REPLACEMENT LAYING IN MARBLED MURRELETS

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SUMMARY

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Replacement laying gives seabirds an opportunity to increase reproductive success. For the Marbled Murrelet (*Brachyramphus marmoratus*), a threatened seabird, estimating productivity is of particular importance to conservation management plans. However, fecundity is not well known, and replacement laying has not been previously recorded. We report on the first confirmed case of replacement laying in the Marbled Murrelet. As well, we used a combination of radio telemetry, physiological analysis of vitellogenin, and brood patch examination, to estimate the frequency of renesting from 1999 to 2001 in Desolation Sound, British Columbia. Replacement laying was estimated to occur at a rate of between 13% to 63% annually. This work demonstrates that additional reproductive capability exists for Marbled Murrelets when first breeding attempts fail, and has implications for other studies of threatened species.

Key words: Marbled Murrelet, *Brachyramphus marmoratus*, telemetry, replacement laying, demography

INTRODUCTION

Renesting and replacement laying following nest failure is common in birds, and can make up a considerable percentage of annual productivity (Thompson *et al.* 2001). Since any given reproductive attempt entails parental costs (Monaghan *et al.* 1998), parents may trade off benefits of renesting in one season against future survivorship and reproductive costs (Williams 1966, Wendeln *et al.* 2000). This decision is especially crucial to temperate-zone birds like the Marbled Murrelet *Brachyramphus marmoratus*, which rear only one brood per season (Wendeln *et al.* 2000). Most long-lived seabirds produce a single clutch of one egg annually, but many seabirds do lay replacement clutches, especially when the failure occurs during incubation (Nelson 1979). Within the Alcidae, murres, guillemots, puffins, Rhinoceros Auklets *Cerorhinca monocerata*, and Cassin's Auklets *Ptychoramphus aleuticus* lay replacement clutches (Astheimer 1986, Gaston & Jones 1998, J.M. Hipfner *et al.* unpubl. data); however, to date, there has been little evidence for replacement clutches in murrelets (Sealy 1975, Gaston & Jones 1998).

Marbled Murrelets are non-colonial, secretive alcids for which nesting biology has been notoriously difficult to study (Cooke 1999). It has been difficult to locate and monitor their nests on the mossy platforms of old-growth trees (Nelson 1997) and therefore difficult to generate demographic parameters (Beissinger 1995, Cam *et al.* 2003). To better support conservation evaluations and provide more accurate fecundity estimates for this species, the influence of replacement laying on nest success requires critical examination (Thompson *et al.* 2001).

There has been no previous clear documentation of replacement laying in Marbled Murrelets (Gaston and Jones 1998). We report the first confirmed replacement laying event for Marbled Murrelets. We then use physiology, morphology, and radio telemetry data to estimate the frequency of replacement laying. Using this combination of research techniques, we believe we can produce a range of these frequency estimates after capturing murrelets away from their nests, in the absence of direct nest-site information. Reproductive status was inferred using the following three parameters.

1) Fecund females could be identified if their blood samples contained an egg-yolk precursor protein, vitellogenin (VTG), which is deposited in the developing egg (Mitchell & Carlisle 1991, Vanderkist *et al.* 2000). Egg production in many alcids takes about 14 days (eg. Astheimer 1986, Murphy 1995, Hipfner *et al.* 1999), and although there have been no studies to confirm this directly for Marbled Murrelets, we assume VTG should be present in the bloodstream for a relatively limited time, i.e. 14 days or less, prior to egg-laying (T.D. Williams, pers. comm).
2) Breeding activity was inferred if birds had fully-developed brood patches. Both males and females incubate (Simons 1980) and have brood patches (Nelson 1997), which are assumed to be defeathered and vascularized if they are currently incubating (Bailey 1952, Ainley & Boekelheide 1990). Brood patches are known to develop rapidly in most species, from within 24-48 hrs of the start of incubation in passerines and some auklets (Bailey 1952, I. L. Jones pers. comm.), to within 10 days of egg-laying in most alcids (Gaston & Jones 1998); thus, we expected brood patches to coincide closely with incubation.
3) Radio telemetry enabled us to locate nests and also independently detect the incubation behaviour of individual birds throughout their breeding cycles (Bradley & Cooke 2001, Bradley *et al.* in press). Using incubation patterns, we looked for direct evidence of replacement laying, and examined the temporal relationships between these

incubation patterns and the expected breeding stage of birds whose plasma VTG levels and brood patch development had been measured when the radios were applied.

Thus, our conclusions depend on the reliability of three assumptions:

(1) that birds with elevated plasma VTG would lay an egg within < 14 days;
(2) that full brood patches indicated incubation had begun; and that full brood patch development would not occur before the onset of egg production (i.e. not more than 14 days prior to egg laying);
(3) that behaviour as determined by radio telemetry gave an accurate assessment of nesting status (Bradley *et al.* 2002).

The objectives of this study were to estimate the frequency of replacement laying by (a) documenting any confirmed renesters in the study area, based directly on egg-laying and radio telemetry evidence; (b) examining incubation patterns based on radio telemetry data for discrepancies implying that replacement laying had occurred; and (c) comparing radio telemetry evidence of incubation timing with that expected based on the identified reproductive potential determined by elevated VTG and/or fully-developed brood patch. Secondarily, we investigated the role of seasonal date in determining the propensity to lay replacement clutches.

METHODS

For the purposes of this paper, 'replacement laying' is considered to be (a) development of a second egg if the first one has been resorbed (while still in the follicle) before ovulation (Astheimer 1986) or aborted just prior to normal laying (eg. after a disturbance) (b) laying a replacement egg after egg loss (eg. due to predators), or (c) relaying following loss of a chick. We do not imply that replacement laying equates with double-brooding, producing and fledging two broods per breeding season. We also could not tell whether the replacement egg was laid in the same nest, or in a new nest site; either could have occured. 'Failure' refers exclusively to failure during the incubation period, not during chick rearing.

Captures, blood-sampling, and radio transmitter attachment

Marbled Murrelets were captured in Desolation Sound, British Columbia, (centre 50º 05'N, 124º 40'W) from 4 May to 11 August 1998, 20 April to 4 September 1999, 19 April to 26 August 2000, and 20 April to 14 August 2001, using a 'dipnetting' technique (Whitworth *et al.* 1997, Vanderkist *et al.* 1999). Blood samples were taken from the brachial vein following Vanderkist *et al.* (1999), and frozen at –20° C until analysis. Radio transmitters with subcutaneous anchors (model 394 in 1998, and model 386 in 1999 - 2001; Advanced Telemetry Systems, Isanti, MN) were attached following Newman *et al.* (1999), but with epoxy instead of sutures to secure the devices (Lougheed *et al.* 2002). All radio transmitters were attached before the end of May (1998, 2000 and 2001) or the end of June (1999), and had an insured minimum lifetime of 45 (model 395) or 80 (model 386) days (Bradley 2002, Lougheed *et al.* 2002).

Yolk precursor analyses, brood patch scoring, and DNA sexing

Plasma was analysed for VTG using a diagnostic kit (Zinc, Cat. No. 435-14909, Wako Pure Chemical Industries Ltd), following the methods of Mitchell & Carlisle (1991) and Vanderkist *et al.* (2000). Egg-producing females were classified as in Vanderkist *et al.* (2000) and McFarlane Tranquilla *et al.* (2003a). Brood patches were scored according to Sealy (1974) and only the fully-developed (i.e. completely defeathered and vascularized) brood patches were considered indicative of breeding. Birds were sexed after the field season using genomic DNA derived from blood samples and subjected to PCR amplification (Vanderkist *et al.* 1999).

Radio-tracking

We used aerial telemetry to search for signals from murrelets with radio transmitters every day subsequent to radio attachment until the end of the field season (August 30), or until the radio transmitter signal disappeared (Bradley *et al.* 2002). The 24-hour incubation shifts of Marbled Murrelets were detected as alternating daily attendance at sea and at the nest site (Lougheed *et al.* 2002), giving a repeating "on-off" pattern of attendance. The day this pattern began for each breeding individual was considered to be its laying date (if not already exhibiting this pattern on the day after capture). Birds were classified as nesters if they showed behavioural evidence of incubation ("on-off" pattern), and as non-nesters if they did not (for a full discussion of inferring incubation using radio telemetry, see Bradley *et al.* in press, Bradley *et al.* 2002).

Classifying breeding status

Radio-tagged individuals (40 in 1998, 100 in 1999, and 75 in each of 2000 and 2001) were divided into breeding status categories as breeders or non-breeders, based on their 24-hour incubation patterns as described above. Then we re-evaluated breeding status using brood patch and VTG information (i.e. other evidence for breeding), and re-classified breeding status into Failed nester, Non-nester, Replacement layer, or Incubator categories, using the following criteria:

1. If radio telemetry classified a bird as 'nester'
   BUT incubation (i.e. "on-off" pattern) ended prematurely and did not restart,
   Then new status = Failed Nester.
2. If radio telemetry classified a bird as 'non-nester'
   BUT brood patch was fully developed and / or VTG was elevated (at capture),
   Then new status = Failed Nester.
3. If radio telemetry classified a bird as a 'nester'
   BUT brood patch was fully developed and/or VTG was elevated (at capture),
   AND nesting behaviour was not seen until > 20 days after capture,
   Then new status = Replacement layer.
4. If radio telemetry classified a bird as a 'non-nester'
   AND if brood patches were anything other than fully-developed and VTG was low,
   Then status remains non-nester
5. If radio telemetry classified a bird as a 'nester'
   AND brood patch was anything other than full and VTG was low,
   OR brood patch was fully-developed and VTG was high BUT bird nested within 14 days,
   Then status remains nester (henceforth called 'Incubator').

Effects of seasonal date on replacement laying

We calculated a replacement laying rate by taking birds that apparently failed and determining what proportion of these appeared to lay replacement clutches. To test whether this probability changed over the season, we classified each failed bird as having laid a replacement clutch or not and calculated a logistic regression (SAS Institute) against date in the season. Because radio telemetry detections were not made past the middle of August, birds captured late in the season had fewer days on which replacement laying could be detected. Hence these birds might show a lower frequency of replacement laying as an artefact of search effort. Our last failed nester was captured 36 days before telemetry observations ended. We therefore also analyzed the data restricting our classification as a replacement layer to those detected within 36 days of failure, which allowed for an equal number of post-failure search days for all failed birds.

Individuals considered in VTG analyses were excluded from the brood patch analyses, and individuals considered to have laid replacement clutches solely by assessing radio telemetry patterns were excluded from the VTG and brood patch analyses.

RESULTS

Confirmed replacement laying

On 9 May 2001, a female Marbled Murrelet laid an egg in the research vessel, after being captured by the research crew (N. Parker, pers. obs.). The individual was radio-tagged and radio tracked daily following capture. Thirty days later, on 10 June 2001, this individual was confirmed to be incubating based on 24-hour "on-off" incubation shift patterns. Its nest site was located on 16 July and at the end of the season, its nest tree was climbed and deemed to have successfully fledged a chick (T. Ainsworth pers. obs., Centre for Wildlife Ecology, SFU, unpublished data). This is the first unequivocal evidence that Marbled Murrelets can lay replacement clutches.

Replacement laying frequency

Estimates from radio telemetry

Daily "on-off" incubation patterns from radio-tagged birds (1999-2001) were examined for premature termination (i.e. before the 30-day incubation period was complete) or other discrepancies. In 1999, seven birds appeared to initiate incubation and fail (R. Bradley, unpubl. data). Of these, one individual appeared to lay a replacement egg. This bird exhibited an "on-off" pattern for 7 days, appearing at sea on alternate days. On the 8th day (the day the bird was expected to be off the water), it was radio tracked to its inland nest site (Fig. 1). This pattern ceased, and the bird was detected daily at sea, for 12 consecutive days. Incubation was then apparently re-initiated, and continued for 32 days, a period of time similar to the estimated incubation period (ca. 28 days, Nelson and Hamer 1995). In 2000, birds at eight failed nests were recorded, none of which appeared to renest. In 2001, nests of seven radio-tagged birds failed during incubation, one of which appeared to lay a replacement (Fig. 1). An incubation pattern began on May 23, and continued for 14 days, after which the bird was consistently detected at sea. On 9 July, 35 days after the first apparent incubation attempt ceased, this individual was detected inland at a nest site and was subsequently detected inland during remote monitoring, presumably provisioning its chick (Fig. 1). Its nest tree was climbed on 9 September and was estimated to have recently fledged a chick (T. Ainsworth pers. obs; Centre for Wildlife Ecology, SFU, unpublished data). Including our one confirmed case, these radio telemetry data produce a replacement laying rate of 14% (3/22) over three years.

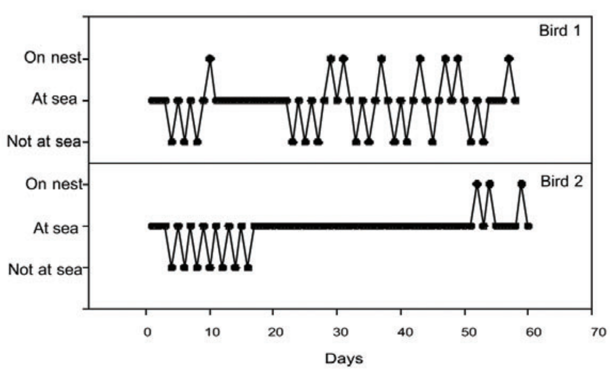

Fig. 1. Time lines for two incubation patterns in Marbled Murrelets, suggestive of replacement laying events. Bird 1: 1999; Bird 2: 2001.

Egg production with follow-up radio telemetry

In 1999 and 2000, VTG levels at capture were available for fourteen radio-tagged females that became nesters and thus had dates of laying assigned. Fig. 2 shows VTG levels at the time of capture, in relation to the estimated timing of egg laying. Of the 14 nesters, three were captured during incubation; as expected, these females all had lower plasma VTG (Fig. 2). Five females with elevated plasma VTG at capture nested within 10 days, within the presumed 14-day window of egg production. However, six females did not nest within this time window, instead nesting between 20 and 35 days after elevated VTG concentrations had been detected in their blood. This discrepancy in the timing of putative first egg production and the detected initiation of incubation suggests that there was enough time for development of a second egg, between the initial blood sample and the subsequent egg-laying event. If assumptions one and three are correct (see introduction), this suggests that 43% (6/14) of egg-producing females laid replacement eggs.

Brood patch development and follow-up radio telemetry

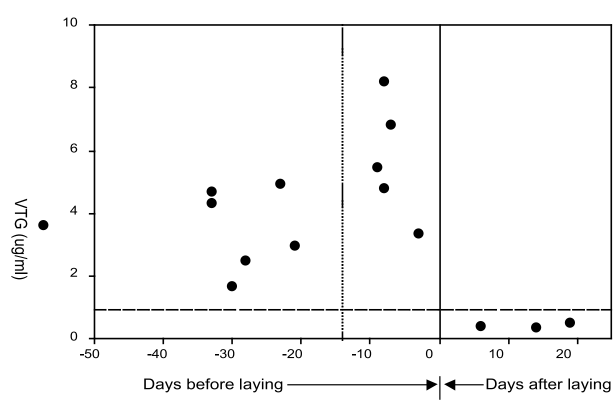

Fig. 2. Vitellogenin (VTG) measured in Marbled Murrelet plasma at time of capture, vs. days between capture and individual's laying date (where negative indicates that the bird was captured before nesting, and positive indicates it was captured after nesting started). Vertical solid line at x = 0 indicates laying date, and vertical dotted line at x = -14 indicates time before which egg production was not expected to occur. Horizontal dashed line indicates threshold VTG associated with laying females (McFarlane Tranquilla *et al.* 2003a). 43% (6/14) had elevated VTG earlier than expected.

From 1998-2001, 38 radio-tagged birds had fully-developed, vascularized brood patches when they were captured. However, 63% (24/38) did not nest within the expected 14-day window for egg production, but instead took 20–59 d to initiate incubation (Fig. 3). The considerable delay between the presence of fully-developed brood patches and the subsequent egg-laying event provides time for replacement laying to occur. If assumptions two and three are correct, 63% of the birds with fully-developed brood patches laid replacement eggs.

Using these three methods and pooling replacement laying events for all radio tagged birds (Table 1), we found that replacement laying occurred after 34% (28/82) of the apparent first nest failures.

Breeding status and seasonal date

We compared the capture timing of failed nesters, replacement layers, and normal incubators. Failed nesters were captured significantly later (by 11 days) than replacement layers, and normal incubators (One-way ANOVA with Tukey's pairwise comparisons, $F_{2,187} = 11.96$, $P < 0.00$) (Fig. 4). The propensity to lay replacements changed with date (logistic regression, df = 1, $P = 0.005$; Fig. 5). Excluding replacement layers for which more time was spent searching for nesting behaviour (i.e. more than 36 days; see methods) decreased our sample of putative replacement layers by 30% (7/23). However, even with the reduced sample, replacement laying was more likely to occur earlier in the season (i.e. before 26 May – see Fig. 5) than later.

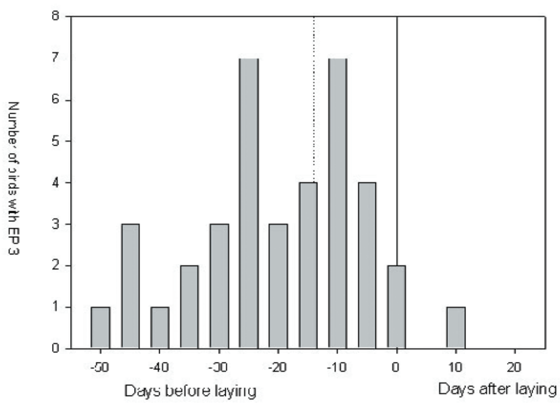

Fig. 3. Number of Marbled Murrelets with fully-developed brood patches vs. days between capture and individual's laying date (where negative indicates that the bird was captured before nesting, and positive indicates it was captured after nesting started). Vertical solid line at x = 0 indicates laying date, and vertical dotted line at x = -14 indicates time before which full brood patch development was not expected. 63% (24/38) brood patches appear to develop earlier than expected.

TABLE 1

Breeding status of radio tagged Marbled Murrelets in Desolation Sound, British Columbia, over four years of study. Replacement laying occurred after 34% (28/82) of the apparent first nest failures.

Status	1998	1999	2000	2001	Total birds
Failed nester	na	21	23	10	54
Non-nester	na	11	16	27	54
Replacement layer	2	10	10	6	28
Incubator	22	37	21	28	118

DISCUSSION

Our data confirm the ability of Marbled Murrelets to lay replacements, following the loss of an egg prior to the start of incubation. For two other birds, radio telemetry data provide strong evidence for replacement laying; and when tallying all radio-tagged birds, we were able to estimate how many first breeding attempts failed and of these, which resulted in replacement laying. Brood patch and vitellogenin data allowed us to further discern between late and timely breeding attempts amongst successful incubators. Thus, our three techniques produce estimates of the frequency of replacement laying of 13%, 40%, 63%, and overall, 34% (Table 1).

Our estimate for the frequency of replacement laying is lower than

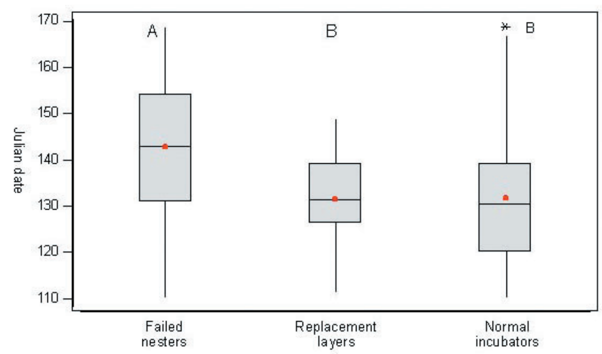

Fig. 4. Radio tagged Marbled Murrelets whose nesting attempt failed were captured 11 days later than replacement layers and normal incubators. Letters indicate groups that are significantly different from each other (Tukey's pairwise comparisons).

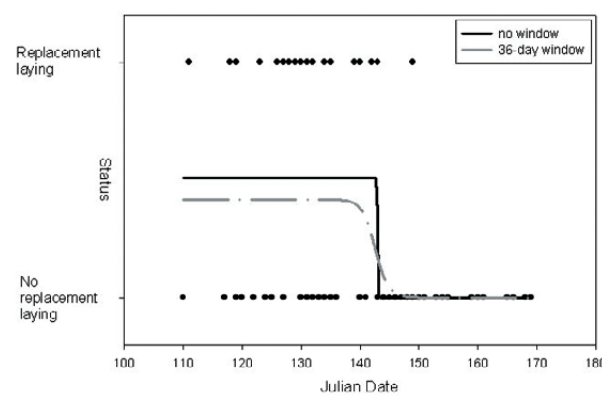

Fig. 5. Replacement laying after nest failure in Marbled Murrelets was more likely to occur earlier in the season (logistic regression where 0 = failed nesting and 1 = replacement laying). Regression lines include data from (1) failed nesters throughout the season ('No window') and (2) failed nesters with enough data to radio track them for 36 d after nest failure ('36-day window'), allowing for equal number of post-failure search days for all failed birds.

that reported for other alcids (81% in Rhinoceros Auklets, 90% in Cassin's Auklets, J.M. Hipfner unpubl. data; 63% in Razorbills and 90% in Thick-billed Murres, Hipfner *et al.* 2001); the difference may be partly due to our indirect detection methods as compared to direct egg removal-replacement studies. Moreover, in all cited studies, the eggs removed were taken from early-laying birds soon after laying. Our estimate of replacement laying frequency would also be too low if any birds (especially the later-captured birds) actually nested and failed prior to capture and radio tagging. Because we captured each individual only once during the study, the methods we used to classify breeding status did not enable us to determine whether birds caught within a few days of laying had already attempted laying prior to capture. This would also deflate our estimate of replacement laying frequency.

Marbled Murrelets have a long and asynchronous breeding season throughout their range (Nelson 1997, Lougheed *et al.* 2002); this in itself suggests that replacement laying may influence breeding chronology for this species (Nelson 1997). The egg production period alone spans 2.5 months in our study area (McFarlane Tranquilla *et al.* 2003a), resulting in a breeding season almost twice the length needed to initiate a nest and fledge a chick. Thus, the environmental and biological factors that permit asynchronous breeding in Marbled Murrelets must also allow ample opportunity during the season for replacement laying. It seems reasonable to assume that attempting to breed in the same season following nest failure is more common than previously thought in this species, especially if the breeding attempt fails early in the season. This is supported by our finding that the propensity to lay replacement clutches decreased as seasonal date progressed (i.e. after May 27; Fig. 5). Seasonal declines in rates of replacement laying are common among some seabirds (eg. Hipfner 2001, Wendeln *et al.* 2000). As with other seabird species, the propensity of Marbled Murrelets to lay replacement clutches probably depends on the quality of the parents, who are also generally the earlier breeders (Sydeman *et al.* 1991, Phillips & Furness 1998, Hipfner *et al.* 1999).

The conclusions drawn from our study depend on the accuracy of three main assumptions presented in the introduction. Firstly, we assumed that egg production in Marbled Murrelets would take 14 d and thus, that high plasma VTG would occur only within 14 days of laying (see introduction). If we have underestimated the amount of time it takes to produce an egg, then our estimates of replacement laying will be inflated. Because we were unable to determine experimentally the duration of egg formation in Marbled Murrelets, the 14-day estimate comes from the closely-related Cassin's Auklet (Astheimer 1986), and compares closely to that of other alcids. As in other alcids, egg production time may vary somewhat in Marbled Murrelets, however, egg formation rarely takes more than 20 days in the other auks (Gaston & Jones 1998). Yolk deposition, the time during which we would expect elevated plasma VTG, occurs at different rates amongst the seabird orders (Grau 1984), from 4 d in small shorebirds to 13-24 d in some gulls and penguins (Gill 1995, Astheimer & Grau 1985). Even in the Brown Kiwi *Apteryx australis*, a species famous for producing a disproportionately large egg yolk (Calder *et al.* 1978), egg production takes only 25 d (Calder 1979). Because yolk precursor production likely has considerable associated metabolic and energetic costs, one would predict close synchrony between yolk precursors produced by the liver and that required for ovarian follicle growth (Challenger *et al.* 2001). Thus, we do not expect VTG to be elevated before it is required, and are confident that birds with elevated plasma VTG levels were ready to lay within approximately 14 d from the time they were captured. It remains possible that our capture and radio-tagging of the birds disrupted their normal breeding schedules, causing an unusual delay, and inflating our estimate of replacement laying rates (see below).

Secondly, we assumed that murrelets with brood patches were incubating, and that fully developed brood patches would not occur before egg production began (i.e. therefore not earlier than approximately 14 d prior to laying). If we have underestimated the amount of time it takes for a Marbled Murrelet to develop a brood patch prior to nesting, our count of replacement laying could be inflated. However, other alcid brood patches generally develop in the last 10 d before egg-laying (Gaston & Jones 1998). After photoperiodic stimulation of gonads early in the breeding season, brood patch development is stimulated by prolactin and other gonadal steriods (Phillips *et al.* 1985). Due to this natural sequence of gonadal- and brood patch-controlling hormones, it seems unlikely that brood patches become fully-developed prior to egg production in the Marbled Murrelet. The timing of brood patch development with breeding activity in Marbled Murrelets has been difficult to interpret (McFarlane Tranquilla *et al.* 2003b), and this may in fact be due to the influence of replacement laying on brood patch development, possibly to prolong its presence in birds laying replacement clutches (as in Cassin's Auklet; Manuwal 1974).

Thirdly, we assumed that behaviour as determined by radio telemetry is accurate. Given that Marbled Murrelets visit the nest site prior to laying and are sometimes detected inland on prospecting flights (S.K. Nelson, pers. comm.), it was imperative to our assumptions that a regular pattern of 24-hour incubation shifts, of at least 4 days, was established before individuals were considered replacement layers (see Bradley *et al.* in press, Bradley *et al.* 2002 for a full discussion). In both cases of inferred replacement laying using interrupted incubation patterns, the first incubation shifts lasted more than 4 days. Because this method depends on the ability to detect birds inland for multiple days (to enable the researcher to pinpoint its inland detection from the air), radio telemetry will be unable to detect most early nest failures. That is, it is very difficult to determine with confidence that brief "on-off" patterns at sea, lasting less than one or two days, are in fact incubation shifts and not inland prospecting visits (Bradley *et al.* in press). Incubation attempts that are terminated during the first day or two after laying are unlikely to be detected due to the short amount of time available to the researcher to find it in a wide expanse of forest. This bias will lead to our actually having underestimated the amount of replacement laying that occurred based on the radio tracking data alone. This might account for the substantially lower estimate determined by this approach.

The research techniques discussed in our study have no doubt affected some individual Marbled Murrelets that were captured, handled, and radio-tagged. The murrelet that laid an egg in the boat undoubtedly did so in response to its encounter with us. As well, the stress of capture may have been the cause of delay between reproductive capability (i.e. elevated VTG and brood patch development) and the actual initiation of incubation, thereby elevating our estimates of natural replacement laying. Many radio-tagged murrelets appeared to completely recover from their brief capture encounter with us, as evidenced by the establishment of 'normal' incubation patterns soon after capture. As well, the influence of individual variation in reaction to capture combined with seasonal effects is not well understood. We could not determine whether radio-tagging led to interrupted incubation patterns or affected foraging or chick rearing, because chronic effects of radio-tagging on incubation patterns and breeding success are unknown. Also we had no untagged control group with which to compare incubation and fledging success, because the latter cannot be estimated for Marbled Murrelets without radio transmitters. However, the effects of investigator-induced disturbance on our estimated replacement laying rate may have been partly offset by our inability to detect first failed nests. If investigator-induced disturbance was not the catalyst for replacement laying, we assume natural factors, such as nest predation or environmental events, were responsible.

The ability of Marbled Murrelets to lay replacement clutches implies that the demographic effects of disruption of the breeding attempt, either by predators or by human activity (Long & Ralph 1998), may be mitigated to some extent. When replacement laying is demonstrated in a species, there is recognition that additional reproductive capability exists when a breeding attempt is interrupted (Azure *et al.* 2000). More work to determine specific replacement laying rates across its range will be invaluable to improving fecundity estimates for Marbled Murrelets.

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REFERENCES

AINLEY, D. G. & BOEKELHEIDE, R.J. (Eds.). 1990. Seabirds of the Farallon Islands; Ecology, dynamics, and structure of an upwelling-system community. Stanford University Press, California.

ASTHEIMER, L.B. 1986. Egg formation in Cassin's Auklet. *Auk* 103: 682-693.

ASTHEIMER, L.B. & GRAU, C.R. 1985. The timing and energetic consequences of egg formation in the Adelie penguin. *Condor* 87: 256-268.

AZURE, D. A., BRININGER, W.L., TOEPFER, J. E., HUSCHLE, G. & CRAWFORD, R.D. 2000. First described renesting attempt by an American Bittern. *Wilson Bulletin* 112: 271-273.

BAILEY, R.E. 1952. The incubation patch of passerine birds. *Condor* 54: 121-136.

BEISSINGER, S. 1995. Population trends of the Marbled Murrelet projected from demographic analyses. In: Ralph, C.J., George, L.H., Jr., Raphael, M.G. & Piatt, J.F. (Eds.). Ecology and Conservation of the Marbled Murrelet, Gen. Tech. Rep. PSW-152. Albany, California: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture: pp. 385-393.

BRADLEY, R.W. 2002. Breeding ecology of radio-marked Marbled Murrelets *Brachyramphus marmoratus* in Desolation Sound, British Columbia. M.Sc. Thesis, Simon Fraser University, Burnaby, B.C., Canada.

BRADLEY, R.W, & COOKE, F. 2001. Cliff and deciduous tree nests of Marbled Murrelets in Southwestern British Columbia. *Northwestern Naturalist* 82: 52-57.

BRADLEY, R.W., COOKE, F., LOUGHEED, L.L. & BOYD, W.S. In press. Inferring breeding success through radio telemetry in Marbled Murrelets. *Journal of Wildlife Management*.

BRADLEY, R.W, MCFARLANE TRANQUILLA, L.A., VANDERKIST, B.A. & COOKE, F. 2002. Sex differences in nest visitation by chick-rearing Marbled Murrelets. *Condor* 104: 180-185.

CALDER, W.A. III. 1979. The kiwi and egg design evolution as a package deal. *Bioscience* 29: 461-467.

CALDER, W.A. III., PARR, C.R., AND KARL, D.P. 1978. Energy content of eggs of the Brown Kiwi Apteryx australis; an extreme in avian evolution. *Comparative Biochemistry and Physiology A* 60:177-179.

CAM, E., LOUGHEED, L.W., BRADLEY, R. & COOKE, F. In press. Demographic assessment of a Marbled Murrelet population from capture-mark-recapture and radio-telemetry data. *Conservation Biology 17: 1118-1126*.

CHALLENGER, W.O., WILLIAMS, T.D., CHRISTIANS, J.K. & VEZINA, F. 2001. Follicular development and plasma yolk precursor dynamics through the laying cycle in the European Starling (*Sturnus vulgaris*). *Physiolical and Biochemical Zoology* 74: 356-365.

COOKE, F. 1999. Population studies of Marbled Murrelets (*Brachyramphus marmoratus*) in British Columbia. In: Diamond, A.W., & Nettleship, D.N. (Eds.). Biology and Conservation of Forest Birds. Society of Canadian Ornithologists. Special publication No. 1. Fredericton, New Brunswick: pp. 43-51.

GASTON, A.J. & JONES, I.L. 1998. The Auks. Oxford University Press.

GILL, F.B. 1995. Ornithology. W.H. Freeman and Company. pp. 349-374.

GRAU, C.R. 1984. Egg formation. In: Seabird Energetics, Whittow, C.G. & Rahn, H. (Eds.). Plenum Press, NY.: pp. 33-57.

HIPFNER, J.M. 2001. Fitness-related consequences of relaying in an Arctic seabird: survival of offspring to recruitment age. *Auk* 118: 1076-1080.

HIPFNER, J.M., GASTON, A.J., MARTIN, D.L. & JONES, I.L. 1999. Seasonal declines in replacement egg-laying in a long-lived, Arctic seabird: costs of late breeding or variation in female quality? *Journal of Animal Ecology* 68: 988-998.

HIPFNER, J.M., GASTON, A.J. & STOREY, A.E. 2001. Nest-site safety predicts the relative investment made in first and replacement eggs by two long-lived seabirds. *Oecologia* 129: 234-242.

LONG, L. L. & RALPH, C.J. 1998. Regulation and observations of human disturbance near nesting Marbled Murrelets. Technical Report, Northwest Forest Plan, U.S.D.A Forest Service, Pacific Southwest Research Station, Redwood Sciences Laboratory, Arcata, California.

LOUGHEED, C., VANDERKIST, B.A., LOUGHEED, L.W. & COOKE, F. 2002. Techniques for investigating breeding chronology in Marbled Murrelets, Desolation Sound, British Columbia. *Condor* 104: 319-330.

MANUWAL, D.A. 1974. The incubation patches of Cassin's Auklet. *Condor* 76: 481-484.

MCFARLANE TRANQUILLA, L.A., WILLIAMS, T.D. & COOKE, F. 2003a. Using vitellogenin to identify inter-annual variation in breeding chronology of Marbled Murrelets. *Auk*. 120: 512-521.

MCFARLANE TRANQUILLA, L.A., BRADLEY, R.W., LANK, D.B., WILLIAMS, T.D., LOUGHEED, L.L. & COOKE, F. 2003b. The reliability of brood patches in assessing reproductive status in the Marbled Murrelet: words of caution. *Waterbirds* 26: 108-118.

MITCHELL, M.A. & CARLISLE, A.J. 1991. Plasma zinc as an index of vitellogenin production and the reproductive status in the domestic fowl. *Comparative Biochemistry and Physiology A* 100: 719-724.

MONAGHAN, P., NAGER, R.G. & HOUSTON, D.C. 1998. The price of eggs: increased investment in egg production reduces the offspring rearing capacity of parents. *Proceedings of the Royal Society (London)* 265: 1731-1735.

MURPHY, E.C. 1995. Seasonal declines in duration of incubation and chick periods of Common Murres at Bluff, Alaska in 1987-1991. *Auk* 112: 982-995.

NELSON, B. 1979. Seabirds their biology and ecology. A&W Publishers Inc., New York.

NELSON, S.K. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). Volume 276. The Birds of North America (A. Poole & F. Gill, editors): The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologist's Union, Washington, D.C.

NELSON, S.K, & HAMER, T.E. 1995. Nesting biology and behaviour of the Marbled Murrelet. In: Ralph, C.J., George, L.H., Jr., Raphael, M.G. & Piatt, J.F. (Eds.). Ecology and Conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-152. Albany, California: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture: pp. 57-68.

NEWMAN, S.H., TAKEKAWA, J.Y., WHITWORTH, D.L. & BURKETT, E.E. 1999. Subcutaneous anchor attachment increases retention of radio transmitters on Xantus' and Marbled Murrelets. *Journal of Field Ornithology* 70: 520-534.

PHILLIPS, J.G., BUTLER, P.J. & SHARP, P.J. 1985. Physiological strategies in avian biology. Blackie & Son Limited, Glasgow. pp. 112-139.

PHILLIPS, R.A. &. FURNESS, R.W. 1998. Repeatability of breeding parameters in Arctic Skuas. *Journal of Avian Biology* 29: 190-196.

SAETHER, B.-E. & BAKKE, O. 2000. Avian live history bariation and contribution of demographic traits to the population growth rate. *Ecology* 81: 642-653.

SEALY, S.G. 1974. Breeding phenology and clutch size in the Marbled Murrelet. *Auk* 91: 10-23.

SEALY, S.G. 1975. Aspects of the breeding biology of the Marbled Murrelet in British Columbia. *Bird-Banding* 46:141-154.

SIMONS, T.R. 1980. Discovery of a ground-nesting Marbled Murrelet. *Condor* 82: 1-9.

SYDEMAN, W. J., PENNIMAN, J.F., PENNIMAN, T.M., PYLE, P. & AINLEY, D. 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding, and year in relation to food availability. *Journal of Animal Ecology* 60: 135-149.

THOMPSON, B. C., KNADLE, G.E., BRUBAKER, D.L. & BRUBAKER, K.S. 2001. Nest success is not an adequate comparative estimate of avian reproduction. *Journal of Field Ornithology* 72: 527-536.

VANDERKIST, B.A., XUE, X.H., GRIFFITHS, R., MARTIN, K., BEAUCHAMP, W. & WILLIAMS T.D. 1999. Evidence of male-bias in capture samples of Marbled Murrelets from genetic studies in British Columbia. *Condor* 101: 398-402.

VANDERKIST, B.A., WILLIAMS, T.D., BERTRAM, D.F., LOUGHEED, L. & RYDER, J.P. 2000. Indirect, physiological assessment of reproductive state and breeding chronology in free-living birds: an example in the marbled Murrelet (*Brachyramphus marmoratus*). *Functional Ecology* 14: 758-765.

WENDELN, H., BECKER, P.H. & GONZALEZ-SOLIS, J. 2000. Parental care of replacement clutches in common terns (*Sterna hirundo*). *Behavioral Ecology and Sociobiology* 47: 382-392.

WHITWORTH, D.L., TAKEKAWA, J.Y., CARTER, H.R. & MCIVER, W.R.. 1997. A night-lighting technique for at-sea capture of Xantus's Murrelets. *Colonial Waterbirds* 20: 525-531.

WILLIAMS, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100: 687-690.