Chapter 5
Nesting Biology and Behavior of the Marbled Murrelet

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Abstract: We summarize courtship, incubation, feeding, fledging, and flight behavior of Marbled Murrelets (*Brachyramphus marmoratus*) using information collected at 24 nest sites in North America. Chick development, vocalizations given by adults and chicks at the nest, and predator avoidance behaviors are also described. Marbled Murrelets initiate nesting as early as March. Females lay a single egg and both adults participate in incubation, exchanging duties every 24 hours at dawn. Most incubation exchanges occur before sunrise. Chicks hatch after 27-30 days. Adults feed chicks single fish up to 8 times daily, but most feedings occur at dawn and dusk. Dawn feeding visits occur over a wider time period than incubation exchanges, with some occurring as late as 65 minutes after official sunrise. The timing of incubation exchanges and feeding visits are affected by weather and light conditions, and adults arrive later on cloudy or rainy days. To minimize the attraction of predators, visits to the nest are inconspicuous, with adults entering and exiting the nest during low light levels, and primarily without vocalizations. Because of this seabird's secretive behavior, our understanding of murrelet demography, nest site selection, and social interactions remain limited.

Marbled Murrelets (*Brachyramphus marmoratus*) are unique among seabirds in that they nest in older-aged coniferous forests throughout most of their range in North America. Little is known about their breeding biology because nest sites have only recently (1974) been discovered and described (Binford and others 1975; Hamer and Nelson, this volume b; Hirsch and others 1981; Nelson and Peck, in press; Quinlan and Hughes 1990; Simons 1980; Singer and others 1991). Marbled Murrelet behavior at the nest has been monitored at 24 of 52 (35 tree and 17 ground) active nests since 1980; however, only a few accounts have been published (Nelson and Peck, in press; Simons 1980; Singer and others 1991, in press). In this paper, we provide a synthesis of information on murrelet behavior patterns, chick development, and vocalizations recorded at these 24 nest sites.

Methods

We compiled all known data on Marbled Murrelet behavior at active nests in North America and combined them with our own studies of murrelet nests. Data were summarized from two ground and five tree nests in Alaska (Hirsch and others 1981; Naslund, pers. comm.; Simons 1980), one tree nest in British Columbia (P. Jones, pers. comm.), two tree nests in Washington (Hamer and Cummins 1991; Ritchie, pers. comm.), nine tree nests in Oregon (Nelson, unpubl. data; Nelson and Peck, in press), and five tree nests in California (Kerns, pers. comm.; Naslund 1993a; Singer and others 1991, in press; S.W. Singer, pers. comm.) (*table 1*). Information on pair bonding and courtship are also summarized.

Active nests were located by observing murrelets land in trees, finding eggshells on the ground and subsequently locating the nest, using radio telemetry, or by incidental observations. Fifteen of the nests were found during the egg stage and 9 during the nestling stage. Some nests were intensively monitored, others only intermittently. Data recorded at many nests included time and duration of incubation exchanges and feeding visits, behavior of chicks and adults, flight behavior, and vocalizations. Weather conditions (percent clouds, precipitation, temperature, wind) were also recorded for comparison with the timing and duration of murrelet activity at the nest. Means, standard errors, and ranges were calculated for numerical data, such as the timing of incubation exchanges and feeding visits in relation to sunrise and sunset, and the length of these encounters at nests.

Results

Pair Bonding and Courtship Behavior

Little is known about when and how Marbled Murrelets pair. Murrelets are primarily observed in groups of two throughout the year, both in the forest and on the water. Many pairs on the water have included a male and female, and were assumed to be mated (Carter 1984; Carter and Stein, this volume; Sealy 1975a). Some of these "pairs" could also be composed of adults in a temporary social association; this is known to occur on the water, especially when birds are not feeding (Carter, pers. comm.). However, we believe that Marbled Murrelets remain paired throughout the year based on these year-round pair groups and data from other alcids (e.g., Harris and Birkhead 1985).

Courtship behavior has been observed on the water in early spring, when some adults are still in winter plumage, as well as throughout the summer. Participation in courtship behaviors while in winter plumage is expected because: (1) the monomorphic plumage in Marbled Murrelets in not a sexually selected trait; and (2) they probably maintain strong pair bonds throughout the year. During courtship, pairs join closely together (<0.5 m), point their bills in the air, partially lift their breasts out of the water, and swim rapidly forward (Byrd and others 1974; Nelson, unpubl. data; Van Vliet, pers. comm.). Pairs also dive synchronously and surface within 1-3 seconds next to one another, suggesting that they remain together under water (Van Vliet, pers. comm.). Preceding the dive or while swimming together in courtship

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Table 1—Marbled Murrelet tree and ground nests by state or province, site, year, and number of days of observation

State/province Site/year	Number of nests	Number of observation days Incubation	 Nestling	Reference
Alaska				
Barren Islands 1978/1979	2	33	56	Hirsch and others 1981 Simons 1980
Naked Island 1991/1992	5	14	0	Naslund, pers. comm.
British Columbia				
Caren Range 1993	1	0	14	P. Jones, pers. comm.
Washington				
Lake 22 1991	1	0	24	Hamer and Cummins 1991
Nemah 1993	1	0	4	Ritchie, pers. comm.
Oregon				
Five Rivers 1990/1991	2	17	14	Nelson and Peck, in press
Valley of Giants 1990/1991	2	26	6	Nelson and Peck, in press
Cape Creek 1991	1	9	0	Nelson and Peck, in press
Siuslaw River 1991	2	0	23	Nelson and Peck, in press
Boulder Warnicke 1992	1	0	8	Nelson and Peck, in press
Copper Iron 1992	1	0	13	Nelson and Peck, in press
California				
Big Basin 1989	2	45	4	Naslund 1993a Singer and others 1991
Father 1991/1992	2	13	25	Singer and others, in press
Elkhead 1993	1	0	12	Kerns, pers. comm.

dances, birds frequently give soft, synchronous nasal vocalizations. Pairs also chase one another in flights just above the water surface throughout the spring and summer, in what may be courtship behavior (see below about similar behaviors exhibited at inland nesting sites).

Copulation has rarely been observed. It is known to occur within trees (n = 1 observation in Alaska; Kuletz, pers. comm.) and on the water where it has been observed at least 15 times (Kuletz, pers. comm.; Naslund, pers. comm; Nelson, unpubl. data; Van Vliet, pers. comm.). Preceding and following copulation, the birds often vocalize with an emphatic, nasal “eeh-eeh” call (Van Vliet, pers. comm.). We expect that copulation primarily occurs at the nest based on observations from other alcids (Sealy 1975a).

Before they lay eggs, pairs probably visit the breeding grounds, not only to pair and copulate, but also to select nest sites. In Oregon, a pair was observed landing on a nest platform for 3 mornings in early May, two weeks prior to laying an egg at that site. Pre-laying visitation to nests, three to four weeks before egg-laying, has been observed in other alcids (Gaston 1992; Nettleship and Birkhead 1985).

Egg-Laying and Incubation Behavior

Marbled Murrelets start to lay eggs as early as March (Hamer and Nelson, this volume a). They lay a single egg weighing approximately 36-41 g (16-18.5 percent of adult weight) (Hirsch and others 1981; Sealy 1975a; Simons 1980). The egg is subelliptical in shape, and measures an average of 59.5 x 37.4 mm (n = 11 eggs) and 0.21 mm in thickness (Day and others 1983; Hirsch and others 1981; Kiff 1981; Sealy 1975a; Simons 1980). The egg has a pale-olive green to greenish-yellow background color, and is covered with irregular brown, black, and purple spots which are more prevalent at the larger end of the egg (Becking 1991; Binford and others 1975; Day and others 1983; Kiff 1981; Nelson 1991, 1993; Nelson, and Hardin 1993a; Reed and Wood 1991; Singer and others 1991).

After the female lays an egg, the pair begins 24-hour shifts of incubation duty; one adult broods the egg while the other forages at sea (n = 12 nests) (Naslund 1993a, pers. comm.; Nelson and Peck, in press; Simons 1980; Singer and others 1991). The incubating adults sit on the egg in a flattened posture and remain motionless on the nest more than 90 percent of the time (n = 4 nests) (Naslund 1993a; Nelson and Peck, in press; Simons 1980). Other behaviors observed during incubation at most nests include turning the egg, re-arranging nest material, and preening. At nests in California (n = 1) and Alaska (n = 5), the average occurrence of these behaviors were 11, 8, and 1 time(s) per day, respectively (Naslund 1993a, pers. comm.).

At a given nest, the two adults appear to have distinct plumage colorations. A light brown and a dark chocolate brown adult (sex of each unknown) have been observed attending nests on 24-hour shifts, indicating possible sexual plumage dichromatism (n = 8 nests) (Fortna, pers. comm.; P. Jones, pers. comm.; Naslund 1993a; Nelson 1991,1992; Ritchie, pers. comm.; Singer and others 1991). In addition, the white patches on the nape of the neck and cheek have varied between adults at a single nest, and individuals at different nests (n = 7 nests) (Fortna, pers. comm.; Hamer and Cummins 1991; P. Jones, pers. comm.; Nelson 1991, 1992; Simons 1980). The variations in these nape and cheek patches may provide a means for identifying individuals.

Murrelets have been observed leaving their egg unattended for 3-4 hours during the morning, mid-day, and evening (n = 4 nests; Naslund 1993a, pers. comm.; Nelson and Peck, in press; Simons 1980). Seabirds often leave their eggs unattended to maximize foraging time and accumulate sufficient energy reserves for lengthy incubation shifts (Boersma and Wheelwright 1979, Gaston and Powell 1989, Murray and others 1983). Murray and others (1993) have hypothesized that the benefits of increased foraging time during egg neglect often outweigh the disadvantages of leaving the egg unattended. Disadvantages of egg neglect include predation, heat loss, and exposure to the elements. In Oregon, an egg was believed to have been taken by a corvid when adults left their nest unattended (Nelson and Hamer, this volume b).

Timing of Incubation Exchanges

Adults usually exchange incubation duties at dawn (n = 12 nests), although Simons (1980) believed exchanges may have taken place at dusk at a ground nest in Alaska. Incubation exchanges generally occur before official sunrise, and often correspond with the first auditory detections of murrelets each morning (Naslund 1993a; Nelson and Peck, in press; S.W. Singer, pers. comm.) (*table 2*). The timing of exchanges were significantly affected by weather patterns and light levels; birds arrived later during overcast or rainy conditions (Naslund 1993a, pers. comm.; Nelson and Peck, in press). In addition, birds arrived earlier in areas of higher latitude likely because of longer periods of twilight. In Prince William Sound, Alaska, incubation exchanges occurred from 37-82 minutes prior to official sunrise ($\bar{x}$ = -52, *s.e.* = 3.1, n = 14 observations at 5 nests) (Naslund, pers. comm.). In Oregon and California, the timing of incubation exchanges ranged from 31 minutes before to 1 minute after official sunrise ($\bar{x}$ = -18.5, *s.e.* = 0.7, n = 85 observations at 7 nests) (Naslund 1993a; Nelson and Peck, in press; Singer and others 1991; S.W. Singer, pers. comm.) (*table 2*). No nocturnal incubation exchanges were observed during intensive observations in California (Naslund 1993a, Singer and others 1991); nocturnal surveys have not been conducted elsewhere.

Incubating birds usually left immediately after the arrival of their mate. Most incubation exchanges lasted 3 to 60 seconds ($\bar{x}$ = 26.0 seconds, *s.e.* = 4.5, n = 76 observations at 7 nests), although at one nest in California one exchange lasted 3 minutes and 40 seconds (Naslund 1993a; Nelson and Peck, in press; S.W. Singer, pers. comm.) (*table 3*). The arriving adult often remained motionless on the nest limb before occupying the nest and commencement of incubation; this waiting period lasted 14 to 357 seconds in California and Oregon (Naslund 1993a; Nelson and Peck, in press).

Egg-Hatching, Brooding Behavior, and Chick Development

The single murrelet chick hatches after 27 to 30 days of incubation (Carter 1984; Hirsch and others 1981; Sealy 1974, 1975a; Simons 1980). Adults become active before the egg hatches, standing and turning more frequently than earlier in the incubation period (Naslund 1993a; Nelson and Peck, in

Table 2—Mean time of incubation exchanges in relation to official sunrise at Marbled Murrelet nests by state[1]

State[2]	Number nests	Number observation days	Mean time before sunrise (min)	Standard error	Range
Alaska	5	14	–52.3	3.1	–82, –37
Oregon	4	49	–18.5	0.8	–30, –8
California	3	36	–18.4	1.3	–31, +1
Total	12	99	–23.2	1.4	–82, +1
Oregon and California only	7	85	–18.5	0.7	–31, +1

[1] Data from Naslund, pers. comm.; Nelson and Peck, in press; S.W. Singer, pers. comm.
[2] Incubation exchanges were not observed in British Columbia and Washington.

Table 3—Mean length of incubation exchanges at Marbled Murrelet nests by state[1]

State[2,3]	Number nests	Number observation days	Mean length (sec)	Standard error	Range (min:sec)
Oregon	4	42	16.3	2.8	0:03-1:07
California	3	34	38.1	1.1	0:02-3:40
Overall	7	76	26.0	4.5	0:02-3:40

[1] Data from Nelson and Peck, in press; S.W. Singer, pers. comm.
[2] Incubation exchanges were not observed in British Columbia and Washington.
[3] Data from Alaska were not available.

press; Simons 1980). Chicks are semi-precocial at hatching, and weigh approximately 32.0-34.5 g (n = 2 chicks) (Simons 1980, Hirsch and others 1981). They are covered with a dense yellowish down, sprinkled evenly with irregular dark spots (brown and black), except on the head where spots are concentrated in large patches, and on their bellies which are covered with a dense, pale grey down (Binford and others 1975, Simons 1980).

Adults usually brood the chick for 1 to 2 days after hatching (n = 4 nests) (Nelson and Peck, in press; Simons 1980; S.W. Singer, pers. comm.), possibly until the chick reaches homeothermy. However, Naslund (1993a) recorded intermittent brooding by adults after daytime and evening feedings at least 3 days after hatching. Naslund (1993a) suggested that the increased brooding may have occurred to protect the chick from predators in the vicinity of the nest. In addition, in British Columbia, Eisenhawer and Reimchen (1990) presented circumstantial evidence that adults returned at night to brood young chicks.

During brooding, adults are active and restless, regularly standing, turning, and repositioning themselves on the chick. Adults do not remove the eggshell from the nest cup, therefore pieces that do not fall out accidentally remain in the nest cup and often are crushed into the nest material by adult and chick activity.

During the first 6 days after hatching, droppings from the chick begin to accumulate around the perimeter of the nest cup (adults are not known to defecate at the nest). By the time the chick fledges, the fecal ring can be up to 51 mm thick. Odor (ammonia and fish) from fecal material can be detected by humans from up to 2 m away.

Murrelet chicks grow rapidly compared to most alcids, gaining 5-15 g per day during the first 9 days after hatching (n = 2 chicks) (Hirsch and others 1981; Simons 1980). As chicks age, the juvenal plumage begins to develop beneath the down; both feather types grow from the same sheath. By day 17, the wing coverts have emerged and down is missing from the forehead and around the mandibles (n = 5 chicks). By day 21, chicks lose most of their belly down, and by day 26, up to 20 percent of body down disappears. Twelve to 48 hours prior to fledging, the murrelet chick, by preening, scratching, and wing flapping, removes the remaining down, revealing their black and white juvenal plumage (n = 10 chicks) (Hamer and Cummins 1991; Hirsch and others 1981; P. Jones, pers. comm.; Nelson and Peck, in press; Simons 1980; Singer and others 1992, in press). This pattern of down loss and feather development is unique among alcids, except the closely related Kittlitz's Murrelet (*Brachyramphus brevirostris*).

Wing length increases rapidly in the last 4 days prior to fledging, and at fledging the chicks wings are 103-144 mm long (86 percent of adult wing length) (Hamer and Cummins 1991; Hirsch and others 1981; Sealy 1975a; Simons 1980). Chicks fledge at age 27-40 days (Hirsch and others 1981; Nelson and Peck, in press; Simons 1980). At this time they still possess an egg tooth, and weigh an average of 146.8-157.0 g ($s.e.$ = 3.6-9.5, n = 4-9), which is 63-70 percent of adult (222 g) weight (Hamer and Cummins 1991; Hirsch and others 1981; Sealy 1975a; Simons 1980). Fledging takes place at dusk, between 11 and 55+ minutes after official sunset (Hamer and Cummins 1991; Hirsch and others 1981; P. Jones, pers. comm.; Nelson and Peck, in press; Singer and others, in press) (*table 4*).

Chicks are thought to fly directly from the nest to the ocean (Hamer and Cummins 1991; Quinlan and Hughes 1990; Sealy 1975a). Hamer and Cummins (1991) radio-tagged a juvenile Marbled Murrelet on a nest in Washington, 37 km inland, and monitored its flight to the ocean. The chick fledged in the evening and was found 18 hours later, 100 m from shore and 2 km north of a direct east-west line between the nest and Puget Sound. The juvenile flew directly to the ocean and did not spend any time in the vicinity of the nest. However, several fledglings have been observed swimming in creeks in California and Washington (Hamer and Cummins 1991; Miller, pers. comm.). It is not known if these fledglings fell from nests, became grounded on their maiden flight to the ocean, or were actually trying to reach the ocean by swimming the creek. Numerous fledging birds in North America appear to have become grounded during flights to the Pacific (Nelson and Hamer, this volume b).

Table 4—Dates and timing of observed Marbled Murrelet fledgings from nests by state and province[1]

State/province	Number nests	Date	Fledging time	Minutes after sunset
Alaska	1	8/16/79	>2200	+21
British Columbia	1	8/20/93	2051	+30
Washington	3	6/22/93	2124	+14
		8/07/91	2046	+11
		8/27/90	2020	+20
Oregon	1	8/29/91	>2050[2]	+55
California	2	6/07/92	2046	+18
		7/03/91	2054	+19

[1] Data from Hamer and Cummins 1991; Hirsch and others 1981; P. Jones, pers. comm.; Nelson and Peck, in press; Singer and others, in press.
[2] Chick fledged between 2050 and 0700 hours.

Many of these grounded fledglings may be unable to take flight again or make it to the ocean by other means. Once juveniles reach the ocean they are thought to be independent and not attended either parent contrary to the suggestion of Ydenberg (1989).

Chick Behavior

Chicks remain motionless or sleep 80-94 percent of the time on the nest (n = 8 chicks) (Hamer and Cummins 1991; Naslund 1993a; Nelson and Peck, in press). Other behaviors include standing, turning, shifting position, preening, stretching, flapping, pecking at the nest substrate or the tree limb, food begging in the presence of adults, and snapping at insects. Behaviors such as wing flapping and preening increase markedly in the week prior to fledging.

On the two evenings prior to fledging, chicks are very active (Hamer and Cummins 1991; Ritchie, pers. comm.; Singer and others, in press). Behaviors during this time include continual rapid pacing on the nest platform, frequent vigorous flapping of the wings, repeated peering over the edge of the nest platform, rapid nervous head movements, and constant preening. After a vigorous session of wing flapping, young birds sometimes hold their wings outstretched and vibrate them rapidly, giving the appearance of shivering wings. These behaviors begin in late afternoon or minutes before sunset, and continue until dark or until the bird fledges.

Low light levels may induce fledging. After a captive reared chick fledged from an artificial nest platform in the dark, it was placed back on the platform and the room brightened by artificial light (Hamer and Cummins 1991). The chick immediately sat motionless and ceased all activity. When the room was darkened again by turning off the light, the chick immediately began the pre-fledging behaviors described above and fledged a second time.

Feeding Frequency, Behavior, and Prey Species

Adults return to feed young up to eight times daily ($\bar{x}$ = 3.2, *s.e.* = 0.4, n = 10 nests) (Hamer and Cummins 1991; Hirsch and others 1981; P. Jones, pers. comm.; Kerns, pers. comm.; Nelson and Peck, in press; Simons 1980; S.W. Singer, pers. comm.) (*table 5*). Chicks are usually fed at least once a day for the 27-40 days they are on the nest, although the frequency is variable and sometimes decreases prior to fledging. The last feeding prior to fledging occurs between 5 minutes (Singer and others, in press) and 2.5 days (Hamer and Cummins 1991) before the young murrelet leaves the nest.

The timing of dawn feedings is more variable than incubation exchanges. First dawn feedings occur from 37 minutes before to 65 minutes after official sunrise ($\bar{x}$ = 6.0, *s.e.* = 3.7, n = 68 feedings at 13 nests) (Hamer and Cummins 1991; Kerns, pers. comm.; Naslund 1993a; Nelson and Peck, in press; S.W. Singer, pers. comm.) (*fig. 1*, *table 6*). Similar to incubation exchanges, weather and light conditions influence the arrival times of the adults, and feedings often occur later on rainy or cloudy days (Naslund 1993a, Nelson and Peck, in press). Second morning feedings occur from 18 minutes before, to 225 minutes (1009 hrs) ($\bar{x}$ = 53.7, *s.e.* = 9.6, n = 40 observations at 13 nests) after, official sunrise. Other feedings take place during the day between the hours of 1100 and 1700 (Hamer and Cummins 1991; P. Jones, pers. comm.; Kerns, pers. comm.; Naslund 1993a; Nelson and Peck, in press; Singer and others 1991)(*fig. 1*). Dusk

Table 5—Mean number of feeding visits observed per day[1] at Marbled Murrelet nests by state and province[2]

State/province[3]	Number nests	Number observation days	Number feedings	Mean per day	Standard error	Range
British Columbia	1	11	44	4.0	0.8	1-8
Washington	1	8	23	2.9	0.4	2-5
Oregon[4]	5	22	61	2.8	0.3	1-5
California[4]	3	21	67	3.4	0.3	1-6
Overall	10	62	195	3.2	0.4	1-8

[1] Not all nests were monitored during mid-day or at night, thus some feeding visits may have been missed. Data include only days where nests were monitored at dawn and dusk on all observation days.

[2] Data from Hamer and Cummins 1991; P. Jones, pers. comm.; Kerns, pers. comm.; Nelson and Peck, in press; S.W. Singer, pers. comm.

[3] No tree nests with chicks were observed in Alaska; data from 2 ground nests in Alaska were not available.

[4] Two nests in Oregon and 1 in California were not monitored at dawn and dusk on the same day.

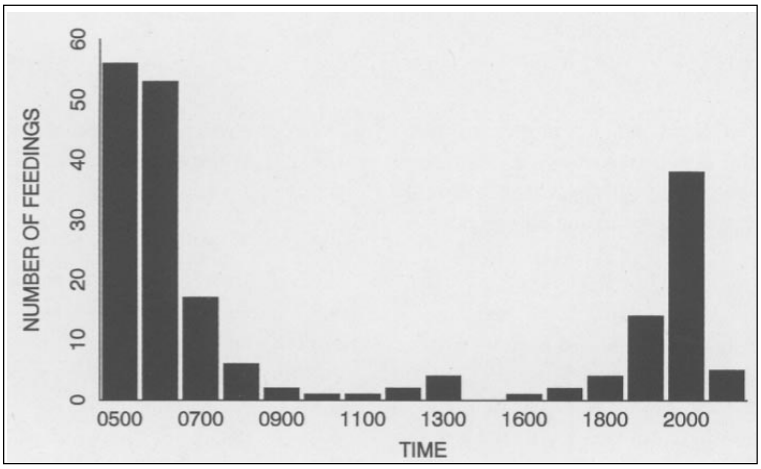

Figure 1—Number of feedings by time of day (0500-2100 hrs) at ten Marbled Murrelet nests in British Columbia, Washington, Oregon, and California (*n* = 206 feedings).

feedings occur from 90 minutes before, to 71 minutes after, official sunset, with the last feeding visit occurring 40 minutes before, to 71 minutes after, official sunset ($\bar{x}$ = 18.4, *s.e.* = 4.1, *n* = 41 feedings at 12 nests) (Hamer and Cummins 1991; Naslund 1993a; Nelson and Peck, in press; Singer and others, in press) (*table 7*). No nocturnal (after dusk) feeding visits were recorded during all-night observations in Washington and California (*n* = 38 nights at 3 nests) (Hamer and Cummins 1991; Naslund 1993a).

On several occasions (*n* = 7 of 68 visits at three nests), two adults arrived at the nest with fish at the same time (Kerns, pers. comm; P. Jones, pers. comm.; Nelson and Peck, in press). In Oregon, when this occurred, one adult flew away, and returned only after the other adult had left. In California and British Columbia, both adults left and returned individually at a later time, or both remained until the chick had eaten one of the fish.

Adults usually carry single fish in their bills, holding it crosswise at the mid-point of the fish's body, or just posterior to the operculum. On several occasions, adults were observed arriving with 2 fish at nests in California and Oregon (*n* = 3)(Buchholz, pers. comm.; Kerns, pers. comm). When adults arrive at the nest with a fish, they often remain in a motionless posture on the landing pad for up to 11 minutes before approaching the nest (*n* = 11 nests) (Hamer and Cummins 1991; Kerns, pers. comm.; Naslund 1993a, pers. comm.; Nelson

Table 6—Mean time of first morning feeding visits in relation to official sunrise at Marbled Murrelet nests by state[1]

State[2,3]	Number nests	Number feedings	Mean time (min)	Standard error	Range
Washington	2	10	– 9.3	11.1	–37,+50
Oregon[4]	7	32	+ 7.9	5.1	–36,+65
California	4	26	+ 9.5	5.9	–31,+62
Overall	13	68	+ 6.0	3.7	–37,+65

[1] Data from Hamer and Cummins 1991; Kerns, pers. comm.; Nelson and Peck, in press; S.W. Singer, pers. comm.
[2] No tree nests with chicks were observed in Alaska; data from 2 ground nests in Alaska not available.
[3] Data from British Columbia were not available.
[4] Does not include one late observation (104 min), assumed to be a second feeding.

Table 7—Mean time of last evening feeding visits in relation to official sunset at Marbled Murrelet nests by state[1]

State[2,3]	Number nests	Number feedings	Mean time (min)	Standard error	Range
Washington	2	4	+ 9.3	22.3	–39,+69
Oregon	7	17	+15.3	5.7	–40,+62
California	3	20	+23.0	5.5	–15,+71
Overall	12	41	+18.4	4.1	–40,+71

[1] Data from Hamer and Cummins 1991; Kerns, pers. comm.; Nelson and Peck, in press; S.W. Singer, pers. comm.
[2] No tree nests with chicks were observed in Alaska; data from 2 ground nests in Alaska not available.
[3] Data from British Columbia were not available.

and Peck, in press; S.W. Singer, pers. comm.). At a nest in Washington, adults rested on the nest platform an average of 2.2 minutes before approaching the chick with food.

In Oregon and Washington, the chick sometimes gave begging calls just prior to the adults landing on the nest platform ($\bar{x}$ = 1.2 minutes before adults arrived, n = 8 observations at 1 nest) and throughout the feeding visit (see vocalizations section) (Hamer and Cummins 1991; Nelson and Peck, in press). At a nest in Washington, the chick spent an average of 10.8 minutes begging during each feeding visit.

After approaching the chick, the adult stands motionless as the chick energetically strokes or nudges the throat and beak of the adult with its beak (Hamer and Cummins 1991; Naslund 1993a; Nelson and Peck, in press). Adults at a nest in Washington held the fish over the chick for an average of 9.7 minutes (*s.e.* = 1.4, n = 16 observations) before the food transfer took place. The adults occasionally give soft whistle or grunt-like vocalizations until the nestling takes the fish (Hamer and Cummins 1991; Nelson and Peck, in press). The time adults spent at nests during feedings ranged from 13 seconds to 80 minutes ($\bar{x}$ = 12.6 min, *s.e.* = 0.7, n = 16) (Hamer and Cummins 1991; Hirsch and others 1981; P. Jones, pers. comm.; Kerns, pers. comm.; Naslund 1993a; Nelson and Peck, in press; Simons 1980) (*table 8*). Fifty percent of feedings lasted > 11 (median) minutes. Chicks held the fish 5 seconds to 2 minutes before swallowing it

Table 8—Mean length of feeding visits at Marbled Murrelet nests by state and province[1]

State/province[2]	Number nests	Number feedings	Mean time (min)	Standard error	Range
Alaska	2	5	5.0	1.7	1.43-10.0
British Columbia	1	38	13.2	2.0	1.00-80.0
Washington	2	24	10.4	1.2	0.30[3]-20.0
Oregon	7	61	16.7	1.3	0.18[3]-46.0
California	4	82	10.4	0.8	0.13[3]-48.0
Overall	16	210	12.6	0.7	0.13[3]-80.0

[1] Data from Hamer and Cummins 1991; Hirsch and others 1981; P. Jones, pers. comm.; Kerns, pers. comm.; Nelson and Peck, in press; Ritchie, pers. comm.; Simons 1980; S.W. Singer, pers. comm.
[2] No tree nests with chicks were observed in Alaska.
[3] Adults may not have fed chicks fish on some of the shorter visits.

head first and whole ($\bar{x}$ = 1.4 minutes at a nest in Washington, n = 4 observations) (Hamer and Cummins 1991; Nelson and Peck, in press). Adults usually leave within 1 minute of the fish exchange.

To provide chicks with fish at dawn, adults probably forage at night, perhaps taking advantage of fish that forage near the water surface during darkness (Carter and Sealy 1987a, 1990). Fish species that have been fed to chicks at nests include Pacific sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea harengus*), and northern anchovy (*Engraulis mordax*) (P. Jones, pers. comm.; Nelson and Peck, in press). Other potential prey species that were not positively identified included capelin (*Mallotus* spp.), smelt (Osmeridae; probably whitebait [*Allosmerus elongatus*] or surf smelt [*Hypomesus pretiosus*]), and herring species (Clupeidae or Dussumieriidae) (Naslund 1993a; Nelson, unpubl. data; Simons 1980; but see Burkett, this volume).

Flight Behavior

Adult murrelets often use similar flight paths on approaches and departures from tree nests. Generally, they follow openings such as creeks, roads or other clearings that allow for direct approaches and departures from the nest (Kerns, pers. comm.; Nelson and Peck, in press; Singer and others 1991; Singer and others, in press). The directions that birds enter and leave nests appear to be related to openings in the canopy or forest around the nest tree, and gaps in the horizontal cover surrounding the nest limb (Naslund, pers. comm.; Nelson and Peck, in press; Singer and others 1991; Singer and others, in press). Birds approach nests below tree canopy at heights as low as 5 m, and usually ascend steeply to the nest in a "stall-out" fashion. Landings are sometimes hard and audible (Nelson and Peck, in press; S.W. Singer, pers. comm.). We have observed and heard murrelets crashing into tree limbs on some occasions during final approaches to nests (Nelson and Peck, in press). In addition, birds occasionally abandoned landings and circled around for second attempts. When leaving the nest, birds usually drop 5-30 m in height before ascending over the canopy to continue their departure flights. They have not been observed departing at nest height or flying upwards on take-off from the nest limb.

When landing on the nest branch, murrelets splay out their webbed feet, lean backwards, and use their wings to slow their forward motion. They land hard enough on the nest limb to create a landing pad, or area where the moss or duff becomes flattened, removed, and worn by repeated landings. Toe nail markings are evident at some landing pads. Landing pads are most often located on the nest limb within 1 m of the nest cup, however they have also been located on adjacent limbs. In the latter case, murrelets hop to the nest limb.

Subcanopy behaviors, including one or more birds flying through, into, or out of the tree canopy, and birds landing in trees, are flight behaviors indicative of nesting and have been noted in nest stands and around nest trees. Landings and departures from trees have been observed at nests, on other branches in nest trees, in trees adjacent to nest trees, and other trees in nest stands throughout the breeding season. These landings may indicate nesting, territorial behavior, searches for nest sites, or resting or roosting behavior (Naslund 1993a). Singer and others (1991), and Naslund (1993a) described an additional four flight patterns observed near nest trees: (1) fly-bys and stall-flights, including single birds or pairs flying by or stalling out next to a known nest tree, at nest branch height; (2) flying-in-tandem and tail-chases, where pairs of birds fly in close proximity to known nest trees; and

(3) buzzing, which includes single birds flying through the canopy making continuous low-pitched buzzing wing sounds.

Several flight behaviors above the canopy are also indicative of nesting. Like other alcids, Marbled Murrelets are often observed circling singly or in groups above the nesting grounds (Gaston 1992). Nesting birds may join with others before returning to the ocean after incubation and feeding visits. Nonbreeders may also accompany nesting birds in these circling flights above the canopy. Murrelets also occasionally create a loud sound, like a jet, during a shallow or steep dive that often originates above the canopy and ends at or below canopy level (Nelson and Peck, in press; S.W. Singer, pers. comm.). In Oregon, this behavior has been observed most often (67 percent) associated with known nest trees. In California, the jet dive during encounters between two murrelets has been observed and may be an aggressive posture or territorial defense.

Predator Avoidance Behavior

The Marbled Murrelet's primary defense against predators at the nest is to avoid detection through their secretive behavior at or near the nest, morphological defense mechanisms, such as cryptic plumage, and location of nest sites in trees and stands with hiding cover. In direct response to calls, silhouettes, or the presence of predators, and other disturbances (e.g., airplanes) at nests, adults and chicks often flatten themselves against the tree branch, holding their backs and heads low and remaining motionless (Kerns, pers. comm.; Naslund 1993a; Nelson and Peck, in press; Quinlan and Hughes 1990; Simons 1980; Singer and others 1991). However, they may also attempt to defend themselves against predators that have located the nest. At a nest in California, a murrelet chick was observed to defend itself against a Steller's Jay (*Cyanocitta stelleri*) by standing erect, turning to face the intruder, and jabbing it with its slightly open bill (Naslund 1993a; S.W. Singer, pers. comm.). In addition, Naslund (1993a) noted that occasionally when a raven flew by a nest, the adult assumed an erect posture as if readying itself to take flight. S.A. Singer (pers. comm.) observed an incubating adult lunge with open bill at a raven as it approached the nest, causing it to veer off instead of landing.

Vocalizations and Wingbeats

Marbled Murrelets primarily give soft or muted calls from the nest limb that are not audible from the ground. They rarely give loud vocalizations from stationary locations or in close proximity to a nest. When loud vocalizations are given at or near a nest, they can be heard from the ground depending on weather conditions and the location of the observer. However, because loud calls are uncommon, using them as a means for locating nests is not feasible with our current understanding of murrelet vocalizations.

Below is a summary of the vocalizations heard from murrelet nests. Most of these vocalizations were heard with the aid of microphones and other recording equipment pointed directly at the nest branch.

Adults and chicks were heard giving soft vocalizations at most nests (n = 14), but loud vocalizations were heard at only seven nests. These calls were given during incubation exchanges and feeding visits. Soft vocalizations include groan or grunt calls (duck-like quacks; previously referred to as alternate calls), whistle calls, and faint peeps. Loud vocalizations consist of keer and groan calls (Nelson and Peck, in press).

During incubation exchanges in Alaska, Oregon, and California, vocalizations were primarily given at the nest as birds arrived or departed the nest limb or during the brief seconds when adults were on the nest limb together. However, an interesting long (13.5 sec) vocal sequence was recorded at one nest in Oregon. First, the incubating adult made soft groans from the nest branch, and at the same time a second adult flying nearby gave short, loud whistle calls. The incubating adult then emitted additional groans, which became increasingly louder and more emphatic. As the flying adult joined the other on the nest limb, one of these two birds gave loud whistle calls.

The frequency of exchanges with vocalizations varied among nests. In Alaska, 10 of 11 incubation exchanges included soft groan and other (undescribed) calls; and adults gave 1-2 loud keer calls when arriving or departing during incubation exchanges on two of 12 mornings (Naslund, pers. comm.). In Oregon, only 10 percent of incubation exchanges included soft or loud vocalizations (n = 59). At a nest in California, adults gave loud, emphatic "keer" and groan calls just before leaving the nest branch on five of 17 incubation exchanges (Naslund 1993a; Singer and others 1991; S.W. Singer, pers. comm.). In addition, several soft grunt calls, sounding like "unh-unh-unh", were heard on one occasion after an adult landed on the nest branch.

During feeding visits in Oregon, Washington, and British Columbia, adults occasionally gave loud keer calls and soft groan and "eeeuh" or "eeea" whistle calls as they flew from the nest branch or while bringing food to a chick at the nest (Hamer, unpubl. data; P. Jones, pers. comm.; Nelson and Peck, in press). The latter calls sounded like a muffled honking that adults gave while holding fish during feeding visits. In addition, in California, a series of soft "chip" notes, duck-like quacks, or short, soft grunts were given after the adult bird arrived to feed the chick (Singer and others 1991; S.W. Singer, pers. comm.). In British Columbia, a one-note bleating call (soft groan) was usually made when two adults were at the nest simultaneously (n = 4 occasions at 1 nest).

Chicks emit a rapid, high pitched begging call during feeding sessions. This begging call was recorded from a captive chick, and heard or recorded from active nests in Oregon and Washington (n = 4). In addition, P. Jones (pers. comm.) described a soft peep or begging call (repeated "puli-puli") that may have been given by the chick during feedings at a nest in British Columbia. We believe begging calls occur during every food delivery, but this sound is not usually audible, especially without microphones placed at or near the nest.

Calls and fly-bys that indicate the impending arrival of an adult may also be given at nest sites. On several occasions in Oregon and Washington, incubating adults or chicks became alert, and chicks gave begging calls, moments before the arrival of the (other) adult (Hamer and Cummins 1991; Nelson and Peck, in press). Naslund (1993a) and Eisenhawer and Reimchen (1990) also mentioned keer and groan vocalizations given by adults prior to incubation exchanges.

Wingbeats have been heard during landings and take-offs from nest branches at all nests, and while murrelets were flying through the tree canopy. Murrelets appear to be able to purposely create the wing sounds, because they are not heard during all landings, take-offs, and flights through the canopy.

Discussion

Marbled Murrelet breeding biology, morphology, and behavior, like that of other alcids, is affected by distance of nest sites from food sources, risk of predation, and other physical and biological factors (Cody 1973; De Santo and Nelson, this volume; Vermeer and others 1987a; Ydenberg 1989). The risk of predation may be the most significant factor in the development of alcid behavior, especially for Marbled Murrelets in their forest nesting environment.

Exposure to predation has influenced the length of incubation shifts, chick feeding frequency, and fledging strategy of alcids (Ydenberg 1989). Predator avoidance may be the driving force behind the long incubation shifts of both the Marbled (24 hours) and the Ancient (48 to 120 hours) Murrelets (*Synthliboramphus antiquus*)(Gaston 1992), as frequent visits to a nest can increase the chances of being discovered by predators and endanger the parents and young. Because of this risk, some species of alcids only feed their chick once in a 24-hour period (nocturnal alcids with semi-precocial young), whereas others (*Synthliboramphus* spp.) produce precocial chicks that are not fed at the nest site. In addition, feeding frequency within a species can vary among nesting colonies, with young in safe sites receiving more food than those in unsafe sites (Ydenberg 1989). Young that receive multiple daily feedings grow faster and fledge earlier than those with lower provisioning rates (Gaston and Nettleship 1981). Early fledging helps to minimize nest mortality (Cody 1971).

Marbled Murrelets have optimized their survival strategies by laying a single egg, feeding their chick relatively frequently, and concentrating most of their activity in the low light levels of dawn and dusk. With multiple daily feedings, murrelet chicks grow relatively rapidly and generally fledge earlier compared with most semi-precocial alcids (De Santo and Nelson, this volume). Despite this earlier fledging, Marbled Murrelet chicks are vulnerable in their open nest sites for 27 to 40 days. Therefore, selection of safe nest sites (Hamer and Nelson, this volume b) and secretive behaviors to avoid predation are also necessary for their survival.

In response to pressures from predation at nesting sites, alcids have developed specific behavioral characteristics (flight behavior, nocturnal activity) and have selected nest sites in inaccessible areas (burrows and crevices). Whereas most alcids are diurnal, nine species, including Marbled Murrelets, are primarily nocturnal or crepuscular (*Synthliboramphus* murrelets, Cassin's [*Ptychoramphus aleuticus*] and Rhinoceros [*Cerorhinca monocerata*] Auklets, Kittlitz's Murrelet, Dovekie [*Alle alle*]). Activity during low light levels (or twilight hours in the high arctic) minimizes predation by diurnal avian predators like gulls and corvids (Ainley and Boekelheide 1990; Gaston 1992; Nettleship and Birkhead 1985). Most alcids nest in inaccessible areas (burrows, crevices) to hide from predators, however, some species nest in the open on rock ledges (Common Murre, Thick-billed Murre [*Uria lomvia*], and Razorbill [*Alca torda*]), and must protect their young by nesting in large colonies or by guarding them during the day (Nettleship and Birkhead 1985).

The *Brachyramphus* murrelets also nest in the open, but they generally nest solitarily. For protection from predation, these murrelets have developed a cryptic plumage and secretive behaviors that allow them to remain hidden. For example, Marbled Murrelets have developed a variety of morphological and behavioral characteristics as defense mechanisms, some of which are shared by Kittlitz's Murrelet and other alcids: (1) concentrating activities in forests during crepuscular periods when light levels are low (i.e., incubation exchanges and feeding visits at dawn and dusk); (2) cryptic coloration of the egg, chick, and adult (breeding plumage); (3) rapid flight into and away from the nest; (4) visiting the nest briefly during incubation and less so during feeding of young; (5) "freezing" behavior exhibited by adults after landing at the nest during incubation exchanges and feeding visits; (6) remaining relatively silent on the nest branch (vocalizations are muted); (7) low, motionless posture of the incubating adult; (8) well developed thermoregulatory capabilities of the chick shortly after hatching allowing for minimal parental care; (9) chick remaining motionless for long time periods; (10) retention of down feathers by chick concealing bright juvenal plumage until just prior to fledging; (11) young fledging just after dusk; (12) long distance indirect flights through the forest canopy to access nests; (13) fly by inspections of nests and nesting area by adults before a nest visit; (14) flying in groups within and above the nesting grounds, which may provide protection from predators and serve as an important social function; and (15) selecting nest platforms with high levels of vertical or hiding cover (see Binford and others 1975; Hamer and Cummins 1991; Hamer and Nelson, this volume b; Naslund 1993a; Nelson and Peck, in press; Sealy 1974, 1975a; Singer and others 1991). The number and diversity of these adaptations suggests that predation has been a selective factor on Marbled Murrelets in the past. Given these predator avoidance strategies, one would expect predation at nests to be low. However, Marbled Murrelets are still vulnerable

to seemingly high rates of predation (see Nelson and Hamer, this volume b). Predation rates on alcid nests are often higher in areas where predators have been introduced, habitat has been modified, or where birds are disturbed by humans (Gaston 1992; Murray and others 1983; Nettleship and Birkhead 1985).

Observations of Marbled Murrelet behavior at nest sites have provided us with a wealth of new information that was not available prior to 1980. Their secretive behavior, rapid flights in low light levels, and the inaccessibility of many of their nests, however, has limited our opportunities to study many aspects of their biology. The paucity of information on some aspects of Marbled Murrelet breeding biology minimizes the accuracy with which land managers can maintain or create suitable habitat for this species. In addition, their secretive behaviors limit our ability to identify nesting sites, especially in stands that contain few birds. Continued research on the biology, demography, and habitat selection of this species should be conducted, in addition to determining the effects of different forest management strategies on nesting success of this unique seabird.

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