all nest sites, not just the 30% of nest sites for which fledging data could be obtained from tree climbing.

We might assume that rates of success in the final stage of chick rearing are similar in ground-accessible and inaccessible sites. However, the higher levels of mid-chick success we observed in inaccessible nests compared to accessible nests (Table 3) suggests that fledging success may be higher in these inaccessible habitats. Bradley (2002) found that higher reproductive success in our radiomarked murrelets was associated with steeper slopes and higher elevations. This suggests that our fecundity estimates from fledging data are likely conservative and actual rates may be closer to mid-chick fecundity values that we reported, since inaccessible sites often are in steep areas at higher elevation.

MANAGEMENT IMPLICATIONS

Our methods allowed the first estimation of reproductive success parameters for marbled murrelets from radiomarked individuals. While estimates of breeding parameters from radiotelemetry may slightly overestimate incubation success and the proportion of nonbreeders, our radiotelemetry results generated robust estimates of fecundity for our population. Fecundity estimates are more important in assessing the demography of avian populations than are nesting success data (Thompson et al. 2001). Management of marbled murrelet populations should, whenever possible, be informed by demographic field data on marbled murrelets and not estimates from other alcids. Although this data is costly and labor-intensive to collect, we have shown that it is possible to obtain. In addition, demographic analyses of survival, which is more important than fecundity for long-lived species, also must be investigated in tandem with studies of reproductive success (Cam et al. 2003) to ensure the most informed management strategy for marbled murrelet populations.

Potential differences in mid-chick-rearing success between accessible and inaccessible habitats suggest that radiotelemetry may help to reduce bias in estimating reproductive success in wildlife populations. We believe that our approach has utility for other species whose behavior and movement patterns might be used to assess breeding status and success. Our study is an example of the

valuable role that behavioral studies can play in conservation biology (Sutherland 1998).

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