

Body mass variation in Marbled Murrelets in British Columbia, Canada

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Body mass was measured in Marbled Murrelets *Brachyramphus marmoratus* from May to August, 1994–1998 at Desolation Sound, and during June and July 1997 at Mussel Inlet, British Columbia, Canada, to assess seasonal, sexual, site and intra-annual variation. Birds were captured by mist-net, and by night-lighting, and were sexed using molecular techniques. The breeding status of females (gravid or not) in 1997 was determined from plasma levels of egg-yolk precursors. Adult males weighed 203.7 ± 14.8 g, $n = 495$ (juveniles 166.6 ± 28.8 g, $n = 31$) and females weighed 201.2 ± 20.5 g, $n = 344$ (juveniles 148.3 ± 23.5 g, $n = 20$). Murrelets caught in mist-nets were significantly lighter than those caught by night-lighting. Female mass was constant across years of the study, but males caught by night-lighting were heavier in 1998 than in 1997. Females declined in mass during the egg-laying period, but when gravid females were removed from the analysis, or when the post-laying data were analysed, no declines were found. Marbled Murrelets appear to maintain mass at a constant level all season, and are probably more income than capital breeders. Variation in body mass in this species may be constrained by the need to fly with speed and agility to avoid aerial predators.

Marbled Murrelets *Brachyramphus marmoratus* are small alcids found along the Pacific north-west of North America from California to Alaska. They are long-lived seabirds with low fecundity (Nelson & Hamer 1995). While a great deal of research has been conducted on Marbled Murrelets in recent years, particularly assessing habitat use, there is still much to be understood about the species. For example, little is known about seasonal and geographical variation in body mass of Marbled Murrelets (Nelson 1997); there is only one published study on body mass variation in this species, carried out at Langara Island (Queen Charlotte Islands – Haida Gwaii), British Columbia during 1970 and 1971 (Sealy 1975).

The purpose of this study was to describe body mass changes in Marbled Murrelets across a number of years and at two sites, thereby providing more information on this poorly understood threatened species. Inter- and intra-annual changes in body mass were examined, as were comparisons between the sexes, sites and different capture techniques.

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METHODS

Marbled Murrelets were captured at Desolation Sound ($50^{\circ}05'N$, $124^{\circ}40'W$) from 1994 to 1998, and Mussel Inlet ($52^{\circ}51'N$, $128^{\circ}10'W$) British Columbia, Canada, during 23 June–12 July 1997. Two capture techniques were used. A floating mist-net system (Kaiser *et al.* 1995) was used to catch birds as they flew through Theodosia Inlet, Desolation Sound at dawn (04:00–07:00 h) and dusk (20:00–23:00 h), from early June to early August (the only period when murrelets could be caught using this technique). Mist-netting was unsuccessful at Mussel Inlet, so 'night-lighting' was used instead. Night-lighting (modified from Whitworth *et al.* 1997), involved searching for birds from an inflatable boat and, once spotted, they were approached slowly and scooped into the boat with a landing net. Night-lighting was conducted between 23:00 and 05:00 h. It was also used to catch birds on the open waters of Desolation Sound from mid-May to mid-August, 1997 and 1998. Night-lighting allowed the capture of birds earlier in the breeding season and, for the first time at Desolation Sound, recently fledged juveniles. All birds were uniquely

banded with US Fisheries and Wildlife stainless steel bands, and weighed using a spring or top-loading balance. A small sample of blood was taken from the tarsal vein for molecular sexing (Vanderkist *et al.* 1999).

The breeding chronology and breeding status of Marbled Murrelets is difficult to determine, as nests are hard to locate and access and, once found, breeding birds are prone to disturbance (Long & Ralph 1998). In order to assess mass changes in relation to breeding chronology, 'core' (> 50% of breeding birds) incubation and chick-rearing periods were used. These core periods were calculated at Desolation Sound in 1996–1998 using several approaches (Lougheed 1999): (1) analysis of plasma levels of egg-yolk precursors; (2) on/off patterns on the water derived from radio-telemetry; (3) timing of the arrival of recently fledged juveniles, and (4) observations of fish-holding behaviour [indicating young being fed] and behaviour in the forest at nest sites. The core incubation period at Desolation Sound is 19 May–8 July, and core chick-rearing is 18 June–4 August (Lougheed 1999). To minimize the overlap between the two periods, 18 June was defined as the end of the egg laying period for these analyses. The breeding status of some females (gravid) during 1997 was determined from plasma levels of egg-yolk precursors measured for another study (Vanderkist 1999).

Because Marbled Murrelets are seldom caught more than once during a season, it was impossible to track mass changes in individuals. Instead, changes in the sampled population were assessed. Comparisons of mass were made between sexes (analysed after 18 June), methods (mist-netting vs. night-lighting) and years, using Analysis of Covariance (ANCOVA, date as a covariate). Comparisons were also made between sites using ANCOVA, but the assessments were made on the entire data set. Similarly, the masses of birds caught in mist-nets while flying into and out of the forest were compared to determine whether murrelets flying into the forest were heavier because they had been foraging. *t*-tests were used for comparisons between groups when date was not relevant. Changes in mass over the breeding season within each sex, site and year were assessed with linear regressions. Recaptured individuals and juveniles (recognized by the presence of an egg tooth and plumage characteristics, Carter & Stein 1995) were treated separately. Changes in mass of recaptured birds were assessed with paired *t*-tests, as between-year recaptures and same-year captures. Data are

reported as mean \pm standard deviation, and a significance level of $P < 0.05$ was accepted throughout.

RESULTS

In total, 839 adults (495 males and 344 females) and 51 recently fledged juveniles (31 males and 20 females) were captured and sexed during this study (Figs 1 and 2). We found no differences in mass between years in females, but males caught by night-lighting were heavier in 1998 (Fig. 3). Overall, the mean mass of adult males was 203.7 ± 14.8 g, and of females (measured after 18 June [to avoid gravid females, see below]) was 201.2 ± 20.5 g. Juveniles were 82% and 74% the mass of adult males and females, respectively (males 166.6 ± 28.8 g and females 148.3 ± 23.5 g). Gravid females (measured only during 1997) were found from mid-May to early July, and were significantly heavier (235.2 ± 24.2 , $n = 24$) than non-gravid females (200.0 ± 19.0 g, $n = 87$, $t = 6.6$, $P < 0.001$). Other than the comparisons between Mussel Inlet and Desolation Sound, all further comparisons of females are made after 18 June, or with gravid and non-gravid females treated separately.

Significant differences in mass were found between females captured by night-lighting and those caught with mist-netting during 1997 and 1998 at Desolation Sound (1997: $F_{1,108} = 26.6$, $P < 0.001$; 1998: $F_{1,130} = 8.8$, $P < 0.004$, Fig. 3). In both years females caught by mist-netting were lighter than those caught by night-lighting (Table 1). During 1998, but not 1997, the masses of males caught by the two techniques differed (1997: $F_{1,139} = 0.1$, ns; 1998: $F_{1,166} = 8.8$, $P < 0.001$). Males caught by mist-netting during 1998 were significantly lighter in mass than those caught by night-lighting (Table 1, Fig. 3).

The masses of birds did not differ with flight direction when captured by mist-net (inland or out to sea) in either 1997 (males: $t_{108} = 0.7$, ns; females: $t_{55} = 1.6$, ns), or 1998 (males: $t_{81} = 1.7$, ns; females: $t_{39} = 0.2$, ns).

No significant difference in female mass was found between years, within each capture method (mist-net: $F_{4,187} = 0.1$, ns; night-lighting: $F_{1,143} = 2.2$, ns). However, while males caught by mist-netting did not differ in mass between years ($F_{4,354} = 0.7$, ns), those caught by night-lighting were significantly heavier in 1998 than in 1997 ($F_{1,130} = 12.4$, $P < 0.001$, Figs 1–3).

There were no significant differences between the masses of males and females during 1994

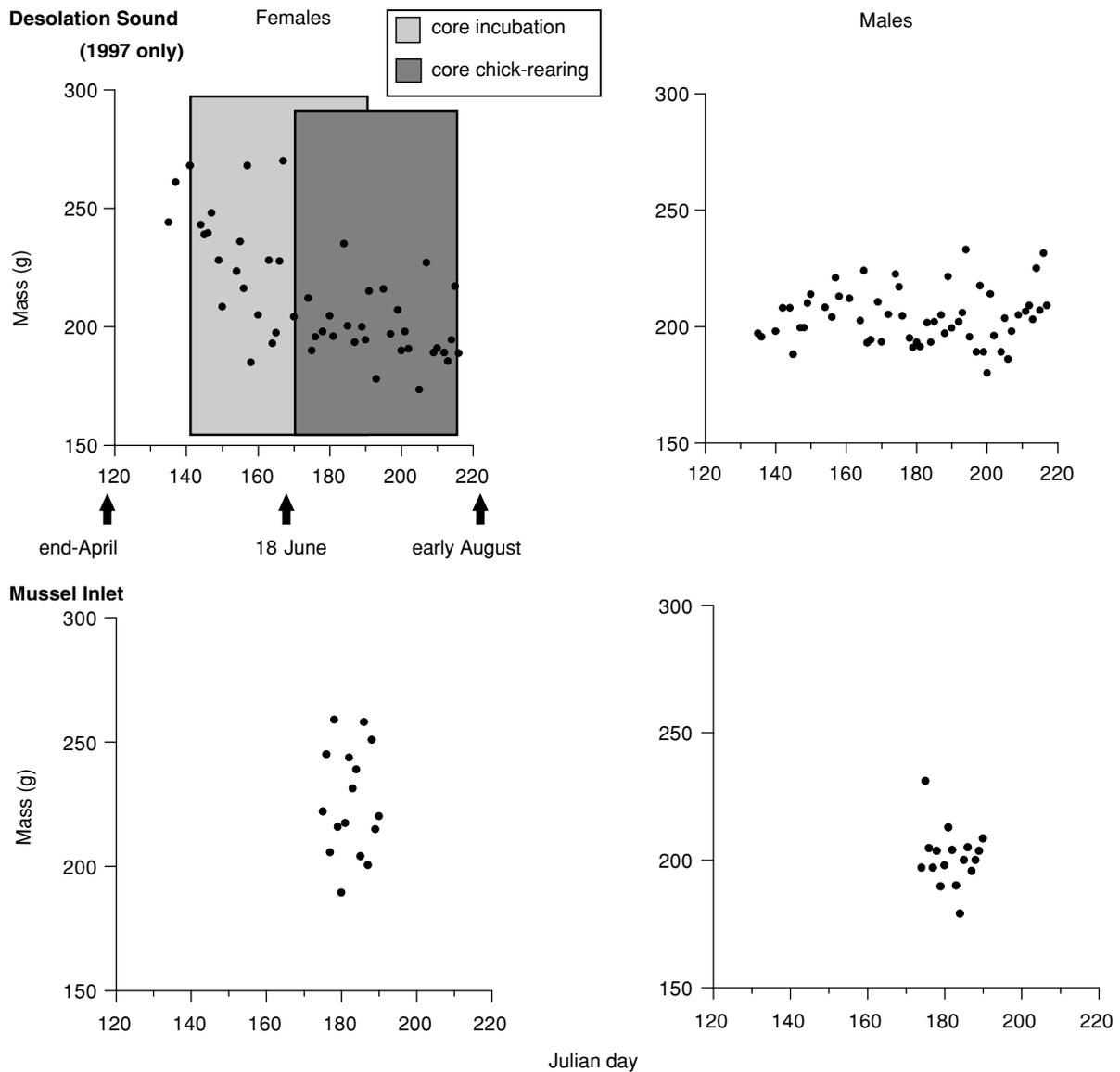


Figure 1. Sex-specific mass of Marbled Murrelets at Desolation Sound (top) and Mussel Inlet (bottom) during 1997. Core incubation and chick-rearing stages are marked (Lougheed 1999, see text for details).

Table 1. Body mass of male and female Marbled Murrelets captured using different techniques during 1997 and 1998 at Desolation Sound.

	Night-lighting	Mist-netting
Females		
1997	219.4 ± 28.2 g	196.5 ± 14.2 g
1998	223.1 ± 27.4 g	197.0 ± 12.1 g
Males		
1997	203.6 ± 15.4 g	202.9 ± 12.6 g
1998	212.5 ± 14.1 g	202.2 ± 15.3 g

($F_{1,198} = 2.1$, ns) and 1995 ($F_{1,112} = 3.2$, ns). However, during 1996, 1997 and 1998 males were significantly heavier than females (1996: $F_{1,91} = 13.1$, $P < 0.001$; 1997: $F_{1,376} = 22.6$, $P < 0.001$; 1998: $F_{1,167} = 5.9$, $P < 0.02$). Females from Mussel Inlet did not differ significantly in mass from males ($t_{83} = 0.8$, ns, Figs 1 and 2).

Similarly, Desolation Sound and Mussel Inlet did not differ significantly in either mean male or female mass (males: $t_{143} = 0.02$, ns; gravid females: $t_{34} = 1.9$, ns; non-gravid females $t_{34} = 1.4$, ns, Fig. 2).

A significant decline in female mass was found during 1997 and 1998 at Desolation Sound, but not

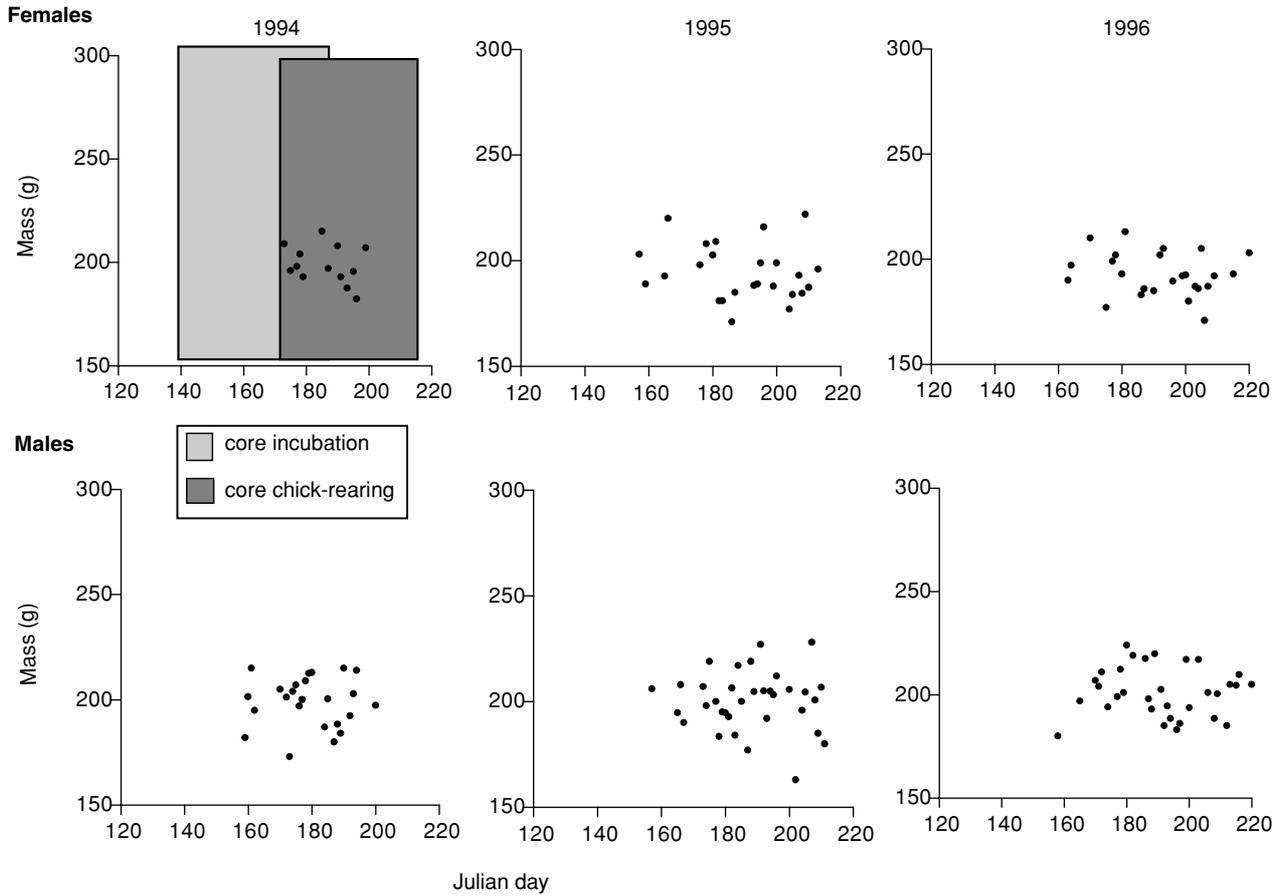


Figure 2. Sex-specific mass of Marbled Murrelets during 1994, 1995 and 1996 at Desolation Sound. Core incubation and chick-rearing stages are marked (Lougheed 1999, see text for details).

Table 2. Results of regressions of mass changes in male and female Marbled Murrelets, through the breeding season during each year of the study. Significant cases are in bold type.

Year and site	Females	Males
Desolation Sound 1994	$F_{1,18} = 2.6, P > 0.05$ $r^2 = 0.13$	$F_{1,46} = 0.5, P > 0.05,$ $r^2 = 0.01$
Desolation Sound 1995	$F_{1,39} = 1.9, P > 0.05,$ $r^2 = 0.05$	$F_{1,73} = 0.003, P > 0.05,$ $r^2 = 0.0001$
Desolation Sound 1996	$F_{1,36} = 0.3, P > 0.05,$ $r^2 = 0.01$	$F_{1,55} = 0.7, P > 0.05,$ $r^2 = 0.01$
Desolation Sound 1997	$F_{1,110} = 48.2, P < 0.0001,$ $r^2 = 0.31^*$	$F_{1,90} = 0.07, P > 0.05,$ $r^2 = 0.001$
Desolation Sound 1998	$F_{1,131} = 82.0, P < 0.0001,$ $r^2 = 0.39$	$F_{1,168} = 6.2, P < 0.01,$ $r^2 = 0.04$
Mussel Inlet 1997	$F_{1,57} = 0.4, P > 0.05,$ $r^2 = 0.08$	$F_{1,51} = 0.13, P > 0.05,$ $r^2 = 0.003$

*Includes all birds, see text for results with gravid females removed.

during the other years, or at Mussel Inlet (Table 2). When gravid females were removed from the 1997 analysis, mass did not change with date ($F_{1,83} = 2.4, ns$). Female mass remained constant after 18 June

during both 1997 and 1998 (1997: $F_{1,68} = 1.2, ns, r^2 = 0.02$; 1998: $F_{1,62} = 3.0, ns, r^2 = 0.05$).

Females captured by night-lighting showed a significant decline in mass over the breeding season

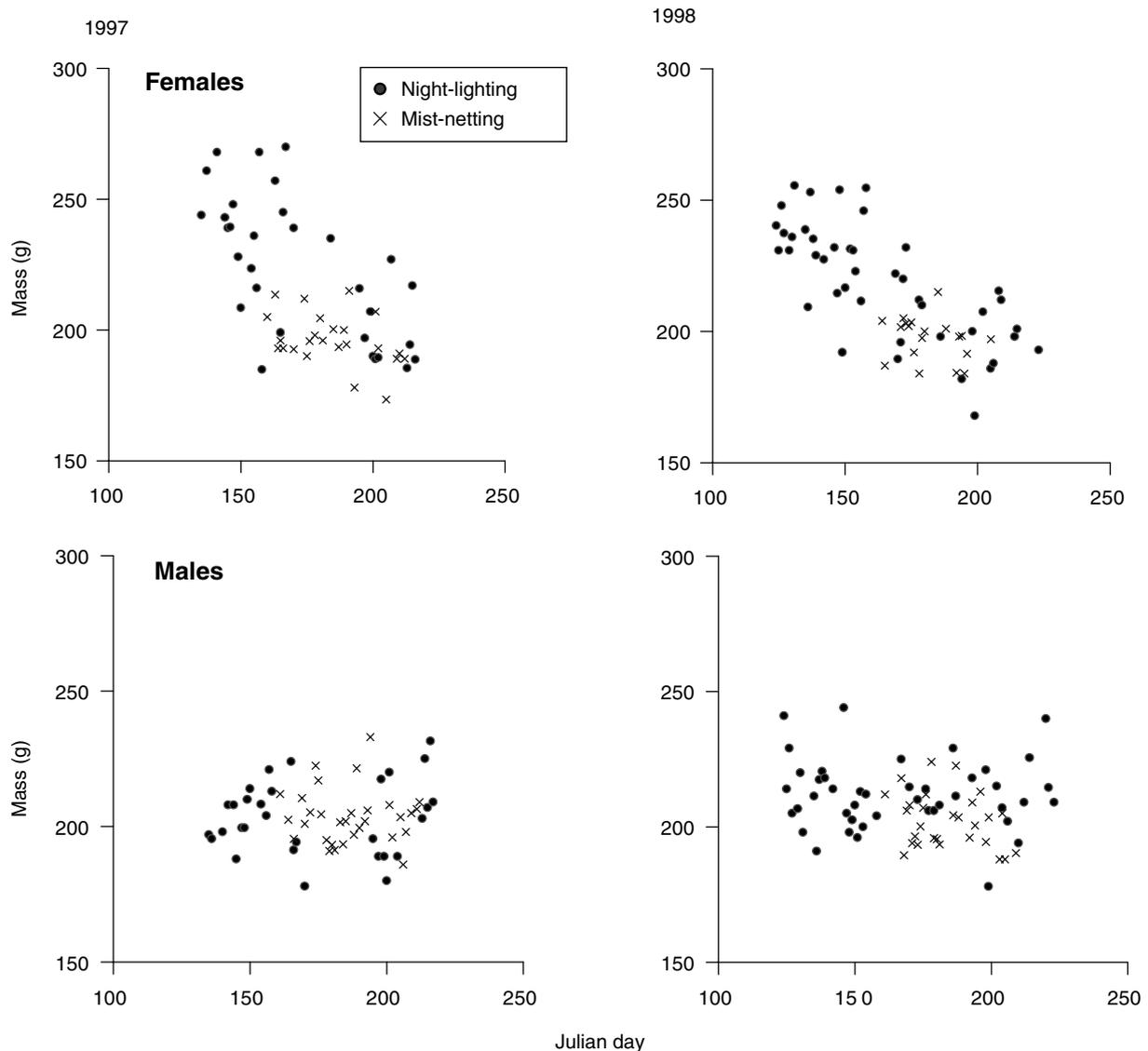


Figure 3. Sex-specific mass of Marbled Murrelets caught by night-lighting and mist-netting at Desolation Sound during 1997 and 1998.

in 1997 and 1998 (1997: $F_{1,52} = 30.7$, $P < 0.001$, $r^2 = 0.4$; 1998: $F_{1,90} = 37.7$, $P < 0.001$, $r^2 = 0.3$), but those caught by mist-netting did not (1997: $F_{1,55} = 3.9$, ns, $r^2 = 0.03$; 1998: $F_{1,39} = 2.7$, ns, $r^2 = 0.06$).

Males did not exhibit a decline in mass either when caught by mist-netting (1997: $F_{1,91} = 0.007$, ns, $r^2 = 0.0$; 1998: $F_{1,85} = 0.9$, ns, $r^2 = 0.01$) or by night-lighting (1997: $F_{1,47} = 1.3$, ns, $r^2 = 0.03$; 1998: $F_{1,81} = 0.007$, ns, $r^2 = 0.0$, Fig. 3).

The masses of juveniles did not differ between 1997 and 1998 (males: $t_{29} = 1.1$, ns; females: $t_{18} = 0.8$, ns). Neither did the masses of juveniles change with capture date (males: $F_{1,29} = 3.3$, ns,

$r^2 = 0.01$; females: $F_{1,18} = 1.4$, ns, $r^2 = 0.07$). However, the masses of recently fledged juvenile males and females did differ significantly ($t_{49} = 2.3$, $P < 0.05$).

A total of 72 individuals were recaptured between years, and 14 were recaptured in the same year. There were no significant differences in the mass of males retrapped between years (paired $t_{51} = 0.5$, ns), nor in females (all data: $t_{19} = 1.7$, ns, assessed after 18 June: $t_{14} = 1.5$, ns). Males and females recaptured in the same year also exhibited no change in mass (paired tests: males $t_{34} = 1.1$, ns, females $t_8 = 1.0$, ns).

DISCUSSION

Male and female Marbled Murrelets in this study weighed 204 g and 201 g, respectively. These are lighter than those weighed by Sealy (1975) at Langara Island (males: 217.0 g, range 196.2–252.5 g; and females: 222.7 g, range 188.1–269.1 g). This difference can be explained, in part, by the inclusion of gravid females in Sealy's (1975) sample. Gravid females in our study were on average 35 g heavier than non-gravid females. Sealy sampled birds across the breeding season, but sample sizes were greater during the egg-laying period, and included breeding females.

The differences in male masses between the two studies are more difficult to explain. Males were lighter in our study perhaps because of site or geographical differences. There are some methodological differences between the studies, with Sealy's birds obtained in the middle of the day when they may have consumed more food than during the night as they are foraging primarily for self-maintenance. In contrast, nocturnal foraging may be primarily to provision chicks and less food may be caught at that time.

Mussel Inlet is at almost the same latitude, and within 200 km of Langara Island, hence the difference is probably not related to latitude, although there may still be a difference between sites. Murrelets could be lighter now than they were in the early 1970s, but this is difficult to confirm due to the paucity of data. Furthermore, recently fledged juveniles were 157 ± 19 g in Sealy's (1975) study compared to 158 ± 26 g in our study, which would counter this explanation.

Marbled Murrelets caught by night-lighting were heavier than those caught by mist-netting, indicating that either these two capture techniques sampled different sections of the population (such as different proportions of breeders and non-breeders, with one group being heavier than the other), or they sampled birds at different stages in the breeding cycle. Recent data from this site have indicated that mist-netted captures include breeding birds, primarily chick-rearing birds (L. Tranquilla unpubl. data, R. Bradley unpubl. data). Therefore, breeding birds may be lighter in mass than non-breeders or failed breeders. These latter birds may be more abundant in the open waters of Desolation Sound caught by night-lighting.

The difference in mass between birds caught with mist-nets and those caught by night-lighting may

occur because birds on the open waters of Desolation Sound (those caught by night-lighting) may still be foraging and have recently caught food for themselves, adding to their mass. However, this explanation does not seem adequate to explain the approximately 20 g difference in mass, although it is unknown how much food Marbled Murrelets consume during foraging, and whether it would be digested prior to their flight to the forest.

Female body mass was constant across years of the study, while that of males was not. Males caught by night-lighting were heavier in 1998 than 1997. Inter-annual variability in mass may have been more difficult to detect in earlier years of the study as night-lighting was not used to catch birds. Night-lighting detects more egg-producing birds than are detected amongst birds caught by mist-netting. However, night-lighting captures birds earlier in the season, hence there are fewer birds producing eggs, although not necessarily fewer breeders. The heavier male masses found during 1998 may be related to improved foraging efficiency due to a greater abundance and distribution of prey. It is unknown why only males exhibited this difference in mass between years.

Birds at Desolation Sound did not differ in mass from those at Mussel Inlet. Desolation Sound is an area of substantially fragmented forest, while Mussel Inlet is near-pristine forest. While there may be differences in the availability of nesting habitat between the sites, the abundance and availability of food may be similar.

The work conducted at Mussel Inlet during the current study was of short duration (23 June–12 July) and, as indicated by the presence of gravid females (determined from egg-yolk precursors in their plasma), it coincided with the egg-laying period. This suggests that the breeding season of Marbled Murrelets at Mussel Inlet during 1997 may have been up to 30–40 days later than at Desolation Sound, and later than Sealy (1975) found at Langara Island. The egg-laying period at Langara Island, determined by the follicular development of 20 females, was thought to extend from 15 May until the end of June (Sealy 1975). The breeding season of Marbled Murrelets is believed to be quite protracted and less synchronous than that of other alcids (Hamer & Nelson 1995, Loughheed 1999). In British Columbia it is thought to last 137 days, extending from mid-June (onset of incubation) until early September (Loughheed 1999).

Male Marbled Murrelets were constant in mass across the breeding season in all years. Females

caught during 1997 and 1998 declined in mass after the expected time of egg laying (mid-June), and then remained at the same level for the rest of the breeding season. Gravid females were on average 35 g heavier than non-gravid females. This difference is equivalent to the mass of an egg, with some of the increase in mass possibly due to enlarged reproductive organs (Marbled Murrelet eggs are 36–41 g, Sealy 1975, Hirsch *et al.* 1981). This pattern of mass loss contrasts with that found by Sealy (1975). He describes a gain in mass prior to egg laying, then a gradual decline in mass in both sexes through the breeding season. However, the declines described by Sealy (1975) were based on five sampling periods, small sample sizes (1–14), and included gravid females.

Marbled Murrelets nest at considerable distances from foraging areas, with nest sites found by radio telemetry at Desolation Sound being between 12 and 102 km from presumed foraging areas (Hull *et al.* 2001). Regular commuting between nests and foraging areas was estimated to be energetically costly, and as flight costs depend upon the mass of individuals (Pennycuik 1975, 1987), expenditure can theoretically be reduced if a bird's mass is lowered. A murrelet with the lowest mass recorded in the current study (159 g) would theoretically expend 41.4 kJ/h during flight at maximum range velocity, while the heaviest (236 g) would expend 76.3 kJ/h during flight (calculated from Pennycuik's 1998 flight program).

This difference in energy expenditure related to mass could provide support for mass loss according to the flight adaptation hypothesis (FAH), under which mass is lost at specific times in the breeding season, thereby helping to minimize the cost of flight. In K-selected species such as Marbled Murrelets, the effect of reproductive effort on future survival is likely to be important, with birds having to minimize the risk of mortality during reproduction (Williams 1966, Johnsen *et al.* 1994). Greater parental effort devoted to reproduction, reflected in increased energetic consumption, could make an adult more susceptible to starvation, predation or disease. Given the low recruitment rate of Marbled Murrelets (Cooke 1999), individuals should presumably minimize stress during reproduction in order not to jeopardize their long-term survival.

According to the FAH, birds lose mass to reduce the cost of flight prior to the most demanding period in the breeding season. Energy costs are reduced as a lower mass decreases wing loading, and reduces the

cross-sectional area of the bird, thereby reducing drag (Freed 1981). If mass loss is adaptive it should decline rapidly in a stepwise fashion prior to the most demanding stage, such as chick-rearing when more flights are made to provision young (Freed 1981, Croll *et al.* 1991). However, mass changes found in this study do not support this hypothesis because: (1) mass loss in females was not greater than the amount of an egg and associated enlarged reproductive tissue; (2) the masses of males were constant through the breeding season (except during 1998, but this difference is most likely due to sampling a different part of the population, non-breeders caught in mist-nests); and (3) mass loss was stepwise in females, but occurred only around the expected time of laying.

Nor was there any evidence to support the reproductive stress hypothesis, which predicts that birds lose mass through the physiological stress of reproduction (Freed 1981, Merilä & Wiggins 1997). Birds that lose mass in this way lose body condition as they allocate limited resources to offspring at the expense of self-maintenance (Moreno 1989). A possible consequence of mass lost through reproductive stress is that it lowers subsequent survival; therefore, a decline in mass is symptomatic of a fitness cost (Freed 1981). Evidence in support of this hypothesis would be a gradual decline in mass over the breeding season, which was not found in this study.

Other factors dictating mass change in Marbled Murrelets appear to be important. The lack of decline in either sex after the laying period suggests that Marbled Murrelets may not have large fat stores, and therefore little opportunity to alter mass (as is found in some male passerines, Moreno 1989). The fact that Marbled Murrelets carry little fat in reserve suggests that they are 'income' breeders (acquiring mass throughout the season) rather than 'capital' breeders (storing energy [capital] for breeding prior to the breeding season) (Drent & Daan 1980). Marbled Murrelets may need to fly fast and with agility to avoid predation when in flight. Long-term studies of small passerines in the United Kingdom reveal that predation risk is an important determinant of mass, with the adjustment of fat being a trade-off between the risks of starvation and predation (e.g. see Gosler *et al.* 1995).

It is possible that the years in which this study was undertaken were influenced by environmental conditions. For example, inshore resources could have been low due to the effect of El Niño or the Pacific Decadal Oscillation, resulting in low masses. Unfortunately,

there are no data available on inshore resources at these sites during these years to explore this point further.

As the ability to capture individual Marbled Murrelets of known breeding status improves, more data will be available to explore other issues related to mass changes in the species. These should include how mass changes with food availability, and the consequences of differences in mass on reproductive success. The vulnerability of this species to predation, and the long distances it commutes between nest sites and foraging areas, also require further study in relation to mass changes.

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