Deciphering the Social Structure of Marbled Murrelets from Behavioral Observations at Sea

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Abstract.—We surveyed Marbled Murrelets (*Brachyramphus marmoratus*) daily from small boats in Auke Bay and Fritz Cove, Alaska, from May through August 1992 and 1993. Differences in numbers of juveniles and in the timing of their presence in the study area between the two years indicated that breeding phenology was late and productivity was low in 1992 compared to 1993. This difference was consistent with variability in the physical environment. Of 99 fish identified in the bills of fish-holding adult murrelets, 81 (82%) were Pacific Sand Lance (*Ammodytes hexapterus*). Counts of fish-holding adult murrelets were significantly higher in the evening than at any other time of day. Time of day had no significant effects on counts of fledglings, indicating that juveniles were moving into and out of the study area during the day. Murrelets were predominantly found in groups of two or more, even during incubation, suggesting that murrelets incur an appreciable benefit, such as increased foraging efficiency, from foraging in groups. For both summers, there was no correlation between counts of murrelets on the water and numbers of murrelet detections in the adjacent forest. We suggest that many behavior patterns of the Marbled Murrelet (displaying, choosing of mates, and pair-bonding, finding of nest sites and successful foraging of juveniles) may be socially facilitated. *Received 13 January 2003, accepted 28 April 2003.*

Key words.—Behavior, *Brachyramphus marmoratus*, Marbled Murrelet, social structure, Southeast Alaska.

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The Marbled Murrelet (*Brachyramphus marmoratus*) nests as solitary pairs in tall, old-growth forest, and it is very difficult to gather data on its breeding biology without the great effort to find nests. Despite its solitary breeding habits, the Marbled Murrelet at sea is social. Murrelets in Alaska commonly gather at sea in groups of up to ten birds to feed, rest, socialize, display, and copulate (Strachan *et al.* 1995; Speckman 1996), and aggregations of hundreds to thousands may be found at important foraging areas (DeGange 1996).

The Marbled Murrelet is threatened by logging of old-growth forest nesting habitat (Kelson *et al.* 1995), oil pollution (Piatt *et al.* 1990; Carter and Kuletz 1995), entanglement in gillnets (Carter *et al.* 1995), and changes in forage fish availability (Piatt and Anderson 1996). We examined aspects of the breeding biology of the Marbled Murrelet and aspects of their behavior and social structure that might be important for overall population stability. Due to inherent difficulties in finding and monitoring murrelet nests in forests, we focused on behavior on the water, such as copulation and fish-holding, and the appearance of newly-fledged juveniles, as indicators of nesting phenology and as proxies for nesting behavior and reproductive success.

Effects of time of day, tide, weather, and season on distribution and abundance of adult murrelets at sea have been presented elsewhere (Speckman *et al.* 2000). Here, we focus on interannual variability in the productivity of the Marbled Murrelet and on the social and behavioral aspects the life history of the Marbled Murrelet. Murrelet courtship behavior, feeding strategies and species composition of prey, and inter- and intra-specific interactions are discussed, and we consider the effects of the physical variables time of day, tide, and season on provisioning of chicks and numbers of juveniles at sea.

METHODS

Study Site.—This study was carried out in Auke Bay and Fritz Cove, an area about 8 km long and 4-5 km wide, located 20 km northwest of Juneau, Alaska, and 130 km from the Gulf of Alaska (Fig. 1). Auke Bay is an

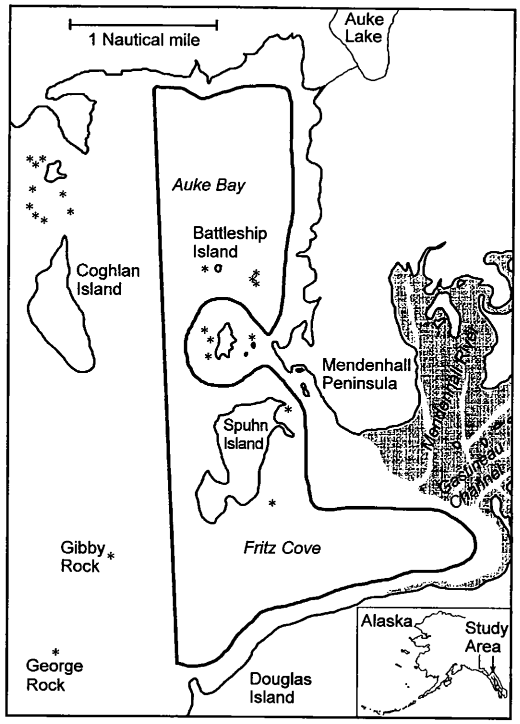

Fig. 1. The study area in Southeast Alaska. The boat transect is indicated by the thick, bold line.

embayment on the coast of Alaska, and Fritz Cove is located between the mainland and Douglas Island, forming the northwestern end of Gastineau Channel. The Mendenhall River flows from the Mendenhall Glacier into Fritz Cove. The shoreline of Fritz Cove, from the head of the bay along the mouths of Gastineau Channel and the Mendenhall River, is lined with broad tidal flats. The remaining shoreline of Fritz Cove and Auke Bay is steep and rocky, rapidly dropping into deep water.

Boat Surveys.—Daily counts of Marbled Murrelets in Auke Bay and Fritz Cove were made from 6 May-15 August 1992 and from 12 May-13 August 1993, spanning the period from courtship through fledging of chicks. These "Morning Boat Surveys" were conducted five or six times a week along a transect line approximately 200 m from shore (Fig. 1). Each survey was approximately 16 km long, started at 05.00 h Alaska Standard Time (AST), and took about 2 h to complete. Because surveys were conducted at the same time each day, tide height during surveys varied. Survey speed was slower in areas with many birds, and the boat was stopped completely when large, concentrated flocks were encountered. Boats used were 5-m long, with outboard motors.

Once a week in 1993, we conducted "Repeated Boat Surveys," for which the boat transect was repeated five times during the day, at low, rising, high, and falling tides. Tide stages are repeated approximately every 12 h, so that the tide stage in the morning survey was resurveyed again in the evening.

Juveniles, fish-holding birds, and displaying birds were recorded, regardless of their distances from the boat. Juveniles were identified by a combination of characters, including presence of the egg tooth, plumage, and behavior. Fish-holding birds near the boat were approached in an effort to identify the fish to species. S.G.S. was the primary observer for all surveys. All sightings and times to the nearest minute were recorded on a tape-recorder, and sea state, weather, observation conditions, and any disturbances were noted for each survey. Surveys were omitted from analyses when fog or high winds reduced visibility. A group was defined as birds within two m of each other. Group sizes were recorded when birds were scattered or in small numbers, but were not recorded for large gatherings of birds.

Dawn Watch Surveys.—Terrestrial dawn watches were conducted on Douglas Island two or three times a week in 1992 and once a week in 1993 from mid-May through mid-August. Three monitoring stations were established along the road leading up the densely forested valley to Eagle Crest Ski Area, about two to three km from Fritz Cove. This valley was chosen for dawn watch surveys because Fish Creek, which runs through the valley, empties into Fritz Cove. We assumed that murrelets traveling up and down this valley were probably the same birds which utilized the at-sea study area, and that chicks fledging from this valley would land on the water in Fritz Cove and elsewhere within the study area before moving on to other areas.

In a modification of the "grid survey" (Naslund 1993), the three inland stations were monitored in the same order each day for 20 min each during the hour preceding official sunrise. Sunrise varied from 02.51 h to 04.21 h AST during the course of the study. The numbers of audio and visual detections of Marbled Murrelets flying in the valley were counted according to established protocols (Naslund 1993). After the dawn watch was completed, we conducted the Morning Boat Survey in Auke Bay and Fritz Cove.

Statistical Analyses.—Counts of juveniles and fish-holders from each Repeated Boat Survey were modified with a square-root transformation after adding 0.5 to each count (Sokal and Rohlf 1995). We analyzed abundance of fish-holding murrelets and juveniles by analysis of variance and variance component procedures in SuperANOVA (1989). Factors considered were date, time of day (02.30-07.00 h, 07.00-11.00 h, 11.00-15.00 h, and 15.00-19.00 h AST) and tide stage. The Tukey-Kramer Honestly Significant Difference procedure (HSD) for unequal sample sizes was used for all pair-wise comparisons where initial tests indicated significance (Sokal and Rohlf 1995).

We used Spearman rank correlation coefficients (SPSS 1990) to test for positive significance of association (both linear and non-linear) between numbers of detections in the forest and numbers of murrelets or numbers of displaying murrelets at sea (1-tailed). To determine percentages of group sizes, all groups were summed for one-week periods, and expressed as percentages of the total number of birds observed.

RESULTS

Phenology and Productivity.—Nests were not observed as part of this study, so all estimates of the timing of breeding activities were made from observations of birds on the water. Timing of the egg-laying period was indicated by sightings of murrelets copulating, the chick-rearing period by sightings of fish-holding adults, and the fledging period by sightings of juveniles. We observed murrelets copulating on the water only six times in Auke Bay and Fritz Cove during this study (Fig. 2). All six observations occurred during Morning Boat Surveys from 05.00 h-07.00 h; no copulations were observed at other times of day. In 1992, G. van Vliet (pers. comm.) observed murrelets copulating on 24 May, and we observed a copulation on 8 June. In 1993, we saw copulating murrelets on 15 May, 20 May, 13 June, and 6 July.

Less than 2% of the murrelets were still molting into breeding plumage in May. Numbers of birds in transitional plumages declined to zero in June and July. By mid-July, birds in the process of molting began to appear again, as some birds began changing into winter plumage. However, only a few birds in advanced molt were present in the study area by mid-August, and this simplified the identification of juveniles, which can be confused with adults in winter plumage.

In 1992, we observed fish-holders (adults carrying fish cross-wise in their bills) twelve times and juveniles nine times during Morning Boat Surveys (Fig. 2). We saw the first fish-holder on 31 May, but did not observe the next fish-holder until 26 June. Thereafter, we saw fish-holders through 3 August, for a span of 39 days (not including the bird in May). No fish-holders were seen during the seven surveys from 4-12 August. The first juvenile was seen during a Morning Boat Survey on 30 July and the last on 11 August. We saw no juveniles during the last two surveys on 13 and 15 August.

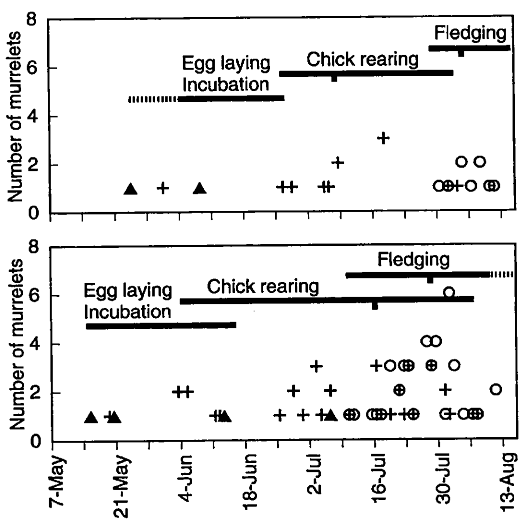

Fig. 2. Observations of at-sea behavior of adults and sightings of juvenile Marbled Murrelets in 1992 (upper) and 1993 (lower panel). Copulations are indicated by triangles, fish-holding murrelets by crosses, and juveniles by open circles. These sightings were used to estimate the timing of the breeding cycle, indicated by horizontal bars. Dashed portions of the bars indicate uncertainty about the duration of that phase.

In 1993, fish-holders were observed 50 times and juveniles 43 times during Morning Boat Surveys (Fig. 2). Two fish-holders were seen on 5 June, and others subsequently until 7 August, spanning a period of 64 days. No fish-holders were seen during the three surveys from 10-12 August. We saw the first juvenile on 10 July and the last on 11 August; none were seen on 12 August, the last morning survey. Sightings of juveniles reached a peak on 2 August.

Juveniles were seen nine times, or an average of 0.9 juveniles/survey (range 1-2), in 1992 during ten Morning Boat Surveys in the 16-day period after the first sighting of a juvenile. In 1993, we observed juveniles 43 times, or an average of 1.7 juveniles/survey (range 1-6) during 25 Morning Boat Surveys during the 34-day period after the first sighting of a juvenile.

Based on the difference between dates of initial sightings of juveniles (29 July 1992 land-based survey; 10 July 1993 Morning Boat Survey), the data suggested that breeding in 1993 began about 19 days earlier than in 1992. We estimate that the duration of the breeding season in Auke Bay and Fritz Cove was about 100 days, from early-mid May until mid-late August, but varied between years.

The egg tooth was seen on the upper bill of ten out of twelve juveniles that were approached closely during Morning Boat Surveys in 1993. Most juveniles were observed close to shore, usually within 10 m of the water's edge. Of the 52 sightings of juveniles in 1992 and 1993, 42 (81%) were alone, two were together but without an adult (4%), six were with one adult (12%), and two were each with two adults (4%).

Juveniles were sighted 53 times during four sets of Repeated Boat Transects (19 surveys total) conducted on 21 July, 28 July, 2 August and 10 August 1993. The numbers of juveniles within the study area did not vary with time of day (r^2_{17} = 0.15, n.s.) or tide stage (r^2_{17} = 0.16, n.s.).

Courtship.—Murrelets exhibit several behavioral activities at sea that appear unique to this species. The "bill-up" display or "heads-up posturing," has been described elsewhere (Byrd *et al.* 1974; Nelson and Hamer 1995; Strachan *et al.* 1995). A pair of murrelets in complete basic (winter) plumage performed the bill-up display on 21 November 1992 in Auke Bay, suggesting that pair-bond maintenance may continue during winter.

The "v-wing" display has not been described. During this display, one bird positions its wings half-opened and extended high over its back, so that from the front or behind, the wings form a "v" shape over the bird's back. Only one member of the pair, probably the male, does the v-wing display, swimming up behind or alongside the other member of the pair. The v-wing display was always accompanied by a buzzing sound. The call is distinctive and when surrounded by a flock of murrelets, we could scan and find a murrelet with its wings over its back. After the v-wing display, which lasted only about 5-10 seconds, both murrelets of the pair performed the bill-up display together. The v-wing display was seen only in early morning.

Murrelets performing the "tail-chase" and "pursuit flight-dive" displays (Singer *et al.* 1991), in groups of up to four individuals, were more common in the study area in late July and early August, when displaying in the forest also increased (Fig. 4). On 19 July 1993, two murrelets chased each other, flying at high speed in a complicated pattern, and then the first crashed into the water without slowing. The second bird flew vertically, and then plunged into the water from about five m above the surface. Both birds then surfaced and flew away. Typically this display involved calling, including the "keer" call and a two-note "keer" call (Nelson and Peck 1995). Tail-chases at sea were restricted almost exclusively to the early morning period and often followed birds arriving from the forest.

Group Sizes.—The number of murrelets used to determine average group sizes for each week ranged from 347 to 3,275 birds per week. Sightings of single murrelets were few in both years of the study, never exceeding 26% of the birds seen in any week (Fig. 3). Sightings of pairs were common, but highly variable, ranging from 34-84% of all groups seen in 1992 and from 34-77% in 1993. Even during incubation, pairs of murrelets made up a substantial proportion of the murrelet sightings. Overall percentages of murrelets in pairs were 55% in 1992 and 47% in 1993, and overall percentages of single birds were 15% in 1992 and 18% in 1993. The distribution of group sizes in both years followed the same general pattern in relation to the breeding cycle. The number of pairs dropped and the number of single birds rose during the egg-laying period (late May to late June in 1992; mid May to mid June in 1993), and the number of pairs rose during hatch (mid June through July in 1992; June through July in 1993; Fig. 2).

Fish-holding Behavior and Species Composition.—All fish-holding murrelets observed were in complete summer plumage, and all birds held a single fish crosswise in their bills. Only twelve fish-holders were seen during Morning Boat Surveys in 1992, compared to

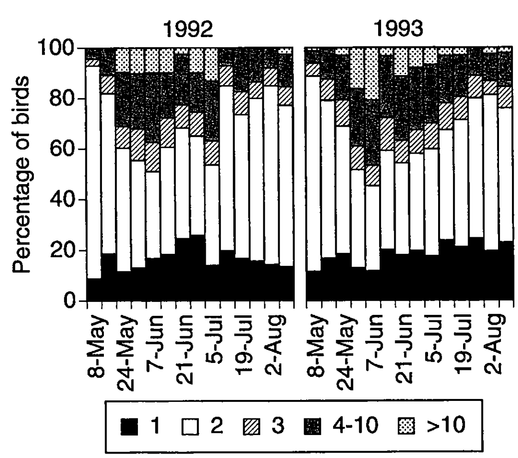

Fig. 3. Percentage frequency of Marbled Murrelet group sizes. Observations grouped into one-week time periods.

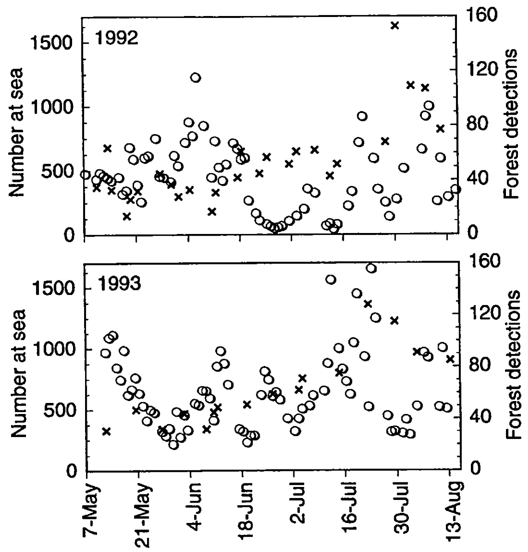

Fig. 4. Numbers of Marbled Murrelets counted on Morning Boat Surveys (open circles) in Auke Bay and Fritz Cove and numbers of forest detections (x) on Douglas Island. There was no correlation between numbers on the water and in the forest.

38 in 1993. A total of 203 fish-holders were observed, including opportunistic sightings as well as sightings during surveys. Of these, 81 (40%) were holding Pacific Sand Lance (*Ammodytes hexapterus*), four (2%) Pacific Herring (*Clupea harengus*), seven (3%) Capelin (*Mallotus villosus*), seven (3%) were holding unidentified fish, but not sand lance, and 104 (51%) were holding an unidentified fish. No demersal or benthic fishes or invertebrates were identified.

Analysis of variance of the Repeated Boat Surveys for a ten-week time period showed that time of day was the most important factor affecting fish-holding behavior (Table 1). The proportion of murrelets holding fish was significantly greater during evening counts than at all other times of day, and was significantly greater during afternoon than late morning counts (Tukey-Kramer HSD test, $P < 0.05$).

Table 1. Analysis of variance of fish-holding Marbled Murrelets. The model included four times of day over a period of eight weeks.

Source	df	P-value	% var. explained
Date	7	<0.01	31
Time of day	3	<0.01	41
Residual	26		23
r^2			0.73

Feeding Assemblages.—Murrelets in Auke Bay and Fritz Cove often participated in mixed-species feeding flocks involving Bonaparte's Gull (*Larus philadelphia*), Glaucous-winged Gull (*L. glaucescens*), and Black-legged Kittiwake (*Rissa tridactyla*). Other species participating in feeding flocks were Common and Pacific Loons (*Gavia immer* and *G. pacifica*), Surf Scoter (*Melanitta perspicillata*), Red-breasted Merganser (*Mergus serrator*), Mew Gull (*Larus canus*), Herring Gull (*L. argentatus*), Arctic Tern (*Sterna paradisaea*), Harbor Seal (*Phoca vitulina*), and Harbor Porpoise (*Phocoena phocoena*). Several times, Bald Eagles (*Haliaeetus leucocephalus*) disrupted feeding assemblages.

On many occasions murrelets were seen feeding in a cooperative manner. For example, on 12 July 1993, six murrelets were feeding on a school of juvenile herring. Only two murrelets came to the surface at a time while the school of fish seethed at the water surface in a tight ball, with many jumping out of the water. It appeared that murrelets were herding fish to keep the school cohesive and trapped against the water surface. In mixed-species feeding flocks, this strategy made fish available to pursuit-divers as well as plunge-divers and surface feeders.

Relation of Forest Attendance to At-sea Attendance and Behavior.—Numbers of combined audio and visual detections in the forest increased significantly through the summer, reaching a peak in late July in both years (Fig. 4; for 1992, $r^2_{24} = 0.72$, $P < 0.01$; for 1993, $r^2_{13} = 0.94$, $P < 0.01$). In neither year was there a significant positive correlation between the total number of detections in the forest and the total number of murrelets on the water a few hours later ($r^2_{23} = -0.23$, n.s. in 1992; $r^2_{13} = -0.08$, n.s. in 1993).

The relationship between the number of forest detections and numbers displaying at sea was not significant in 1992 or 1993 (Fig. 5; for 1992, $r^2_{24} = 0.30$, n.s.; for 1993, $r^2_{13} = 0.28$, n.s.). However, in both years, the amount of displaying at sea increased signif-

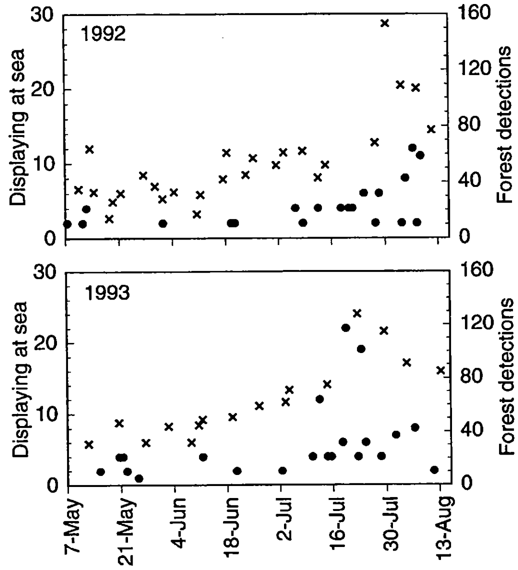

Fig. 5. Numbers of Marbled Murrelets displaying at sea (filled circles) and numbers of forest detections (x). There was no correlation between numbers in the forest and numbers displaying at sea. In both years, however, display activity on the water and in the forest increased through the summer, peaking in mid-late July.

icantly through July 31 (for 1992, $r^2_{59} = 0.30$, $P < 0.01$; for 1993, $r^2_{61} = 0.26$, $P < 0.05$), and in 1993 the number of murrelets on the water was significantly correlated with the number of murrelets displaying on the water ($r^2_{70} = 0.32$, $P < 0.01$). Numbers of displaying murrelets both at sea and in the forest increased sharply in mid or late July. The increase in social displays did not seem to correspond to a phase of the breeding season, but rather to the time of year, and may correspond to the arrival of sub-adult murrelets to the area (Speckman *et al.* 2000).

DISCUSSION

Phenology and Productivity.—Phenologies for 1992 and 1993 constructed from sightings of at-sea behavior and juveniles indicate that breeding in Auke Bay and Fritz Cove is more synchronous than breeding in areas to the south, where the breeding season is more protracted, and may last as long as 170 days in California (Hamer and Nelson 1995).

The contrast in numbers of juveniles observed on the water in 1992 and 1993 suggests that reproductive success in 1993 was nearly double that of 1992. Lower reproductive success in 1992 was accompanied by a delayed breeding phenology. Unfavorable weather in 1992 may have influenced the timing of breeding and reproductive success via an effect on the food supply of murrelets (Speckman *et al.* 2000). Lower than usual density of zooplankton in Auke Bay during 1992 (Hulbert and Sturdevant 1995) is likely to have reduced food biomass up the food chain, resulting in reduced availability of fish to murrelets, and therefore possibly delaying nesting and reducing reproductive success (Speckman *et al.* 2000).

There was no indication that juveniles accumulated in the study area over time, as has been observed in some nursery areas (Beissinger 1995; Kuletz *et al.* 1995; Kuletz and Piatt 1999) where food availability was apparently high (Sealy 1975a; Strachan *et al.* 1995). As in our study, M. McAllister (unpubl. data) found that more than 80% of juvenile murrelets observed in Alaska were unaccompanied by adult birds. In British Columbia, about 50% of juveniles were alone, 22% were with another juvenile, 12% were in groups of three or more juveniles, and the remaining 17% were with adults (Sealy 1974). There is no evidence indicating whether the adults seen with juveniles are their parents; it is possible that juveniles are simply taking advantage of unrelated older birds' foraging expertise. In frequent observations of juvenile-adult interactions in Auke Bay and Fritz Cove, we never observed any behavior that suggested the juveniles were related to nearby adults (e.g., vocal communications, physical contact, coordinated movements) or were fed by them.

Juveniles of many seabird species are less efficient foragers than adults (Burger 1988; Wunderle 1991), and juveniles of some species are known to follow adults to both feeding areas and to specific schools of fish, relying on the adults for their expertise at locating and identifying prey (Drury and Smith 1968; Porter and Sealy 1982). This is especially important during a bird's first year, when survival rates are generally the lowest for most species (Lack 1954). Conspicuous feeding flocks may provide both adult and juvenile murrelets with a dependable means of locating food (Chilton and Sealy 1987).

Group Sizes.—We agree with Strachan *et al.* (1995) that Marbled Murrelets forage cooperatively. Underwater herding behavior has been reported for the Marbled Murrelet (Chilton and Sealy 1987; Mahon *et al.* 1992), murres (Chilton and Sealy 1987; Hoffman *et al.* 1981) and Rhinoceros Auklet (*Cerorhinca monocerata*; Grover and Olla 1983), and serves to maintain feeding flocks by lengthening the amount of time that prey are available. The fact that murrelets were seen most often at sea in pairs, even during the incubation period and during the non-breeding season, may indicate that murrelets forage more efficiently in small groups than as individuals. As few as two murrelets may be able to concentrate a school of fish enough to prolong their feeding opportunity and enhance their foraging success.

Feeding Assemblages.—Murrelets can either initiate feeding flocks themselves, or follow other murrelets and gulls to existing feeding assemblages (Chilton and Sealy 1987; Carter and Sealy 1990; Mahon *et al.* 1992). Feeding flocks were present in Auke Bay and Fritz Cove throughout each summer, but were most common in June and July. Feeding flocks appeared to play an important role for murrelets, judging from their frequency of occurrence and the numbers of murrelets participating. Flocking behavior in murrelets may be driven in large part by murrelet density (Carter and Sealy 1990), so that a positive correlation may exist between murrelet density and the number of feeding flocks (Mahon *et al.* 1992). Foraging in flocks is known to enhance feeding efficiency for many species (Götmark *et al.* 1986).

Fish-holding Behavior and Species Composition.—The species composition of fish held by adult murrelets for later delivery to chicks may not accurately represent their diets, because many adult seabirds select higher quality prey for chicks and consume less nutritious or smaller prey themselves (Sealy 1975b; Baird 1991). Nonetheless, sand lance and Capelin are two of the most important prey for adult murrelets in Alaska and British Columbia (Burkett 1995; Piatt and Anderson 1996). The number of fish-holders was highest on the water in the evening, but birds flew into and out of the forest surrounding our study area at all hours of the day. However, observations at nest sites in Prince William Sound, Alaska, show that most meal deliveries were made before sunrise (Naslund and O'Donnell 1995), when it is difficult to conduct at-sea observations of fish-holding murrelets. A small peak in the number of deliveries occurs just after dusk (Naslund and O'Donnell 1995), and these birds likely wait on the water until it is dark before attempting delivery to the nest, accounting for birds carrying fish in the evening. This means that the temporal patterns of fish-holding on the water observed during this study may not be indicative of when most fish are delivered to nestling murrelets.

Relation of Forest Attendance to At-sea Attendance and Behavior.—In this study, the numbers of murrelets at sea did not reflect forest attendance patterns. Rodway *et al.* (1995) found a positive correlation between numbers of murrelets on the water and numbers of forest detections in one inlet in the Queen Charlotte Islands, British Columbia, but not in a nearby inlet. They cautioned that use of marine areas by murrelets does not necessarily reflect use of the adjacent inland habitat.

Forest activity levels may not be useful as an index to breeding effort by murrelets, because the breeding season is protracted and activity levels in the forest increased while bird were still incubating eggs or rearing chicks (Naslund 1993). Increased forest activity levels in late summer may represent an influx of non-breeding and subadult birds (Naslund 1993; Speckman *et al.* 2000). This is supported by the observation that numbers at sea increased in mid and late July in the study area during both summers (Speckman *et al.* 2000). The significant correlation in 1993 between numbers of murrelets on the water and numbers displaying may indicate that displays are socially facilitated, so that more murrelets display when more murrelets are present.

The murrelets' vulnerability to forest predators has forced them to become secretive and crepuscular in their nesting habits

(Naslund and O'Donnell 1995), and it appears they have transferred many of their social activities from the nest site to the sea. Our results suggest that aggregative behavior at sea may play an important role for murrelets in both foraging strategy and efficiency. Participation in feeding flocks of two or more birds may be an efficient way for murrelets to secure prey, and following other murrelets and gulls to active flocks may ensure both adults and juveniles a dependable and easily exploited food supply (Chilton and Sealy 1987).

Many behavior patterns of the Marbled Murrelet, such as displaying, choosing of mates, pair-bonding, finding of nest sites, and successful foraging of adults and juveniles may be socially-facilitated. Thus, such behavior may become less prevalent or less successful as numbers and densities of murrelets decline. Further research is needed to decipher the importance of social behavior and the impacts of declining forest and at-sea densities on the social structure of the Marbled Murrelet.

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