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DAILY FORAGING BEHAVIOR OF MARBLED MURRELETS

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Abstract. Patterns of at-sea dispersion, flocking, distribution, flights, and fish-holding behavior of Marbled Murrelets (*Brachyramphus marmoratus*) in Barkley Sound, British Columbia, were synthesized into a descriptive model of daily foraging behavior. Murrelets were clumped in coastal and sill areas in Trevor Channel and used the same feeding sites each day. Adults rearing nestlings flew to and aggregated at feeding sites at or before dawn, fed themselves there early in the day, flew to other areas later in the day to search for prey for nestlings, and returned to nest sites to feed chicks mainly at or after dusk. At this time, adult murrelets minimized time required to feed themselves by specializing on abundant and easily-found prey. Consequently, this maximized time to obtain prey for nestlings, which were less abundant and more difficult to locate. This system may be facilitated by solitary foraging.

Key Words: Marbled Murrelet; *Brachyramphus marmoratus*; British Columbia; foraging; habitat selection; flocking behavior.

The foraging behavior of alcids has been difficult to study because the birds typically forage long distances from nest sites over wide expanses of ocean without obvious landmarks. Thus, foraging behavior has been inferred only roughly from diet, patterns of attendance at colonies or nest sites, and general aspects of their distribution at sea (e.g., densities within specific marine habitats) (Brown 1980, Nettleship and Birkhead 1985). While inter-seasonal and inter-year differences in these aspects of alcid biology have been examined (e.g., Gaston and Nettleship 1981; Ainley and Boekelheide, 1990), the daily foraging behavior of any alcid has never been examined directly in the field. Daily foraging behavior causes variation in the numbers and distribution of birds at sea throughout the day and reflects variability of prey resources, foraging movements at sea, and movements to and from nest sites.

The Marbled Murrelet (*Brachyramphus marmoratus*) is a small alcid that uses nearshore waters year round and often aggregates in small, well-defined feeding areas (Sealy and Carter 1984, Carter and Erickson 1988). While we know little about actual nest sites, their accessible feeding aggregations provide a focus on which to examine distribution and movements at sea. Carter (1984) determined that Marbled Murrelets are most aggregated during the nestling period, when the single chicks are left unattended at solitary nests during the day while adults forage at sea (Sealy 1974, Simons 1980). Adults must forage efficiently when feeding themselves and their chicks, and this should be reflected in their temporal and spatial distributions at sea.

We integrated patterns of dispersion, flocking, distribution, flights, and fish-holding behavior with the few known aspects of nesting biology to construct a descriptive model of daily foraging behavior of Marbled Murrelets in Barkley Sound, British Columbia. This unique approach permitted us to infer foraging behavior from direct observations of birds at sea without following focal birds or monitoring attendance patterns at nest sites. Thus, we were able to elucidate factors affecting the selection and use of feeding areas by murrelets that would not have been possible otherwise.

METHODS

CENSUSES

Marbled Murrelets were censused at sea 37 times between 16 June and 6 July 1980 in south Trevor Channel, Barkley Sound, British Columbia. A contiguous-quadrat grid covering 23.7 km^2 of water surface was used (Fig. 1) and the size of all flocks of murrelets on the water was recorded in each of 96 0.25 km^2 quadrats on each census. Flying birds were recorded but not included in quadrat totals. Censuses began at four times (PDT) of day: dawn (05:00, N = 6), morning (10:00, N = 10), afternoon (15:00, N = 9), and dusk (20:00, N = 12). Each census was conducted by HRC from a pneumatic boat powered by an outboard engine. Dawn, morning, and afternoon censuses averaged 2.1, 2.1, and 2.2 hours, respectively, whereas dusk censuses averaged 1.7 hours. One to four censuses were conducted each day and none was carried out on eight days of the 21-day period that generally coincided with the nestling period of Marbled Murrelets in this area (Carter 1984, Carter and Sealy 1984).

A sitting flock was two or more birds observed within 1 m of one another. A flying flock was two or more birds that flew in the same direction, at the same speed, within 5 m of one another, and usually less than 10–15 m above the water. Single individuals were treated as a type of flock for ease of analysis. Flocks landing or taking off were classified as sitting flocks.

Dispersion indices

We used a comprehensive method for analyzing spatial patterns in contiguous grids based on the relation of Lloyd's (1967) mean crowding index (m^*) to mean density (m) (Iwao 1968, 1972, 1977; Iwao and Kuno 1971). The m^*/m ratio is called patchiness (Lloyd 1967) and measures relative concentration. Often, m^* is linearly related to m. The intercept, α, is called the index

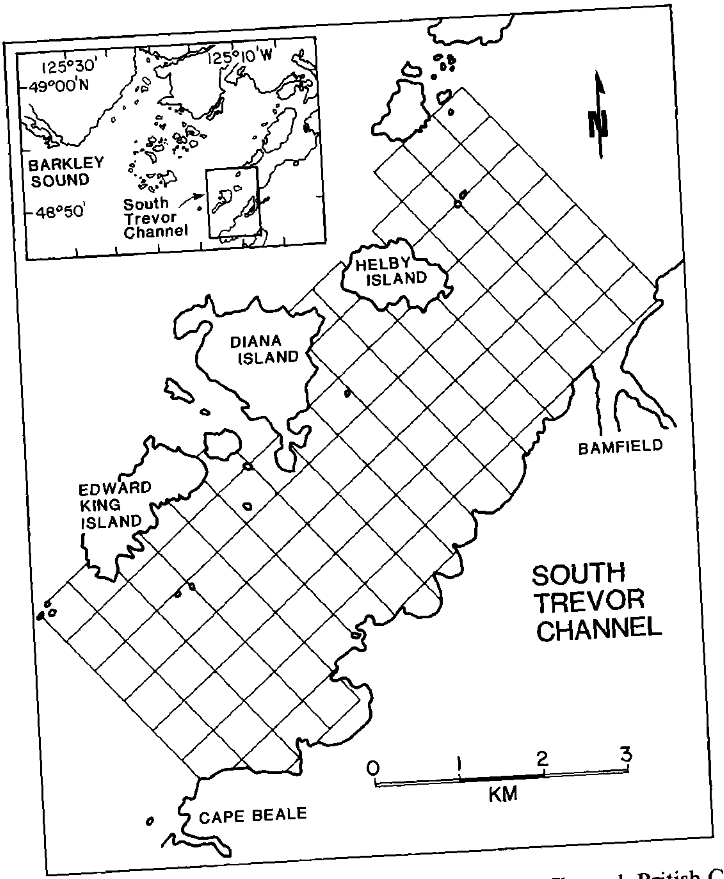

FIGURE 1. Contiguous grid of 96 quadrats in south Trevor Channel, British Columbia.

of basic contagion, and indicates whether a single individual or a group of individuals is the basic component of the distribution. The slope, β, is the density-contagiousness coefficient and indicates how the basic components distribute themselves over the habitat (Iwao 1968). The p index, obtained by successive changes in m^*/m with quadrat size, provides information about the spatial structure of the population (Iwao 1972).

We studied quadrats that differed in size by modifying Greig-Smith's (1952) method for contiguous grids. To use the entire grid, three quadrats were combined first and then quadrat size was increased by a factor of two (see Carter 1984). This method produced six quadrat sizes (q): 0.25, 0.75, 1.5, 3.0, 6.0, and 12.0 km^2.

Grid regions and areas

We divided the grid into 12 regions (see Carter 1984), using three considerations (see Cliff et al. 1975): 1) the system of regions should be simple; 2) the quadrats within a region should be similar to promote homogeneity; and 3) the regions should be compact (i.e., only contiguous quadrats should be combined and they should be closely knit rather than forming a long string). Quadrats in coastline regions were less than 500 m from shore (measured from the center of the quadrat).

Regions were grouped into areas both along and across the channel (see Carter 1984). Murrelets usually flew in straight lines in the grid, typically along or across the channel. The direction of flight was recorded when birds were first observed. Subsequent changes of direction were not examined. Because murrelets flew in small flocks below tree tops, all birds that flew over each quadrat were detected.

The number of birds observed flying depended mainly on how much time the observer spent in each quadrat, which was proportional to the size of the area. Means of 0.5, 0.4, 0.5, and 0.6 hours were spent in south, south-middle, north-middle, and north along-channel areas, respectively, and 0.6, 1.0, and 0.4 hours in west, center, and east across-channel areas, respectively. The number of birds/hr was used to examine flights over different areas of the grid.

Statistical tests

All means in this paper are expressed ± SD (standard deviation). Before analyses, densities (sitting birds/km^2) and numbers of birds flying/hr were transformed logarithmically ($\log_{10}[x + 1]$) because sample variances were greater than sample means; 1 was added to each count (some regions and areas contained no birds). This eliminated the dependence of the variance on the mean, and ensured that the components of the variance were additive. Post-hoc comparison tests (Sheffe's S test and Games-Howell procedure) were used to identify pair-wise differences between means after one-way ANOVA had indicated that differences existed.

To justify using regional changes in mean density (regardless of variation around the mean) to indicate murrelets' use of the grid, the $\log_{10}$(mean density + 1) of Marbled Murrelets was plotted against log S (or variance). The power law states that the variance of a population is proportional to a fractional power of the arithmetic mean. The linear regression $y = 0.13 + 1.89x$ indicated that the log transformation was appropriate because the slope was approximately equal to 2. Log mean density accounted for 87% of the variance of the log variances.

RESULTS

DISPERSION OF MARBLED MURRELETS AT SEA

Quadrat use

Numbers of birds/quadrat were positively skewed with a mean of 2.8 ± 7.9 and ranged from 0 to 161 (Fig. 2A). This indicated that birds were clumped within the grid (χ^2 variance-to-mean ratio test, $d = 310.6$, $P < 0.01$). Also, 61.1% of quadrats censused (N = 3462 [90 omitted due to poor observing conditions]) contained no birds. Similarly, mean numbers of birds/quadrat were positively skewed with a mean of 2.9 ± 5.8 and ranged from 0 to 43.2 ± 28.5 (Fig. 2B). This indicated that birds often were clumped in particular quadrats (χ^2 variance-to-mean ratio test, $d = 33.6$, $P < 0.01$).

Occupied quadrats (N = 1347) were arbitrarily divided into four classes of low, medium-low, medium-high, and high density containing 1–10, 11–30, 31–50, and 50+ birds, respectively. Most occupied quadrats (82.2%) were low-density; medium-low, medium-high, and high-density quadrats represented 13.4%, 2.7%, and 1.7%, respectively. Although Marbled Murrelets were clumped, 38.7% of the population occurred in low-density quadrats; medium-low, medium-high, and high-density quadrats represented 32.3%, 13.8%, and 15.3%, respectively (N = 9626 birds).

Dispersion pattern

The regression of mean crowding (m^*) on mean density (m) (Fig. 3) was linear, $m^* = 4.84 + 5.79\,m$ ($F = 21.2$, $P < 0.001$, $r = 0.38$), showing that birds were dispersed in a density independent pattern over the range of mean densities. Residual plots did not indicate any curvilinear relationship. Separate regression lines of m^* on m for each time of day did not differ significantly (ANOVA, $F = 1.8$, $P > 0.05$), although the dawn line (with highest mean densities) fell below other times of the day indicating that the distribution was less clumped. Numbers of empty quadrats also were lower at dawn (55.0%) than morning, afternoon and dusk (60.1%, 62.3%, and 64.3%, respectively). The slope was significantly greater than 1 ($t = 28.8$, $P < 0.05$), indicating that the dispersion of basic components was non-random, being clumped in some quadrats.

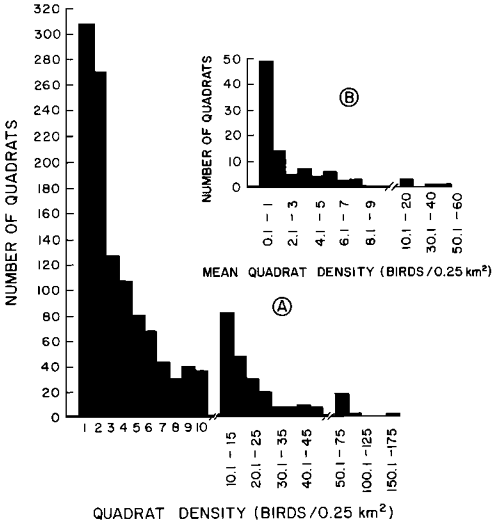

FIGURE 2. Frequency distributions of: A, the number of birds per quadrat (N = 3462 q); and B, the mean number of birds per quadrat (N = 96 q).

Different quadrat sizes

Regressions of m^* on m for each of six quadrat sizes all fitted linear models, although degree of fit increased as quadrat size increased (Carter 1984). Regression lines differed significantly (ANOVA, $F = 17.8$, $P < 0.001$), including differing slopes (ANCOVA, $F = 11.9$, $P < 0.001$) and adjusted means (ANCOVA, $F = 18.9$, $P < 0.001$). All slopes were significantly greater than 1 except at $q = 12.0$ km², indicating clumped dispersions in all but the largest quadrats. Separate regressions for each time of day within each quadrat size did not differ significantly.

In all graphs of mean p-index values by time of day (see Carter 1984) positive correlations resulted between adjacent quadrats. Largest values occurred at smaller quadrat sizes, whereas values fluctuated around 1 at larger quadrat sizes. The general shape of the p-graph indicated that basic components (>1 individual) were clumped and peaks in p-graphs revealed that clumping occurred at 3 spatial levels: ≤0.25, 1.5, and 6.0 km². At the smallest quadrat size ($q = 0.25$ km²),

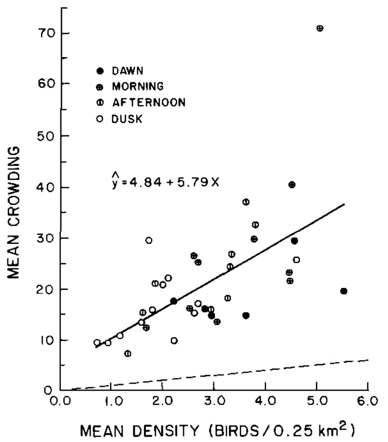

FIGURE 3. Linear regression of mean crowding on mean density. The dashed line indicates the random dispersion of basic components composed of single individuals.

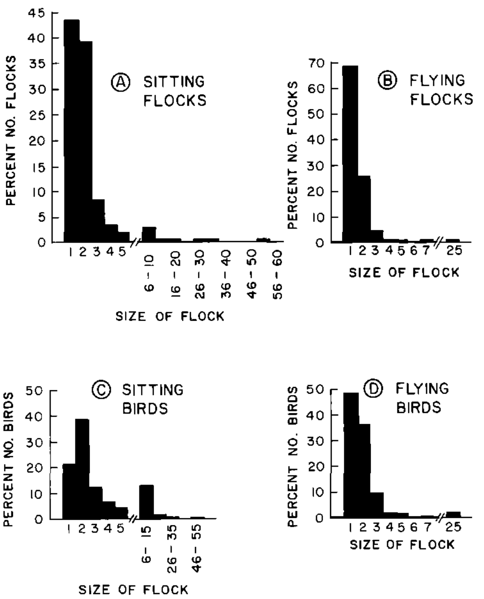

FIGURE 4. Percent frequency distributions per size of flock of: A, the number of sitting flocks (N = 4880); B, the number of flying flocks (N = 885); C, the number of sitting birds (N = 9626); D, the number of flying birds (N = 1248).

the *p* index equalled the m^*/m ratio or Lloyd's patchiness index, which increased from dawn to dusk. This further supported the trend that birds were less clumped at dawn but became more clumped towards dusk.

Flocking Behavior

Flock sizes

Sitting flocks were positively skewed with a mean of 2.0 ± 1.9 and ranged from 1 to 55 individuals (Fig. 4). Of 4880 sitting flocks observed, most were single individuals (43.7%) or pairs (39.0%). Of 9626 sitting birds, pairs contributed most birds (40.7%) followed by single birds (22.5%). Flying flock sizes also were positively skewed with a mean of 1.4 ± 1.0 and ranged from 1 to 25 (Fig. 4). Of 885 flying flocks observed, most were of single birds (68.8%), although pairs were common (25.5%). Of 1248 flying birds observed, single birds were most prevalent (48.8%), followed by pairs (36.2%).

Sitting flock sizes were similar throughout the day but were larger as quadrat density increased ($\chi^2 = 42.6$, $P < 0.01$, Table 1). Flocks in low-density quadrats were excluded from the latter analysis because low numbers alone precluded larger flocks from forming. In fact, the preponderance of low-density quadrats partly accounted for the large proportion of small flocks (90.9% of singles and pairs). Medium-low, medium-high, and high-density quadrats also contained large proportions of singles and pairs (77.7%, 75.7%, and 67.9%, respectively). Flock sizes increased with increasing quadrat density only in morning censuses ($\chi^2 = 32.4$, $P < 0.05$). Flying flocks were largest at dawn ($\chi^2 = 18.9$, $P < 0.05$).

Because sitting flocks were significantly larger than flying flocks ($\chi^2 = 201.8$, $P < 0.01$), most must have formed when flocks coalesced on the water. While flying singles joined other birds in flight or landed beside birds already on the water, pairs often flew and landed alone. Larger flying flocks (maximum 25) invariably broke apart as birds landed and other flock members flew on or landed elsewhere. Large sitting flocks seemed to form only temporarily but did not take off as a unit.

Diving behavior

Only single birds and pairs were observed diving. Members of pairs were often seen swimming towards each other on the surface before diving again. Thus, pairs may have been underestimated if birds were apart or if one was under water. Three or more birds never dove together in a coordinated fashion. They often occurred in side-by-side lines which also suggested that they were not feeding (see Bédard 1969). Larger flocks sometimes included fish-holding birds that were not feeding at the time (Carter and Sealy 1987a), although most birds that held fish were alone (80.0%) or in flocks of two (9.6%).

On 8 and 10 June 1980, between 14:00 and 21:00, behaviors noted above were confirmed through observations of murrelets diving in water 10–30 m deep near Taylor Islet. Dive times of 42 single birds averaged 27.8 ± 12.8 sec (range = 2–87 sec; N = 119 dives). Dive-pause ratios, excluding fish-holding birds, averaged 3.9 ± 3.0 (range = 0.17–24.00; N = 105 dives).

DENSITIES

Numbers of sitting birds averaged 265.8 ± 118.3/census (range = 74–518) and densities averaged 11.3 ± 5.0 birds/km^2 (range = 3.1–21.9). Mean densities were significantly higher at dawn and morning (14.4 and 13.9 birds/km^2, respectively) than at dusk (7.7 birds/km^2) (Sheffe's S Test, $\alpha = 0.05$), whereas afternoon densities were intermediate (11.0 birds/km^2) and did not differ significantly from other times (Table 2). Neither tidal state nor weather affected densities (see Carter 1984). When four censuses were conducted in one day, highest numbers twice were recorded at dawn, twice in the morning, and once in the afternoon; numbers were always lowest at dusk, when only 37.1 ± 16.7% (range 17.5–51.6%) of the highest number counted that day remained in the grid. The number at dusk was higher than at other times of day only once (see Carter and Sealy 1984).

Highest mean densities occurred in regions 2 and 3 (50.0 and 24.6 birds/km^2, respectively). Mean densities were higher in west than east regions of the channel, which partly reflected more coastline habitat on the west (7.3 km^2) than east (4.6 km^2) side. Mid-channel regions generally supported lower mean densities than did coastal regions. Region 5, over the shallow sill, had the highest mid-channel mean density (6.3 birds/km^2). In general, regions near or over the sill at the mouth of south Trevor Channel had the highest mean densities.

Mean densities decreased progressively in most regions from dawn/morning to dusk (Table 2). Significant decreases were found in five regions of intermediate density located across the sill (regions 1, 5, and 9) and in regions 10 and 11 where shallow water extended inwards from the sill. Low-density regions (6, 7, 8, and 12) and high-density regions (2, 3, and 4) did not exhibit significant decreases. The densities in the five regions were similar to high-density regions at dawn and in the morning, whereas they were similar to low-density regions later in the day.

FLIGHTS

The number of flying birds averaged 33.7 ± 29.5/census (range = 7–163), which corresponded to a mean of 16.3 ± 12.7 birds flying/hr (range = 3.0–64.7) (Table 3). More birds flew/hr at dawn (37.4 birds/hr) when highest numbers were on the water; morning, afternoon, or dusk (11.1, 9.3, and 15.2 birds/hr, respectively) did not differ significantly from each other (Table 3). North and south flights accounted for 75.5% of daily flights (Table 3). Most flights occurred over west, center, and south areas of the grid, which were associated with intermediate and high densities of birds on the water.

TABLE 1. NUMBER AND SIZES OF FLOCKS IN QUADRATS OF DIFFERENT DENSITIES OF MARBLED MURRELETS BY TIME OF DAY (N = 4880 FLOCKS)

Time of day	Flock size class	Quadrat density[1] Low	Medium-low	Medium-high	High	Total
Dawn	1	204	156	82	18	477
	2	187	154	54	12	436
	3	23	43	15	2	87
	4+	13	33	17	6	73
Morning	1	322	166	76	49	613
	2	266	192	68	74	600
	3	36	51	23	27	137
	4+	30	54	29	51	164
Afternoon	1	308	99	49	51	509
	2	224	99	62	63	448
	3	45	26	12	18	101
	4+	21	24	19	31	104
Dusk	1	398	91	26	19	534
	2	245	108	42	23	418
	3	27	33	13	4	83
	4+	23	42	19	7	97

[1] Density of birds in 0.25 km^2 quadrats: low (1–10 birds), medium-low (11–30 birds), medium-high (31–50 birds), and high (51–161 birds).

At dawn, more birds flew into the grid from the south and north than flew out of the grid. Many birds flew directly towards the sill and west areas (Fig. 5), where there was no difference between northward and southward flights over south-middle and north-middle areas at dawn. After dawn a few more flights occurred near the sill, when densities decreased there (Table 2). Fewer flights in morning and afternoon represented lower within-channel flights as well as few birds leaving the grid area. Although dusk flights did not differ significantly from morning and afternoon (Table 3), the lowest number of birds were in the grid at this time. Increased flights probably occurred relative to the proportion of flying birds that originated from birds sitting in the grid. Directions of flight were the reverse of those at dawn (Fig. 5).

MURRELETS HOLDING FISH

Sitting birds holding fish averaged 3.9 ± 4.9 individuals/census (range = 0–26) and densities averaged 0.2 ± 0.2 birds/km^2 (range = 0–1.0). Few flying birds that carried fish were counted (range = 0–5 birds/census), corresponding to 0 to 3.3 birds/hr. However, at least one fish-hold-

TABLE 2. Mean (±sd) densities (Birds/km^2) of Marbled Murrelets in each Region of South Trevor Channel by Time of Day (N = 37 Censuses). Mean Log Densities that Were Not Significantly Different Are Underscored by a Line (Scheffe's S Test for All Pair-Wise Comparisons (α = 0.5) or are Indicated by NS (One-Way ANOVA, α = 0.05)

Region	Total	Time of day: Dawn (DN)	Morning (M)	Afternoon (A)	Dusk (DK)	Differences between ranked log means
1	14.2 ± 14.9	23.4 ± 12.4	26.0 ± 19.3	8.7 ± 6.1	3.9 ± 3.3	M DN A DK
2	50.0 ± 24.2	47.6 ± 26.2	61.2 ± 29.4	55.6 ± 21.1	37.5 ± 16.2	NS
3	24.6 ± 15.2	21.0 ± 7.2	29.3 ± 19.3	25.1 ± 15.5	22.2 ± 14.7	NS
4	15.7 ± 12.3	25.7 ± 17.1	16.9 ± 11.3	14.2 ± 8.2	10.9 ± 11.2	NS
5	6.3 ± 6.5	14.2 ± 10.2	7.0 ± 5.5	4.6 ± 4.5	3.1 ± 2.3	DN M A DK
6	2.6 ± 3.4	3.8 ± 2.9	2.8 ± 4.6	0.8 ± 1.0	3.1 ± 3.4	NS
7	2.2 ± 2.2	2.7 ± 2.9	2.7 ± 3.1	1.3 ± 1.2	2.3 ± 1.6	NS
8	1.1 ± 1.3	1.2 ± 1.1	0.6 ± 1.0	1.1 ± 0.9	1.6 ± 1.8	NS
9	11.0 ± 12.4	14.2 ± 8.0	18.4 ± 17.7	8.4 ± 4.9	0.8 ± 0.8	M DN A DK
10	16.1 ± 18.3	23.9 ± 20.1	20.1 ± 22.7	20.5 ± 18.8	5.5 ± 7.1	DN A M DK
11	8.5 ± 7.8	8.7 ± 7.1	10.0 ± 7.3	11.2 ± 5.0	5.1 ± 9.8	A M DN DK
12	0.9 ± 1.4	0.6 ± 1.1	0.6 ± 0.9	1.7 ± 2.3	0.9 ± 0.8	NS
Total	11.3 ± 5.0	14.4 ± 4.8	13.9 ± 4.6	11.0 ± 3.8	7.7 ± 4.1	DN M A DK
Differences between ranked log means^2	2 3 4 10 1 9 11 5 6 7 8 12	2 4 3 1 10 9 5 11 6 7 8 12	2 3 1 10 4 9 11 5 7 6 8 12	2 3 10 4 11 9 1 5 12 7 8 6	2 3 4 1 5 10 11 6 7 8 12 9	

ing bird was observed on 86.5% of the 37 censuses. Fish-holding birds comprised only 1.5% of mean density and only 2.5% of mean birds flying/hr.

Highest numbers of fish-holding birds on the water or flying occurred at dusk (0.27 birds/km^2 and 1.0 birds/hr, respectively), although significant differences were found only between dawn

TABLE 3. Mean (±sd) Numbers of Marbled.Murrelets Flying/Hour by Time of Day and Direction of Flight in Trevor Channel (N = 37 Censuses). Symbols and Tests as in Table 2

Flying direction	Total	Time of day: Dawn (DN)	Morning (M)	Afternoon (A)	Dusk (DK)	Differences between ranked log means
North (N)	6.0 ± 5.2	14.1 ± 6.6	4.3 ± 2.6	2.4 ± 2.0	6.1 ± 3.4	DN DK M A
South (S)	6.3 ± 5.9	14.6 ± 9.8	3.6 ± 2.1	3.6 ± 2.1	6.3 ± 3.7	DN DK A M
West (W)	2.7 ± 2.4	6.6 ± 3.0	2.0 ± 1.5	1.5 ± 1.0	2.4 ± 1.6	DN DK M A
East (E)	1.6 ± 2.5	2.2 ± 1.2	1.3 ± 1.5	1.9 ± 4.5	1.2 ± 1.6	NS
Differences between ranked log means	S N W E	N S W E	N S W E	S N W E	N S W E	
Total	16.3 ± 12.7	37.4 ± 16.6	11.1 ± 5.2	9.3 ± 4.0	15.2 ± 7.5	DN DK M A
Total with fish	0.4 ± 0.8	0.1 ± 0.2	0.1 ± 0.2	0.3 ± 0.2	1.0 ± 1.2	DK A M DN

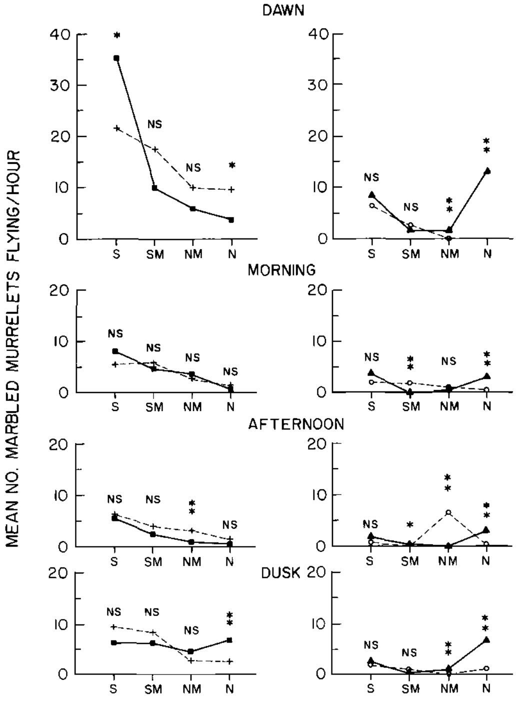

FIGURE 5. Mean numbers of Marbled Murrelets flying/hour by time of day, along-channel area and flight direction. In the left column, the numbers of birds flying north (solid line) are compared with those flying south (dashed line); in the right column, birds flying west (solid line) are compared to those flying east (dashed line). Along-channel areas are coded: S, south; SM, south-middle; NM, north-middle; N, north area. Significant differences between directions of flight in each area are indicated by * (α = .10) and ** (α = .05); nonsignificant differences are indicated by NS (one-tailed t-test).

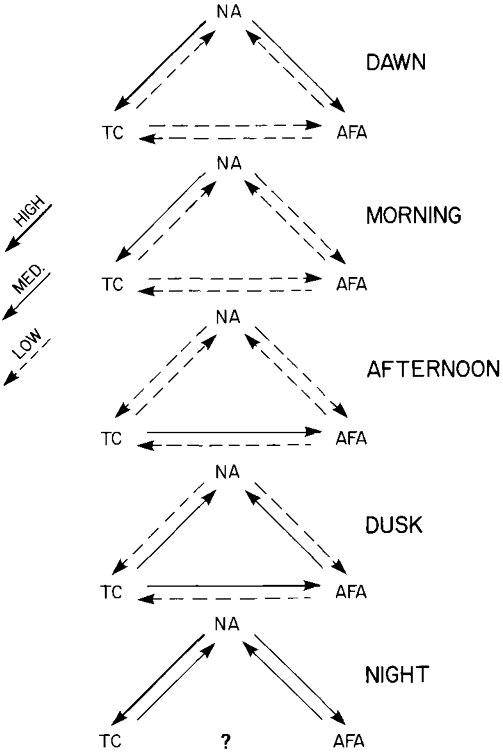

FIGURE 6. Daily movements of breeding Marbled Murrelets between nesting areas (NA), the Trevor Channel feeding area (TC), and alternative feeding areas (AFA) during the nestling period in Barkely Sound, British Columbia. Movements by chick-rearing adults occur throughout the day whereas those by off-duty incubating adults primarily occur between dusk and dawn (see text). Non-breeding birds are assumed not to move in a regular fashion at sea or to nesting areas and are not included.

and dusk (Table 3). The proportion of fish-holding birds increased from 0.2% to 3.5% of mean density and 0.3% to 6.6% of mean birds flying/hr from dawn to dusk. Numbers of sitting and flying birds did not differ significantly between regions or most areas.

DISCUSSION

DIURNAL FORAGING

Each breeding season Marbled Murrelets aggregate daily in south Trevor Channel (Carter 1984, Sealy and Carter 1984). This area evidently provided a reliable source of food because large numbers of murrelets flew there at dawn directly from nesting areas each day (Fig. 6). Adult murrelets fed primarily on juvenile Pacific herring (*Clupea harengus*) and Pacific sandlance (*Ammodytes hexapterus*) in Barkley Sound (Carter 1984). During the murrelets' nestling period these prey are concentrated each year in this traditional nursery area, which is located in sheltered water inside a small-scale oceanographic front at the south entrance of the channel (Hourston 1959; see Carter 1984). Murrelets appeared to travel substantial distances (over sea and land) from nesting areas to reach the feeding area, as indicated by high flight activity over water to the north and south of the grid. Marbled Murrelets probably nest solitarily in trees around Barkley Sound that could be up to 75 km inland (Sealy and Carter 1984, Carter and Sealy 1986). Thus, murrelets in the feeding area probably come from many different nesting areas. While other alcids are known to aggregate at larger-scale prey patches often far from shore (e.g., Schneider et al. 1990), prey availability there is most likely much less stable over time than it is in Trevor Channel for murrelets.

The clumped distribution of foraging murrelets in the grid probably reflected small patches of prey along coastlines and over the sill near the south end of the channel (Hourston 1959; see Carter 1984). The consistent use of specific quadrats and flights directly to intermediate- and high-density regions at dawn indicated that birds returned to known feeding sites or were continually attracted to these sites, perhaps by the continual presence of other birds. However, as the numbers of birds increased, some birds apparently chose not to forage where other birds were clumped, evidenced by the constant dispersion pattern over the range of densities observed, the regular spacing of birds in coastal regions, and the wide use of the feeding area on every census.

Few flights and a distribution similar to that at dawn indicated that birds moved little in the morning and afternoon (Fig. 6). After morning, more birds left than arrived in the feeding area. Flights over the sill after dawn possibly indicated birds shifting to coastal regions as also indicated by clumps of birds being more conspicuous over the sill at dawn but along coastlines later.

FORAGING BY BIRDS FEEDING NESTLINGS

Most murrelets seen holding fish were observed near dusk, just before they fly to their nests to feed nestlings (Simons 1980, Hirsch et al. 1981). A few birds, however, were observed holding fish at dawn and in the morning. Adults that hold fish intended for their nestlings are precluded from capturing more fish until after they have fed the chick. Therefore, we infer that some individuals may feed chicks during the day (Fig. 6), and mainly within a few hours of dawn. This is supported by observations of birds in flight over known nesting areas at these times (Carter and Erickson 1988).

Infrequent fish-holding behavior indicated that prey for nestlings (second-year Pacific sandlance, Pacific herring, and Northern anchovy [*Engraulis mordax*]) in Trevor Channel was less available during the day than the juvenile fish that adults consumed (Carter 1984). Indeed, fish taken for nestlings occur deeper during the day than prey consumed by adults (Hourston 1959, Macer 1965, Baxter 1967).

Increased fish-holding by birds toward dusk coincided with the decrease in overall numbers of birds in the feeding area. The proportion of birds (about 65%) that had left by dusk corresponded roughly to the expected proportion of the population that was feeding nestlings. We presumed that many birds moved to and obtained prey for nestlings later in the day at alternative feeding areas that were distributed widely in Barkley Sound but were used by only a few birds at a time (Carter 1984, Sealy and Carter 1984).

Simons (1980) suggested that murrelets fed nestlings several times on some nights. This was supported further by adults with food in their stomachs being drowned in gill nets at night in Trevor Channel, and by observations of birds apparently feeding at night at inland lakes (Carter 1984, Carter and Sealy 1984, 1986). Thus, if murrelets foraged at night to take advantage of fish (especially for nestlings) closer to the surface, this might explain why some birds were present in the feeding area at dawn.

The foraging behavior of Marbled Murrelets feeding nestlings resembled a "time minimizer" (Schoener 1971, Norberg 1977). By flying directly to Trevor Channel at dawn, birds minimized the time required to feed themselves by specializing on the abundant and easily found resources. This enabled birds to fly to alternative feeding areas some time before dusk and thereby maximized the time needed to obtain less abundant and more difficult-to-locate fish for young on a regular basis. The fast growth rate of nestling Marbled Murrelets compared with other alcids (Simons 1980, Hirsch et al. 1981) may result from regular feedings of relatively large prey loads (Carter and Sealy 1987a), in concert with multiple diurnal and nocturnal feedings, or both, by at least some individuals. This system is enhanced by rearing young when prey are most abundant (Hourston 1959, Carter 1984).

SOCIAL AND FEEDING BEHAVIOR

In Trevor Channel, murrelets occurred primarily as singles and in pairs, as has been reported elsewhere in summer and winter. Pairs probably were mated with chicks at the nest (see Sealy 1975a). Larger flocks of up to 50 individuals also have been reported previously and contain subadults and adults (Sealy 1975b).

Marbled Murrelets apparently fed solitarily because only singles and pairs were observed diving and presumably feeding. Although members of pairs may dive together, this does not imply cooperative foraging. Larger flocks were loafing groups that formed after feeding. Large loafing flocks formed from positive attractions between individual flock members, evidenced by the large sizes of certain flocks (up to 55 birds), increases in flock size with quadrat density, and cohesive formations of flocks on the water. This occurred especially in the morning when fewer murrelets were actively feeding, enabling larger flocks to form and remain together for some time. Larger flock sizes, however, occurred frequently in high-density quadrats regardless of time of day. Larger flocks may involve social interaction, although birds also interact in flight over nesting areas at dawn and dusk (Carter, unpubl. data).

We considered that murrelets were highly solitary feeders because they occurred mainly as singles and pairs in low- as well as high-density quadrats and tended to be more dispersed in the feeding area at higher densities. Thus, murrelets appeared to aggregate where food was clumped but otherwise avoided other individuals while feeding, perhaps to avoid interference or competition (see Leyhausen 1965, Goss-Custard 1970, Duffy et al. 1987).

Feeding solitarily may be necessary to maximize time required for foraging in alternative feeding areas for nestling prey, which occurred in a widely dispersed and low-density fashion in Barkley Sound. Thus, solitary foraging allowed both aggregated and dispersed prey to be exploited efficiently (see Bédard 1969, Asbirk 1979). This may partly account for the continuous occurrence of Marbled Murrelets in high and low densities along much of the coast of the North Pacific, as well as providing a basis for the development of solitary nesting (Day et al. 1983, Sealy and Carter 1984, Carter and Sealy 1987b).

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