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Intraspecific Variation in Commuting Distance of Marbled Murrelets (*Brachyramphus marmoratus*): Ecological and Energetic Consequences of Nesting Further Inland

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ABSTRACT.—Radio transmitters were deployed on Marbled Murrelets (*Brachyramphus marmoratus*) at Desolation Sound, British Columbia, Canada, during the 1998 breeding season to assess individual variation in distance birds nested from foraging areas, and potential energetic and ecological consequences of commuting those distances. Radio-tracking from a helicopter was used to locate nests, and tracking from the air and boats was used to locate murrelets on the water. Twenty-three nests were found, with active incubation at 16, and active chick-rearing at 12. A minimum of 3 nests fledged chicks, 9 were failures, and 11 were unknown. Nests were at an elevation of 806 ± 377 m and a distance of 39.2 ± 23.2 km (range 12–102 km) from locations on the water. Birds spent an estimated 1.2 ± 0.7 h per day commuting to and from nests (range 0.3–3.5 h per day). It was estimated that birds expended $3,883 \pm 2,296$ kJ (range 1,200–10,144 kJ) over the breeding season when commuting to those nests, which was 5–41% of their estimated field metabolic-rate during the breeding season. There was no relationship between distance to nests and breeding success. Either Marbled Murrelets can accommodate that additional energy expenditure, or reduce commuting costs by modifying their foraging behavior. They may forage closer to nest sites when provisioning chicks, thereby reducing commuting costs with a payload, or alter nest visitation rates in relation to distance they nest from foraging areas. Nests further inland may also confer advantages that compensate for the added commuting, or birds might replenish body reserves at the end of the breeding season.

Distance that birds travel between nest sites and foraging areas is an important component of time-energy budgets, particularly during the breeding

season (Drent and Daan 1980, Ricklefs et al. 1986). Birds that use flapping (muscle-powered), or non-gliding flight do not usually commute long distances from nest sites to foraging grounds due to the poor economy of such flight (Pennycuik 1987). Energetic consequences of travelling long distances to foraging grounds using flapping flight may be substantial over the breeding season, especially when parents are regularly provisioning chicks. Added energetic cost of nesting a long distance from foraging grounds may then have ecological consequences for those individuals.

The alcids (family Alcidae) have a high rate of energy expenditure during flight due to their flapping, nongliding technique (Pennycuik 1987). Marbled Murrelets (*Brachyramphus marmoratus*) are small alcids found along the Pacific coast of North America, from northern California to Alaska. In British Columbia, they nest solitarily or in loose associations in large trees of old-growth (>100 years old) forest (Hamer and Nelson 1995). They can nest up to 60 km inland, but are dependent on marine habitat for their primary food, Pacific sand lance (*Ammodytes hexapterus*), which they forage for close to shore (Carter and Sealy 1990). Despite that inshore foraging habit, murrelets have been likened to alcids that forage offshore due to distance they travel between nest sites and feeding areas (Gaston and Jones 1998).

Marbled Murrelets use flapping flight with no gliding. Because that travelling mode involves a high rate of energy expenditure, it is expected that individuals would attempt to minimize time spent commuting (cf. Gaston 1985). However, they exhibit substantial intraspecific variability in distance between nest sites and the sea (Grenier and Nelson 1995, Hamer 1995). Presumably, long flights are energetically costly, increase the risk of predation from aerial predators (Ralph et al. 1995), and detract from time spent in other activities such as foraging. Those factors may result in a trade-off between reproductive investment and adult survival (Stearns 1977).

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The purpose of this study was to address the issue of individual variability in commuting distance of Marbled Murrelets. Effect of commuting distance on breeding success was assessed, and potential energetic cost of commuting varying distances was calculated. Diurnal and seasonal variability in areas used and nest visitation rates were also examined in relation to location of nests.

Methods.—Field work was conducted at Desolation Sound, British Columbia (50°04'N, 124°42'W, Fig. 1) during the 1998 breeding season. Marbled Murrelets were captured on the waters of Desolation Sound using night-lighting (modified from Whitworth et al. 1997 and see Loughheed et al. 2000 for details), between 4 and 19 May 1998. Radio-transmitters were attached to 40 murrelets, which were also weighed using a spring scale, and banded with stainless steel Canadian Wildlife Service/U.S. federal bands. Sex was determined using a molecular sexing technique (Vanderkist et al. 1999), for which a small droplet of blood was collected from a pin-prick in the tarsal vein of birds.

Telemetry transmitters that were used were two-stage, Advanced Telemetry Systems (Isanti, Minnesota) devices that weighed 1.9 g (~1% average mass of Marbled Murrelets), and measured $22 \times 11 \times 7$ mm, with a flexible 120 mm antenna at the posterior end. They were attached to the back of the birds using subcutaneous anchors based on the technique of Newman et al. (2001), although a small amount of epoxy (Bird Adhesive, Titan Corporation) was used to secure the transmitter to body feathers rather than a suture.

Marbled Murrelets were radio-tracked from a boat, a helicopter, and from ground-based stations. Locations on the water (LW) were described from boat and helicopter telemetry, and nest sites were located by tracking from the air and by ground searches.

Boat-tracking was undertaken from a 5 m fiberglass inflatable boat (see Loughheed et al. 2000 for details) from 16 May–13 August, 1998, through 10 stations in Desolation Sound and adjacent inlets. Telemetry runs were conducted three times a day (duration of runs was usually 6 h): morning, or sunrise to noon (AM); afternoon, or midafternoon to sunset (PM); and night, or end of civil twilight (defined as when the center of the sun is geometrically 6° below the horizon, U.S. Naval Observatory) to half an hour before civil twilight the following day (NT), over four consecutive days (usually 12 runs per week, 111 runs in total).

Aerial telemetry was conducted from a Robinson 22 helicopter (see Loughheed et al. 2000 for details). Flights were conducted at an altitude of 200–3,000 m, starting at high altitudes for maximum range to determine presence of a signal and then lower, circling to determine precise locations of signals, with no fixed route being used. Forty-two flights were con-

ducted between 12 May–4 July 1998 (25 in May, 14 in June, and 3 in July). Elevations of nest sites were measured with an altimeter either on the helicopter or at the nest site at the end of the breeding season.

Ground-based telemetry was conducted by placing two people at 11 sites in the forest close to known active nests for three to four days during chick-rearing (late June and early July) to determine number of visits by adults and to describe flight paths to nests. Signals were monitored from an hour before dawn until an hour after dusk each day. Marbled Murrelet flight paths were described by watching paths taken by birds to nest sites and by monitoring signals from transmitters.

The locations of and distances between LW and nest sites were plotted using ArcView GIS (Environmental Systems Research Institute Inc., Redlands, California). Commuting distances were calculated (1) via inlets, the path through inlets on the basis of observations of birds and detections from ground-based radio telemetry, and (2) direct, from LW to nest sites (which gives a minimum estimate of commuting distance). Geometric means of locations on the water were used, which averaged diurnal and seasonal changes in foraging areas, and included coalescing areas (areas where birds gathered, Strachan et al. 1995). We assumed that LW represented foraging areas of Marbled Murrelets. Seasonal changes in LW were assessed by comparing locations between incubation (May) and chick rearing (July and August). Diurnal changes were made by comparing locations on the water from 0400–0600 PDT (around sunrise) and 1900–2100 hours (around sunset).

Radio-tracking from boats was limited in its spatial but not temporal coverage, whereas helicopter telemetry was temporally but not spatially limited. In order to address those sampling biases, number of locations in relation to sampling effort (locations/unit effort [minutes of radio-tracking]) was determined for the period 4–14 June 1998 (incubation) and 4–14 July 1998 (chick rearing). Those times were selected because all birds should have initiated incubation by 4 June (as breeding attempts were recorded between 11 May and 5 June 1998, see below), but no chicks should have hatched (according to the estimated 30 day duration of incubation, Sealy 1975). The 4–14 July was selected because all chicks at successful nests should have hatched by that time, but it was prior to decline in battery life of the transmitters (indicated by slow and erratic pulse rates, which began ~59 days after deployment of batteries, therefore after 15 July).

Breeding success was measured at three stages: active incubation, active chick rearing, and successful chick fledging. Activity implied success during at least part of a stage, but not whether the event was successfully completed. The first two stages were determined by attendance patterns by adults at the nest and on the water (following Nelson and Hamer 1995) from radio telemetry. Successful chick fledging was

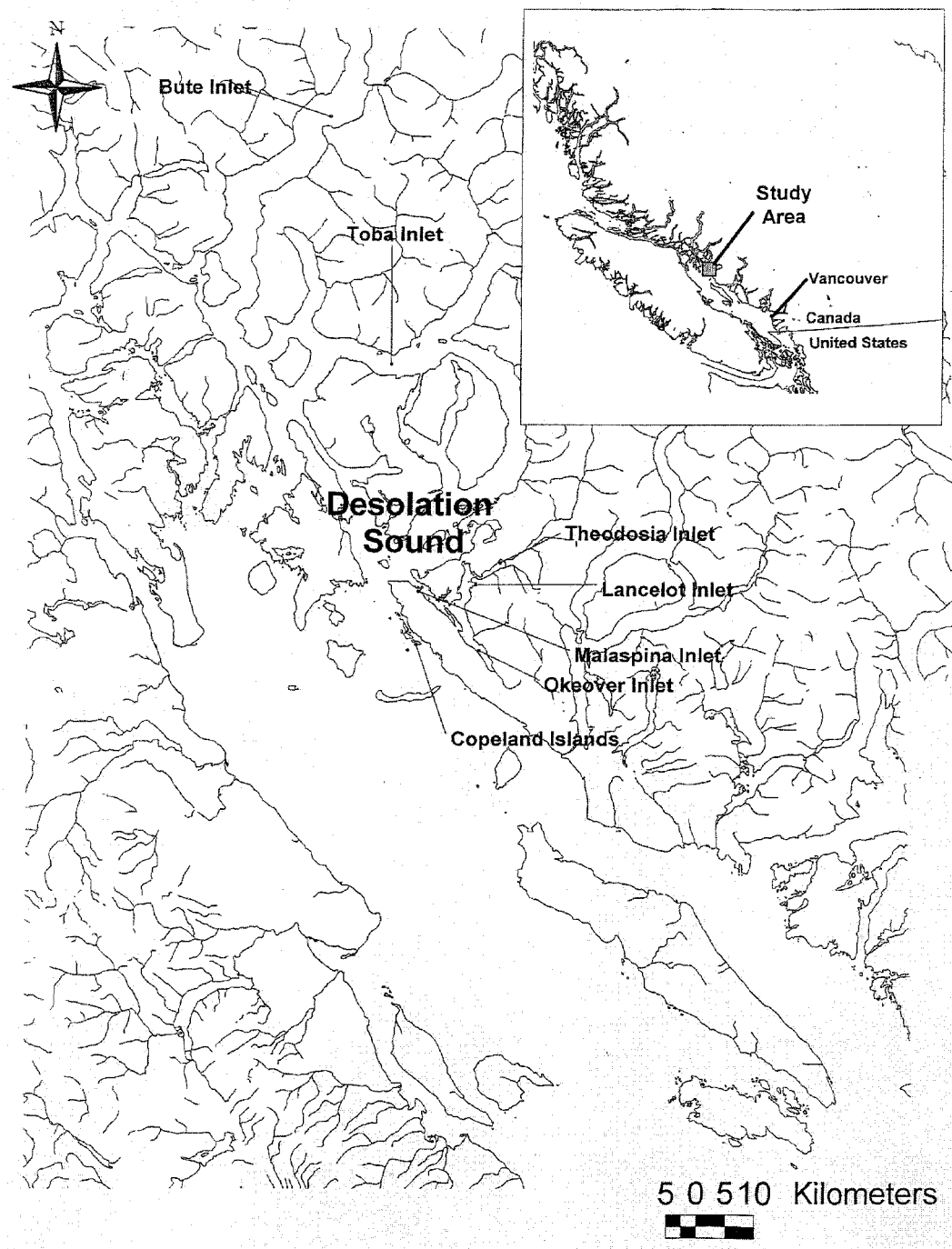


FIG. 1. Study area at Desolation Sound, British Columbia.

determined by climbing nest trees at the end of the breeding season and observing the presence of a fecal ring and chick down at the nest (Manley and Kelson 1995).

Binary logistic regressions on nests where a breeding attempt was made were used to determine if the explanatory variables of elevation, commuting distances (using both methods), and mass (log-trans-

formed) had an effect on success during the three stages. Regressions were performed on nest-visitation rates and commuting distance, and number of LW and commuting distance. Sampling bias between helicopter and boat telemetry was assessed by comparing number of locations per unit effort between methods, and between incubation and chick rearing with Mann-Whitney *U*-tests (due to lack of normality in the data, which transformations did not resolve). Retrospective power analysis was performed to determine if a Type II error may have been made in some of the tests with small sample sizes. Power was set at 0.8 and the effect size at that power determined using PASS (Power Analysis and Sample Size, 1996, NCSS, Statistical Software, Kaysville, Utah).

Theoretical predictions of chemical power (=energy expenditure) during flight were estimated from the program of Pennycuik (1998). Wing span (0.48 m) and wing area (0.0307 m², used to derive aspect ratio) were measured on six Marbled Murrelets from Desolation Sound, and mass (0.20 kg) was obtained by averaging adult birds captured at Desolation Sound during May–July, 1994–1998 (Wildlife Ecology Chair, Simon Fraser University unpubl. data). Other than those, default values in the program were used. Cost of commuting was estimated from energetic values at V_{mr} (maximum range velocity), because those speeds were most similar to ones recorded at that site (see below; G. Kaiser and M. Drever unpubl. data), and it is recommended that values closest to those measured be used (Flint and Nagy 1984). Trips during incubation were calculated from the value of birds without a payload, and those during chick provisioning with a payload of 10 g, which is the approximate size of Pacific sand lance brought to chicks (Burkett 1995, C. Lougheed unpubl. data).

Amount of time spent commuting (*T*) between nests and locations on the water was calculated for both incubation and chick rearing periods, using the formula of Obst et al. (1995): $T = (2 \times C \times R) / V$, where *R* = foraging radius (kilometers per trip), *C* = number of daily trips (see below), *V* = flight speed (average 70 km h⁻¹ in Marbled Murrelets at Desolation Sound; M. Drever unpubl. data).

It was assumed there were 15 flights to and from the nest by each parent during the incubation period (30 days duration, with exchanges every 24 h, Nelson and Hamer 1995). During chick rearing, adults visited nests in this study on average 1.2 times a day (see below). That is a conservative amount, because other studies have found higher visitation rates (Ralph et al. 1995). A 28 day chick-rearing period was assumed (Nelson and Hamer 1995, I. Manley unpubl. data), resulting in adults making 34 trips during that stage.

Results.—Masses of birds at time of capture was 232.8 ± 26.3 g (some of those birds would most likely have been females carrying an egg). Twenty of the birds were sexed. The elevation of nest sites ranged

from 300–1,300 m (mean \pm standard deviation, 806.5 ± 376.7 m) (Appendix).

Six-hundred and forty locations were obtained from boat telemetry, 397 from helicopter (Fig. 2), and 44 from ground-based telemetry. Twenty-three nest sites were located from the 40 radio-marked birds. At one nest site, both members of the pair had transmitters. Of the 23 nests located, one transmitter failed during incubation and two during chick-rearing.

Distance between nest sites and presumed foraging areas via inlets was 12.1 to 102.3 km (39.2 ± 23.2 km), and direct distances were 10.7 to 72.8 km (30.9 ± 15.6 km) (Appendix). The majority of LW were in Desolation Sound, Malaspina Inlet, and around the Copeland Islands (Fig. 2). A linear regression found more detections were obtained from birds nesting closer to LW than those nesting further away ($R^2 = 0.18$, $t = 2.2$, $P < 0.05$; Fig. 3).

Number of visits by each bird to nests during chick rearing varied from 1 to 1.7 per day (average 1.2). The correlation between number of visits to nests and distances between nests and LW (estimated via inlets) was not significant ($F = 0.4$, $df = 1$ and 12 , $P > 0.05$). Nest 19, however, was aberrant in that respect (102 km LW with 1.7 visits per day).

There were no apparent seasonal or diurnal changes in LW (Figs. 4 and 5), although more locations were obtained around sunset (64) than sunrise (23).

Number of locations per unit effort (number of detections per minute of sampling) did not differ between helicopter and boat telemetry during incubation ($U = 4$, $df = 1$, $P > 0.05$), but did during chick rearing with more detections being received from helicopter than boat tracking ($U = 0.0$, $df = 1$, $P < 0.05$). Although there was a decline in number of detections from boat telemetry between the two periods (incubation: 0.020 ± 0.01 detections per minute of sampling, $n = 5$ days; chick rearing: 0.017 ± 0.01 detections per minute of sampling, $n = 6$ days), and an increase in number of locations from helicopter telemetry between those periods (incubation: 0.067 ± 0.07 , $n = 2$ days; chick rearing 0.092 ± 0.02 , $n = 2$ days), the patterns were not significant (helicopter: $U = 4$, $df = 1$, $P > 0.05$; boat $U = 11$, $df = 1$, $P > 0.05$). However, retrospective power analysis revealed that a Type II error may have been made because a difference in means of 0.002 and 0.2 would be required to detect an effect in boat and helicopter telemetry, respectively. Therefore, there may have been biases in telemetry sampling, with birds moving out of the study area surveyed by boat later in the breeding season (after chicks hatched).

Nesting was initiated between 11 May and 23 June. Sixteen of the 23 nests were active during incubation, 12 were active during chick rearing (3 unknown), and 3 fledged chicks (11 unknown). Logistic regressions revealed that mass, elevation of nests, and com-

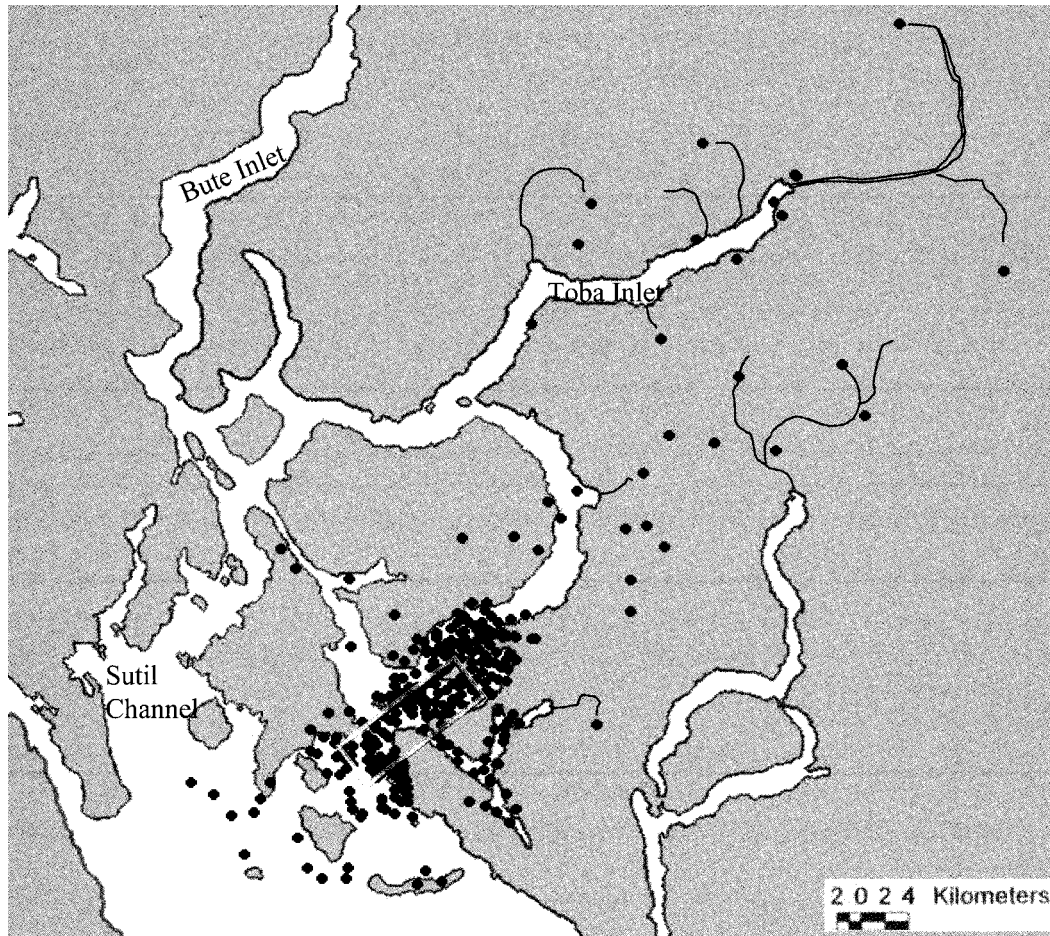


FIG. 2. Nest sites and locations of Marbled Murrelets on the water found using radio telemetry. The rectangle indicates extent of boat telemetry, whereas helicopter telemetry covered the entire area shown.

muting distance were not significantly related to breeding success during the three stages (incubation: G-test, $G = 12.3$, $df = 4$, $P > 0.02$, but Hosmer-Lemeshow goodness-of-fit test was significant $\chi^2 = 20.4$, $df = 8$, $P > 0.09$ [indicating the model was an inadequate fit], chick rearing: $G = 7.7$, $df = 4$, $P < 0.05$; chick fledged: $G = 6.9$, $df = 4$, $P < 0.05$, Fig. 6).

Calculated minimum power speed and maximum range speed for Marbled Murrelets with and without a payload, and energetic costs of flight are provided in Table 1. Calculated time spent commuting to nests across breeding season at the 23 nests ranged from 0.3 to 3.5 h per day (mean 1.2 ± 0.7 h per day, but that does not take into account the higher visitation rates of nests closer to LW) (Appendix). Energetic expenditure of commuting to the nests was estimated to be 1,200 to 10,144 kJ ($3,883 \pm 2,296$ kJ) (Appendix). In terms of prey consumption, that represents 22 to 187×10 g sandlance. Energetic values for those es-

timates are from Montevecchi and Piatt (1987), assuming an assimilation efficiency of 76%, as has been used for the closely related Cassin's Auklet (*Ptychoramphus aleuticus*) (Montevecchi et al. 1984, Hodum et al. 1998).

Discussion.—Radio telemetry used during this study was successful in locating both the nest sites and LW of Marbled Murrelets at Desolation Sound. The 23 nests located represents the largest number of active nests found in one season in a single study area, although many nests have been found after the breeding season in that area using ground searches (Manley 1999). Nests located using radio telemetry are unique in that they are located without a biased expectation of suitable nesting habitat (Ralph et al. 1995).

Commuting distance from nest sites to locations on the water ranged from 12 to 102 km (mean 39 km). Although measurements between nest sites and LW

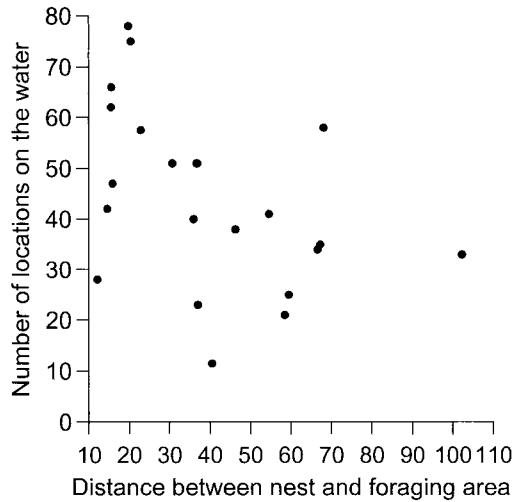


FIG. 3. Number of Marbled Murrelet locations on the water in relation to the distance between nest sites and foraging areas (kilometers).

have not been made before, maximum distances Marbled Murrelet nests have been recorded inland is between 29 to 63 km (Carter and Sealy 1986, Leschner and Cummins 1992, Hamer 1995). Birds in southeast Alaska have been found foraging up to 124 km from probable nesting areas, resulting in 250 km daily round trips (Whitworth et al. 2000), and Burns et al. (1994) found one bird 111 km from its suspected nest site.

The locations of birds were similar across the day, but the number of detections was substantially less at sunrise than sunset. Fewer locations around sunrise can be explained by the fact that birds were outside the range of boat telemetry. Those birds may have been foraging closer to nest sites, a pattern that has been described previously (Carter and Sealy 1990, Nelson and Hamer 1995, Rodway et al. 1995, Strachan et al. 1995).

Seasonal changes in locations of birds on the water were not detected in this study. Changes in locations of murrelets on the water have been found previously at both Desolation Sound and other sites, with more birds in inlets than open waters, and closer to nesting sites later in the season (Carter and Sealy 1990, Burns et al. 1994, Rodway et al. 1995, G. Kaiser unpubl. data). Lack of such a pattern in our study could be due to small sample sizes and sampling biases.

Fewer LW were obtained from birds that nested furthest from their foraging areas because they were outside the range of boat telemetry and therefore not detected. Those birds may have been foraging closer to their nest sites some of the time, or have had different foraging patterns from those nesting closer to LW. It is obvious that Marbled Murrelets have com-

plex use patterns of the marine environment (Rodway et al. 1995), requiring further examination, particularly in relation to location of nest sites.

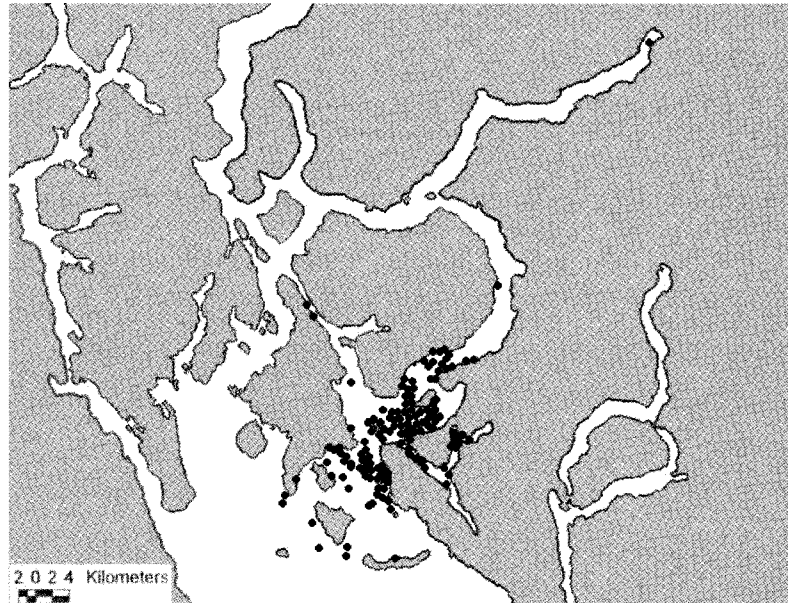
There was not a significant reduction in number of visits to nests by birds nesting further from LW, although a Type II error may have been made due to small sample sizes, and aside from nest 19, there was a trend for nest visitation rates to be higher the closer birds nested to foraging areas. Nests in the Bunster Range (Desolation Sound) are within 5 km of marine areas, and have the highest nest-visitation rates yet reported for murrelets, which is thought to be linked to proximity of foraging areas (Manley 1999).

Due to various assumptions made and unmeasurable values applied to all individuals, the estimated cost of commuting should only be viewed as an approximation of the actual commuting costs. Energetic costs of commuting could differ because the model might not accurately reflect actual costs of flight due to morphological and behavioral adaptations Marbled Murrelets may have, or they may use the environment to reduce cost of flight (Flint and Nagy 1984). The default values of induced power factor, body drag coefficient, profile power ratio, and conversion efficiency in the model may also not be appropriate and require more research (Pennycuik 1998). A constant air density was used, but that changes with altitude, which will affect lift:drag ratios, and therefore energetic expenditure during flight (Pennycuik 1975). A flight speed of 70 km h⁻¹ was used when estimating time spent commuting, yet flight speed in Marbled Murrelets is highly variable between sites, and with the direction birds are travelling (Hamer et al. 1995, Burger 1997, G. Kaiser and M. Drever unpubl. data). Number of foraging trips per day used in our study are low compared to other studies (Ralph et al. 1995), and duration of the breeding season varies considerably, both of which will alter estimates of commuting costs. Changes in mass across the breeding season will also alter costs of flight, as will the weight of food carried during flight.

Whereas the calculated costs of commuting to nests should be viewed with caution, the magnitude of effects can be regarded with greater confidence. There was an eight-fold difference in commuting distance and estimated energetic consumption required to fuel commuting. However, that variation was not reflected in breeding success. Although we did not find an effect, it is possible that chick fledging masses and or first-year survival rates were affected. In some but not all seabirds, an increase in distance between nest sites and the ocean results in a decrease in density of nest sites and reduced breeding success (Eberl and Picman 1993, Obst et al. 1995).

Alternatively, estimated flight costs in Marbled Murrelets may not add a significant burden to their annual energetic budgets. The energetic cost of flight was estimated to be 11 × basal metabolic rate at max-

Locations prior
to 31 May 1998



Locations after
1 July 1998

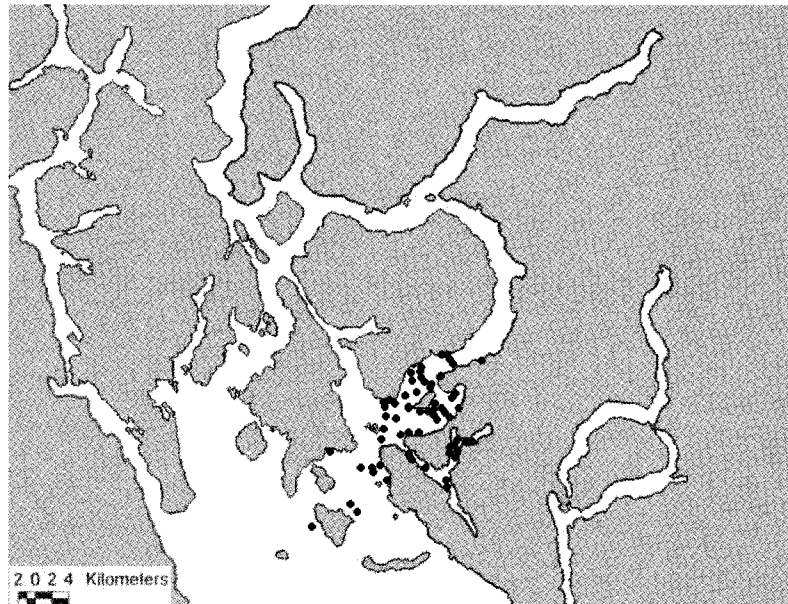


FIG. 4. Locations of Marbled Murrelets on the water during incubation (prior to 31 May) and during chick rearing (after 1 July).

imum power, and $13.8 \times$ BMR at maximum range, with no payload. Empirical studies have found flight costs in birds varies between 4.8 to $11.6 \times$ BMR (Roby and Ricklefs 1986, and references therein). BMR in alcids ranges between 222 to $587.8 \text{ kJ day}^{-1}$ (Johnson and West 1975, Bryant and Furness 1995). Using the allometric equation for BMR in seabirds from the North Atlantic ($2.3 \text{ mass}^{0.774}$, Bryant and Furness

1995), Marbled Murrelet BMR is estimated to be $138.9 \text{ kJ day}^{-1}$ (8,056.2 kJ over the breeding season). Field metabolic rates in seabirds are $3 \times$ BMR (Bryant and Furness 1995), therefore $416.7 \text{ kJ day}^{-1}$ in Marbled Murrelets (24,168.6 kJ over the breeding season). The added cost of commuting to nests was 1,200 to 10,144 kJ over the breeding season, or an additional 5 to 42% (mean 16%) above normal field

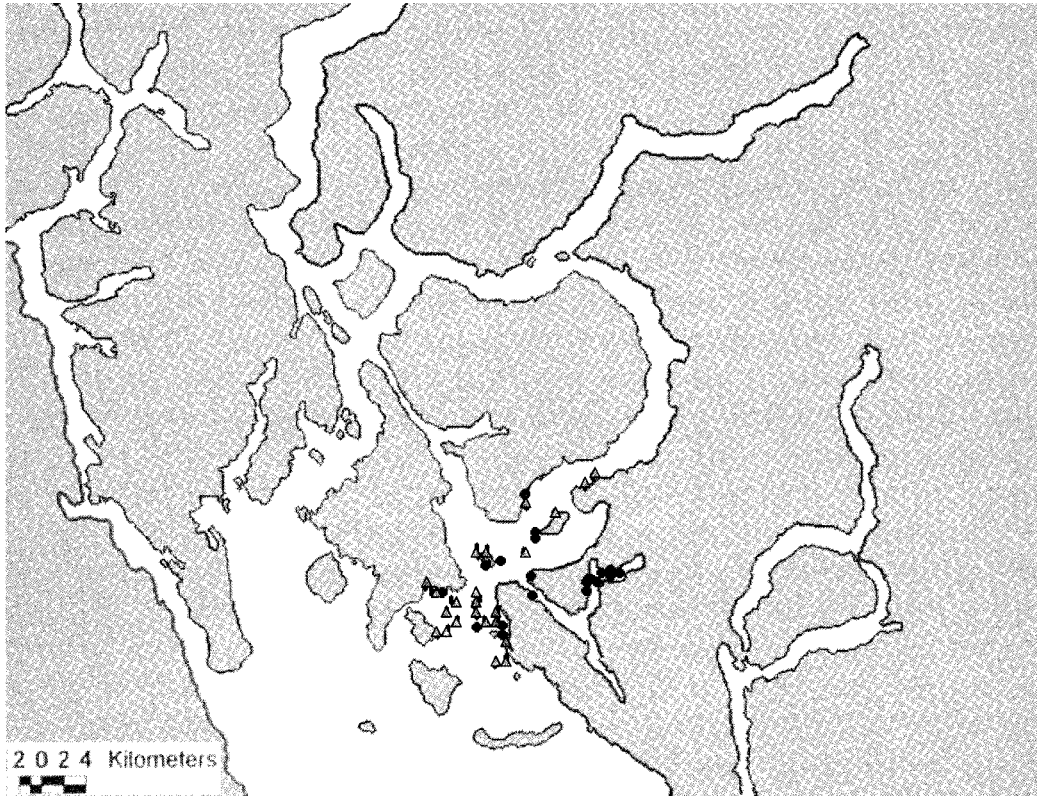


FIG. 5. Locations of Marbled Murrelets on the water during the morning and evening. Circles represent morning (around sunrise), and triangles represent evening (around sunset).

metabolic-rates. Only four of the 24 birds had commuting costs that exceeded 25% of normal field metabolic rates. Because there was no detected effect of distance on breeding success in this study, it suggests that Marbled Murrelets either have sufficient plasticity in their energy budgets to accommodate that additional 5 to 42% cost, or that they employ strategies to reduce costs from what was estimated here. Hence, actual costs may not be as high as estimated. Some of those strategies could be as follows: (1) Changing foraging zones. (Birds nesting further inland may use different foraging areas than those nesting closer to foraging areas. Adults may also forage for food for chicks close to the nest, thereby reducing commuting costs while carrying prey items.). (2) Altering nest visitation rates in relation to commuting distance. However, unless larger food items are brought to chicks at nests further inland, slower growth rates, later fledging (Gaston and Nettleship 1981), or lower fledging masses of chicks may occur, which could have implications for first-year survival of chicks. (3) Other advantages of nests being further from foraging areas. (Nests further inland may be of higher quality, or have lower predation rates than those closer to foraging areas, which compensates

for the added risk; DeSanto and Nelson 1995.) (4) Replenish at the end of the breeding season (see Martins and Wright 1993).

There are currently too few data to conclusively determine which, if any, of the above strategies are employed by Marbled Murrelets to minimize commuting costs, or whether extra costs of commuting are a burden to individuals. Closer examination of individual diurnal and seasonal foraging patterns, time-energy budgets, nest-visitation rates, and nest sites varying distances inland are required to further understand this alcid, which appears to use complex, yet largely undescribed foraging behaviors during the breeding season. Those issues are particularly important if Marbled Murrelets are forced to nest further from foraging areas due to habitat modification. Most of the low elevation old-growth forests at Desolation Sound have been removed by industry. Marbled Murrelets in this study nested at a mean elevation of over 800 m, which is much higher than other sites (332 m, Gaston and Jones 1998) where less habitat modification has occurred. It is unknown if birds in this study were nesting further from foraging areas than murrelets from more pristine sites because there are no comparable data. If there is a limit

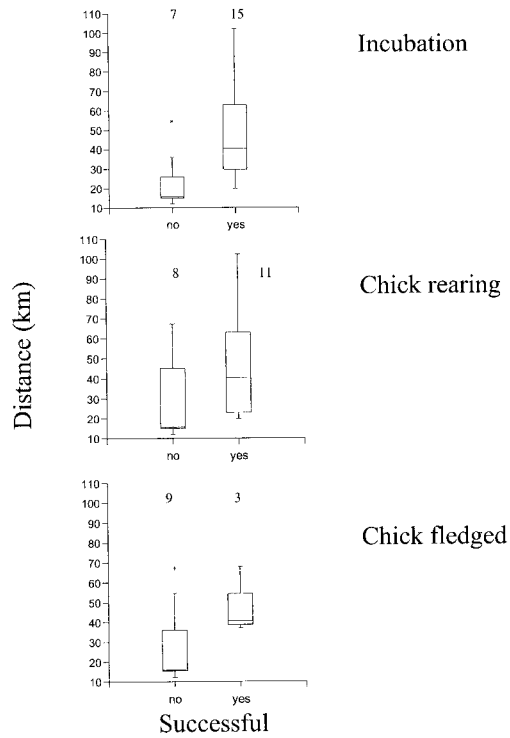


FIG. 6. Boxplots of distance between nest sites and locations on the water in successful and unsuccessful nests, during incubation, chick rearing, and at nests where the chick was known to have fledged. The center line is the median, the length of the box is the range within which the central 50% of values fall. The long lines represent the range in which 75% of values fall. Asterisks are outliers ($1.5 \times$ the interquartile range). Sample sizes are given above boxes.

to the distance Marbled Murrelets can nest from foraging areas due to the added energetic cost of commuting or risk of predation, nesting further inland could influence reproductive output or adult survival. Marbled Murrelets are threatened in Canada and

endangered in parts of the United States (Committee on the Status of Endangered Wildlife In Canada, Federal Register of the United States), and indirect effects of habitat modification such as that need to be considered in management of the species.

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TABLE 1. Estimated maximum range speed (where the ratio of power to speed is least, and although a bird uses more energy, it does less work per unit of distance flown), minimum power speed (the speed at which a bird uses the least power to fly, thereby minimizing the work done per unit distance, Pennycuik 1998) and energetic costs of flight for Marbled Murrelets, from Pennycuik's (1998) model. BMR = basal metabolic rate.

Flight variable	Velocity (km h ⁻¹) no payload	Velocity (km h ⁻¹) with 10 g payload	Power (W), no payload	Power (W), with 10 g payload
Minimum power	43.2	43.9	13.1 (11 × BMR)	14.1 (11.9 × BMR)
Maximum range	71.3	72.4	16.4 (13.8 × BMR)	17.6 (14.9 × BMR)

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APPENDIX. Details of Marbled Murrelets for which nest sites were located during the study. *T* = estimated time spent commuting per individual of a pair per day, based on the formula of Obst et al. (1995); see text.

Nest number	Sex	Mass (g)	Distance, via inlets (km)	Distance, direct (km)	T (h/day)		Elevation (m)	Cost of commuting (kJ)
					Incubation	Chick rearing		
1	Male	204	54.6	35.7	1.6	1.9	600	5414
2	Male	241	59.5	74.4	1.7	2.0	1300	5900
3	Female	238	22.9	22.9	0.6	0.8	900	2271
4	Male	227	36.9	62.6	1.1	1.3	400	3659
5	Female	219	40.5	51.9	1.2	1.4	400	4016
5	Male	300	40.5	51.9	1.2	1.4	400	4016
6	Female	244	14.6	13.6	0.4	0.5	900	1448
7	Female	258	66.6	68.2	1.9	2.3	1200	6604
8	?	204	15.9	15.9	0.5	0.5	700	1577
9	Male	226	68.1	62.2	1.9	2.3	300	6753
10	Male	220	20.4	20.4	0.6	0.7	1200	2023
11	?	270	58.5	58.5	1.7	2.0	1000	5801
12	Female	178	12.1	12.1	0.3	0.4	?	1200
13	Male	217	22.9	22.9	0.7	0.8	1200	2271
14	?	232	67.3	67.3	1.9	2.3	150	6674
15	Female	255	46.3	46.3	1.3	1.6	1000	4592
16	Female	246	19.8	19.8	0.6	0.7	1300	1963
17	Male	234	36.0	33.9	1.0	1.2	1200	3570
18	Male	206	15.5	12.8	0.4	0.5	900	1537
19	Male	220	102.3	102.3	2.9	3.5	1200	10144
20	Female	245	36.7	36.7	1.0	1.3	300	3639
21	Female	200	37.0	54.8	1.1	1.3	300	3669
22	Female	240	15.6	15.6	0.4	0.5	900	1547
23	?	264	30.7	30.7	0.9	1.1	800	3044