

DO TWO MURRELETS MAKE A PAIR? BREEDING STATUS AND BEHAVIOR OF MARBLED MURRELET PAIRS CAPTURED AT SEA

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ABSTRACT.—Marbled Murrelets (*Brachyramphus marmoratus*) observed at sea usually are in pairs throughout the year. Although it has been assumed that these pairs are mates, this assumption has not been formally examined. Using data from three study sites during the breeding seasons of 1997–2001, we found that 92% of the birds that were paired at capture were of male-female pairs, and that paired females were more likely (73%) to be producing eggs than were single females (8%). Fourteen of fifteen pairs were tracked to a single nest location per pair. No pair members caught at sea were found breeding at separate nest sites. One pair was caught in two successive seasons, suggesting that at least some pairs are long lasting. Notably, pair members breeding together and radio tracked throughout the summer were detected without their breeding partners for 77% of the time. Thus, while pairs of Marbled Murrelets observed at sea most likely are members of a breeding pair, single murrelets observed at sea should not be assumed to be unpaired or nonbreeders. *Received 9 September 2002, accepted 5 December 2003.*

At-sea surveying is the technique most often employed to census Marbled Murrelets (*Brachyramphus marmoratus*) and to estimate local productivity and population sizes and trends (Sealy and Carter 1984, Piatt and Naslund 1995, Kuletz 1996, Agler et al. 1998, Kuletz and Kendall 1998, Kuletz and Piatt 1999, Speckman et al. 2000). Productivity indices typically are calculated as the proportion of hatch-year to after-hatch-year birds counted at sea (Kuletz and Kendall 1998, Kuletz and Piatt 1999). However, because breeding, sub-adult, and nonbreeding birds are indistinguishable by plumage (Sealy and Carter 1984), the resulting juvenile:adult ratios are unlikely to

accurately represent productivity and census estimates. Murrelet surveyors have reported that Marbled Murrelets at sea most often occur in pairs, during both summer and winter (Sealy 1972, Nelson and Hamer 1995, Strachan et al. 1995), and return to local areas in spring already paired (Sealy 1974). Individuals in pairs exhibit courtship behavior at sea (Nelson and Hamer 1995, Strachan et al. 1995); forage and loaf together (Sealy 1975a, Strachan et al. 1995); call to each other before, during, and after capture (Strachan et al. 1995, Nelson 1997, LMT pers. obs.); and usually are composed of a male and a female (hereafter M-F; Sealy 1972).

These anecdotes suggest that pairs observed at sea are actually mated, breeding pairs (Nelson and Hamer 1995). However, this assumption has not been confirmed (Gaston and Jones 1998). An estimate of the percentage of pairs observed at sea that are indeed mated and breeding together, and an understanding of the status of single birds observed at sea, would improve the accuracy of productivity indices calculated from at-sea surveys, thus allowing more meaningful interpretation of productivity ratios (Evans Mack et al. in press). In addition, information on pair bond maintenance and duration, and the relative use of marine habitat by pair members during the breeding

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TABLE 1. Most Marbled Murrelet pairs are male-female (M-F). One particular M-F pair was captured in both 1998 and 1999 in Desolation Sound.* Data are from British Columbia, Canada.

Variable	Location			Total
	Mussel Inlet	Desolation Sound	Clayoquot Sound	
Years	1997, 1999	1997–2001	2001	1997–2001
Total number of sexed pairs	23	39	2	64
M-F pairs	20 (87%)	37* (95%)	2 (100%)	59 (92%)
M-M pairs	1	1	—	2
F-F Pairs	2	1	—	3
Pairs with egg-producing females	19 (47%)	12 (75%)	—	31 (58%)
M:F sex ratio in dipnet capture sample	—	0.88 ($n = 943$)	1.19 ($n = 79$)	0.90 ($n = 1022$)

season, could be used to determine the optimal time frame to conduct population surveys in the context of breeding chronology, as well as further our understanding of this elusive seabird for which reliable data are difficult to obtain. Our objectives were to (1) test the assumption that M-F pairs were indeed mated, (2) examine the extent and duration of apparent pair bond behavior throughout the breeding season, and (3) examine the amount of time pair members were alone at sea.

METHODS

Study area and captures.—We captured 74 Marbled Murrelet pairs at three locations in British Columbia, Canada: Mussel Inlet (52° 51' N, 128° 10' W) during May of 1997 and 1999 ($n = 27$ birds); Desolation Sound (50° 05' N, 124° 40' W) from April to September, 1997–2001 ($n = 45$); and Clayoquot Sound (49° 12' N, 126° 06' W) during May 2001 ($n = 2$). We used dipnetting (also called “night lighting”; Whitworth et al. 1997, Vanderkist et al. 2000) to capture pairs at night (23:00–05:00 PST) on the open water; we also captured single murrelets that were either (a) obviously paired but whose pair member escaped capture or (b) apparently single at sea, with no partner nearby.

DNA sexing and identifying egg producers.—We determined the sex of 64 of the 74 pairs captured (Table 1). DNA was extracted from red blood cells following the methods in Vanderkist et al. (1999). Egg-producing females were identified by the presence of an egg yolk precursor (vitellogenin) in the plasma, using a diagnostic kit (Zn, Cat. No. 435–14909, Wako Pure Chemical Industries, Ltd.),

following the methods of Mitchell and Carlisle (1991) and Vanderkist et al. (2000). We obtained blood samples as described by McFarlane Tranquilla et al. (2003). Plasma samples were available only from birds taken at Desolation Sound (1999–2000) and Mussel Inlet (1997). For birds captured in Desolation Sound, we used exact χ^2 tests to compare the frequency of egg-producing females captured in pairs ($n = 64$, including females that were paired but whose partner escaped) to those captured alone (singles; $n = 12$). The mean egg production date plus one standard deviation (16 June) had been previously determined for Desolation Sound (McFarlane Tranquilla et al. 2003), and was used as a cut-off date after which some females would be past egg production and thus were excluded from the analysis. We collected plasma samples in Mussel Inlet during May, within the expected egg-producing period.

Radio tracking.—We used radio telemetry to monitor Marbled Murrelet behavior and daily at-sea attendance and location. Twenty-four Marbled Murrelet pairs received radio transmitters (Model 384 in 1998 and Model 386 in 1999, 2000, and 2001; Advanced Telemetry Systems, Isanti, Minnesota). Transmitters were attached between the scapulars of the birds following the methods of Newman et al. (1999) and Lougheed et al. (2002). The transmitters were deployed during the egg-producing period (20 April to early June), and remained active for a minimum of 80 days. We tracked radio-tagged birds by helicopter every day until 30 August or until the transmitter signal disappeared. Incubating pairs alternate regular 24-h incubation shifts, spend-

ing one day on the nest and the next day at sea, until incubation is complete. Individuals displaying this incubation pattern were classified as breeders; those that did not were classified as nonbreeders (see Bradley and Cooke 2001, Bradley et al. 2002). By monitoring nest attendance patterns, and by extrapolating to the end of incubation and chick-rearing periods (*sensu* Hamer and Nelson 1995), we were able to determine the specific breeding stage (i.e., pre-incubation, incubation, and chick-rearing stages) of radio-tagged pairs. Successful breeders were those radio-tagged individuals for which more than 30 days of incubation shifts were recorded, and were subsequently detected flying inland (presumably to feed chicks) after these incubation shifts ended. Unsuccessful breeders were those whose incubation shifts terminated prematurely and who did not appear to make regular inland flights.

At-sea associations of pair members.—To address the extent and duration of pair member association throughout the breeding season, we compared the behavior of radio-tagged pair members to each other and to other radio-tagged murrelets. We had sufficient data to do this only for Desolation Sound. We used aerial radio telemetry detections for each radio-tagged individual to calculate (1) the amount of overlap of Kernel home ranges between pair members, and (2) direct distances between pair members as detected and geo-referenced from the air. The locations of individuals detected during aerial telemetry flights were geo-referenced to landmarks, and digitized (Bradley et al. 2002) in a Geographic Information System (ArcView ver. 3.2; Environmental Systems Research Inst., Inc. 2000). Because the radio locations spanned the breeding season for most individuals, telemetry locations from each individual were pooled and treated as one record (see Kenward 2001). We used ArcView Animal Movement extension ver. 3.1 (Hooge and Eichenlaub 1997) to calculate the Kernel home range for each radio-tagged Marbled Murrelet having more than 24 telemetry detections, with a nonparametric kernel density estimator, and a fixed kernel method (Seaman and Powell 1996, Seaman et al. 1999, Kenward 2001). We defined core home range (hereafter “home range”) as the 30% kernel home range; we

chose this conservative cut-off for a more accurate representation of primary habitat use (Samuel et al. 1985, Seaman et al. 1999, Shepherd 2001). We used ArcView to calculate the overlap (weighted percent shared home range area) of home ranges between murrelets.

We used individual home range polygons to calculate the extent of habitat use overlap of 16 individual pair members to (1) their pair partner and (2) to other randomly selected, radio-tagged murrelets that originally had been captured in pairs. To control for potential seasonal differences in reproductive status between randomly selected pair members, our selection of pairs included only those birds captured within <2 days of each other. We used two-sample *t*-tests to compare the overlap of home ranges between 8 pairs and between 22 randomly selected pairs (we used 22 because this was the maximum number of pair combinations we could make).

We were not able to address pair association in each separate breeding stage (pre-incubation, incubation, and chick-rearing) because sample sizes for some pairs were insufficient to calculate separate kernel home ranges at each stage. Instead, we used telemetry detections to assess the distance between pair members, as a measure of spatial association during each breeding stage. From the air, radio-tagged pair members appeared to be either (1) at the same location (together), (2) at different locations in the study area (apart), or (3) alone at sea (alone; i.e., their partners were not in Desolation Sound or the surrounding marine area). For the 8 pairs and 22 randomly selected pairs, we used χ^2 analysis to compare the number of times pair members were together, apart, and alone during the study period.

In six cases, telemetry detections were sufficient to further categorize the spatial association of pair members (i.e., together, apart, alone) according to breeding stage (pre-incubation, incubation, or chick-rearing). For these six cases, we used repeated measures ANOVA to compare the amount of time together, alone, and apart during each breeding stage. Daily detections of radio-tagged murrelets in both pair and randomly selected pair groups were made within a few hours.

TABLE 2. Most Marbled Murrelet pair members, radio-tagged at sea, were tracked to the same nest site location and determined to be breeding together. This was the case in all three study sites. Sexes of some birds were unknown, but most likely were members of M-F pairs since they were tracked to the same nest site. Data are from British Columbia, Canada.

Variable	Location			Total
	Mussel Inlet (1999)	Desolation Sound (1998–2001)	Clayoquot Sound (2001)	
Pair members				
Bred together	6	6	2	14
Neither bred	2	7	0	9
Bred separately	0	0	0	0
Only one bred	0	1	0	1
Total pairs radio-tagged	8 unknown	14 (11 M-F, 3 unknown)	2 M-F	24

RESULTS

Sex ratio in pairs.—Ninety-two percent of sexed pairs ($n = 64$) were M-F pairs, and 8% were same-sex pairs (Table 1). Given the sex ratio in the capture sample, this percentage of M-F pairs is greater than one would expect based on random association of pair members (for Desolation Sound: $\chi^2 = 11.25$, $df = 1$, $P < 0.007$; for Clayoquot Sound: $\chi^2 = 27.29$, $df = 1$, $P < 0.001$; Table 1). In Desolation Sound, one M-F pair was captured in both 1998 and 1999, suggesting at least some between-year fidelity.

Egg producers.—Fifty-eight percent of the pairs captured included an egg-producing female (Table 1). We also assessed egg produc-

tion in paired females (i.e., each paired female captured, whether the other pair member was captured or not) compared to single females. Paired females (73%, $n = 64$) were more likely to be producing eggs than single females (8%, $n = 12$; $\chi^2 = 18.41$, $df = 1$, $P < 0.001$).

Radio-tagged pairs.—We detected incubation behavior for 63% (15/24) of the radio-tagged pairs (Table 2). Of the 15 pairs showing incubation behavior, 14 were radio tracked to a single nest location per pair. No radio-tagged pair members were found breeding at separate nest sites (Table 2). In one pair, the female appeared to be incubating a month after capture while the male of this pair behaved as a nonbreeder throughout the season.

At-sea associations of pair members.—The home range size of pairs ($n = 8$) and randomly selected pairs ($n = 22$) was not significantly different (two-sample $t = 0.54$, $df = 33$, $P = 0.59$). However, the percent shared home range area between pair members ($53.3\% \pm 7.1$ SE) was significantly greater than that shared by randomly selected pair members ($30.1\% \pm 5.2$ SE; two-sample $t = 2.64$, $df = 22$, $P = 0.015$). Members of pairs were detected together $40.0\% \pm 6.7$ SE of the time. This was significantly greater than for randomly selected pairs detected together ($11.0\% \pm 1.2$ SE of the time; two-sample $t = 4.27$, $df = 7$, $P = 0.004$).

For six pairs with sufficient data to assess associations during each breeding stage (Fig. 1, Table 3), pair members were detected together more frequently during the pre-incubation stage (34%) than during the incubation

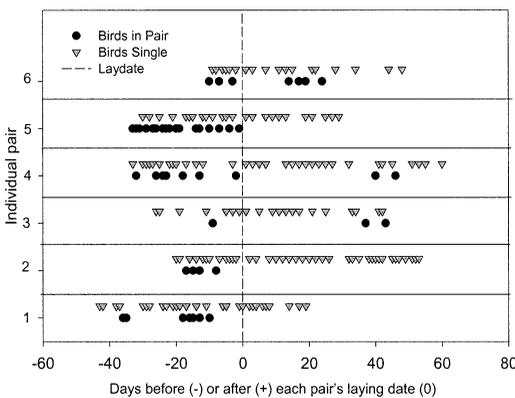


FIG. 1. Marbled Murrelet pair members were detected in pairs (together) prior to laying, and were detected as single birds (either apart or alone) for most of the breeding season. Some pair members were together after the incubation stage. Data are from British Columbia, Canada, 1997–2001.

TABLE 3. The members of six pairs of radio-tagged Marbled Murrelets most often were detected alone (at sea) or apart (in different locations in the same study area), and thus appeared as single birds. Values within the table are percentages of detections; values in parentheses are mean number of detections per pair. Data are from Desolation Sound, British Columbia, Canada, 1998–2001.

Attribute	Breeding stage			Total ($\bar{x} = 67$)
	Pre- incubation ($\bar{x} = 35$)	Incubation ($\bar{x} = 21$)	Chick- rearing ($\bar{x} = 12$)	
Alone	26	93	70	53
Apart	39	2	10	24
Together	34	5	20	23

or chick-rearing stages (repeated measures ANOVA, Wilk's Lambda = 0.38, $F_{2,6} = 4.9$, $P < 0.055$; Table 3). During the pre-incubation stage, pair members would have appeared to the at-sea observer as single (i.e., either alone or apart) for 65% of the time (Table 3). Pair members were alone most often during the incubation stage (93%). One pair appeared to fail during incubation and re-associated after this event (Fig. 1, pair 6). Overall, these six radio-tagged pair members at sea were single (either apart or alone) 77% of the time, and together 23% of the time (Table 3; test for two proportions, $Z = 9.07$, $P < 0.001$). Radio-tagged pair members that were successful breeders ($n = 6$) were detected together for a significantly longer duration (55.0 days \pm 29.4 SD) than those that were unsuccessful breeders ($n = 5$; 19.4 days \pm 18.5 SD); ANOVA, $F_{1,9} = 5.5$, $P = 0.044$).

DISCUSSION

Our data suggest that a large majority of Marbled Murrelets caught or observed together as pairs early in the breeding season are mated pairs. Most pairs at sea were of opposite sex, nested together, associated more at sea, and shared a greater proportion of home range area with each other than with randomly selected pair members. Nevertheless, we found that pair members spent more than half of their time alone or apart from each other at sea. Not only were pair members detected at sea as singles during incubation (as in Sealy and Carter 1984, Evans Mack et al. in press), but they also were single for more than half

of all telemetry detections throughout the breeding season.

Our study confirms the findings of Sealy (1975b), who also found most Marbled Murrelet pairs to be male-female pairs. The few same-sex pairs we found may have been together while their mates were incubating (Evans Mack et al. in press). Although there is little evidence that Marbled Murrelets forage at night (Jodice and Collopy 1999, but see Strachan et al. 1995), Marbled Murrelets often forage together in pairs during the day (Hunt 1995, Strachan et al. 1995), which likely increases foraging efficiency (Sealy 1972). Thus, the occurrence of same-sex pairs at night may be due to associative foraging. Alternatively, same-sex pairs may have been captured together coincidentally.

The strongest support for the assumption that pair members are mated came from the confirmation that all pairs that bred did so together, each pair at a single nest site. Only one pair appeared to divorce; in this case, either the male did not participate in incubation, was replaced as a mate, or may have been captured coincidentally near the female. Additional support that pair members are breeding together comes from our finding that during the laying period, 73% of pairs contained an egg-producing female.

Although murrelets captured in pairs were breeding together, radio-tagged pair members most often were away from their partners at sea. Without concurrent at-sea surveys, we cannot confirm that pair members found alone or apart by aerial radio telemetry were actually separate from other untagged murrelets at sea (as in Evans Mack et al. in press). Despite the amount of time spent alone, the marine home ranges of pair members overlapped more with their mates than with other radio-tagged murrelets. Because the 30% kernel home range is considered an accurate description of the area used most frequently by an animal (Samuel et al. 1985), we are confident that the home range overlap is a real phenomenon. This suggests that although marine "hotspots" are used by many murrelets, paired murrelets maintain a type of home range at sea, perhaps used more for foraging or loafing with their partners than with other murrelets. The significance of fidelity to and

defense of marine home ranges by murrelets is currently unexplored.

Murrelet pair members are assumed to maintain pair bonds throughout the year (Sealy 1974, Nelson and Hamer 1995). However, prior to this study, there have been no confirmed observations of breeding pairs maintaining a pair bond. We found one-third of murrelet pairs together during the pre-incubation stage and after chick rearing (Table 3), and one pair together in consecutive seasons. We also detected three pairs together during incubation at least once; at-sea associations of pair members during incubation may correspond with skipped incubation shifts (Bradley et al. in press). Remaining associated throughout the breeding season probably increases foraging efficiency (Sealy 1972) and promotes pair fidelity for future years (Nelson 1979). However, as in other species, pair bonds may break down following a failed reproductive event. Consistent with this idea, members of successful breeding pairs were detected together for longer than unsuccessful pairs.

As Kuletz and Kendall (1998) suggested, numbers of breeding-plumaged adults present during early incubation would more accurately reflect the local breeding population than those present during late summer. Further, we suggest that the number of pairs observed during the pre-incubation stage can provide an estimate of breeding attempts when calculating productivity, but we caution that failed breeders also may appear in pairs.

Finally, surveyors should be aware that although pairs at sea are likely mated, pair members at sea spent only 20–40% of their time together throughout the breeding season, including during the pre-incubation stage when they are expected to be together the most. Thus, the presence of single murrelets at sea is probably not suitable to infer incubation periods, numbers of nonbreeders, or numbers of failed breeders. However, as Evans Mack et al. (in press) suggest, the proportion of single murrelets during the incubation period may help assess the proportion of nesting murrelets. We support this suggestion because our pairs were separate 95% of the time during incubation (Table 3). At the same time, we caution at-sea surveyors to use additional methods (Hamer and Nelson 1995, Loughheed et al. 2002, McFarlane Tranquilla

et al. 2003) to determine breeding phenology at a local scale in order to make more accurate estimates of breeding pair numbers. Because pairs spent most of their time alone throughout the season, single murrelets in the study area at any time can not be assumed to be unpaired or failed breeders.

ACKNOWLEDGMENTS

We thank the many field assistants involved whose hard work and sleepless nights made this project possible. C. A. Botero, G. A. Keddie, and C. Theissen deserve special thanks for field support and radio tracking. D. Taylor, J. Vandendort, and B. White of E&B Helicopters (Campbell River, British Columbia) skillfully flew helicopters for the radio telemetry component of the study. F. Cooke and three anonymous reviewers provided constructive criticism of the manuscript, and C. Smith and B. Sherman provided logistical support. Generous financial support was provided by Forest Renewal British Columbia, National Sciences and Engineering Research Council, Centre for Wildlife Ecology at Simon Fraser Univ., Canadian Wildlife Service, British Columbia Ministry of Forests, Science Council of British Columbia, Timber-West Forest Ltd., International Forest Products Ltd., Western Forest Products Ltd., Weyerhaeuser, National Council for Air and Stream Improvement, and Pacific Forest Products Ltd.

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