

ESKIMO:  
Tagi-tuekk  
FRENCH:  
Guillemot marbré  
RUSSIAN:  
Dlinnoklyuvii pyzhik  
JAPANESE:  
Madara-umisuzume

# Marbled Murrelet

*Brachyramphus marmoratus*



**T**he Marbled Murrelet is unique among members of the alcid family in its nesting habits. This small seabird nests in trees in coastal, older forests throughout most of its range in North America and Asia. First described by Gmelin in 1789 (as *Colymbus marmoratus*; *Brachyramphus* by Brandt in 1837), this species has been referred to more recently as the “enigma of the Pacific” because of its secretive behavior and elusive nests (Guiguet 1956). After more than a century of unsuccessful attempts by early ornithologists to locate its nest, a \$100 reward was offered for solving one of the last great ornithological mysteries in North America (Arbib 1970). Finally, in 1961 and 1974, the first verified and published nests were reported in Asia and North America, respectively (Kuzynkin 1963, Arbib 1972, Binford et al. 1975).

Referred to as the “Australian Bumble Bee” by fishermen (Gabrielson and Lincoln 1959) and “fogbirds” or “fog larks” by Eskimos and loggers (Bédard 1966, McCarthy 1993), Marbled Murrelets fly at high speeds, attend their breeding sites during periods of low light, and nest solitarily. These behaviors, combined with the challenges of capturing them at sea, have made this species difficult to study. Only in the last decade have some of its secrets been revealed; today more than 160 of its nests are known. Information remains limited, however, on its nesting habits, behavior, habitat

## The Birds of North America

Life Histories for the 21st Century

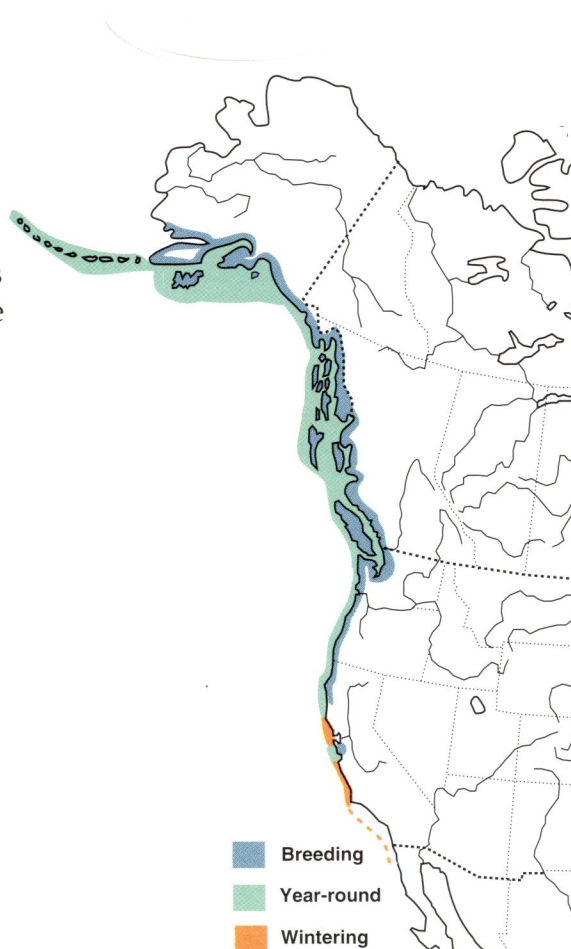


Figure 1.

Distribution of the Marbled Murrelet in North America. This species also breeds in Asia. See text for details. Marbled Murrelets have been recorded in small numbers during the winter south to the dotted line. Individuals have also been recorded at inland breeding sites during the winter north through southeastern Alaska. During the breeding season, nonbreeders occur along the Pacific coast from the Aluetian Islands south to Monterey Bay, California.

associations, and population numbers, and relatively little is known about its demography.

The distribution and numbers of this species have declined primarily because logging and coastal development have removed significant portions of its essential nesting habitat. Gill-net fishing and oil spills also kill this species and threaten its prey. The Marbled Murrelet was listed as a Threatened species in Canada in 1990 and in the southern portion of its range in the United States in 1992 (U.S. Fish and Wildlife Service [USFWS] 1992, M. Rodway unpubl. report).

### **DISTINGUISHING CHARACTERISTICS**

Small alcid (24–25 cm long, wing length 122–149 mm; adult mass 188–269 g); no differences in size between sexes. Asiatic form larger (adult mass 258–357 g) with longer bill (23.5 versus 17.6 mm) than that of North American form. Wings longer, narrower, and more pointed than those of other alcids. Longest primary (outermost) equal to slightly more than half the length of wing. Rapid wing-beats and flight speeds up to 158 km/h create a distinctive appearance in flight. Tail about one-fourth the length of wing, with 14 broad, rounded rectrices of equal length. Adults sexually monomorphic in plumage, but Alternate (breeding) and Basic (winter) plumages are distinct. Breeding adults have sooty brown to brownish black upperparts, rusty margins on the back-feathers (area between rump and nape), and reddish scapulars (Ridgway 1919, Gabrielson and Lincoln 1959, Kozlova 1961, Dement'ev and Gladkov 1968, Carter and Stein 1995). Underparts (chest, sides, flanks) and sides of head to above eye and neck are light, mottled brown (white feathers with broad brown margins). Rectrices and upperwing-coverts dark brown with occasional white margins and brownish dots on outer rectrices. Underwing-coverts and axillaries uniform gray brown. Undertail-coverts white. Winter adults blackish brown above, with bluish gray margins on back-feathers and largely white scapulars (especially inner ones). White underparts, although some brown gray flecking may persist on sides and flanks. White sides of head to above eye, and nearly complete nuchal collar. Rectrices uniformly blackish brown, or outer rectrices edged with narrow white margin (*B. m. perdix*). Axillars and underwing-coverts uniform fuscous, as in summer. Undertail-coverts white. See Systematics: subspecies, below, for differences relating to the Asiatic form.

Juvenal plumage similar to that of adult Definitive Basic plumage, but white underparts (breast, neck, and sides) are speckled with blackish brown spots, more brownish above, and bluish gray margins are less visible. White collar and scapular-patch less distinct than on winter adults. Underwing-coverts are brownish gray with some white. White edges on outer rectrices (*B. m. perdix*); inner vanes pale

brownish. Lores almost wholly dusky. Recently fledged juveniles darker overall, with thicker dark margins on side and flank. Dark neck-band formed by dark-margined feathers on upper breast. Within 2 wk–2 mo after leaving nest, underparts become whiter, upperparts become lighter (dark brown flecking on feather margins is replaced with thick gray margins), and dark neck-band disappears. At this point juveniles are generally indistinguishable from adults in Definitive Basic plumage.

Closely related Kittlitz's Murrelet (*Brachyramphus brevirostris*) is quite similar and is sympatric in central and se. Alaska and in Russia (see Habitat: breeding range). Kittlitz's has shorter bill, averaging about 11 mm on adults whereas Marbled averages over 15 mm (Sealy et al. 1982), white outer rectrices, and white on tips of secondaries, especially on the inner webs. In Russia, *B. m. perdix* is referred to as the Long-billed Murrelet, whereas *B. brevirostris* is referred to as the Short-billed Murrelet. Kittlitz's Murrelet in Alternate plumage further distinguished by grayish upperparts spotted or streaked with buff and tawny, and by overall pale appearance. Kittlitz's in Basic plumage distinguished by white face (dark cap of Marbled Murrelet extends to or below eye) and paler, grayer upperparts. Kittlitz's in Juvenal plumage differs in possessing white on tail and secondaries, grayer plumage, whiter face, less extensive barring on hind flanks and undertail-coverts, and better-defined grayish breast-band (Devillers 1972). In addition, Kittlitz's in Juvenal plumage has pale crescent mark in front of eye and complete white nuchal collar.

### **DISTRIBUTION**

#### THE AMERICAS

**Breeding range.** *B. m. marmoratus* (see Systematics: subspecies, below) nests in forested or rocky areas on islands and on mainland along coast from Near (Attu), Andreanof (Adak, Atka, Kagalaska) and Fox (Unalaska) Is. of Aleutian Archipelago in Alaska; east to Alaska Peninsula, Cook Inlet, Kodiak I., Kenai Peninsula, and Prince William Sound; south through Alexander Archipelago (se. Alaska), and along coasts of British Columbia, Washington, and Oregon, to Santa Cruz Co. in w.-central California (Fig. 1; Kessel and Gibson 1978, Campbell et al. 1990, U.S. Fish and Wildlife Service 1992, Small 1994). A few spring and summer records from north and west of Alaska Peninsula, including Bristol Bay (Bartonek and Gibson 1972), St. Lawrence I. (Kavalghak Bay; Bédard 1966), and n. Bering Sea (near Nome; Bent 1919). A few summer and fall records south in California to Big Sur and occasionally to Point Conception (Santa Barbara), Point Mugu, and Channel Is. (Anacapa and Santa Cruz; Ainley 1976, Garrett and Dunn 1981, Small 1994, H. Carter pers. comm.).

A large gap in inland distribution occurs in California between s. Humboldt Co. and Half Moon Bay (Santa Cruz Co.), a distance of about 450 km. Occurs as far as 88 km inland, or farther; e.g., 3 possibly vagrant records known from Oregon 96–129 km inland (SKN) and 1 grounded juvenile from 101 km inland in British Columbia (Rodway et al. 1992). Other far-inland sightings (56–88 km) are primarily from Washington and Oregon. Farthest inland nest at only 50 km in Oregon (SKN unpubl. data).

Widely distributed in nearshore waters on West Coast of North America. Occurs primarily within 5 km of shore (Alaska, within 50 km), and primarily in protected waters, although distribution varies with coastline topography, river plumes, riptides, and other physical features (Burger 1995, Piatt and Naslund 1995, Ralph and Miller 1995, Strong et al. 1995, Speckman 1996). See Food habits: feeding, and Habitat: marine range, below. Distribution appears also to be associated with presence of suitable forest habitat (Nelson et al. 1992, Ralph and Miller 1995). Concentrations during breeding season occur along Kodiak Archipelago, Prince William Sound, Yakutat Bay, and Alexander Archipelago in Alaska (Gabrielson and Lincoln 1959, Agler et al. in press, S. Klosiewski and K. Laing unpubl. data), sheltered and exposed nearshore waters off Queen Charlotte Is., Desolation Sound, and sw. Vancouver I. (especially at Amphitrite Bank off Barkley Sound) in British Columbia (Morgan et al. 1991, Burger 1995), Straits of Georgia and Juan de Fuca, and San Juan Is., WA (Speich and Wahl 1995), central Oregon coast between Cascade Head (s. Tillamook Co.) and Cape Arago (Coos Co.; Strong et al. 1995), and n. California coast off Del Norte and Humboldt Cos., and Point Año Nuevo (Santa Cruz Co.; Ainley et al. 1995, Ralph and Miller 1995). The farthest offshore sightings in summer are from 75 km offshore Vancouver I., British Columbia (Morgan et al. 1991).

**Winter range.** Poorly documented, but present near breeding sites year-round in most areas, except portions of Alaska and British Columbia, where many individuals move to protected waters, offshore areas (Alaska), or unknown locations (see Habitat: winter range, below). In Prince William Sound, AK, for example, only 25% of breeding population is present in winter (Agler et al. in press, S. Klosiewski and K. Laing unpubl. data). Casual winter visitor to St. Paul I. and Pribilof Is., AK (Hanna 1920, Kessel and Gibson 1978). Occurs south to s. California (Carter and Erickson 1992) and n. Mexico (extreme nw. Baja; Erickson et al. 1995). In this area, regularly found off Santa Barbara Co., but less common farther south (Fig. 1). Generally more dispersed and found farther offshore in winter in some areas (Alaska), although highest concentrations still occur close to shore and in protected waters. Farthest offshore records are 35 km in California (Farallon Is.; Small 1994) and at least

300 km in Alaska (Piatt and Naslund 1995). Known areas of winter concentration include Alexander Archipelago, Kodiak Archipelago, Cook Inlet, Prince William Sound, and some areas out to 300 km in the Gulf of Alaska (Piatt and Naslund 1995); Hecate Strait, La Pérouse Bank, Saanich Inlet and portions of Strait of Georgia including Jarvis Inlet, Howe Sound, and around islands in the Northern Strait in British Columbia (Campbell et al. 1990, Morgan et al. 1991, Burger 1995); and southern and eastern end of Strait of Juan de Fuca (primarily Sequim, Discovery, and Chuckanut Bays), San Juan Is., and Puget Sound, WA (Speich and Wahl 1995). Winter surveys are not available for Oregon and California (but see Ainley et al. 1995). See Migration: timing and routes for rare sightings of *B. m. perdix* in North America.

**Summer nonbreeding range.** Nonbreeding adults and subadults are thought to occur in similar areas as breeding adults (both marine and forested habitats), although difficulties in differentiating nonbreeders from breeders has limited distribution information (see Appearance: molts and plumages, below).

#### OUTSIDE THE AMERICAS

**Breeding range.** Asiatic form (*B. m. perdix*; see Systematics: subspecies, below) breeds from Kamchatka Peninsula, Russia (northernmost sighting at Litke Strait) and Commander (Kommandorski) Is. in north, southward through Kuril Is., along northern and western coasts of Sea of Okhotsk (Magadan to Sakhalin I.), south to Hokkaido I., Japan, and south and east along coast of Primorski Krai, Russia and Sea of Japan to Vladivostok (Konyukhov and Kitaysky 1995). Also, an immature bird captured in summer along sw. Korea coast (Austin 1948, Kozlova 1961). Southernmost nest site known from Ol'ga Bay on Primorski Krai coast, 274 km north of Vladivostok (Labzyuk 1987). Breeding and activity sites have occurred as far as 30 and 40 km inland, respectively (Nechaev 1986). In summer, most common along northwestern and southwestern coasts of Sea of Okhotsk, especially Shantarskie and Sakhalin Is., s. Kuril Is., along e. coast of Kamchatka Peninsula, and nw. coast of Hokkaido I. (Kozlova 1961, Nechaev 1986). Rare on southeastern and southwestern coasts of Hokkaido I. and Primorski Krai coast south of Amur River.

**Winter range.** In winter, individuals move south from n. Russia and are found primarily off Sakhalin I., Hokkaido, Honshu, Kyushu, Amami-o-shima, and Kume-jima Is. (Japan), Primorski Krai coast in Seas of Okhotsk and Japan, Korea, and n. China (Vaurie 1959, Kozlova 1961, Dement'ev and Gladkov 1968, Brazil 1991). A pair of *B. m. marmoratus* were seen and 1 bird collected at Ildidlya I. near Kolyuchin Bay on northern coast of Chukotski Peninsula in ne. Siberia (Bent 1919), and 1 bird was collected on 19 May at Diomedea Is. in Bering Strait (Kozlova 1961).

## HISTORICAL CHANGES

Few data, but in North America scarce or absent in areas where once plentiful, including s.-central Alaska (Agler et al. in press, S. Klosiewski and K. Laing unpubl. data), w. Vancouver I., British Columbia (Burger 1995, Kelson et al. 1995), sw. Washington (Grays Harbor and Pacific Cos.; Leschner and Cummins 1992), n. (Clatsop Co.) and s.-central (Coos Co.) Oregon (Nelson et al. 1992), and n.-central California between Humboldt and Santa Cruz Cos. (Carter and Erickson 1992). In winter, also rare off Monterey and Santa Barbara Cos., CA, where numbers were once plentiful (Carter and Erickson 1992). Range and population numbers appear to be in steady decline (USFWS 1992, 1995, 1996, Ralph 1994, Ralph et al. 1995). Information on historical changes in distribution from Asia not available.

## FOSSIL HISTORY

No information. *Brachyramphus* thought to be one of oldest alcid genera, having evolved during late Miocene, 7–12 million years ago (Piatt and van Vliet 1992). Many subfossil remains of Marbled Murrelets dating from 1,600–4,000 yr before present are known from numerous archaeological digs along West Coast of North America (British Columbia, Washington, and Oregon; Calvert 1980, DePuydt 1983, Greenspan and Wigen 1987, 1991, Greenspan and Crockford 1992).

## SYSTEMATICS

## GEOGRAPHIC VARIATION

North American race differs from Asiatic race in size and plumage, but no geographic variation in size or plumage apparent within North America (Pitocchelli et al. 1995). Populations north and west of Prince William Sound, AK, nest on ground, whereas those from Prince William Sound east and south nest in trees. Two unusual ground nests are known from se. Alaska, however (Prince of Wales and Catherine Is.; Ford and Brown 1995, T. DeGange pers. comm.), and several tree nests are known from Kodiak I. (Naslund et al. 1995). See Breeding: nest site, below.

## SUBSPECIES

Two subspecies currently recognized (Nettleship 1996). Although long regarded as separate species, the 2 were considered conspecific by Am. Ornithol. Union (1957). Recent molecular genetic evidence suggests that the 2 again merit recognition at species level (Friesen et al. 1994, 1996b, Piatt et al. 1994).

*BRACHYRAMPHUS MARMORATUS MARMORATUS* (GMELIN, 1789). Breeds from Aleutian Archipelago, AK, south to Santa Cruz Co., CA, and winters from Bering Sea in Alaska to extreme nw. Mexico. Reported rarely in summer to ne. Siberia. Bill shorter (exposed culmen <18.0 mm) than that of *B. m. perdix* (see below) and not

longer than tarsus (see discussion of *B. m. perdix* for plumage differences).

*BRACHYRAMPHUS MARMORATUS PERDIX* (PALLAS, 1811). First described as *Cephus perdix*, the Partridge Auklet. Genus *Cephus* then included many smaller Alcidae, not just guillemots, as presently construed. Breeds from Kamchatka Peninsula and Commander Is. in Russia to Hokkaido, Japan, and s. Primorski Krai in Russia, and winters from Sakhalin I., Hokkaido, Honshu, Kyushu, Amami-o-shima, and Kume-jima Is., Japan, and along s. Primorski Krai coast (s. Russia) to Korea and n. China. Very rare along Pacific Coast of North America and at inland localities, where nominate *marmoratus* unrecorded, eastward across North America (see Distribution, above, and Migration: timing and routes of migration, below). Larger size (20% larger in mass) and longer bill (exposed culmen >18.0 mm) than that of *B. m. marmoratus*, bill longer than tarsus (Ridgway 1919, Dement'ev and Gladkov 1968, Sealy 1975a, Sealy et al. 1982). In Alternate plumage, *perdix* spotted or barred with buff on upperparts, lacking the rusty margins on back, scapulars, rump, and uppertail-coverts that are seen on *marmoratus*; underparts show more white mottling and throat paler on *perdix* (Ridgway 1919). In Basic plumage, *perdix* lacks nearly complete white nuchal collar and large black margin below eye, typically has partial or broken white eye-ring (white arcs either below or above and below eye; but may not be reliable field mark), and has narrow, white marginal stripe on outermost rectrix of tail (Sibley 1993, Konyukhov and Kitaysky 1995, Di Labio 1996). Overall, *perdix* appears more extensively dark on head, nape, forehead, and lores (above gape), whereas nominate *marmoratus* has more capped appearance. White smudges or patches on back of head and color of lores above gape are variable in both taxa during molt, so not useful in subspecific identification in spring and fall (Erickson et al. 1995, Di Labio 1996, S. Sealy pers. comm., SKN).

Udvardy (1963) considered these subspecies to have disjunct sub-boreal distributions, but Sealy et al. (1982) suggest, on basis of a few records of *B. m. perdix* from Commander Is. and suspected breeding of *B. m. marmoratus* at Adak I. in Aleutians, and observations of individuals as far west as Attu I. (Kessel and Gibson 1978), that known breeding ranges of subspecies are only geographically separated by Near Strait, a distance of 500 km.

## RELATED SPECIES

North American race of Marbled Murrelet is thought to be most closely related to Kittlitz's Murrelet. Analyses of both cytochrome *b* sequences and allozymes suggest that these are sister taxa that diverged 1.6 million yr ago, forming a monophyletic group, excluding *B. m. perdix* which diverged from other brachyramphine murrelets 5–6 million yr ago (Friesen et al. 1996b). Studies of mitochondrial DNA

also reveal differences between North American and Asiatic Marbled Murrelets (Zink et al. 1995) and a recent divergence, about 2.2 million yr ago, between Kittlitz's and North American Marbled Murrelets (Pitocchelli et al. 1995). All share the unique characteristic of molting from cryptic Alternate plumage in summer to black-and-white Basic plumage in winter (see Appearance, below). Within Alcidae, the *Brachyramphus* murrelets form a well-defined group (Moum et al. 1994, Friesen et al. 1996a).

## MIGRATION

### NATURE OF MIGRATION IN THE SPECIES

Few data, but some at-sea surveys have revealed seasonal shifts in distribution consisting primarily of small-scale migratory movements. In these limited movements, individuals move seasonally from outer coastal to protected waters (i.e., into Puget Sound), from inland waters to unknown locations, or south from breeding areas (Rodway et al. 1992, Small 1994, Burger 1995, Piatt and Naslund 1995, Speich and Wahl 1995, Kuletz 1996). In Alaska, concentrations still remain inshore near some breeding sites (Kodiak and Alexander Archipelagos), but in other areas individuals move to points south, areas farther offshore (out to 300 km), or unknown locations; for example, 50–75% of birds in Prince William Sound move to other areas in winter (Agler et al. in press, S. Klosiewski and K. Laing unpubl. data, K. Kuletz unpubl. data). Long-distance migrations (mostly north to south) occur after breeding season in British Columbia, where most individuals move from northern coast and waters along western coast of Vancouver I. and Queen Charlotte Is. inland and south to Hecate Strait, lower Straits of Georgia and Juan De Fuca, and into Washington (Rodway et al. 1992, Speich et al. 1992, Burger 1995, Speich and Wahl 1995); an adult banded in Desolation Sound, British Columbia, in Jul was captured in late Sep in San Juan Is., WA (G. Kaiser pers. comm.). In British Columbia, some birds found farther offshore in spring and fall than winter (Morgan et al. 1991). Long migrations also occur in e. North Pacific, where most individuals leave n. Russia for areas off s. Russia, Japan, Korea, and n. China (Vaurie 1959, Kozlova 1961, Brazil 1991, Konyukhov and Kitaysky 1995). While much of Alaska Range remains ice-free in winter, birds are forced south from n. Russia by extensive ice cover and ice floes. Documented as far south as n. Mexico in winter, 756 km south of their breeding range in California (Erickson et al. 1995). See also Habitat: winter range, below.

### TIMING AND ROUTES OF MIGRATION

Limited information. Most large- and small-scale movements begin after breeding season, usually in late Jul or early Aug (Burger 1995, Kuletz 1996). Some

movements occur only during Prebasic molt (Jul–Nov); for example, in Auke Bay, AK, no individuals are sighted between 15 Sep and 31 Oct (G. van Vliet pers. comm.). Small-scale movements may also occur throughout winter in association with prey availability. In large-scale migrations, numbers decline or increase (depending on location) steadily throughout Aug and Sep and increase or decline again between Mar and May (Bent 1919, Sealy 1975a, 1975c, Campbell et al. 1990, Burger 1995, S. Klosiewski and K. Laing unpubl. data, K. Kuletz unpubl. data; see Fig. 5). For example, during spring in Kachemak Bay and Prince William Sound, AK, numbers increase throughout Apr and reach summer abundance by early May. In fall, numbers decline throughout Aug and are low by mid-Sep (K. Kuletz unpubl. data). In British Columbia, breeding areas on outer coast are vacated in late summer as individuals move to inshore waters; numbers increase again in April (see Fig. 5; Sealy 1974, 1975a, 1975c). In Russia, moves south in Sep and Oct (Konyukhov and Kitaysky 1995). Sightings from winter range in s. California (Santa Barbara to nw. Mexico; Fig. 1) recorded between Oct and Jan (Garrett and Dunn 1981, Small 1994, Erickson et al. 1995). Exact distances and routes of migration unknown. See also Habitat: winter range, below.

All records >130 km inland from Pacific Coast are of Asiatic form (*B. m. perdix*) and occur primarily in late summer and fall during migration from breeding areas, when individuals are probably carried to North America during westerly storms. At least 22 definitive records between Jul and Mar (1979–1996), including Denali National Park, AK; Mono Lake, CA (4 records); Saskatoon Lake, Alberta; Yellowstone National Park, WY; Natrona Co., WY; Jefferson Co., CO; Pitkin Co., CO; La Porte Co., IN; Monroe Co., IN; Seneca Co., OH; Plymouth Co., MA; Montreal, Quebec; Cornwall, Ontario; Chatham Co., NC; Georgetown Co., SC; Levy and Pinellas Cos. FL (4 records; Jehl and Jehl 1981, Sealy et al. 1991, Sibley 1993, Di Labio 1996, unpubl. data). Also at least 9 records from Pacific Coast between Alaska and California (north of San Francisco) between Jun and Feb (1845–1995; Konyukhov and Kitaysky 1995, C. Strong pers. comm., D. Fix pers. comm.).

### MIGRATORY BEHAVIOR

No information available.

### CONTROL AND PHYSIOLOGY

No information available.

## HABITAT

### BREEDING RANGE

Habitat characteristics based on (1) >160 nests throughout range in North America and Russia, (2) records of downy and recently fledged young at

inland sites, and (3) records of murrelet vocalizations and visual sightings at inland sites, mostly via surveys following Pacific Seabird Group's inland survey protocol (Paton et al. 1990, C. J. Ralph, S. K. Nelson, M. Shaughnessy, S. Miller, and T. Hamer unpubl. data).

On basis of nest sites, this species breeds in coastal forests and sea-facing talus slopes or cliffs on islands and mainland (see Breeding: nest site, below). Most nest in trees, a few on the ground (in Alaska about 3% of population; Piatt and Ford 1993). On Kenai Peninsula, Cook Inlet, Barren I., and Kodiak I., 9 ground nests were found in the open, under vegetation, or in cavities on rock scree slopes or cliffs either with no vegetation except a few scattered shrubs or small trees—primarily Sitka alder (*Alnus crispa*) and dwarf Sitka spruce (*Picea sitchensis*) or in conifer forests—within 6.2 km (most <1 km) of shore (Simons 1980, Hirsch et al. 1981, Day et al. 1983, Johnston and Carter 1985, K. Kuletz unpubl. data, J. Hughes pers. comm.). To the west in Prince William Sound (Naked and Perry Is. and Port Nellie Juan) and se. Alaska (Prince of Wales and Catherine Is.), 4 ground nests were found in or near forests and 1 in a rock crevice (Ford and Brown 1995, Kuletz and Marks in press, K. Kuletz unpubl. data, J. Hughes pers. comm., M. Cody pers. comm.). All these nests were located on cliffs or rock outcroppings; 1 nest was on tree root adjacent to cliff. Two ground nests also reported in Russia (A. Kistchinski unpubl. data) and Japan (Mt. Mokoto, Hokkaido I.; Brazil 1991, Kon-yukhov and Kitaysky 1995). The Russian ground nest was found on an open scree slope in mixed-conifer/broad-leaved forest at 700 m elevation and 30 km inland above Shelikhova Bay, near Magadan. The authenticity of the ground nest found in a mixed deciduous-coniferous forest, at 400 m elevation and 24 km inland, on Mt. Mokoto, Hokkaido I., Japan is questionable; 3 eggs collected from nest were not murrelet eggs, but an adult, supposedly attending the nest, was collected and later confirmed to be a Marbled Murrelet.

An overlap in ground and tree nesting occurs in the region between Kodiak and Prince of Wales Is., AK. South of se. Alaska, known to nest only in trees. In North America, >136 tree nests found within 50 km (most within 30 km; 6.4 km in Alaska) of coast (Quinlan and Hughes 1990, Singer et al. 1991, 1995, Hamer and Nelson 1995a, Naslund et al. 1995; additional papers in Nelson and Sealy 1995; I. Manley unpubl. data, S. Singer unpubl. data, SKN unpubl. data). These tree nests have occurred in old-growth conifer forests and in mature conifer forests with old-growth components (remnant trees) or large branch platforms created by normal tree growth, disease, damage, or mistletoe (*Arceuthobium* sp., primarily *A. tsugense*). Two nests in Oregon found in young conifer forests (60–70 yr old) consisting of western hemlock (*Tsuga heterophylla*) trees with extensive mistletoe infections (SKN unpubl. data). In Prince William Sound, AK, many nests found in dense old-growth forests at heads of bays (Naslund

et al. 1995, K. Kuletz unpubl. data). Elevations of nest sites range from sea level to >1,100 m. In some areas of Alaska, presence of high mountains and glaciers near coast, where tree line occurs within only a few kilometers of shore, limits inland distribution of nests. In Russia, 4 tree nests found on intertwined small branches of Dahurian larch (*Larix gmelini*, formerly *L. dahurica*) in taiga forests up to 12 km inland (Kuz'yakin 1963, Arbib 1972, Nechaev 1986, Labzyuk 1987, Kondratyev and Nechaev 1989). In general, breeding range believed to be limited by distribution of taiga forest in coastal areas of region (Kistchinski 1968), although information on general habitat characteristics is limited. See also Breeding: nest site, below.

On basis of forest surveys and locations of grounded juveniles, breeding habitat consists of mature and old-growth coniferous forests, or forests with old-growth components, including, but not limited to, large trees with large limbs or large platforms created by damage, disease, mistletoe, or other factors; moss or other nesting substrate (e.g., needles, lichen); and multilayered canopies (Hamer and Nelson 1995a). Because adults do not build nests and depend on availability of large platforms, abundance of large platforms with moss or other thick substrate, such as piles of needles collected on limb near tree bole (for protection from weather and enlarging platform size), are key habitat components; absence of these factors may limit this species' distribution and habitat use. Specific habitat attributes from each state and province in North America are as follows. In Alaska, location relative to heads of bays, percent epiphyte cover on trees, tree diameter, presence of suitable nesting platforms, and amount of cover of large old-growth trees were variables that best predicted nesting habitat or the probability of detecting birds at a site (Kuletz et al. 1995). Elevation, slope, and aspect were also important. Less abundant in unforested areas in Prince William Sound. In British Columbia, coastal, low-elevation western hemlock and Sitka spruce forests, mean tree diameter, and moist stands with well-developed epiphytic mosses present were key habitat components (Burger 1995). In Washington, number of potential nest platforms, percent moss on dominant trees ( $\geq 81$  cm in diameter), percent slope, density of dominant trees, and mean diameter of western hemlock best characterized habitat (Hamer 1995). Presence of birds decreased with increasing stand elevation, distance inland, lichen cover, and canopy cover. In Oregon, density of large dominant trees ( $\geq 81$  cm diameter), dominant tree height, midstory tree diameter and cover, and percent canopy closure were important habitat components (Grenier and Nelson 1995). Nest sites had fewer trees per hectare and less canopy closure than did random sites. In California, percent old-growth canopy cover and tree species composition (>50% coast redwood [*Sequoia sempervirens*]) were most important predictors of occupancy and presence (Miller and Ralph 1995).

Habitat along major drainages and at lower elevations also key in large stands of old growth.

#### MARINE RANGE

In summer, forages primarily in bays, inlets, fjords (rarely in protected harbors), and open ocean within 5 km of shore (Alaska 50 km). Usually in widely dispersed concentrations: singles or pairs of birds. Seems to prefer shallow water, usually <60 m deep (Sealy 1975c, Ainley et al. 1995, K. Kuletz unpubl. data), but known to forage in water up to 400 m deep in fjords and 300 km offshore (Gulf of Alaska), generally in areas with underwater sills, shelf edges, or strong tidal currents (Piatt and Naslund 1995, Strachan et al. 1995, K. Kuletz unpubl. data). Highest use in upwelling areas, mouths of bays, over underwater sills, tidal rips, narrow passages between islands, shallow banks, and kelp beds (*Nereocystis* sp.; Sealy 1975a, Ainley et al. 1995, Burger 1995, Strong et al. 1995, K. Kuletz unpubl. data). Juveniles found closer to shore than adults; rarely found >1 km offshore (Beissinger 1995, K. Kuletz unpubl. data). Distribution and location of concentrations at sea are likely influenced by proximity to nesting habitat (especially off noncomplex shorelines), by prey availability, and by environmental factors (e.g., weather). Some feeding areas used consistently on daily and yearly basis (Carter and Sealy 1990). Also known to feed on coastal freshwater lakes (>70 records), primarily in British Columbia and Alaska (Carter and Sealy 1986) and on Kamchatka Peninsula and Sakhalin I. in Russia (Nechaev 1986, Konyukhov and Kitaysky 1995). Most lake records are within 20 km of ocean (farthest 75 km inland in British Columbia) and during breeding season (but at least 18% are winter records). In Alaska and British Columbia (areas with convoluted shorelines), travel from nesting areas on or near water to foraging sites can be as far as 75 km, but generally <20 km (mean distance traveled by 6 radio-tagged nesting adults in Alaska was 16 km; K. Kuletz unpubl. data, G. Kaiser pers. comm.). In other areas, travel (over land and sea) to foraging sites can be greater, depending on distance of nest from coast. See also Food habits: feeding, below.

#### OVERLAP WITH RELATED SPECIES

In North America, inland and at-sea ranges overlap with those of Kittlitz's Murrelet between Glacier and Bristol bays, and in Bering Sea, AK (including Prince William Sound, Cook Inlet, Kachemak Bay, Shelikof Strait, Alaska Peninsula, and Aleutian Is.; Agler et al. in press). In Russia, Kittlitz's Murrelet and Marbled Murrelet (*B. m. perdix*) overlap primarily in Sea of Okhotsk, and perhaps ne. Russia. In marine habitat, both forage in inshore waters on similar prey, but Kittlitz's Murrelet concentrates its foraging at glacial outfalls (Gabrielson and Lincoln 1959). In inland habitat, Kittlitz's Murrelet nests only on barren, open, rocky slopes (ground nests) above timberline. These

2 species overlap somewhat in this area, but Kittlitz's generally nests at higher elevations and farther inland (Ewins et al. 1993), and is not found in inland forests.

#### SPRING AND FALL MIGRATION

Few data on marine-habitat preferences during spring and fall, but similar to preference during breeding season in many areas. See Winter range, below, and Migration, above, for details on migratory movements. See Marine range, above, and Food habits: feeding, below, for habitat preferences.

#### WINTER RANGE

Few data. Marine habitat similar to breeding-season habitat; most individuals forage in stratified waters (i.e., tidal rips, river mouths) close to shore. Locations of foraging shift, however, as individuals from some regions move from exposed outer coasts into protected waters, where large concentrations usually occur during winter months. Also found farther offshore in some areas in Gulf of Alaska (out to 300 km). See Marine range, above.

Use of forested habitat documented during winter in some areas, especially in southern portion of range in North America, where individuals, presumed to be experienced local breeders, fly into coastal forests during winter, perhaps to maintain nest sites, territories, and pair bonds, or to select nesting areas (Carter and Erickson 1992, Naslund 1993b). Roosting and landing in trees during winter has not been documented.

## FOOD HABITS

#### FEEDING

**Main foods taken.** BREEDING SEASON (ADULTS AND CHICKS). Small schooling fish, including Pacific sand lance (*Ammodytes hexapterus*), northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea harengus*), capelin (*Mallotus villosus*), surf smelt (*Hypomesus* sp.), and viviparous seaperch (*Cymatogaster aggregata*).

WINTER AND SPRING. Euphausiids (e.g., *Thysanoessa spinifera*, *T. inermis*, *T. raschii*, *Euphausia pacifica*), mysids (e.g., *Acanthomysis* sp., *Neomysis* sp.), gammarid amphipods (Scorpaenidae; e.g., *Atylus tridens*), capelin, smelt, and herring are dominant prey (Burkett 1995). Also known to consume Pacific sardine (*Sardinops sagax*), walleye pollock (*Theragra chalcogramma*), Pacific sandfish (*Trichodon trichodon*), rockfishes (Scorpaenidae; e.g., *Sebastes* sp.), codfishes (Gadidae), pricklebacks (Stichaeidae), squid (e.g., *Loligo opalescens*), shrimp (e.g., *Pandalus borealis*), and sockeye (*Oncorhynchus nerka*) and Kokanee (*O. n. kennerlyi*) salmon from freshwater lakes (Carter and Sealy 1986, Burkett 1995). Probably also feeds on eulachon (*Thaleichthys pacificus*) and California needlefish (*Strongylura exilis*). See Diet, below.

**Microhabitat for foraging.** Inhabits nearshore and protected coastal waters throughout the year, including bays, inlets, fjords, lagoons, coves, and exposed outer coasts. Rarely found in harbors, centers of broad straights, and open pelagic waters (> 60 km [300 km in Alaska] from shore). Found near shore, usually within 5 km, and in water <60 m deep (Sealy 1975c, Ainley et al. 1995, K. Kuletz unpubl. data). On exposed outer coasts, generally found closer to shore (<2 km) than in sheltered waters (up to 60 km; Burger 1995, Ralph and Miller 1995, Strong et al. 1995). Often aggregates in small, well-defined feeding areas (Sealy and Carter 1984); clumped at-sea dispersion and seasonal movements may be response to localized food concentrations. Returns to known feeding sites, perhaps guided by continual presence of other birds and prey species (Carter and Sealy 1990). May obtain prey from throughout water column, including near bottom (Sanger 1987), but on basis of association primarily with shallow, nearshore waters and short dive times (see below), foraging depth may be within only 50 m of surface (Sealy 1975c, Thoresen 1989). May forage in deep waters only when upwelling, tidal rips, and daily activity patterns of prey concentrate prey near surface (K. Kuletz unpubl. data). Although quantitative information on associations with oceanographic features is limited, distribution and abundance (location of local concentrations) may be influenced by dynamic and changing physical and biological oceanic processes that concentrate prey, such as at upwellings, ocean floor substrate (sand or mixed rock and sand), outflows of large rivers, shelves at mouths of inlets, shallow banks, rip currents, tidal eddies, water temperature, water depth, and headlands (Kaiser et al. 1991, Ainley et al. 1995, Burger 1995, Strong et al. 1995, K. Kuletz unpubl. data). For example, peak numbers of birds in Auke Bay, AK, coincided with high or falling tides, perhaps because of abundance of sand lance during those times (Speckman 1996). Activity patterns and foraging location probably also affected by weather, climate, time of day, season, and light intensity, factors that affect prey availability (Speckman 1996). Moves into and out of foraging areas usually at dawn and midmorning; limited movement during late morning and afternoon (Carter and Sealy 1990). In Alaska and British Columbia, found in association with kelp beds, especially juveniles (Sealy 1975a, Strachan et al. 1995, Speckman 1996). Juveniles observed closer to shore than adults and most often alone or in small groups (Ralph and Long 1995, Speckman 1996).

Also feeds in freshwater lakes of varying sizes and depths (up to 75 km inland) in Russia, Alaska, British Columbia, and Washington, primarily during breeding season ( $n > 70$  records; Carter and Sealy 1986, Nechaev 1986, Konyukhov and Kitaysky 1995). Winter use of lakes, however, may be related to pair-bond maintenance and prospecting (Carter and Sealy 1986),

similar to use of inland forests in winter (Naslund 1993b). For some individuals, freshwater prey appear important during several weeks in summer and may facilitate more frequent chick feedings, especially for those that nest far inland (Hobson 1990).

**Food capture and consumption.** Forages mostly individually and in twos throughout year; aggregations most common during nestling period, and single birds more common in winter in some areas (Carter 1984, Carter and Sealy 1990). Found in groups of  $\geq 2$ , even during incubation, suggesting that individuals benefit from foraging in groups (Carter and Sealy 1990, Speckman 1996). In northern portion of range and in protected waters, forms larger foraging aggregations at all times of year; in southern areas and in exposed waters, more dispersed (Hunt 1995, Strachan et al. 1995). Flock size likely related to prey availability, abundance of birds, and oceanographic features, such as upwellings and rip currents. Largest flocks and flocks with birds in long lines not usually feeding (Carter and Sealy 1990, Speckman 1996). Subadults may feed singly in early spring but join with adults later in summer (Sealy 1975c). Hatch-year birds usually forage alone after fledging (K. Kuletz unpubl. data), but because plumage becomes indistinguishable from after-hatch-year birds by late fall (see Appearance, below) their flocking tendencies are unknown. Mixed-species flocks that include Marbled Murrelets occur in Alaska and British Columbia and in protected waters (Chilton and Sealy 1987, Carter and Sealy 1990, Mahon et al. 1992, Hunt 1995, Strachan et al. 1995); rare in other areas of range. See Behavior: social and interspecific behavior, below.

Forages day and night (Carter and Sealy 1986, 1990, K. Kuletz unpubl. data). Radio-tagged individuals known to have nests are more active at night than other radio-tagged individuals (K. Kuletz unpubl. data). Congregations gather on water near breeding sites at dawn and dusk in predictable areas close to shore (Sealy 1975c, Carter and Sealy 1990, Strachan et al. 1995, SKN). Individuals, alone or in flocks of 2, often observed holding fish during these periods, but most often at dusk (Carter and Sealy 1987a, 1990, Speckman 1996, K. Kuletz unpubl. data, SKN). Adults, themselves, generally feed on abundant, small (13–63 mm long) fish during day, but they feed their nestlings the less abundant, more-difficult-to-locate, but higher-quality, large prey (60–110 mm long; Sealy 1975c, Carter and Sealy 1987a, 1990, Burkett 1995). Adults forage for these larger fish at dawn, dusk, and night to take advantage of their abundance near surface (they occur deeper during the day; Carter and Sealy 1990). Carrying heavier prey reduces number of trips to nest and sustains high chick growth rates (Carter and Sealy 1987a; see Breeding: young birds, below). Nesting adults may use primarily water close to nest site as staging and foraging areas (as shown in radio-tagged birds in Alaska; K. Kuletz unpubl. data),



but fly to more distant areas when prey is not available and during searches for larger prey for chicks (Carter and Sealy 1987a).

Limited information on underwater foraging behavior. Dives beneath sea surface and pursues prey by flying underwater. Body shape and long, narrow, pointed wings allow for agile and rapid pursuit of prey. Groups of 2 birds often dive simultaneously; vocalize to one another when separated at surface (see Behavior: sexual behavior, below). On basis of association with shallow, nearshore waters and rapid foraging dives (see below), thought to forage within 50 m of surface (Thoresen 1989, Sealy 1975c). Dives are short in duration (mean 20–44 s, range 2–115,  $n = 6$ –119 dives) but vary with water depth (Thoresen 1989, Carter and Sealy 1990, Strachan et al. 1995, K. Kuletz unpubl. data, SKN). Mean surface interval between dives  $26.9 \text{ s} \pm 53.8 \text{ SD}$  ( $n = 181$  dives of 20 individuals, K. Kuletz unpubl. data). Dives and surface interval shorter for juveniles (mean  $17.1 \text{ s} \pm 20.0 \text{ SD}$  and mean  $10.9 \text{ s} \pm 25.4 \text{ SD}$ , respectively;  $n = 330$  dives of 1 individual; K. Kuletz unpubl. data).

#### DIET

**Major food items.** Considered an opportunistic feeder rather than a specialist (Sanger 1987, Burkett 1995). Seems to prefer euphausiids in spring and fish in summer, however. Consumption of forage fish coincides with nestling and fledgling periods (Sealy 1975c, Carter 1984).

Pacific sand lance are the most important prey species in summer, followed by northern anchovy, Pacific herring, osmerids (capelin and surf smelt), and seaperch. Also feeds on Pacific sardine, walleye pollock, rockfish, and squid during breeding season. Euphausiids are key prey in spring (Sealy 1975c), and during breeding season in some years (L. Krasnow and G. Sanger unpubl. data). Euphausiids, mysids, gammarids (amphipods), osmerids, and herring are dominant prey in winter (Munro and Clemens 1931, Sanger 1987, Vermeer 1992). Also feeds on rockfish, squid, and shrimp during winter. Feeds on salmon (sockeye and Kokanee) in freshwater lakes, primarily in summer (Carter and Sealy 1986).

**Quantitative analysis.** **BREEDING SEASON.** Near Langara I., British Columbia, Pacific sand lance dominates diet of adults and subadults (67%; frequency of occurrence), followed by euphausiids (27%), viviparous seaperch (3%), scorpaenids (2%), and osmerids (1%; Sealy 1975c). Hatch-year birds also prefer sand lance (65%) and seaperch (35%); euphausiids (and amphipods) are small proportion of diet. Along w. Vancouver I., breeding adults feed primarily on sand lance (63%) and herring (36%), including larval and juvenile fish (Carter 1984). In contrast, hatch-year birds feed primarily on herring (81%), less on sand lance (13%). Molting birds consumed herring (90%) in greater quantities than

sand lance (7%), but also fed on northern anchovy (4 fish in 1 bird). In Prince William Sound, AK, sand lance (36%) and walleye pollock (21%) were most important prey in late 1970s; now (1980s to 1996) pollock make up 85% of diet (K. Kuletz unpubl. data).

**WINTER.** Near Kodiak I., AK, feeds mostly on Osmeridae fish (L. Krasnow and G. Sanger unpubl. data). Euphausiids (primarily *Thysanoessa inermis*), mysids, and gammarids also in diet. In Kachemak Bay, AK, capelin and other osmerids dominate diet in winter (Sanger 1987). Euphausiids, mysids, unidentified gammarid amphipods, and sand lance (in order of importance) also consumed. On western coast of Vancouver I. (Quatsno Sound), British Columbia, feeds primarily on fish (71.2%, mostly herring) and invertebrates (28.7%, euphausiids including *Thysanoessa spinifera* and *Euphausia pacifica*; Vermeer 1992).

In freshwater lakes, feeds on yearling Kokanee, sockeye, and other species of juvenile salmon (*Salmo* spp.; Brooks 1928, Carter and Sealy 1986).

#### FOOD SELECTION AND STORAGE

No information on food selection. No evidence of food storage.

#### NUTRITION AND ENERGETICS

No information available.

#### METABOLISM AND TEMPERATURE REGULATION

No information available.

#### DRINKING, PELLET-CASTING, AND DEFECATION

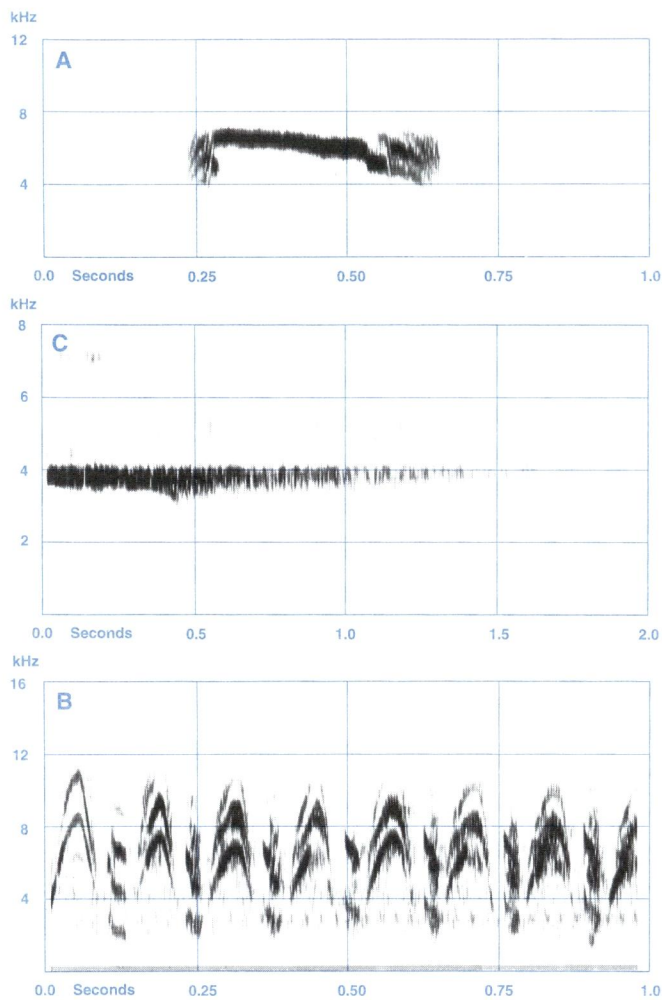
No information available on drinking. Pellet-casting not known. At nests, chicks defecate in circle around nest cup; after 4–5 wk on nest, fecal ring can measure up to 51 mm thick and smell strongly of fish. Adults rarely defecate at nest.

## SOUNDS

#### VOCALIZATIONS

**Development.** No information.

**Vocal array.** Highly vocal at inland nesting sites, and more vocal at sea compared to other alcids. Few data on vocalizations available from inland areas (forests and unforested sites) and at sea; no information available from ground nests or from Asia. Adults appear to give 3 general categories of vocalizations: (1) Keer Calls, (2) Whistle Calls, and (3) Groan Calls, with a total repertoire of at least 11 calls (unless otherwise noted, data are from Nelson and Hamer 1995a, Nelson and Peck 1995, SKN and S. W. Singer unpubl. data). Categories of vocalizations include many highly variable combinations of calls. No sexual differences or geographic variation in vocalizations are known, although quantitative comparisons are limited.



**Figure 2.** Representative vocalizations of Marbled Murrelets (from Oregon and California, SKN and S. W. Singer). A. Keer Call. B. Whistle Call. C. Begging Call of chicks. Prepared by the staff of the Borror Laboratory of Bioacoustics, Ohio State University.

**KEER CALLS.** Figure 2A. Most common vocalizations at nesting sites, while flying, and at sea. Sound phonetically like *keer*, *kee—or*, and *kee-ee-er* (*keea*, *ke—ea*, and *kee-ee-ea*, respectively, when terminal element is lacking). Some calls are smooth and clear; others have distinct separation between first and second syllables and harsher sound (*keeRUH*) when terminal element is accented. Birds exchange variations of Keer Calls, and these calls are sometimes combined with Whistle and Groan Calls. Generally, these calls are intermediate in length (about 345 ms) and consist of 2 or 3 elements.

**WHISTLE CALLS.** Figure 2B. Given by adults during incubation exchanges and other visits to nest site. Whistlelike quality, but generally abrupt and forceful (*kee* or *eya*). Typically consist of 2 or 3 basic elements, including relatively short (25–40 ms), broad-band introductory element followed by narrow-band

whistle. Unique to this group of calls is a whistle element that shows very little frequency modulation.

**GROAN CALLS.** Emitted by individuals in flight and at nest sites; given as single calls, as calls in sequence, or as duets with other birds. Individuals at nest sites recorded giving groans in sequence and in combination with Whistle Calls. Relatively long in duration (404–556 ms); high, plaintive whining quality (*eeh-eeh*).

Chicks give distinctive Begging Call during feeding interactions, which includes rapid, high-pitched breathy sounds (Fig. 2C). This call consists of a 2-note phrase repeated at the rate of 5/s. First note appears as 2 vertical, chevron-shaped bands that lasts approximately 75 ms. Second note consists of 4 downward, sweeping frequency bands lasting approximately 33 ms.

**Phenology.** Highly vocal at dawn and near nesting sites throughout breeding season. Gives few to no calls during midday and evening visits to breeding sites, although may call softly on nests. Calling increases with increased social behavior (larger groups in flight, more circling, increased landing in trees) during peak of breeding season (Jun and Jul; Eisenhower and Reimchen 1990, Rodway et al. 1993, Marks et al. 1995, Naslund and O'Donnell 1995, O'Donnell et al. 1995); increased vocalizations and activity in late summer may be related primarily to influx of subadults and nonbreeders in forests. Number of calls per bird or group of birds is greater in winter (Oct–Feb) than in summer (O'Donnell et al. 1995, SKN unpubl. data).

Vocalizations during flights to inland nesting areas and at nest sites have also been recorded during nonbreeding season (Naslund 1993b, O'Donnell et al. 1995, SKN unpubl. data). Number of calls per bird or group of birds is greater in winter (Oct–Feb) than in summer (O'Donnell et al. 1995). Also known to vocalize at sea in winter.

**Daily pattern of vocalizing.** More vocal at dawn than at dusk (Eisenhower and Reimchen 1990, Rodway et al. 1993, Naslund and O'Donnell 1995). Peak levels of activity (flights and vocalizations) occur within 1 h around dawn, but early activity includes more silent birds, solitary calls, and wing sounds than later (after sunrise). Generally calls from 45 min before to 75 min after sunrise (90 min before to 40 min after in Alaska), but earliest calls can occur 90 min before sunrise (120 min in Alaska). Calling at dusk (rare) occurs from 90 min before to 45 min after sunset, although occasionally heard throughout night in Alaska during breeding season. Calling can last 1–2 h, and usually begins earlier, lasts longer, and reaches peak levels on cloudy or foggy days.

During breeding season, the 3 general types of vocalizations (see above) are given with varying intensity and loudness depending on proximity to

nest sites and number of birds present (Nelson and Hamer 1995a, Nelson and Peck 1995). Frequently vocalizes loudly at dawn at inland breeding sites, primarily when  $\geq 2$  birds are flying above or through forest canopy, but rarely from nests. Soft or muted calls (which are rarely heard from ground or without sophisticated recording equipment) are frequently given at and near nests during incubation exchanges at dawn and feeding visits, when birds arrive or depart nest limb, or during brief seconds when adults are on nest limb together (Nelson and Hamer 1995a, Nelson and Peck 1995). In addition, chicks frequently vocalize softly during food exchanges. During most of year, individuals give loud and soft vocalizations at sea, especially when 2 birds (not known if they are paired) become separated (G. van Vliet pers. comm.).

**Places of vocalizing.** Highly vocal at breeding sites in forest, especially while flying over and through canopy (Eisenhawer and Reimchen 1990, Naslund 1993a, O'Donnell 1993, Rodway et al. 1993, SKN unpubl. data). Also vocalizes during flights from ocean to inland nesting areas, and at sea. Because this species nests solitarily or in low densities and is active in forests primarily when light levels are low, vocalizations may serve an important social function, but this must be balanced with need to remain cryptic at nests. Nesting birds are more discrete in their vocalizations, giving muted calls presumably to minimize discovery of nest by predators (Nelson and Hamer 1995a, 1995b, Nelson and Peck 1995). Also vocalize during feeding and courtship (see Behavior: sexual behavior, below, and Food habits: feeding, above), and when a pair is physically separated, by boats or other disturbance, at sea.

**Repertoire and delivery of songs.** Not known if types of calls vary with season or time of day, although a form of Whistle Call known as "que call" and Groan Calls may be given more frequently during late Jun and Jul, the peak of nesting season (O'Donnell et al. 1995, SKN and S. W. Singer unpubl. data). Preliminary analyses show no geographic variation in vocalizations between Oregon and California, although individuals may have distinct vocalizations; incubating adults and chicks were observed to change behavior or vocalize on nest limb just before arrival of the (other) adult, suggesting that birds on nest recognized calls of incoming mate or parent (Nelson and Peck 1995, SKN and S. W. Singer unpubl. data). Determining repertoire size is difficult; lack of individually marked birds has prevented attributing variation in calls to different call types or individual variation.

**Social context and presumed functions of vocalizations.** No information available on sexual differences in calls, social context, or call function.

#### NONVOCAL SOUNDS

Can deliberately create sounds with wings while flying over and through forest canopy at nesting

areas. Sounds are similar to rapid twirling of rope in air or shaking of long, wide metal saw blade; this unique sound can be used to identify this species in forests. Also occasionally creates loud, whooshing sound, like jet, during shallow or steep dives that usually originate above canopy and end at or below canopy. This behavior has been observed above active nests and during encounters between 2 individuals (Nelson and Peck 1995, S. W. Singer pers. comm.). Function of these "jet dives" not known; may be to maintain pair bonds, or may be aggressive posture or for territorial defense.

## BEHAVIOR

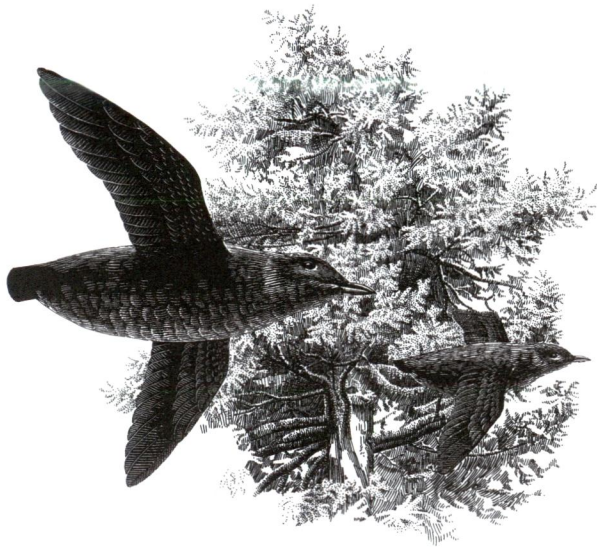
### LOCOMOTION

**Walking, hopping, climbing, etc.** Not considered agile on land, although nesting birds can walk along tree limbs and hop from one limb to another in nest tree. Grounded individuals (that have fallen from nests or crashed on inland flights) may walk hundreds of meters on ground in search of suitable launching areas (opening in forest, elevated location). Not known to climb.

**Flight.** Flies with rapid wing-beats at speeds up to 158 km/h (mean 73–136, SD 9.5–21.4, range 40–158,  $n = 7-91$ ) and altitudes  $>1,000$  m (Burger in press). Unusually long, narrow, and pointed wings (for an alcid) aid flight performance. Takes flight relatively easily from nest tree or cliff and sea surface, although agility increases with height above ground. Observed taking flight directly after surfacing from underwater dive (Gabrielson and Lincoln 1959). Fledglings and adults that become grounded in forest may not be able to take flight again, but some birds observed taking off directly from ground in open areas (T. Hamer pers. comm.). Flight paths from ocean to nest sites usually follow ridges and river corridors (not always the case in California) and are used relatively consistently (SKN unpubl. data, C. J. Ralph pers. comm.).

At nesting stands, usually small groups (2–12 birds) seen flying above canopy. Below canopy, usually 1–3 birds. Groups of birds often display together in large circles, dives, and loud vocalizations; may include nesting birds that have joined with others before returning to ocean after incubation and feeding visits. Nonbreeders, subadults, and birds from other areas may also accompany nesting birds in these circling flights above canopy. Flight below canopy most common during breeding season (Naslund 1993a, O'Donnell 1993). Flock size largest in Jul ( $\geq 2$  birds); smaller (1–2 birds) groups seen in May and Jun, and in winter (O'Donnell 1993, Rodway et al. 1993).

Uses consistent flight paths to enter and exit nest sites (Naslund 1993a, Naslund et al. 1995, Nelson and Peck 1995, Singer et al. 1995). Generally, follows openings, such as creeks, areas of blowdown, and



**Figure 3.**  
Marbled  
Murrelets  
flying by  
their nest  
tree.  
Drawing by  
John  
Megahan.

gaps, that allow for direct approaches and departures from nest. The directions that birds enter and leave nests are related to openings in canopy or forest around nest tree, and gaps in horizontal cover surrounding nest limb. Birds approach nests below tree canopy at heights as low as 2 m, before steeply ascending to nest in "stall-out" fashion. Landings are sometimes hard and audible; often creates "landing pad," or area where moss or duff becomes flattened, worn, and sometimes marked with toenail scratches from repeated landings (Nelson and Peck 1995). Landing pads are most often located on nest limb within 1 m of nest cup, but also on adjacent limbs. When leaving nest, usually drops 5–30 m before ascending over canopy to continue departure flights. Several flight behaviors adjacent to nests: (1) Fly-bys and Stall Flights, including single birds or pairs flying by or stalling out next to known nest tree, at nest branch height (Fig. 3), (2) Flying-in-Tandem and Tail Chases, in which pairs of birds fly near known nest trees, and (3) Buzzing, which includes single birds flying through canopy and making continuous low-pitched buzzing wing sounds (Singer et al. 1991, Naslund 1993a).

**Swimming and diving.** Spends most time at sea swimming, loafing, or resting on ocean surface. Sits on water with head drawn back, neck compressed, and tail cocked. When foraging or moving, head raised higher, and short neck more apparent. Dives underwater to forage by using wings to propel itself. Known to dive to depths of at least 50 m; dives generally short in duration (20–44 s; Thoresen 1989, Strachan et al. 1995, K. Kuletz unpubl. data). See also Food habits: feeding, above.

#### PHENOLOGY AT INLAND SITES

Flight and vocalization activity at inland sites varies dramatically throughout year, but is greatest during

breeding season (Naslund 1993a, O'Donnell 1993, O'Donnell et al. 1995). Peak activity in Jul (Eisenhawer and Reimchen 1990, Rodway et al. 1993, O'Donnell et al. 1995); this influx may include nonbreeders, subadults, and adults that have completed breeding at other sites. Smaller peak of activity occurs in May in Alaska and Oregon (SKN unpubl. data, K. Kuletz unpubl. data). Activity is highly variable on daily basis; number of birds heard or seen is affected by weather (activity begins later and lasts longer on cloudy and foggy days) and date (more activity in summer than in winter, and in Jul compared to May, Jun, and Aug; Eisenhawer and Reimchen 1990, Naslund 1993a, O'Donnell 1993, Rodway et al. 1993). Activity lasts longer in breeding season; in winter, dawn activity usually ends before sunrise. Attendance during winter is variable and flights below canopy are rare. Visits to breeding sites in winter may include high proportion of resident breeders participating in nest-site selection or maintaining pair bonds (Naslund 1993b). Activity is lowest during Feb–Mar and mid-Aug–Oct, when Prealternate and Prebasic molts occur (Naslund 1993a, O'Donnell 1993).

Flight and vocalization activity is greatest at dawn and dusk, but is lower and more sporadic at dusk (Eisenhawer and Reimchen 1990, Naslund 1993a, Rodway et al. 1993, SKN unpubl. data). Although adults travel inland to feed chicks during midday, they are rarely seen or heard except at their nest. Activity in forests generally begins 45 min before sunrise and lasts until 90 min after sunrise (Alaska: 90 min before to 40 min after; Naslund and O'Donnell 1995); however, recent radar and radio-telemetry research shows that peak flights into forests occur 40–80 min before sunrise in Washington and British Columbia and begin as early as 120 min before sunrise in Alaska (Burger in press, B. Cooper and K. Kuletz unpubl. data). Dusk activity occurs from 90 min before to 45 min after sunset, although individuals in Alaska occasionally are active throughout night during breeding season. No inland activity recorded with radar or video cameras at night (>80 min after sunset and <95 min before sunrise) in British Columbia and California (O'Donnell et al. 1995, Burger in press). Morning flights begin later and are shorter in duration in Aug than in Jun and Jul (Eisenhawer and Reimchen 1990, Naslund and O'Donnell 1995). Flight below canopy and occurrence of single, silent birds are more common before sunrise; larger groups fly and call above canopy primarily after sunrise (Naslund and O'Donnell 1995, I. Manley unpubl. data, SKN unpubl. data).

#### SELF-MAINTENANCE

Few data. During nesting season, incubating adults and chicks spend >80% of time on nest sleeping (Naslund 1993a, Nelson and Hamer 1995a, Nelson and Peck 1995, T. Hamer unpubl. data). After-hatch-year and nonbreeding adults may roost in areas along

periphery of forest nesting sites; groups of birds observed landing and loafing on small limbs of young and mature conifer trees in Jun and Jul at 2 sites in Oregon (multiple observations over 2 seasons) and 1 in British Columbia (multiple observations in 1 yr; J. Deal unpubl. data, SKN unpubl. data).

#### AGONISTIC BEHAVIOR

Limited information on physical and communicative interactions. At nest sites in forests, birds observed chasing one another (tail-chasing; Singer et al. 1991, Naslund 1993a) or creating loud sounds, like jet, during shallow or steep dives directed at another individual (mostly seen or heard from lone individuals, but also seen as interaction between birds above or near nests; Nelson and Hamer 1995a, Nelson and Peck 1995). Also chase one another at sea (see Sexual behavior, below). These flight behaviors may sometimes be aggressive postures or territorial defenses (SKN unpubl. data, S. W. Singer pers. comm.). Highly vocal (see Sounds: vocalizations, above).

#### SPACING

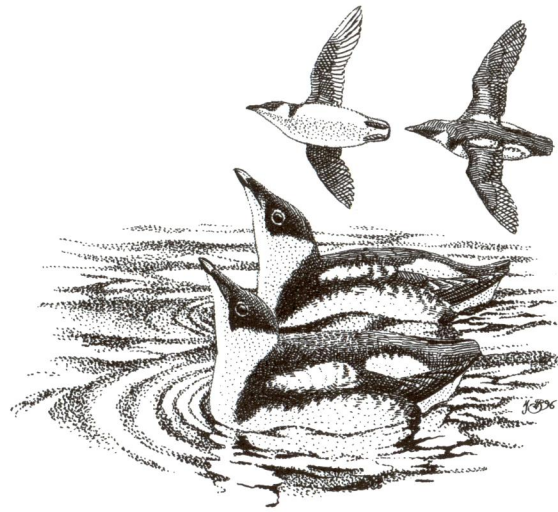
**Territoriality.** No information, although pairs may have terrestrial home ranges, including >1 nest site that they maintain throughout year (SKN). Birds (not known if same individuals) return annually to nesting areas (forest stands) and sometimes reuse historic nest sites (see Breeding: nest, below). Activity below canopy observed to increase at nest sites that recently failed in Alaska; could be form of territoriality (K. Kuletz pers. comm.).

**Individual distance.** Birds nest solitarily, especially at ground nesting sites, but >1 pair occur in single forest stand. Two simultaneously active tree nests were located 30–100 m apart ( $n = 3$  sets; T. Hamer unpubl. data, I. Manley unpubl. data, SKN unpubl. data); also 6 old nests were within 40 m in Oregon and 4 nest or landing trees within 50 m in Alaska (Naslund et al. 1995, SKN unpubl. data). Three radio-tagged tree-nesting adults nested within 1 km of each other, but 3 radio-tagged ground-nesting adults were 6–12 km apart (K. Kuletz unpubl. data).

#### SEXUAL BEHAVIOR

**Mating system and sex ratio.** Suspected to be socially monogamous. Limited information on sex ratios from British Columbia indicates 1.03:1 to 2:1 male-to-female ratio ( $n = 73$ , Sealy 1957;  $n = 237$ , T. Williams and G. Kaiser unpubl. data, respectively).

**Courtship.** Court at sea in early spring, when some adults are still in winter plumage, and throughout summer. Courting behavior also seen in winter (Speckman 1996, G. van Vliet pers. comm.). Number of pairs displaying increases sharply in late Jul, when nonbreeders and subadults are thought to be present. During courtship, male and female join closely together (<0.5 m), extend their necks vertically and point their



**Figure 4.** bills in air (Bill-Up Display, Fig. 4), partially lift their breasts out of water, and swim rapidly forward and together for as long as 30 s (Byrd et al. 1974, G. van Vliet pers. comm., SKN). Pairs also dive synchronously into water and surface within 1–3 s next to one another, suggesting that they remain together underwater. They often resurface and repeat bill-posturing (Strachan et al. 1995). Before the dive or while swimming together in courtship dances, birds frequently give soft, synchronous nasal vocalizations. At dawn, V-Wing Display, lasting 5–10 s, given immediately before Bill-up Display; in the former, one bird extends half-open wings over back to form V while swimming behind or next to mate and giving unique buzzing call (Speckman 1996). Pairs also chase one another in flights just above water surface, primarily at dawn, throughout spring and summer, in what may be courtship behavior. This flight behavior is usually accompanied by vocalizations and sometimes combined with diving (pursuit flight dives), where 1 bird crashes into water from flight, the other flies up into air and then plunges into water, then both surface and fly away (Gabrielson and Lincoln 1959, Strachan et al. 1995, Speckman 1996). An increase in this behavior in late Jul corresponds with increase of activity in forests. Copulation rarely observed (seen <20 times); occurs both in trees (K. Kuletz pers. comm.) and on water (Strachan et al. 1995, Speckman 1996, SKN, G. van Vliet pers. comm.). Before and after copulation, one or both birds usually vocalize with emphatic, nasal eeh-eeh call (G. van Vliet pers. comm.).

**Pair bond.** Limited information. Observed in groups of 2 throughout year, both in forest and on water. Many pairs shot on water have included a male and female, and were assumed to be mated (Sealy 1975a, Carter 1984, Carter and Stein 1995). Observations of courtship in winter suggest that pair bond is maintained throughout year (Speckman 1996, G. van Vliet pers. comm.).

**Extra-pair copulations.** No information.

**Bill-up Display and Pursuit Flight courtship behaviors of the Marbled Murrelet, which often start courtship in winter plumage.** Drawing by N. John Schmitt.

## SOCIAL AND INTERSPECIFIC BEHAVIOR

**Degree of sociality.** Nests solitarily (one pair to a tree or cliff area, but see Harris 1971), but usually occurs in groups (>1 pair per stand) in forest nesting habitat. Socializes (interacts in flights, displays, and vocalizations) in groups of up to 12 individuals during dawn display flights over forest nesting grounds. See also Locomotion, above. Sociality at ground-nesting sites unknown. On water, where maintaining secrecy to avoid predation is not as important as in forests, highly social, especially in winter and in northern portion of range (British Columbia and Alaska). In Alaska, concentrations usually <50, but sometimes as many as 5,000, gather to feed, rest, socialize, display, and copulate (Strachan et al. 1995, Speckman 1996); off Oregon and California, usually occurs in groups of 2–3 (Strong et al. 1995). Flocks larger in late summer (Jul) than in spring and early summer. Believed to forage cooperatively, by herding fish underwater Chilton and Sealy 1987, Mahon et al. 1992, Speckman 1996). Largest flocks often not foraging, however (Carter and Sealy 1990, Speckman 1996). Flock size may be function of bird density, presence of aggressive species (e.g., Common Murre [*Uria aalge*]), and prey abundance (Chilton and Sealy 1987, Carter and Sealy 1990, Mahon et al. 1992). Maintenance of feeding flocks thought to maximize length of time fish are vulnerable and to play important role in foraging efficiency, which contributes to juvenile and adult survival (Chilton and Sealy 1987).

**Play.** None observed, but few data.

**Nonpredatory interspecific interactions.** Limited interactions with other species south of British Columbia, where forages primarily in small groups with conspecifics. Found in mixed feeding flocks with variety of species (e.g., Black-legged Kittiwake [*Rissa tridactyla*], Bonaparte's Gull [*Larus philadelphia*], Glaucous-winged Gull [*L. glaucescens*]) in British Columbia and Alaska (Chilton and Sealy 1982, Speckman 1996, W. Ostrand and J. Maniscalco unpubl. data). Either initiates feeding flocks and attracts others, such as kittiwakes, or follows other seabirds to existing feeding assemblages (Chilton and Sealy 1987, Carter and Sealy 1990, Mahon et al. 1992, W. Ostrand and J. Maniscalco unpubl. data). Feeding flocks may provide birds with dependable and conspicuous means of locating food (Chilton and Sealy 1987). See also Food habits: feeding, above.

## PREDATION

**Kinds of predators; manner of predation.** Predators contribute substantially to nest failure in North America (43% of 32 nests, Nelson and Hamer 1995b; 71% of 14 nests, I. Manley pers. comm.). Eggs may be preyed on when nests are neglected for short periods of time or abandoned, or if adult is chased off nest. Adults are vulnerable during incubation and during flights to nests. Chicks may be preyed on anytime

during the 27–40 d they are alone on nest (see Breeding, below).

Avian predators (1) of eggs: include Common Ravens (*Corvus corax*) and Steller's Jays (*Cyanocitta stelleri*), (2) of chicks: include Common Ravens, Steller's Jays, and Sharp-shinned Hawks (*Accipiter striatus*), (3) of adults on nest: include Common Ravens and Sharp-shinned Hawks, and (4) of adults flying in forests: include Peregrine Falcons (*Falco peregrinus*; Singer et al. 1991, Marks and Naslund 1994, Nelson and Hamer 1995b, D. Suddjian pers. comm.). Remains of this species found at nests of Northern Goshawks (*Accipiter gentilis*) and Peregrine Falcons in Alaska (K. Kuletz pers. comm.). Gray Jays (*Perisoreus canadensis*), Common Crows (*Corvus brachyrhynchos*), Great-horned Owls (*Bubo virginianus*), and Cooper's Hawks (*Accipiter cooperii*) are suspected predators at nests (SKN). No mammalian predators documented at nest sites, although mice and squirrels are potential predators. Avian and mammalian predators of adults and juveniles at sea include Peregrine Falcon, Bald Eagle (*Haliaeetus leucocephalus*), Western Gull (*Larus occidentalis*), and northern fur seal (*Callorhinus ursinus*; Campbell et al. 1977, Vermeer et al. 1989, Rodway et al. 1992, H. Carter pers. comm., K. Kuletz pers. comm.).

**Response to predators.** Avoids detection through behavior on nest and at nest site, and via cryptic plumage (see Breeding: incubation, and Breeding: hatching, below, as well as Sounds: vocalizations, above). In response to calls or presence of predators, adults and chicks often flatten themselves against tree branch, holding their backs and heads low and remaining motionless (Naslund 1993a, Nelson and Peck 1995). Will defend against predators that have found a nest by standing erect, turning to face the intruder, and jabbing at it with bill.

Displays variety of morphological and behavioral characteristics as defense mechanisms against predation, including concentrating activities in forests during periods of low light; cryptic coloration of egg, chick, and adult; retention of cryptic down by chick until just before fledging; rapid flight patterns to nesting sites and near nests; minimal parental care at nest; adult and chick remaining relatively silent (muted vocalizations) and motionless on nest branch; departing nest primarily at dusk; and selecting nest sites with high levels of cover (above and adjacent to nest). Despite these adaptations, species is vulnerable. Predation rates may be higher when nests are located in or near fragmented habitat (Nelson and Hamer 1995b).

## BREEDING

## PHENOLOGY

**Pair formation.** Few data. Courtship activity observed in early spring and throughout summer; also seen in winter. Pairs observed on ocean and in

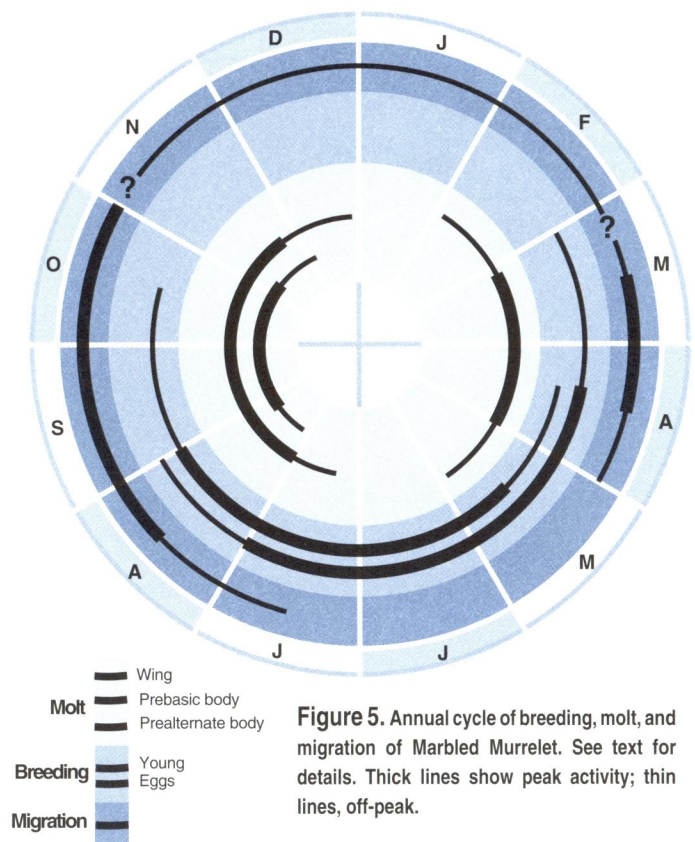
forest year-round near breeding sites in most areas. Migrating birds arrive at breeding areas in Mar and Apr (K. Kuletz pers. comm., G. van Vliet pers. comm.). Pairs visit breeding grounds prior to egg-laying; in Oregon, a pair was observed landing on a nest platform for 3 mornings in early May, 2 wk before laying an egg at that site (Nelson and Hamer 1995a). Interannual variability in timing of breeding is likely affected by food availability and variability in environment (e.g., weather, ocean conditions); there is some indication that birds breed later or not at all during years of low food abundance (e.g., during El Niño ocean conditions; Speckman 1996, K. Kuletz unpubl. data). See also Behavior: sexual behavior, above.

**Nest-building.** Nesting initiated early Mar–mid-Jul (Fig. 5). Asynchronous in initiation of breeding; entire nesting period lasts about 170 d in California, 149 d in Oregon, and 106 d in Alaska (Hamer and Nelson 1995b, Nelson and Peck 1995). Unknown if lack of synchrony is related to renesting after failure, occurrence of second brood, or variation in nest initiation as affected by local food availability.

**First/only brood per season.** Egg-laying Mar–Aug (Fig. 5). Egg-laying and incubation estimated to begin and end as follows in each state and province in North America: California, third week of Mar to mid-Aug; Oregon, late Apr–late Aug; Washington, late Apr–late Jul; British Columbia, early May–mid-Jul; Alaska, mid-May–late Jul (Hamer and Nelson 1995b). No information available for *B. m. perdix*. In California (and less so in Oregon), 2 breeding periods, separated by 1–2 wk, may exist because of double-brooding, renesting after failure, or variation in individual initiation (Hamer and Nelson 1995b). First and second breeding periods (egg to fledging) in California estimated to last 103 d and 89 d, respectively.

#### NEST SITE

The first published, verified ground and tree nests in North America were reported from East Amulti I., AK, in 1978, and Big Basin Redwoods State Park, CA, in 1974, respectively (Binford et al. 1975, Simons 1980). In Asia, the first verified nest was found in tree in 1961 (Kuziyakin 1963, Arbib 1972). Later reviews of literature revealed that 7 potential ground nests with eggs were reported between 1893 and 1963 from Russia, Alaska, and Washington (Taczanowski 1893, Bent 1919, Booth 1927, Gabrielson and Lincoln 1959, Hoeman 1965, Day et al. 1983), but their authenticity is questioned by Kiff (1981) and Day et al. (1983) because of lack of details. Adults with eggs or young also reported falling out of trees felled during logging in 1953 and 1967 from Queen Charlotte Is. and Vancouver I., British Columbia, respectively, but actual nests never found (Drent and Guiguet 1961, Harris 1971, Carter and Sealy 1987b). More than 160 nests are now known; at least 140 tree and 15 ground nests in North America and 4 tree and 1 ground nest



**Figure 5.** Annual cycle of breeding, molt, and migration of Marbled Murrelet. See text for details. Thick lines show peak activity; thin lines, off-peak.

in Russia (Kuziyakin 1963, Day et al. 1983, Nechaev 1986, Labzyuk 1987, Kondratyev and Nechaev 1989; also see references in Appendix 1.)

**Selection process.** Exact process unknown, but pairs and individuals prospect (landing on and flying near tree limbs) in early spring (Mar–May) and midsummer (Jul; Nelson and Hamer 1995a). Non-breeding birds and subadults may participate in this activity during midsummer. Birds also visit nesting areas during winter and may select nest sites during this time (Naslund 1993b).

**Microhabitat; site characteristics.** In areas where they nest on ground (tundra or forested habitat in n. and nw. Alaska, and Russia), suitable nesting habitat consists of rock scree slopes, cliffs, and boulder fields near ocean. Nests on top of rocks, in rock cavities, or crevices in the open or under vegetation (Simons 1980, Hirsch et al. 1981, Day et al. 1983, Johnston and Carter 1985, Kuletz and Marks in press, A. Kistchinski unpubl. data). In Alaska, open nests often at base of Sitka alder or dwarf Sitka spruce; crevice nests also occasionally protected by alder (K. Kuletz unpubl. data). Four nests on or near ground have also been located in forested areas in s.-central and se. Alaska; these nests were on rocks, mats of moss, or tree roots on cliffs of rock outcroppings near ocean (Ford and Brown 1995, T. DeGange pers. comm.).

At tree-nesting sites in North America (see Fig. 6), suitable habitat consists of large-diameter limbs or



platforms created by normal tree growth, disease, mistletoe, deformed branching (especially in coast redwood trees), collections of needles and debris, or other factors in large conifers ( $\geq 30$  cm diameter in Alaska;  $\geq 76$  cm diameter south of Alaska; Quinlan and Hughes 1990, Singer et al. 1991, Hamer and Nelson 1995a, additional papers in Nelson and Sealy 1995; see Appendix 1). Generally in old-growth trees ( $>200$  yr old,  $>81$  cm in diameter), although in Oregon, individuals have been found nesting in mature (95–200 yr old;  $n = 5$ ) and young (66 yr old;  $n = 1$ ) western hemlock trees with large branches formed by mistletoe (SKN unpubl. data). Tree species, in descending order of number found, include Douglas-fir (*Pseudotsuga menziesii*), Alaska yellow cedar (*Chamaecyparis nootkatensis*), western hemlock, Sitka spruce, mountain hemlock (*Tsuga mertensiana*), coast redwood, and western red cedar (*Thuja plicata*; see Appendix 1). Nests usually in middle to top third of live crown ( $>12$  m in height; in Alaska,  $>9$  m). Key characteristics of tree nest sites include large platforms, moss, vertical cover above nest cup, and horizontal access to nest limb. In some forests, especially younger mature forests, these characteristics occur only in small pockets or niches with suitable growing and moisture conditions. Nest trees typically the largest trees in stand. See Habitat: breeding range, above, for detailed stand characteristics.

**Figure 6.** Marbled Murrelet incubating egg on large, moss-covered nest limb. Drawing by Brian Woodbridge.

In Asia, all tree nests found (4) have been in larch trees in mixed coniferous-deciduous forests (Kuzynkin 1963, Arbib 1972, Nechaev 1986, Labzyuk 1987, Kondratyev and Nechaev 1989); at heights ranging from 2.5 to 7.0 m above ground and within 50 cm of tree bole. Information on tree diameter and height is available for only 1 nest (17 cm and 12 m, respectively). See Habitat: breeding range, above.

#### NEST

**Construction process.** Does not add material to nest (but see Naslund 1993a). Nest consists of small depression (formed by weight of egg and adult) in rock or soil on talus slope or cliff (if possible), or in moss or duff on tree platform or tree root. Method, time of day, and length of time for creation unknown.

**Structure and composition matter.** Nests on talus slopes or rocky areas have included rock, soil, and matted vegetation. Those on ground in forests or in trees are composed of moss, lichen, needles, small sticks, or other materials present at the site or that have fallen from branches above. One nest found on pile of small sticks (probably was an old Band-tailed Pigeon [*Columba fasciata*] nest) and 1 nest was on an old western gray squirrel (*Sciurus griseus*) nest (Singer et al. 1991, S. W. Singer unpubl. data). Two nests in California included no substrate; eggs were laid directly on bark of tree branch (S. W. Singer pers. comm.). In Asia, nests on lichen, twigs, needles, and dry deciduous leaves.

**Dimensions.** Limited information on ground nests; 1 nest cup was 15 cm in diameter (Simons 1980). In North America, nest cups in trees are 2.5–26.0 mm long (mean  $10.6 \pm 3.5$  SD,  $n = 117$ ) by 3.1–20.0 cm wide (mean  $9.4 \pm 2.9$ ,  $n = 117$ ), and 0.5–8.0 cm deep (mean  $3.7 \pm 1.5$ ,  $n = 108$ ; Hamer and Nelson 1995a, SKN unpubl. data; see Appendix 1). In Asia, nest cups in trees were at least 5.5 cm long by 3.5 cm wide and 2.5 cm deep ( $n = 2$ ; Kuzynkin 1963, Arbib 1972, Nechaev 1986). Substrate depth at 1 nest was 4.0 cm (Kuzynkin 1963, Arbib 1972).

**Microclimate.** No quantitative information. Tree nests generally located near tree bole or on limb where vertical and horizontal cover provide the most shade and protection from the elements (see Appendix 1). No apparent preference for nest orientation, although in some close coastal areas, nests are located away from prevailing winds (Naslund et al. 1995, SKN unpubl. data). Moss and other substrate material may provide insulation for the egg, especially in cold climates like Alaska (Naslund et al. 1995). The distribution of moss, the most commonly used substrate, is limited to forests influenced by coastal fog and heavy winter rains. Areas without moss or abundant substrate material may have more limited nesting opportunities.

**Maintenance or reuse of nests, alternate nests.** Nests generally not reused in consecutive years, although



>15 records of birds returning to same tree (6 to same nest platform) in successive or later years (birds may not be same pair or individuals; Nelson and Peck 1995, Singer et al. 1995, I. Manley unpubl. data). At 1 of these nests, in Big Basin State Park, CA, individuals returned to same tree (2 different platforms) for 5 consecutive years, although nests were not successful in all years. In another example in Oregon, birds used 1 tree limb in 1991 and nested on different limb in 1993; tree was not used in 1992. Birds (not known if the same individuals) have high fidelity to nesting areas and may reuse existing platforms on rotating basis; this behavior is consistent with that of other adult alcids, which exhibit high level of philopatry, returning to same nesting area and often same site over many years (Nettleship and Birkhead 1985).

*Nonbreeding nests.* Not known to occur.

#### EGGS

*Shape.* Subelliptical.

*Size.* Average length and breadth (mm):  $59.8 \pm 2.2$  SD (range 57.0–63.0)  $\times$   $37.6 \pm 1.4$  SD (range 35.0–39.5;  $n = 11$  eggs); shell thickness 0.21 mm (Sealy 1975b, Simons 1980, Hirsch et al. 1981, Kiff 1981, Day et al. 1983). Similar sizes reported for Asiatic form, except 2 eggs that were  $63.6 \times 39.3$  and  $66.2 \times 39.0$  (Kuzyakin 1963, Arbib 1972, Nechaev 1986).

*Mass.* Approximately 36–41 g (16–19% of adult weight;  $n = 5$ ; Sealy 1975b, Simons 1980, Hirsch et al. 1981, Kiff 1981). Asiatic form 48–53.7 g ( $n = 2$ ; Kuzyakin 1963, Arbib 1972, Nechaev 1986).

*Color.* Pale olive green to greenish yellow background color; nonglossy; covered with irregular brown, black, and purple spots, which are more prevalent at larger end of egg (Binford et al. 1975, Kiff 1981, Day et al. 1983, Becking 1991, Reed and Wood 1991, Singer et al. 1991, SKN). Amount and distribution of brown, black, and purple spots appear to vary greatly among individual eggs. No information on variation with respect to geography.

*Surface texture.* Smooth and nonglossy to slightly glossy.

*Eggshell thickness.* Limited information on thickness; one known measurement 0.21 mm (Kiff 1981). No information related to contaminants.

*Clutch size.* Only 1 egg. Not known if individuals lay replacement eggs after failure or lay >1 clutch per year, although circumstantial evidence suggests renesting after failure at 1 nest in Alaska (Naslund et al. 1995), and bimodal peak in nesting chronology in California suggests renesting after failure or double-brooding (Hamer and Nelson 1995b).

*Egg-laying.* No information on time of day, rate of deposition, or parental behavior.

#### INCUBATION

*Onset of broodiness and incubation in relation to laying.* No information.

*Incubation patches.* Breeding adults of both sexes have 1 medial brood patch with mean dimensions of  $37.5 \times 28.3$  mm ( $n = 14$ ) when fully developed (Sealy 1974). Brood patches from birds mist-netted in Prince William Sound, AK, had mean dimensions of  $23.5 \pm 3.5$  SD (range 16.0–30.0)  $\times$   $27.0 \pm 3.9$  SD (range 16.0–35.0,  $n = 48$ ; K. Kuletz unpubl. data). Brood patches are thought to develop over several weeks. In Alaska, 4 individuals in Basic plumage had fully developed brood patches, and several were paired with birds in Alternate plumage (K. Kuletz unpubl. data, G. van Vliet unpubl. data).

*Incubation period.* 28–30 d (Sealy 1974, Simons 1980, Hirsch et al. 1981).

*Parental behavior.* Incubation shared equally by male and female, who exchange incubation duties every 24 h at dawn; one adult broods egg while other forages at sea. Incubation exchanges occur generally before official sunrise, but timing is affected by weather patterns (birds arrived later during overcast or rainy conditions) and latitude (because of longer periods of twilight). In Prince William Sound, AK, incubation exchanges occurred 37–82 min (mean  $52 \pm 11.6$  SD) before official sunrise ( $n = 14$  observations at 5 nests; N. Naslund pers. comm.). In Oregon and California, timing of incubation exchanges ranged from 31 min before to 1 min after (mean 18.5 min before  $\pm 6.5$  SD) official sunrise ( $n = 85$  observations at 7 nests; Singer et al. 1991, pers. comm., Naslund 1993a, Nelson and Hamer 1995a, Nelson and Peck 1995). No nocturnal incubation exchanges observed, despite some nocturnal watches.

Interaction between adults during exchange is limited, although they do vocalize with one another (see Sounds: vocalizations, above). Incubating birds generally leave within 3–60 s (mean  $26.0 \pm 39.2$  SD;  $n = 76$  observations at 7 nests) of arriving bird (Naslund 1993a, Nelson and Peck 1995, S. W. Singer pers. comm.). Arriving adult often remains motionless on landing platform for up to 5 min before initiating incubating posture. Incubating adults sit on egg in flattened posture and remain motionless or asleep >90% of their time on nest (Naslund 1993a, Nelson and Peck 1995). Adults also observed turning egg (up to 11 times/d), pecking at platform substrate, and preening.

*Hardiness of eggs against temperature stress; effect of egg neglect.* Observed leaving egg unattended for 3–4 h during morning, midday, and evening in California, Oregon, and Alaska (Simons 1980, Naslund 1993a, Nelson and Hamer 1995a, Nelson and Peck 1995). In Oregon, an egg was believed to have been taken by a corvid during period of egg neglect. No specific information on egg hardiness.

#### HATCHING

*Preliminary events and vocalizations.* No information. Adults become active just before hatching of

egg, standing and turning more frequently than earlier in incubation period (N. Naslund pers. comm., SKN).

**Shell-breaking and emergence.** Timing from first pipping to emergence unknown. Eggs appear to hatch in evening or at night (SKN). Chicks hatch within 28–30 d of laying, usually between Apr and late Aug (Fig. 5). Nestling period estimated to begin and end as follows in each state and province in North America: California, mid-Apr–mid-Sep; Oregon, mid-May–late-Sep; Washington, late May–late Aug; British Columbia, early Jun–late Aug; Alaska, mid-Jun–late Aug (Hamer and Nelson 1995b).

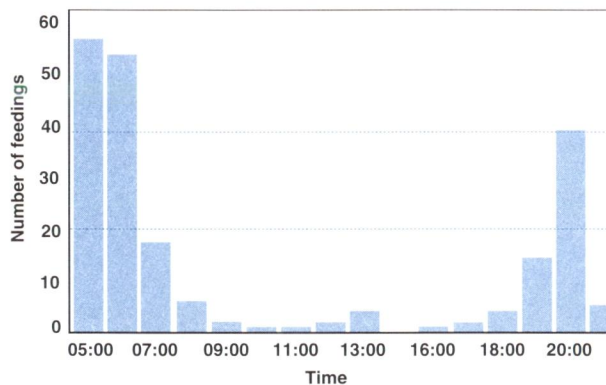
**Parental assistance and disposal of eggs.** No information on parental assistance. Adults do not remove eggshell from nest cup, so eggshells are often found in small pieces in nest cup following fledging. Some fragments fall from tree nests and can be found (although rarely) on forest floor or on adjacent branches within 25 m of nest.

#### YOUNG BIRDS

**Condition at hatching.** Semiprecocial; mass 32.0–34.5 g (15–16% of adult mass;  $n = 2$ ; Simons 1980, Hirsch et al. 1981). Fully feathered and covered with thick yellow down dotted with brown and black spots. Spots on head are concentrated in large patches, and down on belly is pale gray. Beak black, feet dark gray. See Appearance: molts and plumages, below. Chicks are vulnerable on nest, especially during first 6 d, when predation rates are high and their lack of agility increases their chances of falling from tree nests (SKN). Often retain egg tooth until after leaving nest.

**Growth and development.** Brooded by adults for only 1–2 d after hatching, so chicks probably attain thermoregulatory independence in first few days after hatching. Chicks grow rapidly during first 9 d (especially on days 7 to 9) after hatching, gaining 5–15 g/d (Simons 1980, Hirsch et al. 1981). After that, generally gain 1–5 g/d. Grow faster than other alcid chicks, perhaps because of regular feedings of relatively large prey loads (see Food habits: feeding, above; Carter and Sealy 1987a). As chicks age, Juvenal plumage begins to develop beneath down; both feather types grow from same sheath. Wing-coverts emerge, and down begins to fall off forehead and around mandibles by end of second week. During third week, chicks lose most of down on abdomen; 8–48 h before nest departure, chicks preen or scratch off remaining down, revealing black and white Juvenal plumage (Simons 1980, Hirsch et al. 1981, Nelson and Hamer 1995a, Singer et al. 1995). Chicks leave nest after 27–40 d, at 58–71% of adult mass: mean  $146.8 \text{ g} \pm 7.2 \text{ SD}$  ( $n = 4$ ; Simons 1980, Hirsch et al. 1981, T. Hamer unpubl. data), or  $157.0 \text{ g} \pm 28.5 \text{ SD}$  ( $n = 9$ ; Sealy 1975a), although 1 chick in Alaska weighed only 118 g the day before departing its nest (Kuletz and Marks in press).

**Chick behavior.** Chicks remain motionless or sleep 80–94% of the time on nest (Naslund 1993a, Nelson



**Figure 7.** Number of feedings by time of day (05:00–21:00) at 10 Marbled Murrelet nest sites in British Columbia, Washington, Oregon, and California ( $n = 206$  feedings).

and Hamer 1995a). Other behaviors include standing, turning, shifting position, preening, stretching, flapping, pecking at nest substrate or tree limb, snapping at insects, and begging for food in presence of adults. Wing-flapping and preening increase substantially in week before nest departure (T. Hamer unpubl. data). Chicks vocalize softly during feeding bouts and sometimes before arrival of adult at nest (SKN unpubl. data). See Sounds: vocalizations, above.

#### PARENTAL CARE

**Brooding.** Adults brood chick for only 1–2 d after hatching (Simons 1980, Nelson and Hamer 1995a, Nelson and Peck 1995). May also return at night to brood young chicks during first 5 d after hatching (Eisenhawer and Reimchen 1990, Naslund 1993a). During brooding, adults are active and restless, regularly standing, turning, and repositioning themselves on chick.

**Feeding.** Both adults feed young, although they rarely arrive at nest together. Generally carry single fish in bill (rarely  $\geq 2$ ), holding it crosswise just behind operculum. After arriving on nest limb, adult carrying fish often remains frozen on landing pad (up to 11 min) before approaching nest. After approaching chick, adult stands motionless as chick energetically strokes adult's throat and beak with its beak. Time adults spend at nests during feedings: 13 s to 80 min (mean  $12.6 \text{ min} \pm 2.8 \text{ SD}$ ,  $n = 16$ ; Nelson and Hamer 1995a). Chick holds fish for up to 2 min before swallowing it headfirst and whole. Adults usually leave immediately after fish exchange.

Chicks are fed 1–8 times/d (mean  $3.2 \pm 1.3 \text{ SD}$ ) at dawn, dusk, and midday ( $n = 10$  nests; Nelson and Hamer 1995a; Fig. 7). Dawn feedings occur from 37 min before to 65 min after official sunrise (mean 6.0 min after  $\pm 30.5 \text{ SD}$ ;  $n = 68$  feedings at 13 nests). Midday feedings take place between 11:00 and 17:00. Dusk feedings occur from 90 min before to 71 min after official sunset (mean 18.4 min after  $\pm 26.3 \text{ SD}$ ;  $n = 41$  feedings at 12 nests; Nelson and Hamer 1995a). Timing of feedings at dawn is affected by weather conditions; birds arrive later on cloudy or rainy days (Nelson and Peck 1995).

**Nest sanitation.** Adults rarely defecate at nest; chicks defecate in ring around the outside of nest cup. After 27–40 d, ring can be up to 51 mm thick and smell strongly of fish. No information on invertebrate associates in nest.

#### COOPERATIVE BREEDING

Not known to occur.

#### BROOD PARASITISM

Not known to occur.

#### FLEDGING STAGE

**Departure from the nest.** Chicks leave nest at age 27–40 d, at 58–71% adult weight. Variation in time on nest may be related to food-provisioning rates. Depart nest mid-May–late Sep (as early as mid-Apr in California). Chicks begin arriving at sea in May, with numbers increasing rapidly mid-Jun–mid-Jul and peaking late Jul–mid-Aug (Sealy 1975c, Hamer and Nelson 1995b, K. Kuletz unpubl. data). On the 2 evenings before departure, chicks are very active (Nelson and Hamer 1995a, Singer et al. 1995, T. Hamer unpubl. data). Behaviors during this time include constant rapid pacing on nest platform, frequent vigorous flapping of wings, repeated peering over edge of nest platform, rapid nervous head movements, and continuous preening. These behaviors begin in late afternoon or near sunset, and continue until dark or until bird leaves nest. Departs nest at dusk, between 11 and 55+ min after official sunset (Hirsch et al. 1981, Nelson and Hamer 1995a, Singer et al. 1995), although at a cliff nest in Prince William Sound, AK, chick left between 01:00 and 09:00 (Kuletz and Marks in press). Chicks are thought to fly directly from nest to ocean (on basis of observations of 1 radio-tagged fledgling; T. Hamer unpubl. data). At cliff nest in Alaska, referred to above, radio-tagged chick departed by hopping into water during high tide (Kuletz and Marks in press). Generally arrive at sea with remnants of egg tooth on upper mandible and some with wisps of natal down adhered to Juvenal plumage.

**Growth.** Wing length increases rapidly in last 4 d before nest departure; at departure, wings are 103–144 mm long (86% of adult wing length; Sealy 1975a, Simons 1980, Hirsch et al. 1981). At nest departure, chicks weigh average of  $146.8 \text{ g} \pm 7.2 \text{ SD}$  ( $n = 4$ ; Simons 1980, Hirsch et al. 1981, T. Hamer unpubl. data) to  $157.0 \text{ g} \pm 28.5 \text{ SD}$  ( $n = 9$ ; Sealy 1975a), but see Young birds, above.

**Association with parents or other young.** Chicks fledge alone; no evidence of parental care after departure. Last feeding visits by adults occur 10 min to 2 d before chick fledges (Singer et al. 1995).

**Ability to get around, feed, and care for self.** Few data. Numerous fledging birds in North America appear to become grounded during flights from nest to Pacific (Nelson and Hamer 1995a, 1995b). Many of

these grounded fledglings may be unable to take flight again or make it to ocean by other means (but see Behavior: locomotion, above). Once juveniles reach ocean, they are independent and not attended by either parent. A radio-tagged chick stayed within a 12-km<sup>2</sup> area of its nest site for at least 2 wk (Kuletz and Marks in press).

#### IMMATURE STAGE

Limited information on hatch-year (HY) and after-hatch-year (AHY) birds. Plumage indistinguishable from that of adults after fall of first year. Prebreeders are thought to fly into inland nesting areas in Jul and participate in social circling and calling behavior (O'Donnell et al. 1995). HY birds spend more time foraging (less time on surface and shorter dives) than AHY birds (K. Kuletz unpubl. data). Occur closer to shore and more often alone or in small groups than AHY birds (Ralph and Long 1995, Speckman 1996, K. Kuletz unpubl. data). No information on daily habits or time budgets.

## DEMOGRAPHY AND POPULATIONS

#### MEASURES OF BREEDING ACTIVITY

**Age at first breeding; intervals between breeding.** No data. Age at first breeding believed to be 2–4 yr, on basis of data from other alcids (Beissinger 1995, De Santo and Nelson 1995). Birds may not nest every year, especially when food resources are limited.

**Clutch.** One egg. Not known if pairs reneest after failure or lay >1 clutch (but see Breeding: eggs, above).

**Annual and lifetime reproductive success.** Existing information from observations of tree nests in North America indicates that overall nesting success (% eggs laid that produce fledged young) is only 28% ( $n = 32$  nests with known outcomes; Nelson and Hamer 1995b). In North America, hatching success (% eggs laid that hatch) is 67% ( $n = 20$ ), and fledging success (% young hatched that fledge) is 45% ( $n = 19$ ; De Santo and Nelson 1995, Nelson and Hamer 1995b). Most nests (43%) failed because of predation during egg and nestling stages. Ratios of HY to AHY birds on water range from 0.1 to 17% (Ralph and Long 1995, Strong 1995, Kuletz 1996, unpubl. data, SKN and J. Kelson unpubl. data). No data on lifetime success.

**Number of broods normally reared per season.** Unknown; probably 1 (on basis of information from other alcids; but see Breeding: eggs, above).

#### LIFE SPAN AND SURVIVORSHIP

No mark-recapture information; mark-recapture research is just beginning in British Columbia (G. Kaiser pers. comm.). Adult and first-year juvenile survivorship estimated to be 81–88% and 70%, respectively (on basis of information from other alcids; Beissinger 1995).

## DISEASE AND BODY PARASITES

No information.

## CAUSES OF MORTALITY

*Exposure.* No information.

*Predation.* See Behavior: predation, above, for list of known predators. Predation is major cause of nest failure (43% of 32 nests; Nelson and Hamer 1995b). Fragmentation of conifer or mixed-species forests throughout range may contribute to these high predation rates; nests along forest edges may be especially vulnerable (Nelson and Hamer 1995b).

*Competition with other species.* No information.

*Other.* Nest abandonment by adults, the fall of chicks from nests, and the death of nestlings (1 bird died of burst aorta). In addition, fledglings discovered on ground at varying distances from ocean during breeding season (up to 101 km inland; Nelson and Hamer 1995a). These juveniles are believed to have crash-landed because of exhaustion or difficulty navigating during their relatively long flights from nest to ocean. At least 5 adults probably were killed by cars or trucks while flying low over roads, 3 may have crashed into electric transmission lines, and 1 may have been killed by a dog (in Alaska and Oregon; Balmer 1935, Kuletz unpubl. data, G. van Vliet unpubl. data, SKN unpubl. data). More than 5 records of adults found stunned or dead after trees were felled in s.-central Alaska and British Columbia (Drent and Guiguet 1961, Harris 1971, K. Kuletz pers. comm.). Individuals also killed at sea in gill-nets (Carter and Sealy 1984, Carter et al. 1995) and oil spills (Piatt et al. 1990, Carter and Kuletz 1995, Kuletz 1996). Numerous individuals (adults and HY birds) wash up on beaches each fall and winter; cause of death is unknown, but some are believed to have died of starvation (e.g., in Oregon; R. Lowe pers. comm.). See Conservation and management: effects of human activity, below.

## RANGE

*Initial dispersal from natal site.* Few data. From observations of 2 radio-tagged fledglings in Washington and Alaska, they appear to remain in shallow waters directly offshore from nest sites (Kuletz and Marks in press, T. Hamer unpubl. data). Washington chick flew 41 km due west of nest to Puget Sound and remained there until signal was lost 2 d later. Alaska chick hopped into water at high tide from its cliff nest and stayed within 12 km<sup>2</sup>, primarily along 4 km of shoreline until the signal was lost 2 wk later. See Breeding: fledging stage, above.

*Fidelity to breeding site and winter home range.* Species (not known if the same individuals) has high fidelity to nesting areas (forest stands); same sites in Alaska, Oregon, and California occupied for 5, 10 and 20 yr, respectively (i.e., every year surveyed; Divoky and Horton 1995, K. Kuletz pers. comm.). Also faithful to nest trees (see Breeding: nest, above). Limited data

on fidelity at sea, but in Alaska, radio-tagged adults ( $n = 31$ ) repeatedly used same foraging areas and stayed within 91 km (most within 17 km) of capture sites; off Oregon, by contrast, 3 of 5 adults with radios moved frequently (on hourly and daily basis) up to 132 km from capture sites (breeding-season observations; K. Kuletz unpubl. data, P. Jodice unpubl. data). In winter, individuals (suspected to be experienced local breeders) repeatedly return to forest nesting areas (Naslund 1993a, 1993b, O'Donnell 1993). No information on fidelity at sea in winter.

*Dispersal from breeding site or colony.* No information.

*Home range.* No information.

## POPULATION STATUS

*Numbers.* Exact numbers unknown. In North America, total population, based on numbers below, is 263,000–841,000 individuals; estimated at 300,000 individuals by Ralph et al. (1995). In each state and province, population has been estimated from partial or complete surveys, but survey techniques and assumptions have not been consistent among areas, and methods still need refinement. Population estimates vary widely in Alaska and Oregon.

Estimates of number of individuals: Alaska—200,000–758,000, 67–90% of population (Piatt and Ford 1993, Agler et al. in press); British Columbia—45,000–50,000 (Rodway et al. 1992); Washington—5,000–6,500 (Speich et al. 1992, Speich and Wahl 1995, Varoujean and Williams 1995); Oregon—6,600–20,000 (Strong et al. 1995, Varoujean and Williams 1995); California—6,450 (Ralph and Miller 1995).

Distribution and abundance in summer: (1) Alaska: densities 0.1–14.9/km<sup>2</sup> in n. Gulf of Alaska; 75% of birds occur off se. Alaska (Alexander Archipelago) and 97% off this area (Alexander Archipelago), Prince William Sound, and Kodiak Archipelago (Mendenhall 1992, Piatt and Ford 1993, Agler et al. in press); (2) British Columbia: densities 0.3–16/km<sup>2</sup>; highest numbers occur in Queen Charlotte Is. and along western coast of Vancouver I. (Burger 1995); (3) Washington: densities 0.01–5.6/km<sup>2</sup>; >50% of birds occur in Puget Sound and Straits of Juan de Fuca and Georgia (Speich et al. 1992, Speich and Wahl 1995, Varoujean and Williams 1995); (4) Oregon: densities 12.5–130.5/km<sup>2</sup> (from vessel surveys); largest concentrations occur along central coast between Cascade Head and Cape Arago (Strong et al. 1995); (5) California: highest densities (4.0/km<sup>2</sup>, 62% of population) occur between Oregon border and Trinidad (Ralph and Miller 1995). No estimates for Asian population, but probably in the tens of thousands (Konyukhov and Kitaysky 1995). Surveys in Sea of Okhotsk, Russia, found 0.5–2.0 birds/km of coastline in summer (Babenko and Poyarkov 1987).

*Trends.* Historical data limited. Species currently rare and uncommon in areas where it was common or abundant in early 1900s, especially along southern

coast of Washington, northern coast of Oregon, and coast of California south of Humboldt Co. (Sealy and Carter 1984, Marshall 1988, Carter and Erickson 1992, Nelson et al. 1992, Ralph 1994). Mostly absent from historical range in Mendocino, Sonoma, and San Mateo Cos., CA. Populations in n. Gulf of Alaska appear to have declined by 50–73% over last 17–20 yr (Piatt and Naslund 1995, S. Klosiewski and K. Laing unpubl. data). On western coast of Vancouver I. (Clayoquot Sound), Kelson et al. (1995) suggest, on basis of 2 sets of surveys 10 yr apart, that populations may have declined 40%. Population trends projected from demographic analyses suggest that populations are declining throughout their range in North America as much as 4–7%/yr (Beissinger 1995). No information on population trends in Asia (for causes of decline, see Conservation and management: effects of human activity, below).

#### POPULATION REGULATION

K-selected species (long-lived, slow to mature, low reproductive rate), whose population stability is sensitive to adult mortality (Beissinger 1995). Major threats include logging or modification of habitat, entanglement in gill-nets, and oil spills and other pollution (Carter and Sealy 1984, USFWS 1992, Carter and Kuletz 1995, Fry 1995, Kelson et al. 1995). Predation of eggs, chicks, and adults is significant factor limiting populations in North America (see Causes of mortality, above). The cumulative effects, exacerbated by fluctuations in prey availability, as effected by oceanographic changes (e.g., El Niño ocean conditions) and other physical and biological factors, threaten nesting attempts, reproductive success, and adult survival (Ainley and Boekelheide 1990).

## CONSERVATION AND MANAGEMENT

#### EFFECTS OF HUMAN ACTIVITY

*Shooting and trapping.* No information.

*Pesticides and other contaminants/toxics.* Mortality due to oil pollution is considered one of the major threats to populations, although effects of large oil spills and chronic oil pollution, and their lethal and sublethal impacts, have been poorly documented. Rated as one of the most vulnerable species to oil spills because it feeds close to shore (King and Sanger 1979); oiling not only causes direct mortality but also has sublethal, physiological, and reproductive consequences that affect local populations. Large spills could extirpate populations from portions of their range. At least 8,400 *Brachyramphus* murrelets (most of which were *B. m. marmoratus*; 3.4% of the Alaska population and 6–7% of population in spill zone) were estimated to have been killed in the *Exxon Valdez* oil spill in Prince William Sound, on basis of recovery of 1,025 carcasses (Carter and Kuletz 1995, Kuletz

1996). This spill appeared to affect breeding at Naked I.; lower ratios of HY to AHY birds found in postspill years (Kuletz 1996). Hydrocarbon concentrations found in livers of birds within spill area but not in those in unoiled areas (K. Oakley unpubl. data). Many birds killed in other spills throughout range in North America in 1980s and 1990s, including but not limited to: (1) British Columbia: 1988 *Nestucca* spill from Washington killed 143 birds off Vancouver I.; (2) Washington: 1985 *Arco Anchorage* spill off Port Angeles killed 1 bird, 1988 *Nestucca* spill off Grays Harbor killed 2 birds, and 1991 *Tenyo Maru* spill off Olympic Peninsula killed 45 birds; (3) Oregon: 1983 *Blue Magpie* spill in Yaquina Bay killed at least 2 birds; (4) California: 1984 *Puerto Rican* and 1986 *Apex Houston* spills off San Francisco killed 1 and 11 birds, respectively (Burger 1995, Carter and Kuletz 1995, Fry 1995). Fewer than 10% of birds are likely recovered in spills because of their small body size and other factors (Fry 1995). Oil transport and development, mining, and pulp mills contribute to pollution and bioaccumulation of toxins and heavy metals in ocean, which could affect local populations and availability of food resources (Carter and Kuletz 1995, Fry 1995, Speckman 1996). No quantitative information on other contaminants, but Fry (1995) discusses possibility of effects on murrelets related to organochlorines, other industrial pollutants, plastics, and marine debris.

*Ingestion of plastics, lead, etc.* No information.

*Collisions with stationary/moving structure or objects.* Sometimes hit by cars or trucks on logging roads and highways ( $n > 5$ ; Balmer 1935, G. van Vliet pers. comm., SKN); individuals approach nests from below, so traffic is threat where nests are located near roads. One murrelet believed killed by collision with transmission line in Mapleton, OR, and 2 near Juneau, AK (G. van Vliet. pers. comm., SKN).

*Fishing nets.* Inshore gill-net mortality may have significant impacts on local populations. In Alaska, 3,300 birds (0.5–2% of population) captured annually in gill-nets (Carter et al. 1995, Piatt and Naslund 1995). In Barkley Sound, British Columbia, at least 6.2% ( $n = 175$ –250 birds) of breeding population was captured in nets in single season (Carter and Sealy 1984). Smaller numbers (10–100 annually), but limited data, captured off Washington (Speich and Wahl 1989) and California (Carter et al. 1995). No gill-net fishing occurs off Oregon. Recent changes in regulations (e.g., fishing closures implemented by California Department of Fish and Game) in California have significantly reduced threat, so greatest threat occurs from Washington north. Despite impacts, little has been done to develop long-term solutions to limit or eliminate gill-net mortality. Mariculture operations in Alaska and British Columbia may also kill individuals in nets and cages, and affect local prey species abundance (Rodway et al. 1992, Speckman 1996). No quantitative data available from other fisheries or concerning threats in Asia.

**Degradation of habitat.** Logging of nesting habitat and elimination of habitat through development along coast have been identified as greatest threats to Marbled Murrelets because they directly affect populations by removing essential nesting habitat (USFWS 1992). These activities also fragment habitat. Small islands of nesting habitat remain in many areas; these sites may be subjected to greater predation rates, changes in microclimate that affect distribution of epiphytes, and other edge effects (Nelson and Hamer 1995b). Not known if individuals can shift to new sites when previously used habitat is gone. At sea, oil spills may pose significant threat to this species (Piatt et al. 1990, Carter and Kuletz 1995, Kuletz 1996), but long-term impacts of oil on prey resources and foraging habitat have not been quantified. Some declines in forage fish species (e.g., juvenile Pacific herring), however, were noted after *Exxon Valdez* oil spill in Prince William Sound, AK (Carter and Kuletz 1995, Kuletz 1996). Changes in prey availability may have impacted nesting success in spill area (e.g., Naked I.; Kuletz 1996). See discussion of pesticides and other contaminants, above, for more information on oil effects.

**Disturbance at nest sites.** Limited information. In a few places, species nests in state parks and other recreation areas with consistent human activity. Unsuccessful nests in these forest areas may result not because of noise or direct disturbance (nests are usually >12 m high in trees), but by presence of predators attracted to human refuse. Observation of nests by researchers may also attract predators (but see Nelson and Hamer 1995b). Birds at tree nests do not flush when observations are made from ground, but they may flush if nest branch is approached by tree climber (Binford et al. 1975, K. Kuletz pers. comm.). In contrast, ground-nesting murrelets are easily disturbed by human activity; individuals flush when approached (Ford and Brown 1995, D. Marks pers. comm.).

**Human/research impacts.** No impacts known that would affect large numbers of birds or local populations. Low-altitude aircraft and boat activity disturbs individuals, especially adults holding fish; makes birds dive and affects activity and distribution (Kuletz 1996, Speckman 1996).

#### MANAGEMENT

**Conservation status.** Listed as Threatened in Oregon, Washington, and California under federal Endangered Species Act in 1992 (USFWS 1992). Also listed as Threatened in British Columbia (M. Rodway unpubl. rep.), and in Washington and Oregon (Washington Administrative Code 232-12-001, 1993; Oregon Administrative Rule 635-100-125, 1995). Listed as Endangered by state of California (Calif. Fish and Game Comm. 1992).

**Measures proposed and taken.** Given the federal listing of this species as Threatened in Washington, Oregon, and California in 1992, a series of protection

measures must be taken in these states. First, federal agencies are required to consult with the USFWS on any action, such as a timber sale, that would affect murrelets. To assess the impacts of timber harvest, these agencies are conducting surveys for murrelets in proposed timber sales using a protocol designed by the Pacific Seabird Group to assess murrelet use of an area (C. J. Ralph, S. K. Nelson, M. Shaughnessy, S. Miller, and T. Hamer, unpubl. data). Some state agencies and private companies also are conducting surveys. On basis of these surveys, some stands with murrelets have been temporarily removed from timber production.

Second, in 1992 President Clinton hosted a Forest Conference to deal with the region's timber issues, and a Forest Plan was developed that provides long-term habitat for Marbled Murrelets (U.S. Depts. of Agriculture and Interior 1993). The plan is just beginning to be implemented, so its effectiveness is unknown at this time (1996).

Third, a Recovery Team was established to write a Recovery Plan (USFWS 1995), and Critical Habitat (habitat that is critical for nesting and recovery) was designated by the USFWS (1996). Designation of Critical Habitat helps in regulating land use activities (on federal lands) and identifying areas for special management or protection. The final Recovery Plan has not been released or implemented yet, but recovery objectives include increasing population productivity, minimizing threats to survivorship (e.g., by protecting habitat), and conducting research and monitoring to fill in missing information for developing specific delisting criteria (criteria by which to remove this species from the endangered species list).

Fourth, U.S. Forest Service published a volume of information on the species, which in addition to presenting biological data, outlines management strategies similar to those in the Recovery Plan (Ralph et al. 1995). Strategies include: (1) stabilizing the current amount of suitable forested habitat and managing at-sea habitats, both measures to ensure that quality, quantity, and distribution of habitat are adequate to sustain demographic and population size goals; (2) surveying suitable habitat to identify high-use areas; and (3) creating buffers and future habitat to maximize stand size and minimize fragmentation.

Fifth, in 1994 an observer program was established in Washington to assess impacts of gill-net fishing on murrelets in Puget Sound. The program is ongoing and no results are available.

See USFWS (1995) for a complete summary of these conservation measures.

## APPEARANCE

#### MOLTS AND PLUMAGES

Our understanding of the annual cycle of hormones, molt, and breeding is limited. Adults have

incomplete Prealternate molt (body-feathers) before breeding season (Feb–May) and complete Prebasic molt (body, tail, wing) after breeding season (Jul–Nov; see Fig. 5; Bent 1919, Kozlova 1961, Carter and Stein 1995). During Prebasic molt, loses all remiges relatively synchronously and is flightless for up to 2 mo (Bent 1919, Kozlova 1961, Carter and Stein 1995). Entire Prebasic molt takes 2–3 mo; molt of primaries, secondaries, and rectrices requires about 65 d (range 45–75 d; Pimm 1976). Molt of body-feathers generally begins slightly before and ends slightly after remigial molt, and rectrix molt generally follows primary molt (Carter and Stein 1995). Body molt proceeds from anterior to posterior in ventral and dorsal tracts (e.g., back of head and chin before abdomen and back). Some ventral feathers retained as late as Dec (after molt of other body- and wing-feathers is complete). First 6 primaries molt in order and almost simultaneously; outer 4 primaries are lost later (Carter and Stein 1995). Limited information on sequence of Prealternate molt suggests it also proceeds from anterior to posterior in ventral and dorsal tracts (Carter and Stein 1995). Sexes appear identical in all aspects of plumage. However, differences in shading of breeding plumage (dark chocolate brown versus lighter brown) between adults at known nests may indicate gender or individual variation in plumage (SKN).

Timing of molts varies from year to year and location to location, presumably in association with prey resources, stress levels, and reproductive success; Prebasic molt may occur earlier and faster in stressed or failed breeders. Prealternate molt may occur later in subadults and nonbreeders (Kozlova 1961, Sealy 1975a) and vary with the individual; some individuals in Basic plumage observed as late as Jun (S. Sealy unpubl. data, SKN). Examples of individual variation in timing of molt include observations of (1) individuals in Alternate plumage paired with others in Basic plumage, (2) individuals in full Basic plumage with brood patches, and (3) an adult in Basic plumage (completely white breast; paired with adult in Alternate plumage) landing at nest in Aug in Oregon (K. Kuletz unpubl. data, G. van Vliet unpubl. data, J. Witt unpubl. data). No data on whether timing of molt varies geographically, but Prebasic molt would be expected to begin earlier in southern part of range, on basis of earlier known nesting dates (Carter and Stein 1995, Hamer and Nelson 1995b). No differences in timing or molt sequence known for Asiatic form.

**Hatchlings.** Covered with thick, cryptic, downy plumage that is yellowish and sprinkled evenly with irregular dark spots (brown and black), except on head, where spots are concentrated in large patches, and on belly, which is covered with pale gray down (Binford et al. 1975, Simons 1980). Down covers developing Juvenal plumage and is retained until just before nest departure.

**Juvenal plumage.** Grows on same shafts as down

feathers. Develops during the 27–40 d chick is on nest. Chicks pluck and preen down off body 8–48 h before leaving nest (Nelson and Hamer 1995a). Reproductive success can be assessed only by determining percentage of juveniles that appear on ocean after breeding season. It is therefore crucial to be able to distinguish birds in Juvenal plumage from older birds.

Crown, nape, ear coverts, back, rump, and uppertail-coverts are blackish brown; throat and scapulars are white. White neck-collar and scapular patch less distinct than in winter adults. Lores dusky. Underparts (chest, breast, sides) and sides of head to below eye are white with fine dusky barring which does not conceal white ground color. Remiges and upperwing-coverts dark brown to blackish brown. Underwing-coverts are brownish gray with some white. Rectrices dark brown. Outer rectrices edged with white (*B. m. perdix*), inner vanes pale brownish. Undertail coverts white. Recently fledged juveniles are generally darker than older juveniles with dark brown to black feathers on upperparts, and white feathers with dark margins on head, neck, breast, sides, and abdomen, giving juvenile a speckled appearance. Also have dark neck-band formed by dark feather margins or entirely dark feathers, and retain egg tooth for unknown period of time. In contrast, older juveniles (similar to adults), are whiter on neck and breast. Within a month or 2 of fledging, the flecks of black and gray on most of the neck, breast, sides, and abdomen, and the dark neck-band begin to disappear, and upperparts become lighter (dark brown feather margins replaced with gray). It is unclear how some of these plumage changes occur or how long they take. They could result from feather wear and/or a partial Prebasic I molt. At this point, juveniles resemble Definitive Basic adults; the 2 are indistinguishable from a distance. In the hand, however, remnant speckling on breast can be visible as late as Feb in some birds.

**Subadult plumages.** Juvenal plumage slowly changes during months following fledging so that by late fall, HY birds closely resemble Definitive Basic adults. Unknown whether this transition in appearance results from molt and/or feather wear. As far as is known, all subadult plumages are similar or identical to adult plumage during breeding and nonbreeding periods. However, age by which adult (Definitive Basic and Alternate) plumages achieved uncertain, but Definitive Prebasic molt probably occurs by age 1.

**Definitive Basic plumage.** Definitive Prebasic molt complete (see above); occurs Jul–Nov, and plumage is retained throughout winter.

Dark brownish above; back feathers have blue gray margins, and scapulars are white (Ridgway 1919, Gabrielson and Lincoln 1959, Carter and Stein 1995). Underparts, sides of head to above the eye (including malar, auricular, and suborbital regions and lower half of loreal region), and feathers below nape are white (nearly complete nuchal collar). Some brown

gray flecking may persist on sides and flanks. Lores generally white. Remiges dark brown; upperwing-coverts brownish-gray or blackish-gray. Axillars and underwing-coverts uniform fuscous, as in summer. Rectrices uniformly blackish brown, or outer rectrices edged with narrow white margin (*B. m. perdix*). Undertail-coverts white.

**Definitive Alternate plumage.** Definitive Prealternate molt incomplete; includes body-feathers (see above), occurs Feb–May, and plumage is retained throughout summer.

Sooty brown to brownish black upperparts, rusty margins on back-feathers, and reddish scapulars (Ridgway 1919, Gabrielson and Lincoln 1959, Carter and Stein 1995). Head, hindneck, and ear coverts dark brown, forming indistinct cap. Chin and throat paler brown, marbled with buff and white. Lores generally brown. Underparts, sides of head, and neck mottled brown (formed by white feathers with brown margins). Remiges (retained from Definitive Basic plumage) and upperwing-coverts dark brown. Underwing-coverts and axillaries uniform gray brown. Rectrices dark brown, although some outer feathers have white margins with brownish dots (*B. m. perdix*). Undertail coverts white.

#### BARE PARTS

Bare parts are similar for adults and juveniles.

**Bill and gape.** Black. Culmen small and narrow with greatest depth less than half the length of exposed culmen. Convex near base, shorter than tarsus in *B. m. marmoratus* and longer than tarsus in *B. m. perdix*. Edges of bill near tip of upper mandible bear distinct incisions. Nostril broadly oval, pyriform, or triangular, near anterior end of feathered nasal fossa.

**Iris.** Dark brown.

**Legs and feet.** Legs and toes flesh pink to dark gray; feet anteriorly dark grey with bluish tinge. Webbing between toes and rear of tarsus black. Toenails jet black. Tarsus short and stout, shorter than middle toe without nail. Outer toe (without nail) as long as middle toe. Legs have reticulated scale pattern.

#### MEASUREMENTS

##### LINEAR

Sexually monomorphic in characters (Appendix 2). No difference within North American or Asia, but Asiatic murrelets have longer bills and wings than American form. HY birds have shorter bills and wings compared to adults.

##### MASS

No differences between sexes. Asiatic murrelet significantly larger in size. HY birds weigh 58–71% of adult weight. No information on seasonal fluctuations or geographic variation (within North America or within Asia) in mass.

British Columbia, summer: adults—males 217.0 g (range 196.2–252.5,  $n = 37$ ), females 222.7 g (188.1–269.1,  $n = 37$ ); fledglings (mid-Jul)—157.0 g  $\pm$  28.5 SD ( $n = 9$ ; Sealy 1975a). Alaska, summer: adults—204.9 g  $\pm$  19.8 (121.0–250.0,  $n = 51$ ; K. Kuletz unpubl. data). Asia: males 295.8 g (258.0–357.0,  $n = 8$ ; Shibaev 1990).

#### OTHER

Species important in some Native American folklore along West Coast of North America. In Tlingit culture of se. Alaska (Yakutat area), Marbled Murrelet (and perhaps other murrelets) is considered “mother of Raven,” a position of great power and mystique (de Laguna 1972). Birds so respected that these natives never eat them. Translation for one of murrelet’s Tlingit names is “they just ruffle up the water.” This tribe also has a carved wooden ceremonial hat with a murrelet depicted on top.

#### PRIORITIES FOR FUTURE RESEARCH

*B. m. marmoratus*, classified as Threatened or Endangered in the southern portion of its range, clearly needs continued research on demography, population status, and habitat associations. Top priorities for future research include (1) monitoring populations at sea to determine size, trends, productivity, and distribution, especially in Alaska, where >67% of the population occurs and the species is not protected, despite indications of population decline; (2) developing appropriate and consistent methods for at-sea sampling; (3) conducting basic life history studies to learn more about food habits and demographics; (4) determining distribution and abundance of prey species, including effects of physical and biological ocean processes on availability; (5) monitoring the behavior of individuals and local populations through banding, radio-telemetry, or radar, and developing successful telemetry and radar techniques (but see Burns et al. 1995, Hamer et al. 1995, Kaiser et al. 1995); (6) determining factors that limit population growth in terrestrial and marine habitats; (7) determining key components of terrestrial and marine habitat, extent of inland habitat use (i.e., distance inland), and habitat carrying capacity; (8) surveying forest habitat to identify nesting areas, especially in se. Alaska; (9) determining risk of nest predation relative to forest structure and size; (10) developing baseline information on murrelet numbers and distribution for assessment of oil impact, and developing ways to improve documentation of postspill damages; (11) determining other factors of human-caused mortality at sea; and (12) continuing genetics research on North American and Asiatic forms (Ralph et al. 1995, USFWS 1995, SKN). All these aspects of research should also be conducted on *B. m. perdix* in Russia, Japan, and areas to the south.



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**Appendix 2.** Morphological measurements (mm) of Marbled Murrelets. Data shown as Mean  $\pm$  SD (range; *n*).

Measurements	Age	Sex	Alaska <sup>a</sup>	British Columbia <sup>b</sup>	Pacific Northwest <sup>c</sup>	Asia
Culmen	adult	unknown	15.2 $\pm$ 1.0 (13.3–17.6; 51)			20.7 (19.5–23.5; 4) <sup>d</sup>
		male		15.5 $\pm$ 0.9 (13.2–17.4; 36)	15.1 (13.5–16.5; 10)	20.2 (18.9–22.2; 8) <sup>e</sup>
		female		15.3 $\pm$ 1.1 (13.7–17.6; 32)	15.4 (15.0–16.0; 6)	18.5 (18.0–19.0; 2) <sup>d</sup>
	subadult	male	15.4 $\pm$ 0.5 (14.8–16.3; 6)			19.0 (18.0–21.0; 6) <sup>e</sup>
		female	15.0 $\pm$ 1.0 (13.6–15.9; 8)			19.7 (19.0–20.0; 3) <sup>d</sup>
	juvenile unknown	unknown	12.9 $\pm$ 0.6 (–; 9)			20.3 $\pm$ 1.4 (18.2–22.2; 6) <sup>f</sup>
Bill depth	adult	unknown	5.6 $\pm$ 0.3 (4.8–6.6; 51)	6.0 $\pm$ 0.3 (5.4–6.6; 26)		
		female		5.8 $\pm$ 0.2 (5.3–6.8; 23)		
	subadult	male	6.2 $\pm$ 0.5 (5.8–7.0; 6)			
		female	6.0 $\pm$ 0.6 (5.4–6.9; 8)			
	juvenile unknown	unknown	5.7 $\pm$ 0.5 (–; 9)			6.4 $\pm$ 0.3 (6.0–6.6; 5) <sup>f</sup>
		unknown				
Wing length	adult	unknown	131.2 $\pm$ 2.9 (125–138; 51)			142.1 (135–155; 11) <sup>d</sup>
		male		134.2 $\pm$ 3.0 (128–140; 25)	126.1 (121.5–129.0; 10)	141.2 (136–147; 8) <sup>e</sup>
		female		132.6 $\pm$ 4.3 (122–139; 23)	121.7 (112–127; 6)	141.1 (138–147; 5) <sup>d</sup>
	subadult	male	127.8 $\pm$ 5.7 (121–135; 5)			138.3 (130–145; 6) <sup>e</sup>
		female	123.2 $\pm$ 3.8 (120–129; 5)			139.5 (138–141; 2) <sup>d</sup>
	juvenile unknown	unknown	114.8 $\pm$ 3.5 (–; 9)			141.6 $\pm$ 4.0 (135–146; 7) <sup>f</sup>
Tarsus length	adult	unknown	18.5 $\pm$ 1.2 (16.6–22.5; 51)	16.2 $\pm$ 0.6 (15.1–17.6; 37)	15.9 (15.5–16.5; 10)	18.1 (17.0–18.7; 8) <sup>e</sup>
		female		15.9 $\pm$ 0.9 (13.9–17.3; 39)	15.5 (15.0–16.0; 6)	18.0 (16.8–19.0; 6) <sup>e</sup>
	subadult	male	15.9 $\pm$ 5.8 (15.1–16.8; 6)			
		female	15.7 $\pm$ 0.8 (14.9–16.8; 8)			
	juvenile unknown	unknown	16.1 $\pm$ 0.6 (–; 9)			17.4 $\pm$ 0.9 (15.9–18.5; 6) <sup>f</sup>
		unknown				
Tail length	adult	unknown			30.0 (–; 1) <sup>g</sup>	
		male			31.3 (29–33; 10)	
		female			30.5 (28–33; 6)	
	subadult	male				
		female				
	juvenile unknown	unknown	32.8 $\pm$ 2.2 (28–38.9; 35)			34.5 $\pm$ 1.1 (32.7–35.6; 7) <sup>f</sup>

<sup>a</sup> K. Kuletz unpubl. data.  
<sup>b</sup> Sealy 1975a.  
<sup>c</sup> Ridway 1919; samples from Alaska, British Columbia, and Washington.  
<sup>d</sup> Dement'ev and Gladkov 1968.  
<sup>e</sup> Shibaev 1990.  
<sup>f</sup> Sealy et al. 1982.  
<sup>g</sup> SKN unpubl. data; sample from Oregon.

**Appendix 1.** Characteristics of Marbled Murrelet tree nests in North America. Data shown as mean  $\pm$  SD (range; sample size).

Characteristic	California <sup>1</sup> <i>n</i> = 14	Oregon <sup>2</sup> <i>n</i> = 45	Washington <sup>3</sup> <i>n</i> = 6	British Columbia <sup>4</sup> <i>n</i> = 51	Alaska <sup>5</sup> <i>n</i> = 20	Overall <i>n</i> = 136
Number of nests in:						
Douglas-fir	4	32	3	2	0	41
Alaska yellow cedar	0	0	0	37	0	37
Western hemlock	1	11	3	5	6	26
Sitka spruce	0	1	0	6	5	12
Mountain hemlock	0	0	0	1	9	10
Coast redwood	9	0	0	0	0	9
Western red cedar	0	1	0	0	0	1
Tree diameter (cm)	308.7 $\pm$ 156.1 (139.0–533.0; 14)	164.7 $\pm$ 52.6 (76.0–279.0; 45)	149.5 $\pm$ 45.4 (88.5–220.0; 6)	119.4 $\pm$ 58.5 (60.0–370.0; 51)	65.9 $\pm$ 22.5 (26.7–120.0; 20)	147.3 $\pm$ 93.5 (26.7–533.0; 136)
Tree height (m)	73.1 $\pm$ 10.4 (48.8–86.5; 14)	61.5 $\pm$ 13.6 (36.0–85.1; 45)	57.4 $\pm$ 8.2 (45.1–65.0; 5)	33.2 $\pm$ 14.0 (16.5–79.4; 51)	24.0 $\pm$ 4.8 (15.0–34.0; 20)	46.3 $\pm$ 21.1 (15.0–86.5; 135)
Tree diameter at nest height (cm)	103.2 $\pm$ 48.2 (70.0–199.0; 6)	67.6 $\pm$ 24.9 (29.3–122.0; 39)	78.4 $\pm$ 26.4 (40.5–110.0; 6)	58.1 $\pm$ 31.8 (25.5–209.0; 45)	62.7 $\pm$ 11.5 (51.0–74.0; 3)	65.9 $\pm$ 31.2 (25.5–209.0; 99)
Nest branch height (m)	46.9 $\pm$ 11.6 (31.7–67.5; 14)	41.9 $\pm$ 14.7 (13.6–74.8; 44)	33.9 $\pm$ 13.4 (20.1–52.9; 6)	22.7 $\pm$ 7.2 (12.5–42.0; 51)	14.5 $\pm$ 3.8 (9.2–24.0; 19)	30.9 $\pm$ 15.6 (9.2–74.8; 134)
Nest branch diameter at trunk (cm)	44.0 $\pm$ 13.1 (21.0–61.0; 8)	24.6 $\pm$ 10.4 (11.6–56.0; 42)	38.3 $\pm$ 13.9 (13.5–50.5; 6)	29.0 $\pm$ 11.7 (8.0–62.0; 50)	15.4 $\pm$ 5.8 (6.9–27.1; 17)	27.0 $\pm$ 12.7 (6.9–62.0; 123)
Branch diameter at nest (cm)	24.5 $\pm$ 7.6 (16.0–37.0; 6)	33.7 $\pm$ 13.5 (10.0–63.0; 12)	29.4 $\pm$ 15.3 (10.7–46.0; 4)	17.5 $\pm$ 3.5 (15.0–20.0; 2)	19.5 $\pm$ 5.0 (11.8–28.3; 11)	26.3 $\pm$ 11.7 (10.0–63.0; 35)
Branch diameter proximal to nest (cm)		25.0 $\pm$ 10.0 (10.0–50.0; 31)		29.0 $\pm$ 10.2 (15.0–62.0; 47)		27.4 $\pm$ 10.2 (10.0–62.0; 78)
Branch length (m)	4.2 $\pm$ 3.9 (0.9–15.0; 13)	4.9 $\pm$ 2.4 (1.0–12.2; 42)	4.1 $\pm$ 2.7 (1.1–7.5; 5)	3.9 $\pm$ 2.0 (0.6–9.7; 51)		4.3 $\pm$ 2.4 (0.6–15.0; 111)
Branch crown position (%)	64.3 $\pm$ 12.2 (50.0–91.0; 14)	67.8 $\pm$ 17.5 (26.0–98.0; 44)	63.4 $\pm$ 17.2 (41.0–82.0; 5)	71.0 $\pm$ 12.8 (40.0–95.0; 51)	59.7 $\pm$ 12.3 (40.0–79.0; 19)	67.3 $\pm$ 14.9 (26.0–98.0; 133)
Branch orientation (°)	(30–360; 14)	(20–360; 43)	(110–342; 5)	(0–360; 49)		(0–360; 111)
Distance to nest from trunk (cm)	23.1 $\pm$ 39.3 (0–122.0; 14)	100.2 $\pm$ 130.4 (0–762.0; 44)	22.0 $\pm$ 27.2 (0–57.0; 5)	46.5 $\pm$ 78.5 (0–340.0; 50)	79.9 $\pm$ 70.6 (0–224.0; 18)	65.7 $\pm$ 98.1 (0–762.0; 131)
Nest platform length (cm)	24.3 $\pm$ 11.6 (9.5–41.9; 10)	55.4 $\pm$ 47.8 (7.5–250.0; 44)	30.7 $\pm$ 17.1 (10.0–57.0; 6)	52.3 $\pm$ 31.7 (8.0–128.0; 44)	36.3 $\pm$ 24.4 (9.0–65.0; 4)	49.2 $\pm$ 38.3 (7.5–250.0; 108)
Nest platform width (cm)	19.7 $\pm$ 12.6 (6.5–50.8; 10)	26.8 $\pm$ 11.2 (7.0–51.0; 44)	25.0 $\pm$ 11.5 (10.0–39.0; 6)	19.1 $\pm$ 7.7 (7.0–41.0; 44)	29.5 $\pm$ 15.2 (10.0–46.0; 4)	23.0 $\pm$ 10.7 (6.5–51.0; 108)
Nest cup length (cm)	11.0 $\pm$ 2.9 (8.3–16.5; 6)	11.0 $\pm$ 4.0 (5.0–26.0; 43)	12.4 $\pm$ 5.6 (5.9–20.0; 6)	9.9 $\pm$ 2.9 (6.0–20.0; 49)	10.3 $\pm$ 2.3 (8.0–15.0; 13)	10.6 $\pm$ 3.5 (5.0–26.0; 117)
Nest cup width (cm)	9.3 $\pm$ 2.7 (6.5–14.0; 6)	10.0 $\pm$ 3.0 (3.3–18.4; 43)	11.7 $\pm$ 6.1 (3.1–20.0; 6)	8.7 $\pm$ 2.4 (4.0–14.5; 49)	9.4 $\pm$ 2.0 (7.0–15.0; 13)	9.4 $\pm$ 2.9 (3.1–20.0; 117)

Nest cup depth (cm)	3.5 ± 2.2 (2.0–8.0; 7)	3.5 ± 1.7 (0.5–7.1; 38)	2.6 ± 0.7 (1.8–3.6; 6)	3.9 ± 1.3 (1.0–6.0; 46)	4.5 ± 1.3 (2.0–7.0; 11)	3.7 ± 1.5 (0.5–8.0; 108)
Number of landing pads	0.6 ± 0.5 (0–1; 8)	1.2 ± 0.6 (0–3; 43)	2.0 ± 1.0 (1–3; 3)	0.6 ± 0.8 (0–3; 51)		0.9 ± 0.8 (0–3; 105)
Percent moss on platform	42.2 ± 51.1 (0–100; 12)	89.5 ± 15.1 (50–100; 31)	58.0 ± 44.2 (5–100; 5)	88.9 ± 22.9 (2–100; 37)		80.7 ± 32.3 (0–100; 85)
Moss depth on platform (cm)	1.2 ± 2.4 (0–8.1; 12)	4.7 ± 2.7 (0–12.0; 43)	1.4 ± 1.5 (0–3.5; 5)	4.9 ± 1.8 (1.0–10.0; 48)	6.1 ± 3.3 (2.5–15.0; 17)	4.5 ± 2.7 (0–15.0; 125)
Duff and litter depth on platform/nest cup (cm)	4.2 ± 5.7 (0–20.0; 11)	3.0 ± 3.0 (0–12.0; 30)	2.5 ± 0.9 (1.6–3.8; 5)	4.9 ± 2.8 (0.8–10.0; 8)	5.2 ± 3.4 (2.0–15.0; 16)	3.9 ± 3.6 (0–20.0; 70)
Cover above nest (%)	87.1 ± 28.5 (5.0–100; 13)	78.1 ± 21.2 (5.0–100; 41)	89.2 ± 10.7 (70.0–100; 6)	77.7 ± 15.3 (30.0–100; 47)	84.0 ± 20.6 (25.0–100; 12)	80.1 ± 19.7 (5.0–100; 119)
Distance to cover above nest (cm)	210.7 ± 204.5 (1.3–444.4; 10)	71.8 ± 79.4 (2.5–300.0; 40)	104.8 ± 143.4 (19.0–360.0; 5)	96.0 ± 79.6 (10.0–350.0; 45)		98.2 ± 107.2 (1.3–444.4; 100)

<sup>1</sup> Data from Binford et al. 1975, Kerns and Miller 1995, Singer et al. 1991, 1995, unpubl. data, S. Chinnici unpubl. data.

<sup>2</sup> Data from Hamer and Nelson 1995a, S. K. Nelson unpubl. data.

<sup>3</sup> Data from Hamer and Nelson 1995a, T. Hamer unpubl. data. Data for 4 other nests not available.

<sup>4</sup> Data from Jordan and Hughes 1995, Manley and Kelson 1995, A. Burger unpubl. data, I. Manley unpubl. data.

<sup>5</sup> Data from Quinlan and Hughes 1990, Ford and Brown 1995, Naslund et al. 1995, K. Kuletz, M. Brown, and K. Russell unpubl. data.

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