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Author(s): Laura A. McFarlane Tranquilla, Russell W. Bradley, David B. Lank, Tony D. Williams, Lynn W. Lougheed, and Fred Cooke

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The Reliability of Brood Patches in Assessing Reproductive Status in the Marbled Murrelet: Words of Caution

LAURA A. MCFARLANE TRANQUILLA[1,5], RUSSELL W. BRADLEY[2], DAVID B. LANK[1], TONY D. WILLIAMS[1], LYNN W. LOUGHEED[3] AND FRED COOKE[4]

[1]Centre for Wildlife Ecology, Department of Biological Sciences, 8888 University Drive, Simon Fraser University Burnaby B.C., V5A 1S6, Canada

[2]Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94971, USA

[3]Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY 14853, USA

[4]Larkin's Cottage, 6 Lynn Road, Castle Rising, Norfolk, PE31-6AB UK
[5]Email: lat@sfu.ca

Abstract.—The assumption that brood patches identify incubating birds is a pervasive one in avian literature, and as a result, brood patches are often used to infer breeding status. Although the developmental stages of the brood patch with specific reproductive stages in passerines have been described, this information for seabirds is not often reported. Thus, for birds whose breeding activities are not easily observed, it is difficult to confirm (1) that it is valid to assume that a bird which has some stage of brood patch is a nester or putative nester, and (2) whether specific stages of brood patch development reflect specific stages of the breeding cycle. We tested the utility of brood patch scores to infer breeding status in a non-colonial seabird, the Marbled Murrelet *(Brachyramphus marmoratus*), a species always captured away from the nest site. We confirmed the breeding status of murrelets with brood patches, and assessed the specific stages of brood patch development to the timing of egg-production (using a physiological analysis) and the onset of incubation (using radio telemetry). Murrelets with brood patches were not always nesters or putative nesters (58% of birds with brood patches were producing eggs, and 56% of radio-tagged birds with brood patches began incubation), and brood patch score did not predict which birds were more likely to become egg-producers or incubators. Specific brood patch stages did not always correlate with specific breeding stages (e.g., the brood patch of egg-producers ranged from absent to fully-developed). Birds with fully developed brood patches took from 3-30 days to start incubation. Brood patch development accurately depicted the average population incubation time, but we caution against using brood patches to predict the timing of an individual breeding attempt, and suggest that when possible, researchers should try to confirm breeding activities using other methods. *Received 24 June 2002, accepted 12 October 2002.*
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A brood patch is an area of highly vascularized, bare skin found on the abdomen of incubating birds (Bailey 1952; Phillips *et al.* 1985), which transfers heat directly from the parent to the egg or chick. Many birds lose abdominal down within a few days of egg-laying (Bailey 1952; Manuwal 1974; Gill 1995), and the close timing of vascularization of the brood patch with the onset of incubation can provide criteria for determining lay-date (Ainley *et al.* 1990). For this reason, using brood patches to assess breeding status is common practice (see Deviche 1997; Ainley *et al.* 1990). However, in a few species of seabirds, pre-breeders lose abdominal down (Bailey 1952; Ainley *et al.* 1990; Gaston and Jones 1998), which complicates assessment of breeding status made from brood patches alone. In addition, partial or incomplete brood patch development that may occur in nonbreeding adults, young pre-breeders, or brood patches remaining after breeding failure, will complicate breeding status assessments. These problems can be addressed when the study species are colonial seabirds, for which breeding can be directly assessed using other methods. However, in non-colonial species, confirming breeding status that has been inferred by presence of a brood patch is more difficult. Although breeding timing is well studied in birds (Birkhead and Nettleship 1982; Ainley and Boekelheide 1990; Murphy 1995; Hipfner 1997; Hipfner *et al.* 1999), few studies report the developmental stages of seabird brood patches with respect to specific reproductive stages. Likewise, confirmation of breeding status that has been remotely assessed using a brood patch is rarely reported. We assessed the utility of brood patches to infer reproductive status in non-colonial, forest-nesting alcid, the Marbled Murrelet (*Brachyramphus marmoratus*), for which breeding status is difficult to confirm (Cooke 1999).

As in studies of many other forest-nesting birds, Marbled Murrelets are always captured away from the nest (Kaiser *et al.* 1995; Vanderkist *et al.* 2000) and thus, examined in the absence of any direct information on breeding status. Because remote assessment is the only practical option for studying Marbled Murrelets (Speckman *et al.* 2000), and because both pre-breeders and adults have identical plumage during the breeding season (Sealy 1975), brood patches are the only external physical sign that might be used to infer breeding status at the time of capture. However, it is not known how long a brood patch takes to develop and regress in Marbled Murrelets, nor how long a fully-developed brood patch is present, making it difficult to use brood patches to infer the onset of incubation for individuals. Thus, this study compares stage of brood patch development to both the propensity to breed and the timing of breeding, using two additional remote assessments of breeding status. (1) Analysis of the amount of vitellogenin (VTG), an egg-yolk protein present in the plasma of egg-producing females (Deeley *et al.* 1975; Redshaw and Follett 1976), allows identification of egg-producing murrelets (Vanderkist *et al.* 2000). Egg-development in alcids takes about 14 days (e.g., Cassin's Auklet [*Ptychoramphus aleuticus*; Astheimer 1986], Common Murre [*Uria aalge;* Murphy 1995], Brunnich's Guillemots [*Uria lomvia*; Hipfner *et al.* 1999] and VTG is elevated before the egg is completed (i.e. during rapid yolk development; Challenger *et al.* 2001). (2) Radio telemetry, often used to study movement and habitat use (Bunck and Pollack 1993; Kenward 2001), was used to track the daily activities of Marbled Murrelets throughout the breeding season, allowing us to detect the onset of incubation (Hull *et al.* 2001; Bradley *et al.* 2002; Lougheed *et al.* 2002). The objectives of this study were to assess the direct correlation of specific brood patch scores with egg-production and incubation, and whether a brood patch score could be used to correctly infer the reproductive status of an individual.

We generated a series of predictions based on six simple assumptions: (1) that brood patch development usually occurs rapidly, within a few days (in passerines, Bailey 1952; and in auklets, I. Jones pers. comm.); (2) that birds initiating brood patch development are likely to become incubators; (3) that egg-production, as indicated by elevated VTG, should precede incubation; (4) that a fully-developed brood patch indicates a bird is incubating, or will be incubating within 1-2 days; (5) that VTG and brood patch measurements provide an assessment of reproductive status prior to capture; and (6) that capture and handling do not substantially affect the subsequent timing and probability of starting incubation. Our predictions were:

(1) If brood patch development coincides with egg-production, then elevated VTG should be seen when brood patches are developing.

(2) If the onset of a fully-developed brood patch coincides with the beginning of incubation, then a fully-developed brood patch should first occur on or just prior to the date of egg-laying, and continue for the duration of incubation (approx. 30 days).

(3) If natural causes (i.e. predator disturbance, re-nesting) alter the timing of egg-laying or influence egg loss, there will be disagreement between predicted (VTG and brood patch) and observed (radio-telemetry) lay-dates for individuals. The result will be a poorer apparent relationship between predictions (1) and (2), but no disagreement between our three study methods (i.e., brood patch, VTG, and radio-telemetry), because all groups will be similarly affected by natural disturbance.

(4) If radio-tagging affects alter the timing of egg-laying or influence egg loss, there will be disagreement between the population's predicted timing of reproductive stages based on VTG or brood patch scores, and observed laying dates based on radio telemetry information. The result will be a poorer apparent relationship between predictions (1) and (2), and overall disagreement between three study methods.

METHODS

Captures and Study Area

Marbled Murrelets were captured using "dip netting" (Whitworth *et al.* 1997; Lougheed *et al.* 1998) in Desolation Sound, British Columbia (50°05'N, 124°40'W). Captures occurred at night (between 22.00h and 05.00h PDT) from 20 April to 4 September 1999, and 19 April to 26 August 2000. Captures also occurred in 1998 (5 May to 11 August), but due to missing nesting data, that year is reported only briefly in the results.

Study Species and Brood Patch Scoring

Marbled Murrelets are unique among Alcidae, in that they nest at largely inaccessible sites, high in old-growth coniferous trees (Nelson 1997). Their cryptic nesting sites and crepuscular behavior (Nelson 1997) allow few opportunities to observe breeding activities such as egg-laying, incubation, or chick-feeding. Both male and female Marbled Murrelets incubate the egg and have brood patches that are identical in appearance (Sealy 1972). For the Marbled Murrelet, inclusion of breeding status and thus, reproductive output, (Thompson *et al.* 2001) would allow better fecundity estimates for demographic analyses. A simple field measurement such as a brood patch score that could provide reliable information on reproductive potential would be very valuable.

Marbled Murrelets have one large central brood patch (Sealy 1972); Nelson (1997) and Gaston and Jones (1998) incorrectly reported two lateral patches. For all 522 birds captured in 1999 and 2000, we assigned a single score to the brood patch, from BP 0-6, according to Sealy (1972):

BP0 = no evidence of defeathering (similar in appearance to BP 6, but occurs early in breeding season).

BP1 = beginning loss of down and contour feathers.

BP2 = almost complete loss of down and most contour feathers, vasularization beginning.

BP3 = complete loss of feathers, heavy vascularization; fully-developed.

BP4 = regression beginning with down appearing, especially around the edges, sheaths of new contour feathers appearing.

BP5 = most of the area down-covered, contour feathers beginning to break out of sheaths.

BP6 = complete regression; looks like BP 0, but occurs at the end of the breeding season.

In the field, BP0 can be confused with BP6 since they look alike (Sealy 1972), but the distinction is made using relative timing, with BP6 only occurring late in the season. However, to make a distinction between the two, the frequency distributions of BP0 and BP6 (i.e., 'no BP') as scored in the field were plotted, and the seasonal overlap between the two was assessed to determine a cutoff date after which the absence of a BP would be classified as BP6 (L. McFarlane Tranquilla, unpubl. data). For some analyses, we pooled brood patch scores into four developmental stages (see Bailey 1952): absent (BP0), developing (BP1-2), fully developed (BP3-4) and regressing/regressed (BP5-6). BP4 was included in the "fully developed" category because a definite distinction between BP3 and BP4 was sometimes difficult. This study used the following terms, based on assumptions of what brood patch scores indicate, to describe the breeding status of birds: "pre-breeders" (expected to have BP0) describes young birds that are reproductively immature; "early breeders" (expected to have BP0) are reproductively mature, but have not yet initiated breeding; "breeders" (could have BP1-5) are reproductively mature and have begun a breeding attempt; and "post-breeders" (BP6) have presumably completed their breeding attempt.

Vitellogenin Analysis and DNA Sexing

From 150 of 522 birds captured, blood samples (1-2 ml) were taken from the brachial vein, centrifuged, the plasma removed, and red blood cells and plasma frozen at -20°C until transportation to laboratory facilities for further analysis. VTG concentration in the plasma was determined indirectly, following the methods of Mitchell and Carlisle (1991) and Vanderkist *et al.* (2000). Vitellogenic zinc (VTG-Zn), measured in micrograms per milliliter ($\mu g\ ml^{-1}$), was used as an index for VTG, and identified egg-producers, as described and validated for Marbled Murrelets (Vanderkist *et al.* 2000). Because VTG is elevated during yolk development (Challenger *et al.* 2001) and the egg probably takes 14 days to make (as in other alcids), we estimated that, on average, egg production was detected when birds were halfway through egg-production (i.e., about seven days before egg laying would occur).

Radio Attachment

Radio transmitters (weight 3 g, Advanced Telemetry Systems, model 386, Isanti, Minnesota) were attached to 175 birds with subcutaneous anchors in 1999 and 2000, following the methods of Newman *et al.* (1999), but without sutures or anesthetic. Instead of sutures, each radio was glued with a small amount of Bird Epoxy (Titan Corporation, USA) to the dorsal feathers. In 1998, radios (model 384, ATS) were attached to 45 birds. All radio transmitters were attached before the end of June (1999) or the end of May (1998, 2000). They had a lifetime of about 80 days, and usually remained secure on the birds for the duration of the breeding season (four to five months) in 1999 and 2000.

Determining Lay-Date

Lay-dates were determined for 24 birds in 1998, 36 birds in 1999, and 29 birds in 2000. Lay-date (used synonymously with "egg laying" and "onset of incubation") was assigned based on data from aerial radio telemetry, which tracked the presence of radio-tagged birds on the water (foraging/staging area) and in the forest (nest site) (Bradley 2002). The presence or absence of individual radio-tagged birds on the water was noted daily throughout the study (April to August). Because male and female Marbled Murrelet pairs incubate their single egg in equal, regular incubation shifts of 24 hours (Nelson 1997; Bradley *et al.* 2002), incubating birds are detected at sea on alternate days, spending one day on the nest during the incubation shift, and the next day at sea foraging (Bradley 2002). Radio telemetry detected this pattern of presence and absence of radio-tagged birds in the foraging area (Lougheed *et al.* 2002). Prior to incubation, the radio-tagged individuals were detected at sea daily, but once incubation began, each radio-tagged bird established a regular pattern of alternate daily at-sea attendance; the day that these regular patterns began was considered to be lay-date (Bradley 2002; Lougheed *et al.* 2002). Birds with active radios remaining in the area were considered not breeding if this activity pattern was not established. Daily patterns of presence and absence at sea were confirmed by numerous inland flights, to detect the radio-tagged birds at nest sites on the appropriate day, i.e. when it was absent at sea (Bradley 2002). In addition, the male and female of a few pairs were both radio-tagged, and were detected at sea on alternate days, exhibiting the 24-hour incubation pattern (Bradley *et al.* 2002). Birds failing immediately following laying would not have been detected as "failed breeders", as the daily presence-absence patterns would not have been present long enough to infer the laying date.

Comparing Dates of Egg-Production, Egg-Laying, and BP3

To assess the relative timing of egg-production, egg-laying, and incubation (i.e. address prediction 3), we compared seasonal dates on which birds were detected as egg-producers (via VTG), egg-layers (via radiotelemetry), and putative incubators (BP3). Because radio-tagged birds were only captured early in the breeding season, for this comparison, we restricted the other two datasets (VTG and BP3) to that window of time in which the radio-tagged birds were captured. Thus, the comparison was made for three groups of birds, captured in the same window of time (19 April-16 June). We described and compared the timing of breeding activity as assessed in each of these three groups. "Egg-production" dates describe when females had elevated VTG; this describes dates that eggs were produced, but had not yet been laid. "Lay-date" was the date that radio-tagged birds started incubation, as determined by radio telemetry. "BP3" was the date (between 19 April-16 June) when birds had fully developed brood patches, and were thought to be incubating. We expected the mean dates and/or the distribution of dates for each of the three measures of nesting activity to be closely related (prediction 3), with expected mean egg-production preceding mean lay-date (by approx. half the time it takes to make an egg), and mean BP3 coinciding with mean lay-date.

Statistical Analyses

All birds in this study were captured only once; thus analyses of sequential brood patch scores are based on data from different individuals. Brood patch scores and blood samples for physiological analyses were taken at the time of capture, while egg-laying dates were determined using radio telemetry after capture; thus, all brood patch and physiological measurements were made without prior knowledge of reproductive status. All statistical analyses were made using Minitab 13 for Windows, or SAS (SAS Institute, version 8). Data on plasma VTG came from a group of birds containing both radio-tagged and non-radio-tagged individuals; however, not all radio-tagged birds were bled. Data on incubation status was available only from radioed birds. There were no discernible differences in brood patch development between males and females (Sealy 1972, this study), or between years, so brood patch scores were pooled by sex (except in VTG analyses) and year. Normality was tested using the Anderson-Darling Normality test. ANOVA with Tukey's pairwise comparisons were used to test differences between mean dates for egg-producers, lay-dates, and presence of fully developed brood patch. The median dates of breeding chronology were tested for significant differences, but did not vary between 1999 and 2000 (Kruskal-Wallis test, $H = 0.82$, n.s.) so years were pooled. Logistic regressions (providing chi-square values) were used to (1) assess differences in proportion of egg producers by brood patch score, and (2) differences in proportions of incubators by brood patch score. For the latter analyses, BP5 and BP6 were not present early in the season when radio-tagging took place, nor did they ever correspond with egg-production, thus BP5 and BP6 were left out. ANOVA with Tukey's pairwise comparisons were used to test VTG in groups with different brood patch scores and to test significant differences between brood patch scores in respect to lay-dates. Logistic regression was used to test the relationship between brood patch score and nearness to lay-date.

Where applicable, results are reported as means $\pm$ SE. In all box-plots, the box represents the middle 50% of the data. The line through the box represents the median, and dotted lines or dots in the box indicate means. The lines (whiskers) extend to the 10th and 90th percentiles of the data. The 5th and 95th percentile outliers are represented by asterisks (*).

RESULTS

During the study, three fully-formed eggs were laid at the time of capture, from females with BP2-3 (consistent with prediction 1). Larger sample sizes came from the comparisons of indirect (brood patch), direct (VTG), and remote (radiotelemetry) assessments of reproductive status.

Seasonal Distribution of Brood Patch Scores.

Marbled Murrelets ($N = 522$) were captured with brood patches in all stages of development, from BP0-BP6, with the largest proportion (37%) having BP3. The seasonal distribution (1999 and 2000 pooled) of brood patch scores is shown in Fig. 1. Birds lacking brood patches (BP0 and BP6) occurred throughout the breeding season (end of April through early September, Fig. 1). Mean dates for BP3 through BP6 were significantly different from each other (ANOVA with Tukey's pairwise comparisons, $P < 0.001$), showing a seasonal progression of brood patch stages. Mean dates for BP1 and BP2 were not significantly different, probably due, in part, to the difficulty in grading the difference between them in the field. Birds with BP3 (fully developed) were found from 27 April to 6 August.

How Well Do Brood Patches Predict Breeding Status?

Prediction 1: Coincidence of brood patch development with egg-production. Egg-producers (N = 54) had BP0-BP4, but never BP5-BP6. There were no differences in the proportion of egg-producers vs. non-egg-producers in BP0 through BP4 ($\chi^2_4 = 5.23$, N = 122, n.s.) (Table 1). As females progressed through brood patch stages, plasma VTG levels progressed as described in Table 2 (one-way ANOVA, $F_{6, 143} = 4.45$, $P<0.001$ with Tukey's pairwise comparisons). When pooled by developmental stage, VTG in females with BP0 was not significantly different from that in birds with developing brood patches (BP1 and BP2) (Fig. 2) (Mann-Whitney, W = 142, n.s.), contrary to prediction 1. However, consistent with the prediction, birds with fully developed brood patches (BP3-4) had lower VTG than those with developing brood patches (BP1-BP2) (Mann-Whitney, W = 1677, $P < 0.05$) and had significantly higher VTG than birds with regressing brood patches (BP5-BP6) (Mann-Whitney, W = 5305, $P < 0.01$) (Fig. 2). However, there remained an unexpectedly large proportion of egg-producing females with BP3-BP4 (Table 1).

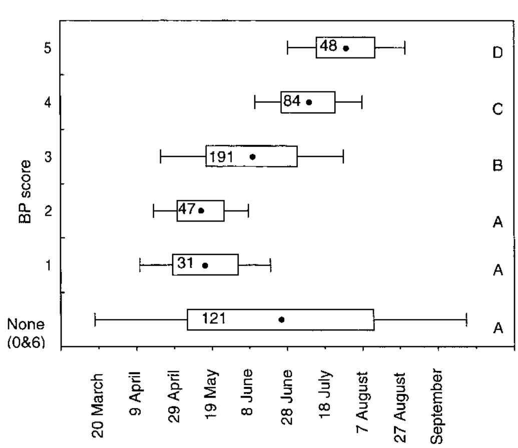

Figure 1. Brood patch (BP) scores versus seasonal date in all Marbled Murrelets (1999 and 2000 pooled data). BP0 and BP6 are pooled (see methods) into the "None" category. Numbers inside boxes indicate sample size. Different letters indicate boxes with means (indicated by dotted lines) that are significantly different, while the same letter indicates means are not significantly different.

Prediction 2: Brood patch development with proximity to lay-date. We assessed the brood patch scores of 139 radio-tagged Marbled Murrelets when captured and their subsequent incubation behavior, detected using radio tracking (Table 1, Fig. 3), and 56% of these individuals were detected as incubating birds. There was no relationship between at-capture brood patch score and probability of being detected subsequently as an incubator ($\chi^2_4 = 2.91$, N = 139, n.s.) (Table 1). The remaining birds (i.e., the "non-incubators") remained in the study area, but showed no evidence of incubation activity.

Radio-tagged birds caught before lay-date had brood patches ranging from BP0-BP3 (Fig. 3). The average estimated number of days for a bird with a specific brood patch score to reach its subsequent lay-date were as follows: BP0 = 25 ± 3; BP1 = 23 ± 6; BP2 = 17 ± 3; BP3 = 13 ± 3 days from capture to lay-date (Fig. 3). In spite of this trend towards higher brood patch scores as time to reach lay-date decreased, brood patch score overall did not vary significantly with proximity to lay-date ($\chi^2_1 = 3.35$, N = 80, n.s.). Brood patch development (BP1-BP2) and the occurrence of BP3 with respect to individual lay-dates (prediction 3) were highly variable. Forty-six percent of birds had developing (BP1-BP2) or developed (BP3) brood patches greater than 20 days (up to 65 days) in advance of observed lay-dates (Fig. 4). While this implies a

TABLE 1. Percentage egg-producing (i.e. not radio-tagged, N = 122) and percentage incubating (i.e. radio-tagged, N = 139) Marbled Murrelets in each brood patch category. Data is from 1999 and 2000 pooled. Egg-producers were detected using plasma VTG concentrations, and incubation was detected using radio-telemetry. Percentages of egg-producers and incubators does not vary significantly with brood patch score (logistic regression, χ^2 = 5.23, n.s.; χ^2 = 2.91, n.s., respectively).

	Females with plasma VTG assessed		Radio-tagged murrelets (both sexes)	
BP score	N	Percentage egg-producers	N	Percentage incubating
0	12	50%	30	47%
1	10	70%	19	68%
2	15	68%	23	65%
3	69	58%	65	53%
4	16	32%	2	50%
Total	122	44%	139	56%

long period of brood patch development, 7% of birds had BP0-BP2 only five days before lay-date, suggesting the ability to reach full brood patch development quickly.

Inconsistencies between predicted and observed incubation times

Prediction 3: Natural Variation of Lay-dates. Given the unexpected variability in the relationship between brood patch development and the timing of lay-date (i.e., inconsistencies within prediction 2), we asked whether date in the season might account for some of the variation in apparent brood patch development time. Days to lay-date varied significantly with Julian date overall (brood patch scores BP0-BP3 pooled, least squares regression, y = -51.5 + 0.67x, df = 79, r^2 = 0.3, P < 0.01), with fewer days between capture and laying for birds caught later in the season. However, there was no significant interaction between individual brood patch scores and lay-dates, in relation to Julian date (date*BP interaction, $F_{1,3}$ = 1.16, n.s.).

Table 2. Plasma VTG concentrations in females with brood patch scores BP0-BP6. Data are in µg/ml of VTG ± SE.

Brood patch class	N	Plasma VTG
BP0	12	3.02 ± 1.0
BP1	10	3.36 ± 1.2
BP2	15	3.36 ± 0.8
BP3	69	1.95 ± 0.2
BP4	16	1.70 ± 0.6
BP5	16	0.27 ± 0.1
BP6	12	0.40 ± 0.1

Prediction 4: Effect of radio-transmitters. To address what might influence prediction 3, we compared the population-level breeding phenology detected by mean dates of egg-producers, birds with BP3, and lay-dates, captured at the same time in the season (see methods). Figure 4 shows the temporal distributions of egg-production (determined using VTG analyses, data from 1999 and 2000; N = 54), lay-dates (determined using radiotelemetry, data from 1998, 1999, and 2000; N = 89), and BP3 (data from 1999 and

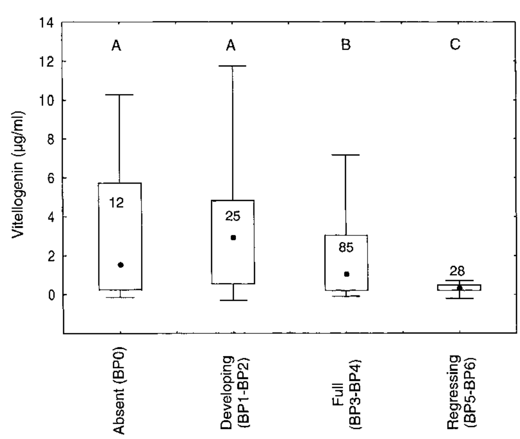

Figure 2. Vitellogenin concentration in plasma of female Marbled Murrelets, with corresponding BP score (1999 and 2000 pooled data). BP scores are pooled according to developmental stages (described in methods). Dot in box indicates median, and boxes enclose two quartiles around the median; lines extend to fourth quartiles from the median, and numbers in boxes indicate sample sizes. Different letters above the boxes indicate groups that are significantly different from each other, while same letters indicate that means are not significantly different (Mann-Whitney tests).

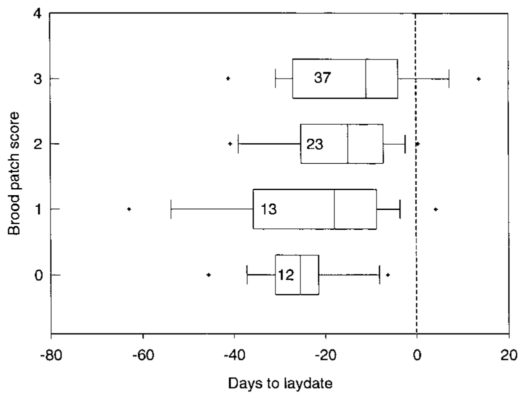

Figure 3. Brood patch (BP) with corresponding lay-date (as determined by radiotelemetry) in radio-tagged Marbled Murrelets. Lay-date = 0 on the horizontal axis. Most birds were captured before lay-dates (and thus, have a negative number on the horizontal axis), but some were caught after they had started incubating (and thus, have a positive number on the horizontal axis). Line in box indicates median, boxes enclose two quartiles around the median, lines extend to fourth quartile from the median, and numbers in boxes indicate sample sizes.

2000, N = 119). Mean egg-producing date was May 18 + 2 days, mean lay-date was May 28 ± 1 days, and mean BP3 was May 26 ± 1 day (Fig. 4). Mean egg-producing date was ten days earlier than mean lay-date, while mean BP3 was not significantly different from mean lay-date (ANOVA with Tukey's pairwise comparisons, $F_{2, 261} = 8.12$, $P < 0.001$).

DISCUSSION

Although fully developed brood patches accurately described the mean timing of incubation (as compared with egg-production and egg-laying), brood patch scores did not always accurately predict breeding status and timing of incubation in individual birds. Previous work on Marbled Murrelets has suggested that, as assumed for other breeding birds, nearly- or fully-developed brood patch are closely associated with the end of egg-production (Sealy 1972), corroborated in this study by three murrelets who laid fully-formed eggs at the time of capture. Despite this apparently clear relationship, we found substantial variation in the predictive ability of brood patches with respect to breeding status, a point that should be kept in mind when assessing brood patches.

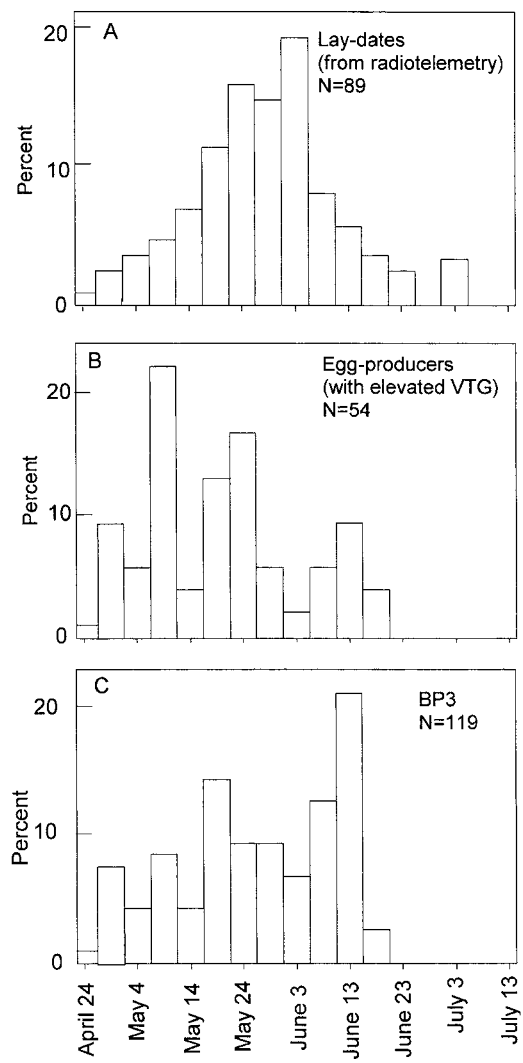

Figure 4. Percentage frequency histograms describing the seasonal distribution of (A) Lay-dates, derived from radiotelemetry; (B) Egg-producers, derived from VTG analyses and (C) BP3, derived from physical examination of Marbled Murrelets at the time of capture. Data are grouped in 5-day intervals. Data for each graph were derived independently, and each dataset excludes birds that were captured after the date radio-tagging efforts ceased (see methods).

Seasonal Distribution of Brood Patch Scores

Generally, brood patch scores in Marbled Murrelets progressed as expected during the breeding season, and appeared to be reflective of underlying biological events (as in Bailey 1952). Brood patch scores also reflected the breeding asynchrony described previously for this species (Nelson 1997; McFarlane Tranquilla 2001; Lougheed *et al.* 2002). As Sealy (1972) also found, birds in this study without brood patches occurred throughout the season (from April to September), but without radio tags, there was no way to determine if they were breeders caught pre- or post-incubation, adult nonbreeders, or true immature pre-breeders. However, we suspect it was a combination of these possibilities, with both adult nonbreeders and immature pre-breeders present in the study area throughout the breeding season, as is often the case for colonial seabirds (Ainley and Boekelheide 1990; Warham 1996; Cadiou 1999).

How Well Do Brood Patches Predict Breeding Status?

Unexpected Nonbreeding. Assessing egg-production using VTG analyses, and incubation using radio-telemetry (Table 1) indicated a ~50% occurrence of nonbreeding in this population, which was unexpected given that the majority of birds had some evidence for a brood patch. These two independent research techniques showed equal proportions of non-egg producers and non-incubators, suggesting that the extent to which apparent "nonbreeding" occurs is not solely explainable by the presence of immature pre-breeders; if pre-breeders had BP0, and if there were enough present to explain the overall 50%-occurrence of nonbreeding observed, then we would expect the numbers of birds with BP0 that were *not* egg-producing or incubating to be much higher than was observed (in Table 1). It must therefore be concluded that those birds classified as apparent nonbreeders included failed breeders, whose early breeding attempt went undetected by radiotelemetry. Other data suggest that early breeding failure is common in Marbled Murrelets, with up to 40% of the breeding attempts attributed to renesting after failure (Centre for Wildlife Ecology, unpubl. data).

Prediction 1: Coincidence of brood patch development with egg-production. Generally, the process of egg-production in all birds is assumed to precede full brood patch development. In Marbled Murrelets, egg-producing females had almost all brood patch scores, from absent, to just beginning to regress. Although eggs and brood patches developed at roughly the same time (prediction 1), we did not expect elevated VTG to occur in birds that had not yet begun brood patch development (Fig. 2). This suggests either that brood patch development is completed during the time it takes to produce an egg, or that birds sometimes begin incubation before reaching BP3. On the other hand, we detected many egg-producers (Fig. 2) with brood patch scores indicating incubation should have started (i.e., BP 3-BP4) (Table 1). This suggests either that full brood patch development sometimes occurs before completion of the egg and onset of incubation, or that some birds can renest, producing VTG a second time after the brood patch is ready for incubation. If egg loss occurs commonly, laying replacement clutches could explain the combination of late brood patch scores with elevated VTG; likewise, high rates of egg loss would explain the equal (and low) proportion of birds in each brood patch class proceeding to incubation (Table 1).

Prediction 2: Brood patch progress with nearness to lay-date. Brood patch development in birds is assumed to progress toward lay-date in a somewhat predictable manner. Our analysis of radio-tracked individuals throughout the season revealed substantial variation in the relationship of brood patch scores to egg-laying dates. Defeathering of brood patches always occurred in advance of lay-dates, and in some cases, abdominal down was lost 40-65 days before laying (Fig. 3). Early defeathering of brood patch has been seen in some breeding birds (storm petrels and Adelie Penguins [*Pygoscelis adeliae*] Ainley *et al.* 1990), but also in physiologically immature pre-breeders (Ainley *et al.* 1990; Gaston and Jones 1998). The latter explanation can be ruled out in our case, because each bird in question was a confirmed incubator. It is possible that early defeathering in Marbled Murrelets is normal, or that these birds were renesters. We have no evidence to refute the latter possibility, and in fact, support from this conclusion is drawn from the elevated VTG with late brood patch scores.

In contrast with protracted brood patch development, some birds with absent or developing brood patches were within five days of lay-date. This suggests either that Marbled Murrelets are able to defeather brood patches quickly, or that they are able to incubate eggs with poorly functional brood patch, as sometimes occurs in Cassin's Auklets (*Ptychoramphus aleuticus*; Manuwal 1979) or Yellow-eyed Penguins (*Megadyptes antipodes;* T. Williams, pers. obs).

Murrelets with higher brood patch scores were not necessarily closer to lay-date (Fig. 3), and the proportions of egg producers and/or incubators were not predicted by any one brood patch score (Table 1). In Marbled Murrelets, even a fully-developed brood patch did not always indicate that a bird was incubating. We could find no descriptions in the literature suggesting that this was either normal or abnormal for most bird species. Curiously, some radio-tagged individuals had BP3 some 40 days prior to the onset of incubation (see Fig. 3). This may be partly explained by variation in the length of time individuals retain BP3. More likely, the discrepancy between "readiness" for incubation (i.e., BP3) and onset of incubation is caused by natural or unnatural disturbances influencing egg-laying, difficulty finding nests, and/or renesting.

The same conflicts arise from both predictions above: (1) that full brood patch development can occur quickly, within the time it takes to make an egg; (2) that full brood patch development may not be complete when incubation starts; (3) that brood patch development takes weeks to complete and starts long before egg-production begins; (4) that renesting often occurs. These force the conclusion that brood patch scores are inaccurate measures of breeding status and timing, however, accuracy may increase if researchers understand the causes of disagreement between brood patch scores and other measures of reproductive status.

Predictions 3 and 4: Disagreement between predicted and observed incubation times. When pooled overall, the timing of lay-dates coincided closely with the timing of egg-production (VTG) and incubation (BP3). This comparison refutes the suggestion that the mismatch between predicted and subsequent lay-date on an individual basis is due to investigator-induced disturbance (prediction 4). Disturbance has been well studied at seabird colonies (see review in Carney and Sydeman 1999), but it is not known if brief disturbance during at-sea capture versus disturbance at a colony have equivalent consequences; the current study suggests not. Likewise, this result supports the prediction (3) that the disagreement between predicted and observed incubation times is due to natural disturbance of breeding, which would affect radio-tagged and non-radio-tagged birds alike. The mismatch between predicted and subsequent lay-dates may be common among murrelets, or even among seabirds, but to our knowledge, no detailed study has documented this.

These contradictory findings are purposely reported here so that researchers using brood patch assessment be aware that the dynamics of brood patch development may not be as clear as previously thought. Specifically for Marbled Murrelets, we suggest that both the observed delay (i.e., discrepancy between BP3 and lay-dates) in nesting birds, and the large number of non-egg-producing birds or non-incubating birds, may be common, and possibly, may be contributing factors in the observed population declines in some parts of its range. On an individual basis, using brood patches to predict the *timing* of a breeding attempt during a remote assessment of Marbled Murrelets is not recommended. Using brood patches to infer reproductive status can neglect reproductive individuals pre-or post-breeding, misinterpret re-laying attempts, and cannot pinpoint the exact lay-date for individuals.

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