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The role of Marbled Murrelets in mixed-species feeding flocks in British Columbia.—Studies off the west coasts of Vancouver Island and the Queen Charlotte Islands indicate that Marbled Murrelets (*Brachyramphus marmoratus*) usually feed singly or in pairs (Carter 1984, Carter and Sealy 1990, Sealy 1973, 1975). Marbled Murrelets participated in mixed-species feeding flocks (Carter 1984; Carter and Sealy 1987, 1990; Chilton and Sealy 1987; Porter and Sealy 1981, 1982; Sealy 1973, 1975) but were not as prevalent as other species (Sealy 1973, Hoffman et al. 1981, Porter and Sealy 1981) and infrequently initiated the flock (Porter and Sealy 1982, Chilton and Sealy 1987). We describe events in a dense concentration of murrelets (Kaiser et al. 1991) in the more sheltered waters of the Strait of Georgia, east of Vancouver Island, where Marbled Murrelets were the major initiators and participants of mixed species feeding flocks.

Study area and methods.—The Okeover Inlet study area (50°5′N, 124°45′W) includes several small inlets and fiords on the southwestern coast of British Columbia (Fig. 1). It is sheltered from major Pacific storms by Vancouver Island and more locally by numerous small islands and peninsulas, creating a protected inshore habitat. The area is characterized by rugged, broken coastline, deep inlets and fiords and moderate tidal currents. Open sound, channel, inlet, and estuarine habitats were included within the study area. During the summer, the area had a resident population of about 370 Marbled Murrelets and 200 Glaucous-winged Gulls (*Larus glaucescens*) with respective densities of 10.4 and 5.6 birds km^{-2} (Kaiser et al. 1991, Campbell et al. 1990). Other fish-eating birds constituted less than 10% of summer observations.

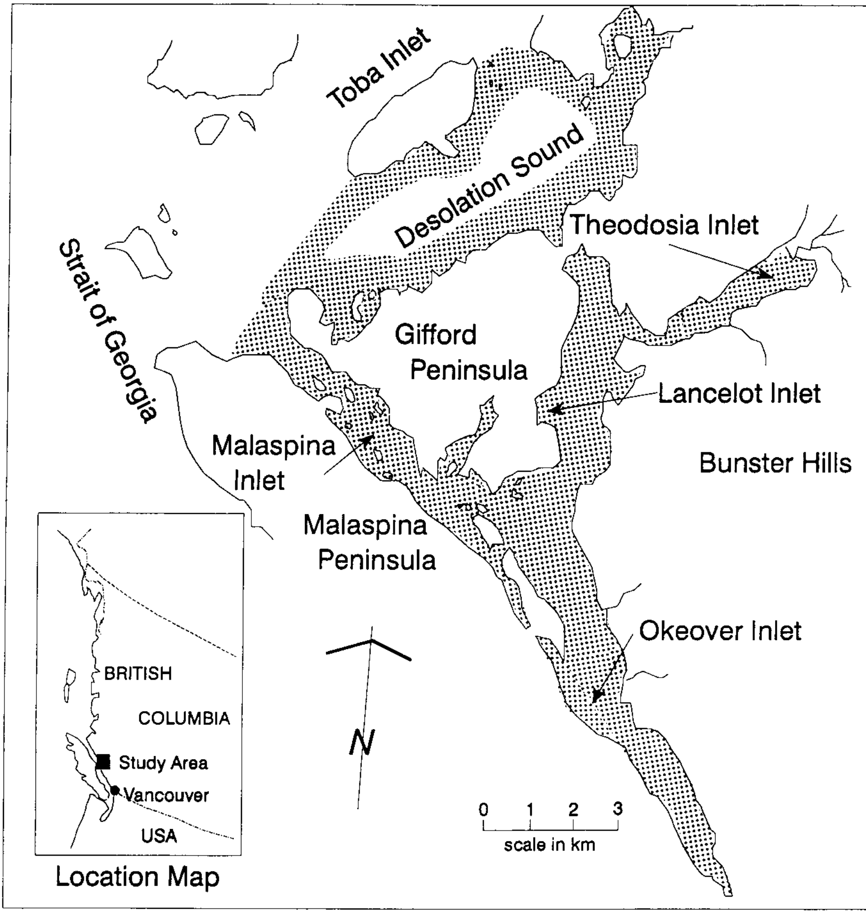

FIG. 1. Map of the Okeover Inlet study area on the eastern shore of the Strait of Georgia, British Columbia. Systematic surveys were made parallel to the shoreline to cover the entire shaded area. Additional observations of feeding flocks were made in the same area.

Between 6 June and 8 August 1991, we conducted 27 surveys along a 72.4 km transect route to determine the composition and density of mixed feeding flocks. We travelled at a continuous speed of 20 km h^{-1} and made observations out to 250 m on either side of the boat for an effective transect width of 500 m. Observations of flock duration and chronology, species' roles and interactions, and feeding methods were made independently of the surveys while stationary on the water about 50 m away from feeding flocks. Prey were identified visually with binoculars when they were driven to the surface by murrelets and when they were captured by gulls.

Results.—We observed 126 feeding flocks in whole or in part. The frequency of feeding flocks seen per survey was positively correlated to the total number of Marbled Murrelets observed per survey (Pearson correlation, $r = 0.66$, $N = 23$, $P < 0.01$). In 100 of the feeding flocks Marbled Murrelets and Glaucous-winged Gulls were the only participants. Bonaparte's Gulls (*L. philadelphia*) were also present in 18 flocks, Common Mergansers (*Mergus merganser*) and Pigeon Guillemots (*Cepphus columba*) were each in three flocks, and Mew Gulls (*L. canus*) and Pelagic Cormorants (*Phalacrocorax pelagicus*) were each in one flock. California Gulls (*L. californicus*), Common Loons (*Gavia immer*), Pacific Loons (*T. pacifica*), and Surf Scoters (*Melanitta perspicillata*) occasionally were seen but did not participate in mixed-species feeding flocks. The proportion of murrelets seen per survey feeding in mixed species feeding flocks ranged between 1 and 22%, and was not correlated with murrelet density ($r = 0.19$, N = 23, $P > 0.05$).

The initiation of 27 mixed-species feeding flocks was observed. In every case, Marbled Murrelets feeding singly or in small groups (<5) initiated the flocks by driving a school of sand lances (*Ammodytes hexapterus*) to the surface where they thrashed briefly in a tightly packed "boil." This attracted one or two Glaucous-winged Gulls to the site, and if the sand lances kept resurfacing more gulls quickly arrived. Additional murrelets were also attracted but generally arrived more slowly than most of the gulls. Arriving singly or in groups of less than five, these murrelets usually swam, or less commonly flew, to the edge of the feeding area and began diving. Generally, murrelets were distributed loosely at the flock periphery, while gulls concentrated in a tight group in the center. Diving by murrelets appeared to keep the school of fish near the surface and accessible to gulls. Marbled Murrelets foraged by pursuit-diving while Glaucous-winged Gulls fed by dipping, surface seizing and surface plunging (Ashmole 1971). Throughout the duration of the feeding flock, both gulls and murrelets called frequently. No other diving birds were observed causing boils of fish, however similar boils by harbor seals (*Phoca vitulina*) did attract gulls but did not result in feeding flock formation.

First-year sand lances (6–10 cm) were the only prey identified in feeding flocks. Three SCUBA dives made in the vicinity of feeding flocks confirmed the presence of schools of sand lances within 5 m of the surface. In the evenings, we saw murrelets holding larger sand lance (14–18 cm), Pacific herring (*Clupea harengus*), and shiner perch (*Cymatogaster aggregata*), which likely were destined for nestlings (Carter and Sealy 1987), but none of these species was taken during mixed-species feeding events.

Feeding flocks were generally small, with a mean of 7.7 murrelets (range 1–48) and 5.9 Glaucous-winged Gulls (range 1–33, N = 126). The largest feeding flock consisted of 48 murrelets and 14 gulls. There was a significant positive correlation between the numbers of murrelets and gulls in each mixed-species flock (Fig. 2). The relationship was non-linear and the best fit was obtained with a logarithmic curve indicating that gull numbers approached an asymptote despite increasing numbers of murrelets (Fig. 2, $r = 0.76$, N = 46, $P < 0.005$). The ratio of gulls to murrelets in flocks with up to 16 murrelets was approximately one to one but declined with increasing flock size.

Mixed-species feeding flocks lasted 1–79 minutes. Flock duration was positively correlated with the number of participating murrelets ($r = 0.94$, N = 41, $P < 0.005$). Feeding ended abruptly. Most murrelets simultaneously ceased to dive and slowly drifted away from the feeding area. Gulls also dispersed on the water as the murrelet's diving activity ceased, and they flew away after 1–2 min if no new boils of fish appeared.

Discussion.—Our observations of murrelets contrast sharply with low flocking tendencies (0.2%, Porter and Sealy 1981) and infrequent feeding flock initiation (1.4%, Porter and Sealy 1982; 15.9%, Chilton and Sealy 1987) seen on the west coast of Vancouver Island. Similarly, in Washington and Alaska, Marbled Murrelets participated in only 2% and 0.6%, respectively, of mixed-species feeding flocks and were never seen to initiate such flocks (Hoffman et al. 1981). In the Okeover Inlet Area in 1990, however, the murrelets frequently participated in mixed-species feeding flocks and initiated all of the flocks we saw from the start.

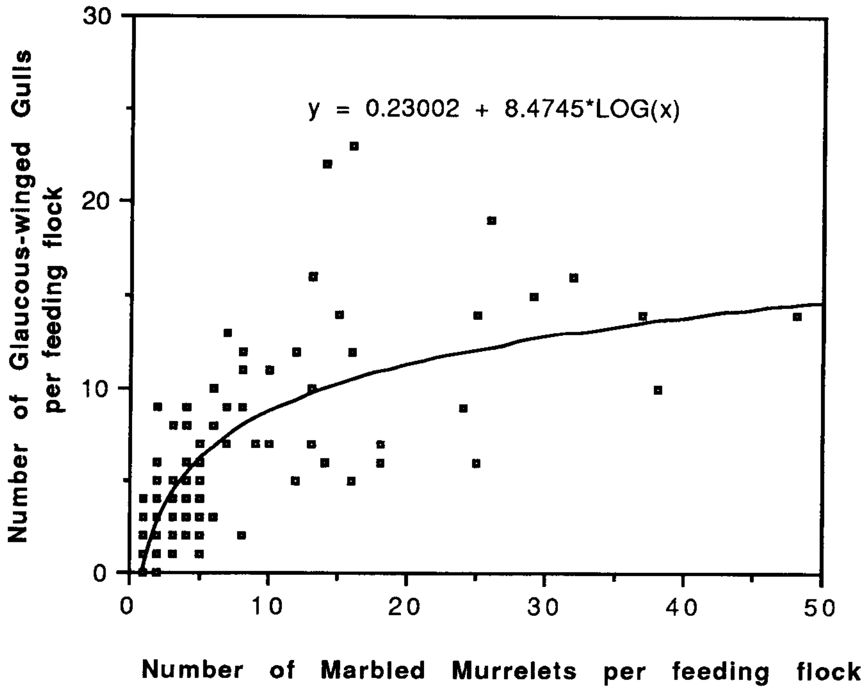

FIG. 2. Numbers of Marbled Murrelets and Glaucous-winged Gulls recorded in feeding flocks. The equation and line show the best-fit logarithmic relationship.

Several factors may have encouraged greater flocking behavior by murrelets in the study area. First, larger more aggressive alcids, such as Common Murres (*Uria aalge*) which can disrupt feeding in smaller alcids (Chilton and Sealy 1987, Piatt 1990), were absent. Second, the study area contained very high densities of murrelets (10.4 birds km^{-2}, Kaiser et al. 1991) which may be important because we found a positive correlation between murrelet density and the number of feeding flocks. Third, prey were locally concentrated and their behavior of balling up at the surface when attacked likely facilitated flock formation (Grover and Olla 1983). It seems unlikely that the prey type itself could explain the flocking behavior, since sand lances are common prey for murrelets in Barkley Sound where murrelets rarely join mixed-species flocks (Carter and Sealy 1990).

The aggregation of murrelets over schools of sand lances may be an example of intraspecific cooperative foraging. Fish schools may be more vulnerable when attacked by several birds (Gotmark et al. 1986). We found that flock persistence was positively correlated to the number of murrelets in the flock. The "boiling" of dense schools of fish at the surface is believed to confuse underwater predators and reduce the surface area of the school available for exploitation (Grover and Olla 1983, Girsa and Danilov 1976). However, alcids have been seen herding sand lances (Angell and Balcomb 1982) and may be able to control surface concentrations by preventing their escape, thus increasing the period during which the fish can be exploited (Hoffman et al. 1981, Grover and Olla 1983).

The frequent association of Glaucous-winged Gulls with individuals and pairs of diving murrelets and the gulls' immediate response to "boils" of sand lance suggests that some gulls have learned to monitor the murrelets. Once a flock is initiated, the conspicuous white plumage and active feeding method of gulls serves as a catalyst for the attraction of other flock participants (Armstrong 1971, Gotmark et al. 1986).

Flocks with up to 16 murrelets usually had equal numbers of gulls and murrelets. As the number of murrelets increased, the number of gulls remained approximately stable although new individuals arrived and displaced gulls already feeding. This dynamic equilibrium appeared to be established through interference competition among the gulls for a limited area on the water where they could successfully exploit the ball of sand lance. The number of murrelets did not show a similar plateau probably because they foraged in three dimensions with a larger exposure to the ball of fish (Baltz and Morejohn 1977). In addition, physiological limitations of diving reduced the total time murrelets could exploit the school underwater. For 126 dives the dive : pause ratio was 2:1.

Initiators are species which locate prey concentrations and typically include surface feeders such as Glaucous-winged Gulls (57%, Chilton and Sealy 1987) or Black-legged Kittiwakes (*Rissa tridactyla*) (76%, Hoffman et al. 1981). Although Glaucous-winged Gulls were numerous and schools of sand lances were observed near the surface, Marbled Murrelets started all of the mixed-species feeding events we observed in the Okeover Inlet area.

This study demonstrates that Marbled Murrelets can regularly feed in flocks under favorable conditions where interference from larger diving birds is lacking. Our study also emphasizes the important, often underestimated role that diving birds play in initiating and maintaining mixed-species feeding flocks of seabirds.

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Arthropod feeding by two Dominican hummingbird species.—Hummingbirds are predominantly floral nectar feeders (Montgomerie and Redsell 1980) and are thought to be closely tied to flowers through most or all of their life cycle (Wolf 1970). Although hummingbirds forage extensively on insects and other arthropods (Wagner 1946; Stiles and Wolf 1970, 1979; Feinsinger and Colwell 1978; Montgomerie and Redsell 1980), arthropods as food are not well known in comparison with nectar (Remsen et al. 1986). Because nectar is high in calories and because hummingbirds have great energy requirements, detailed studies of hummingbirds have assumed that energy is the most important variable determining their behavior. Arthropods may not be a crucial or limiting resource for hummingbirds (Feinsinger 1976, Wolf et al. 1976, Feinsinger and Colwell 1978) and may represent only a limited energetic component of diets (Wolf and Hainsworth 1971). Hainsworth (1977), however, suggests that an equal time flycatching by hummingbirds, even with low efficiency rates of 40%, can provide more energy than nectar feeding.

Detailed foraging studies (reviewed in Gass and Montgomerie 1980) report foraging for insects by hummingbirds as generally less than 15% of feeding time (Wolf and Hainsworth 1971, 1977; Hainsworth 1977), however, other studies report searching for arthropods as the bulk of foraging effort (Young 1971) or, at times, the only food taken (Kuban and Neill 1980). Several studies of hummingbirds show that under field conditions some humming-