BEHAVIOR OF MARBLED MURRELETS AT NINE NEST SITES IN OREGON

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ABSTRACT—Between 1990 and 1992, 9 active marbled murrelet (*Brachyramphus marmoratus*) tree nests were found in western Oregon. Incubation was shared equally between adult birds with each bout lasting approximately 24 hr. Incubation exchanges took place during a relatively narrow time period, 30 to 8 min prior to official sunrise, and on average lasted 16 sec. Feedings occurred primarily at dawn, but adults also returned to feed nestlings at dusk and occasionally during mid-day. In contrast to incubation exchanges, the time adults arrived at nests to feed nestlings varied, both within and among nests, and occurred within 104 min and 90 min of official sunrise and sunset, respectively. The duration of feeding visits was also highly variable and ranged from 18 sec to 46 min in length ($\bar{x}$ = 16.7 min, SE = 1.3). Weather influenced arrival times of adults during incubation and nestling stages; on average birds arrived earlier on clear (≤ 75% cloud cover) than cloudy (> 75%) mornings. Murrelets at each nest used consistent flight paths when entering and exiting nest trees. Soft vocalizations from adults ("groan" and "whistle" calls) and chicks ("begging") were heard at all nests during incubation and feeding visits. In contrast, loud calls ("keer" and "groan"), which were frequently uttered by adults in flight, were uncommon and detected at only 3 nests. The behaviors observed at murrelet nests were secretive and probably designed to minimize detection by predators. While these behaviors pose challenges for locating nests in forests, knowledge of marbled murrelet activity patterns and behaviors associated with nesting will aid in monitoring efforts and in identifying areas that are used for nesting.

The behavior of marbled murrelets (*Brachyramphus marmoratus*) at nest sites is poorly known. The first marbled murrelet ground and trees nests were not found until 1959 and 1974, respectively (Day et al. 1983, Binford et al. 1975). Locating nests for study has proved difficult because murrelets nest solitarily or in loose aggregations, and are active primarily in low light levels (Sealy and Carter 1984, Eisenhawer and Reimchen 1990, Rodway et al. 1993, Naslund et al. 1995, Nelson and Hamer 1995a). In addition, tree nesting murrelets nest on naturally occurring branch platforms high in the canopies of large, mature conifers (Singer et al. 1991, 1995, Nelson and Hamer 1992, Hamer and Nelson 1995a, Jordan and Hughes 1995, Kerns and Miller 1995, Manley and Kelson 1995, Naslund et al. 1995). The marbled murrelet was recently listed as a threatened species in Washington, Oregon, and California (U. S. Fish and Wildlife Service 1992) and information on its activity patterns and behaviors at nests is needed to develop monitoring protocols and define future research directions.

Prior to 1992, the characteristics of marbled murrelet nests and nesting sites had been documented and described at 10 ground nests in Alaska and 6 tree nests from southcentral Alaska to central California (Binford et al. 1975, Simons 1980, Hirsch et al. 1981, Day et al. 1983, Johnston and Carter 1985, Carter and Sealy 1987b, Quinlan and Hughes 1990, Singer et al. 1991). However, information on the behavior and activity patterns of murrelets at nests was summarized at only 4 of these sites. At 2 ground nests in Alaska, Simons (1980) and Hirsch et al. (1981) described the timing and frequency of feeding visits and measured growth of nestlings. More recent observations of 2 tree nests in central California (Singer et al. 1991, Naslund 1993) provided details on the timing and frequency of nest visits, and descriptions of adults and chicks during feeding bouts at the nest. Additional information on

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murrelet nesting chronology (30-day incubation period and 28-day nestling period), clutch size (1), and developmental stage of nestling at hatching (semi-precocial) are known from observing and collecting murrelets at sea, studying nests, and summarizing anecdotal observations of grounded chicks and fledglings (Sealy 1973, 1974; Simons 1980; Hirsch et al. 1981; Hamer and Nelson 1995b). While these studies provided some information, additional details are needed before the behavior of marbled murrelets at nests can be fully understood.

No active nests were located in Oregon prior to 1990, although 2 chicks and 2 fledglings had been found on the ground at inland sites (summarized in Nelson et al. 1992). Between 1990 and 1993, intensive surveys of murrelet activity at inland locations and implementation of methods developed specifically for locating nests, resulted in the discovery of the first nests in Oregon. Eleven nests were located, 9 of which were active (contained an egg or chick) when found. Our objectives were to monitor and describe the behaviors of adult and nestling murrelets at and near their nests during the breeding season. This paper summarizes behaviors of adults, during incubation and feeding of nestlings and while flying to and from nest sites, behavior of nestlings, and vocalizations of adults and nestlings.

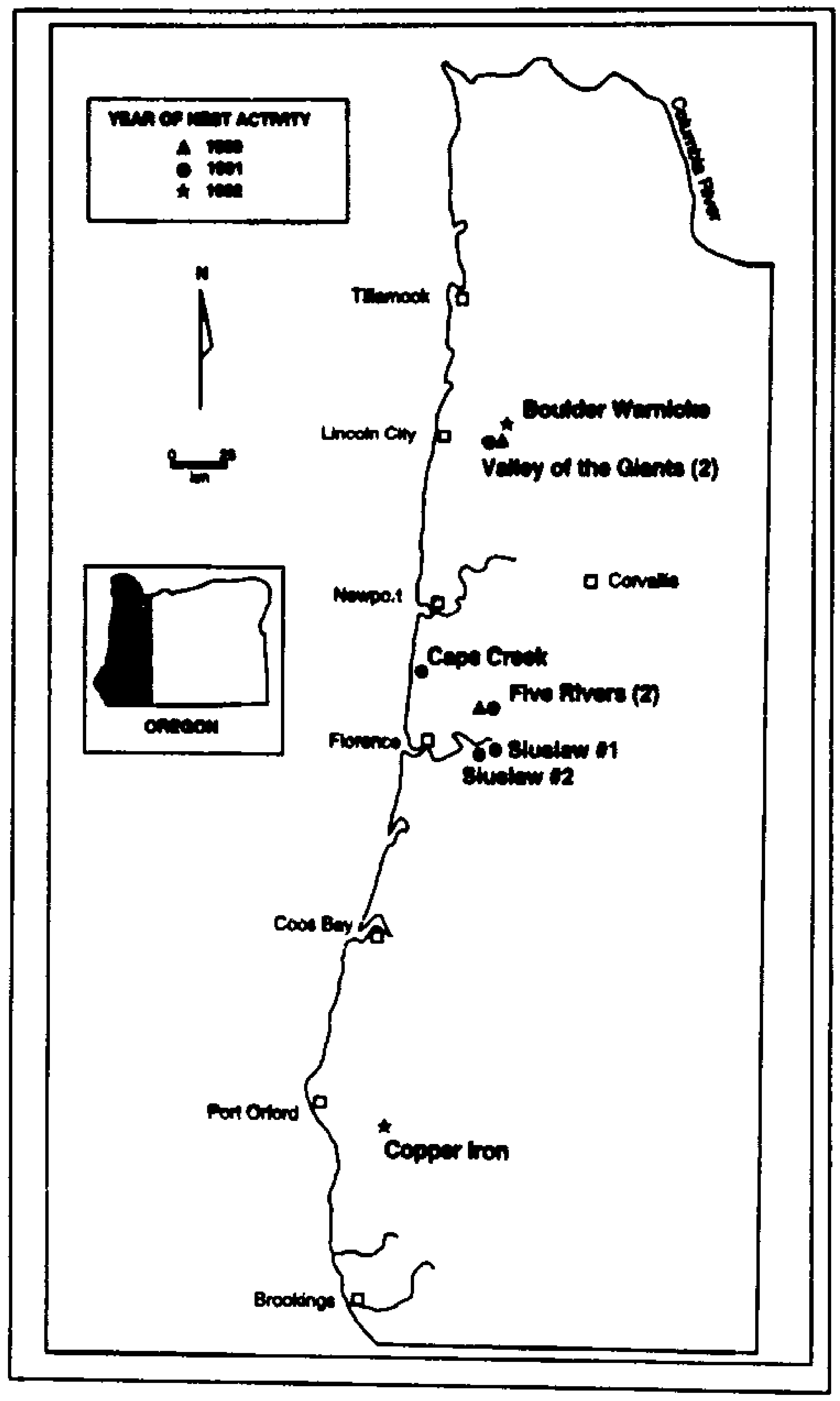

FIGURE 1. Map of coastal Oregon showing the location of 9 marbled murrelet nests found between 1990 and 1992.

METHODS

Nest sites were located in the Coast Ranges and Siskiyou Mountain provinces of western Oregon (Fig. 1). These provinces are characterized by rugged, mountainous terrain, with steep slopes and deeply cut river and creek drainages. Elevations range from sea level to > 1200 m. These areas are primarily forested, although they have been intensively logged since the early 1900's. The landscape consists of a mosaic of young (trees < 46 cm dbh) and mature forests (trees ≥ 46 cm dbh). Old-growth trees (≥ 81 cm dbh) and forests are generally restricted to small, isolated patches. Douglas-fir (*Pseudotsuga menziesii*) is the dominant canopy-forming tree species in the north, whereas a variety of evergreen species are dominant in the south (Franklin and Dyrness 1973).

Seven nests were found by observing birds landing in trees, and 2 nests were located by finding eggshells on the ground. Dawn and dusk surveys (Paton et al. 1990) were used to find areas where murrelets were flying through the canopy. Observers also listened for sounds of murrelets landing or departing from trees as cues for narrowing down our search areas. Once activity areas were located, 2–4 observers were stationed around groups of trees to pinpoint branches where birds were landing. Observers looked for eggshells by systematically or randomly searching around the base of suitable nest trees (limbs > 18 cm dbh) in areas where birds were seen flying through the canopy.

Once a nest tree was located, adjacent trees were climbed to determine nesting stage (incubation or nestling) and nest location. Subsequent observations of nest trees were made primarily from the ground, but where activity on the nest limb could not be observed from the ground, monitoring was also conducted from within the canopy of adjacent trees. Spotting scopes and recordings from a video camera were used to observe and document behavior at nests. Sound recording equipment (Marantz PMD-221 and 430 portable cassette tape recorders with omnidirectional Sennheiser ME-20 [with Sony 33 cm parabolic dish] and ME-88 microphones, respectively) was used to record vocalizations and verify landings and departures from the nest. Disturbance was minimized by stationing observers > 25 m from nest trees.

Nest monitoring was primarily conducted during the sunrise activity period (45 min before, to 90 min after, official sunrise [SR −45 to SR +90]), although all nests were monitored periodically (1–5 nights/wk) at sunset (30 min before, to 45 min after, sunset [SS −30 to SS +45]), and some were monitored continuously ($N = 2$ nests) or occasionally ($N = 3$ nests) during daylight hours (SR +90 to SS −30; official sunrise and sunset hours were determined using the Nautical Almanac for each year). The 2 nests located in 1990 were watched nearly every day from the time of discovery until the nests were no longer active, while the other nests were watched more discontinuously. Nest trees were also monitored in years subsequent to discovery (1991–1993) to document reuse. Monitoring in these cases involved conducting intermittent dawn surveys and climbing trees following the breeding season to look for fecal rings, eggshell fragments, landing pads, or other evidence of nesting.

Data collected at all nests included the time of day adult birds arrived for incubation duties or nestling feeding visits (referred to as timing), duration of feeding visits, behavior of adults and chicks on or near the nest (resting, feeding, flight), routes adults used to enter and exit nest trees, and vocalizations heard near or on nests. In addition, close-range observations of adults and chick on the nest were made by observers, tree climbers, or video cameras at 5 nests, 2 during incubation (Five Rivers 1990 and Valley of the Giants 1990), and 4 during the nestling stage (Valley of the Giants 1990, Siuslaw River #1, Boulder Warnicke, and Copper Iron). These detailed observations provided additional information on the length of resting or activity bouts, behavior before, during, and after incubation exchanges and feeding visits, fish species fed to nestlings, and nestling development and plumage changes.

Temperature, wind speed, cloud cover, and precipitation were recorded during each observation period. Degree of cloud cover was classified as clear (≤ 75%) or cloudy (> 75%) and was based upon conditions at the beginning of each observation period. Light levels (footcandles) at the time of incubation exchanges or morning feeding visits were recorded at 4 nests, and were measured from the ground in openings near nest trees using Sekonic and Quantum Instruments illuminometers.

Data on the timing and duration of incubation exchanges and feeding visits were summarized (means, SE, range) for all days, and for clear and cloudy days. The amount of cloud cover was compared to the arrival time of adults at nests, and the duration of feeding visits was compared among nests and between sunrise and sunset. In addition, the time adults arrived at nests for incubation exchanges and feeding visits was compared to the location of nests with respect to distance inland. Because the length of dawn observation periods each day varied within and among nests, data included in comparisons of dawn activity were limited to the longest observation period used consistently among all nests. Thus, the morning survey period lasted 90 min (SR −45 to SR +45). However, on occasion the first morning feeding visit occurred after the 45-min limit had ended (+100 min in some cases). In these situations, the observation period was extended to include the time of the first feeding visit. No limits were placed on evening observation periods as they were consistent among all nests (SS −30 to SS +45).

RESULTS

Nine active murrelet nests were located between 1990 and 1992. Eight of these nests were found in Douglas-fir trees and 1 was located in a Sitka spruce (*Picea sitchensis*) tree (Table 1). Nests were active over a period of about 6 mo, with the earliest nesting activity recorded on 14 May 1991 (egg stage; Valley of the Giants nest) and the latest ending on 2 September 1991 (predation on chick; Siuslaw River #2 nest). However, at the Cape Creek nest, a pair of birds was observed landing on the nest limb on 3 occasions in early May. After an absence of approximately 2 wk they returned to lay an egg at the site (23 May).

Four nests were located while in the egg stage and 5 were found during the nestling stage. Chicks hatched from 2 of the eggs, while 2 eggs disappeared from nests (Table 1). Young were believed to have fledged from 3 nests based on nestling development, loss of down feathers and presence of juvenal plumage (Carter and Stein 1995), and behaviors exhibited by the nestling, such as pacing on the nest limb (Nelson and Hamer 1995a). The actual fledgings were not observed because of darkness. Albumen or blood on eggshell fragments, or the premature disappearance of the egg or chick, suggested that predation caused the failure of 5 nests (Nelson and Hamer 1995b).

The 4 nests active during the egg stage were observed for an average of 16 days (range 7–25), and the 7 nests active during the nestling stage were watched for an average of 10 days (range 6–17). No nests were observed for the entire incubation period. One nest was monitored for all or most of the nestling period; the chick at the Copper Iron nest was observed for

TABLE 1. Characteristics of 9 marbled murrelet nests found in Oregon between 1990 and 1992.[a]

Nest location	Year	Distance from coast (km)	Habitat type	Nest tree	Status when found	Dates of observation (no. days)[b]	Suspected outcome
Five Rivers	1990	26	mature/ old-growth	Douglas-fir	egg	19 May–15 Jun (23)	chick fell off nest
Valley of the Giants	1990	25	old-growth	Douglas-fir	egg	12 Jul–06 Aug (25)	predation on chick
Cape Creek	1991	2	mature/ old-growth	Sitka spruce	egg	23 May–14 Jun (9)	predation on egg
Five Rivers	1991	26	mature/ old-growth	Douglas-fir	nestling	14 Jun–22 Jun (8)	chick fledged
Siuslaw River #1	1991	40	mature/ old-growth	Douglas-fir	nestling	13 Aug–29 Aug (17)	chick fledged
Siuslaw River #2	1991	39	mature/ old-growth	Douglas-fir	nestling	20 Aug–02 Sep (6)	predation on chick
Valley of the Giants	1991	25	old-growth	Douglas-fir	egg	14 May–04 Jun (7)	predation on egg
Boulder Warnicke	1992	25	old-growth	Douglas-fir	nestling	17 Jun–07 Jul (8)	predation on chick
Copper Iron	1992	27	old-growth	Douglas-fir	nestling	09 Jun–07 Jul (13)	chick fledged

[a] Two additional nest platforms were found at the Five Rivers 1991 and Valley of the Giants 1992 nest trees in 1992 and 1993, respectively, but they did not contain an egg or chick.

[b] Actual number of days of observation between dates listed.

40 days, suggesting it was found shortly after hatching.

None of the active nest platforms in this study were reused in subsequent years (1991–1993). However, 2 of the nest trees were used for nesting in more than 1 yr. Eggshells were found at the Five Rivers 1991 nest tree in 1993 on a nest platform that was inactive in 1991 (tree included at least 2 nest platforms). Based on the degree of weathering, this nest was assumed to have been active in 1992. Additionally, the 1992 Valley of the Giants nest tree had 3 nest platforms, 1 that was used for nesting in 1992 (failed) and 1 in 1993.

Behavior During the Egg Stage

Adult birds equally shared incubation duties and each brooding bout lasted approximately 24 hr. Each morning near sunrise, the non-incubating adult flew to the nest tree and landed on an established landing area (where the moss or duff had been flattened or removed by repeated landings) on or adjacent to the nest platform, to replace the adult currently incubating the egg. Nest exchanges often corresponded with the first vocalizations detected each morning within the stand and occurred during low light levels (< 1 footcandle). Adults overlapped little at the nest during the exchange; the incubating bird usually left the nest platform within seconds after the arrival of the incoming adult ($\bar{x}$ = 16.3 sec, SE = 2.8, N = 42 exchanges). On 2 occasions incubating adults were observed to change behavior or vocalize on the nest limb just prior to arrival of the other adult. Wingbeats were often heard as birds landed on or took flight from the nest limb. The arriving adult generally remained still for up to 5 min on the landing pad before settling down on the egg, and remained motionless (for > 90% of the time) and quiet throughout the incubation bout. Exchanges were observed on all days that nests were watched, except one, but we may have missed that exchange because of limited visibility during rain. Although observations of nests throughout the day were limited, an egg at the Cape Creek nest was observed unattended for 3–4 hr on 2 occasions by a climber in an adjacent tree. Ground observers confirmed that the adult was not flushed from the nest by the climber.

All incubation exchanges took place 30–8 min before official sunrise (Table 2). Weather appeared to influence the time that incoming birds arrived at nests; the mean exchange time for all nests combined was earlier on clear than

TABLE 2. Summary of times (min in relation to sunrise) adult marbled murrelets exchanged incubation duties during the morning observation period (±45 min around sunrise). Times are separated into clear and cloudy periods.

Nest location	Clear				Cloudy			
	N	Earliest	Mean (SE)	Latest	*N*	Earliest	Mean (SE)	Latest
Five Rivers: 1990	2	−26	−22.0 (4.0)	−18	14	−22	−14.9 (1.1)	−9
Valley of Giants: 1990	14	−30	−23.0 (1.6)	−8	4	−20	−19.5 (0.3)	−19
Cape Creek: 1991	2	−22	−18.0 (4.0)	−14	7	−23	−17.3 (1.7)	−9
Valley of Giants: 1991	4	−21	−17.8 (1.7)	−14	2	−18	−14.0 (4.0)	−10
All nests combined	22	−30	−21.5 (1.2)	−8	27	−23	−15.7 (0.8)	−9

cloudy mornings (Fig. 2A; $\bar{x}$ = SR −21.5 and SR −15.7, respectively, N = 49 observations). Although exchanges were consistently earlier on clear mornings at each nest, differences among nests were found. For example, the mean exchange time at the Valley of the Giants 1990 nest was earlier on cloudy mornings than it was on clear mornings at the Cape Creek and Valley of the Giants 1991 nests (Table 2). However, there appeared to be no difference in the average time of incubation exchanges based on the distance that nests were located from the coast (Tables 1 and 2).

Behavior During the Nestling Stage

Adults were considerably more active (turning and standing frequently) just prior to hatching of the chick than earlier in the incubation stage. They were also restless during brooding of the nestling. Brooding by an adult was observed only on the first day after hatching (N = 2 nests). Subsequently, and at all other nests with chicks, adults were observed at the nest only while feeding the nestling.

Most feeding visits were observed at dawn or dusk, but visits were also observed at other times of the day. Overall, visits were observed 45 times within 104 min of sunrise (Fig. 2B), 25 times within 90 min of sunset (Fig. 3), and 5 times during mid-day (at 0941, 1009, 1248, 1311, and 1355 hr at the Siuslaw #1 and Copper Iron nests). At the 3 nests where the chick could be observed from the ground, adults fed chicks on 22 of 23 dawn observation periods and 13 of 17 dusk observation periods. These chicks were fed 1–5 times per day ($\bar{x}$ = 2.2, SE = 0.3, N = 45 observations; includes only nests monitored at dawn and dusk on all observation days).

Adults generally arrived individually at nests, but sometimes they both provided fish to chicks at dawn and dusk within 60 min of each other. These consecutive feeding visits were ob-

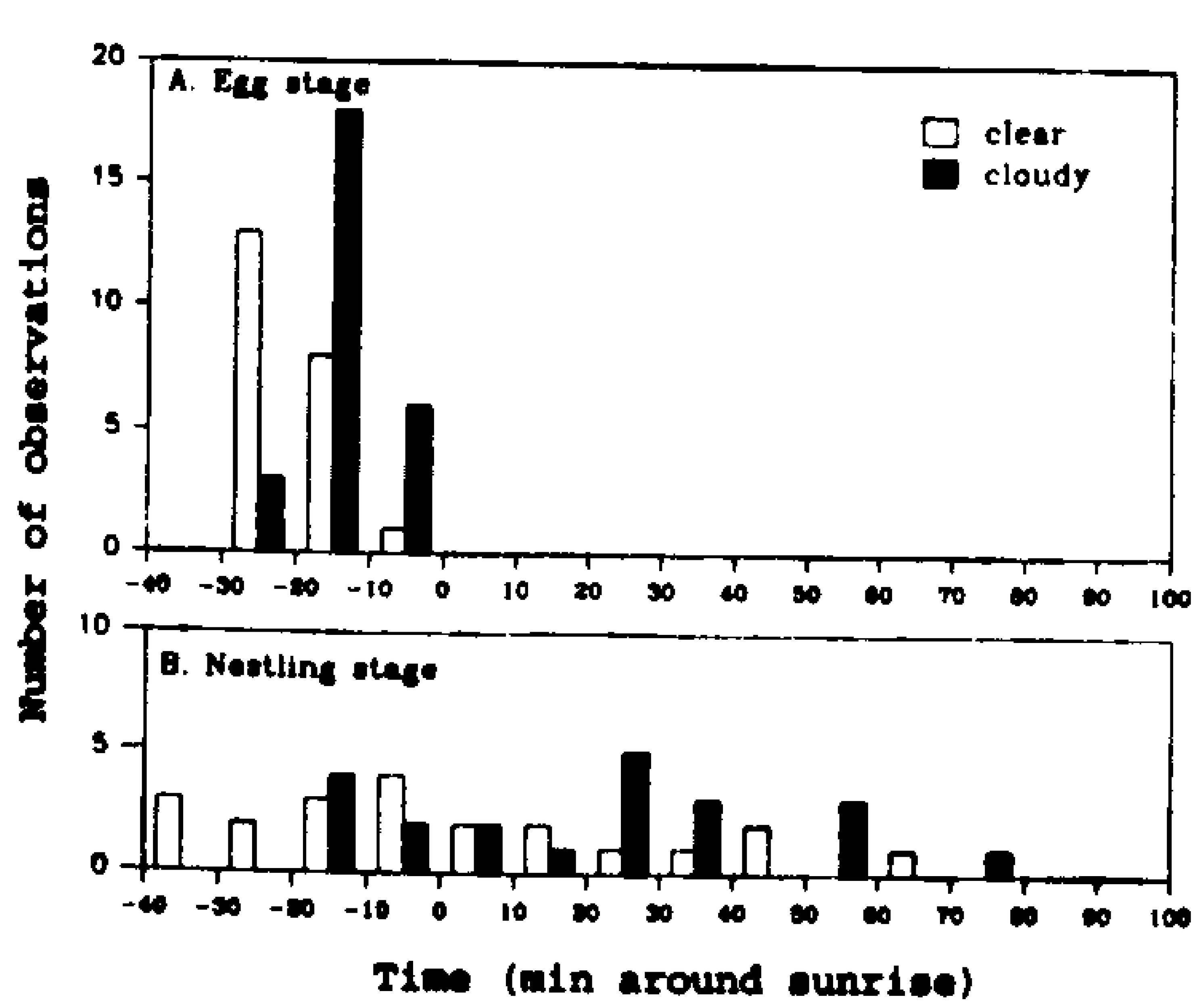

FIGURE 2. Distribution of morning arrival times at the nest by adult marbled murrelets during (A) the egg stage on clear (N = 22) and cloudy (N = 27) days, and (B) nestling stage on clear (N = 21) and cloudy (N = 21) days. Three nestling stage observations were not included because they were second feeding visits and occurred > 45 min after official sunrise.

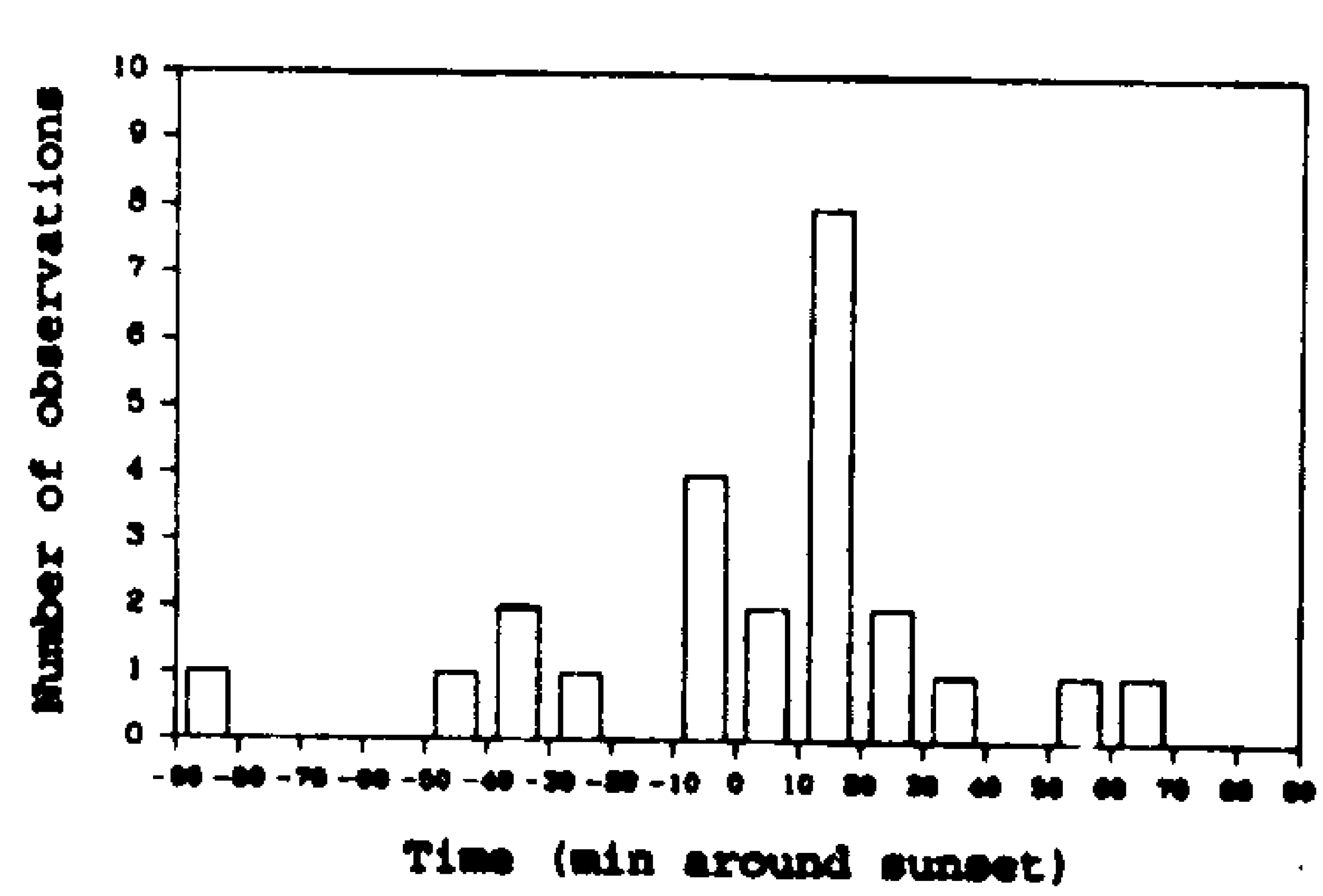

FIGURE 3. Distribution of arrival times at the nest by adult marbled murrelets bringing food to nestlings during the evening observation period (N = 24). One sunset feeding was not used because exact time of arrival was unknown.

TABLE 3. Summary of times (min in relation to sunrise) adult marbled murrelets arrived at nests to feed nestlings during the morning observation period.[a] Times are separated into clear and cloudy periods.

Nest location	Clear				Cloudy			
	N	Earliest	Mean (SE)	Latest	N	Earliest	Mean (SE)	Latest
Five Rivers: 1990	1		−32.0		5	−10	+15.2 (6.4)	+25
Valley of Giants: 1990	8	−33	−7.4 (6.6)	+24	1		−15.0	
Five Rivers: 1991	2	−27	−19.0 (8.0)	−11	2	−1	+27.0 (28.0)	+55
Siuslaw #1: 1991	4	−36	+3.5 (16.3)	+42[b]	9	−18	+20.3 (11.0)	+79
Siuslaw #2: 1991					2	+29	+42.5 (13.5)	+56
Copper Iron: 1992	1		−17.0		1		+37.0	
Boulder Warnicke: 1992	5	−7	+30.4 (12.2)	+65	1		+4.0	
All nests combined	21	−36	+1.0 (6.1)	+65	21	−18	+20.2 (5.9)	+79

[a] Morning observation period restricted in this summary to ±45 min around official sunrise except where first visit occurred after this time. Three second feeding visits were not included because they occurred >45 min after official sunrise.
[b] Second feeding visit of morning; first visit at +12 min after sunrise.

served at least once at 5 of the 6 nests. Overall, 20 pairs of consecutive visits were seen: 14 within 79 min of sunrise, 1 at mid-day, and 5 within 56 min of sunset. The time of arrival at the nest was determined for both birds on 13 of these occasions and the average time interval between these visits was 28.5 min (SE = 4.5, range 4.0–56.0). Twice at the Siuslaw #1 nest, both adults arrived simultaneously. However, on both occasions, 1 adult immediately left the nest, circled above the stand, and returned to the nest after the other adult had departed.

In contrast to the relatively narrow distribution of exchange times during egg incubation (Fig. 2A), the time at which adults arrived at the nest to feed nestlings at dawn was highly variable, both within and among nests ($\bar{x}$ = 10.6, SE = 4.5, range SR −36–SR +79, N = 42 observations; Fig. 2B, Table 3). At dawn, mean arrival times for feeding visits on clear mornings were earlier than on cloudy mornings ($\bar{x}$ = SR +1.0 and SR +20.2, respectively; N = 42 observations; Table 3). However, mean arrival times at the Boulder Warnicke nest were earlier on cloudy than clear mornings (SR +4.0 *vs.* SR +30.4). Evening feeding visits were observed at 4 of the 6 nests. The mean arrival time of evening visits was near sunset ($\bar{x}$ = SS +4.0, SE = 6.6, N = 24), ranging from SS −90 to SS +62 (Fig. 3). Similar to times of incubation exchanges, there appeared to be no correlation between average arrival times for dawn and dusk feedings and distance between nests and the coast (Tables 1 and 3).

After arrival with a single fish held in their bill, adults generally stood erect and relatively motionless on the landing pad for up to 10 min before approaching the chick. During most observations (82%, N = 61), adults stayed on the nest for 5–30 min before releasing the fish to the chick. Adults remained motionless at the chick's side during this time, whereas nestlings were often heard or seen "begging" (*e.g.*, calling, poking at fish, stroking the adults neck with its bill) throughout this period. Adults generally departed from the nest immediately after giving the fish to the nestling. Nestlings held the fish for 5 sec to 2 min ($\bar{x}$ = 15.2 sec, SE = 7.2, N = 16 feedings) before swallowing it. Video recordings and direct observations of feedings revealed that nestlings were fed Pacific sandlance (*Ammodytes hexapterus*) and Pacific herring (*Clupea harengus*), but may also have been fed other prey species that were not identified.

The length of time adult birds spent at the nest during feeding visits was variable within and among nests (Table 4). Many visits (N = 22 observations) lasted more than 20 min, but individual visits ranged from 18 sec to 46 min ($\bar{x}$ = 16.7 min, SE = 1.3, N = 61). No pattern was found between dawn and dusk, except at the Siuslaw #1 nest where the mean length of visits were longer near sunrise ($\bar{x}$ = 26.4 min, SE = 2.7, N = 11) than sunset ($\bar{x}$ = 17.1 min, SE = 2.1, N = 9).

Nestlings remained still during more than 80% of the day, but occasionally picked at nesting substrate, changed position on the nest platform, snapped at flying insects, begged in the presence of adults, preened, stretched, and flapped their wings. On 5 occasions at 2 nests, chicks were observed to rapidly change their behavior (*e.g.*, from sleeping to awake and rest-

TABLE 4. Summary of length of time (min) adult marbled murrelets spent at the nest during feeding visits at sunrise, at sunset, and for all feeding visits combined.[a]

Nest location	Sunrise *N*	Sunrise Mean (SE) (range)	Sunset *N*	Sunset Mean (SE) (range)	Combined *N*	Combined Mean (SE) (range)
Five Rivers: 1990	6	7.9 (2.0) (2.9–14.2)	1	5.1	7	7.5 (1.8) (2.3–14.2)
Valley of the Giants: 1990	6	8.4 (3.5) (0.2–21.0)	6	4.1 (0.6) (0.3–7.0)	12	6.2 (1.8) (0.2–21.0)
Five Rivers: 1991	2	10.0 (3.0) (7.0–13.0)			2	10.0 (3.0) (7.0–13.0)
Siuslaw #1: 1991	11	26.4 (2.7) (11.0–45.0)	9	17.1 (2.1) (9.0–26.0)	24[b]	22.3 (1.7) (9.0–45.0)
Siuslaw #2: 1991	2	26.0 (4.0) (22.0–30.0)			2	26.0 (4.0) (22.0–30.0)
Copper Iron: 1992	1	25.0			1	25.0
Boulder Warnicke: 1992	7	19.4 (5.0) (4.0–46.0)	6	20.6 (2.9) (11.0–30.0)	13	19.9 (2.9) (4.0–46.0)

[a] Number of feedings with known duration less than total number of feedings.
[b] Includes 4 mid-day observations (1009, 1248, 1311, and 1355 hr); 1 mid-day observation (0941) did not include duration data.

less) just prior to arrival of an adult. Nestlings defecated around the perimeter of the nest cup; after about 20 days the accumulated feces created a thick ring. Three-wk old chicks began to loose the down feathers on their belly, forehead and around their mandibles, revealing their black-and-white juvenal plumage. Just prior to fledging, behaviors such as preening and flapping increased in frequency. Remaining down was preened or scratched off 24–48 hr before they left the nest. Nestlings fledged in the evening in low light levels (*e.g.*, between SS +55 on 29 August and SR −45 on 30 August at the Siuslaw #1 nest).

Flight Behavior

Murrelets at each nest used consistent flight paths through the forest when approaching or exiting their nest. Although the direction of arrival and departure of individual birds often differed, the routes used by each bird tended to be consistent among visits. Where available, birds appeared to use open "corridors" (*e.g.*, creeks, rivers, ridges, roads) to approach or leave the nest. The location of foliage adjacent to the nest limb also appeared to influence the direction of approach and departure. Murrelets generally flew towards each nest at heights lower than the nest branch (as low as 5 m above the ground), rising to "stall" just prior to reaching the landing pad. Landings could sometimes be heard from the ground. Occasionally, birds approached the nest at nest-branch level, which caused them to crash through the foliage to land or to abort the landing. Outgoing birds dropped 5–30 m before ascending above the forest canopy. After taking flight, birds flew directly or circled away from the nest tree.

Flight patterns observed in association with nests and nest stands included flights through, into and out of the forest canopy, landing in trees, calling from stationary locations, circling through or above the forest canopy, and flying straight above or below the canopy. Landings and departures in trees near known nests were often seen throughout the breeding season, although most of this activity occurred in July. In addition, birds were observed landing on nest limbs or other limbs in known nest trees in years subsequent to discovery. For example, a bird was observed landing on the Valley of the Giants 1990 nest limb in 1992 and 1993, but birds did not nest there in those years.

Murrelets sometimes also created sounds with their wings during landings and take-offs from trees, and while flying through and over the canopy. In addition, on 3 occasions, a rapid, steep dive combined with a loud sound, similar to a jet engine of an airplane, was heard adjacent to nests.

Vocalizations From the Nest

Murrelets frequently vocalized when flying over and through nesting sites and from nests.

However, vocalizations given while flying were loud, whereas vocalizations given on nests were usually muted (soft) and difficult to detect without ground- or tree-based microphones, or by observers in trees adjacent to the nest. Soft vocalizations ("groan" and "whistle" calls) were heard at all 9 nests, and were given by lone adults or between 2 adults at the nest, and by chicks "begging" for food. Loud calls ("keer" and "groan") from the nest were uncommon, but were heard at 4 nests. These loud calls were thought to have only come from adults and were generally associated with birds entering or exiting the nest tree. Soft and loud vocalizations were heard at 3 of the 4 nests watched during the egg stage and all 7 nests watched during the nestling stage. Loud vocalizations also were recorded from a pair of birds at the Cape Creek nest limb about 14 days before an egg was laid.

Adult vocalizations.—During incubation, adults vocalized when exchanging duties with their mates. Calls were heard while both adults were in the nest tree, just before the incubating bird departed. For example, at the Valley of the Giants 1991 nest, we recorded a 13.5-sec sequence of vocalizations associated with an exchange. A single bird on the nest gave 6 soft "groan" calls. Overlapping these calls, a second bird uttered a series of loud "keer" calls while flying toward the nest. The calls continued until the incoming bird joined the incubating bird at the nest. Four soft "whistle" calls were then heard and 16 sec later the incubating bird silently left the nest.

During the nestling stage, adults holding fish in their bills at the nest often produced muted, nasal sounding "groan" calls. At 1 nest, an adult gave 3 series of soft "groan" calls (of 8, 6, and 8 calls, respectively) that lasted about 4 min. Approximately 1 min after the last series of calls, the adult released the fish to the chick and quietly departed from the nest. Similar vocalization events during evening feeding visits also were heard on 3 occasions at other nests.

Nestling vocalizations.—Nestling calls were heard at least once from each nest that contained a chick. Most calls were made when an adult carrying food was present. For example, on 23 August at the Siuslaw #1 nest, the nestling uttered an incessant "squeaky, rubber-like begging" call as it stroked the throat of the adult or tugged at the fish in the adult's bill during a mid-morning (1034 hr) feeding visit. Soft vocalizations were heard also from chicks on several occasions (four times at 2 nests) moments before the arrival of an adult at the nest.

Discussion

Nesting Chronology

In Oregon, active nests were found between 14 May to 2 September. Based upon a 30-day incubation and 28-day nestling periods (Sealy 1974, Simons 1980, Hirsch et al. 1981), nesting was estimated to have spanned a period of 149 days, from 26 April to 21 September. In comparison, the murrelet nesting season was estimated to span at least 170 days in California (mid-March to late September) and 106 days in Alaska (mid-May to late August) based on similar incubation and nestling periods (Hamer and Nelson 1995b). However, in Oregon, the Copper Iron chick was monitored over 40 days, which is the longest time a chick has been recorded at a nest. Based on a 40-day nestling period, the length of the nesting season would be longer than estimated above.

The presence of nesting activity throughout the spring and summer months for all known nests suggests that there is little synchrony among pairs. This lack of synchrony was clearly shown in Oregon during 1991, as the activity period of 5 nests ranged from 14 May to 2 September, and young fledged or were estimated to have fledged over a period of 49 days (22 June–9 September). Sealy (1974) estimated that egg laying occurred over 40–50 days in the Queen Charlotte Islands, British Columbia, also indicating a prolonged nesting period. In contrast, the timing of nesting of other alcid species is often more synchronous (Nettleship and Birkhead 1985, Ainley and Boekelheide 1990). For example, colonial common murres (*Uria aalge*) nesting in coastal Oregon sites and in the Farallon Islands, California, initiate nesting, and ultimately complete rearing young at the colony, within 10–21 days of each other (Ainley and Boekelheide 1990; R. W. Lowe, pers. comm.). Synchronous nesting of common murres, as well as other colonial and semi-colonial nesting alcids, is generally thought to be driven by either a seasonal increase in food availability or as protection against predation (Nettleship and Birkhead 1985, Ainley and Boekelheide 1990). It is not clear why marbled murrelet nests are not as synchronous as other alcids, but it may be related to differences in the time at which physiological preparedness for nesting occurs. As murrelets feed on a variety of fish and invertebrate species throughout the year (Sealy 1975b, Sanger 1983, Carter 1984, Burkett 1995), changes in the availability of individual prey species may not affect timing of nesting. Alternatively, birds may initiate nesting at similar times each year, but because of double-clutching or renesting after a failed attempt, the nesting period may be prolonged. Too little is known about the nesting biology of murrelets to identify the mechanism(s) underlying the prolonged nesting season.

Activity Patterns

Knowledge of the relationship between activity at marbled murrelet nests and general activity at nesting sites is important for developing nest-search techniques and implementing forest monitoring projects. At dawn, murrelets arrived at nests during low light levels, generally between SR −33 and SR +65, although sometimes as late as SR +104 on cloudy days. Birds returning to their nests were among the first to arrive in the forest each morning, and their arrival often corresponded with the first auditory detections. Breeding birds may vocalize loudly when approaching or flying through nesting stands, but then, in general, become more secretive and silent in close proximity to their nest trees. Arrivals at nests did not appear to be affected by distance inland, which suggests that murrelets nesting farther inland leave the ocean earlier (in lower light levels) or fly faster to arrive at nest sites near sunrise. While adults left nests almost immediately after incubation exchanges and within 46 min of initiating feeding visits, detections in forest sites often continued for long periods of time during the dawn activity period (up to 200 min after sunrise). Nesting birds probably fly and circle in the vicinity of their nests prior to returning to the ocean accounting for this prolonged activity. In addition, because groups up to 10 birds were often observed during dawn surveys, nesting birds may form flocks with other nesters or non-breeding murrelets to circle and vocalize over and within the forest. Although murrelets apparently nest solitarily (one nest per tree or group of trees; but see Harris 1971), this group behavior suggests they may be semi-colonial in forests. Social flight behavior, including circling over colonies and vocalizing loudly, is common for many alcids (*e.g.*, crested auklets [*Aethia cristatella*]; see Jones 1993).

At dusk, few murrelets were heard or seen, and those that were observed generally flew individually and directly in and out of the nesting area. The extended activity periods (beyond the timing of feeding visits) and group circling behavior recorded at dawn were not observed during dusk surveys. Evening activity appeared to be limited to birds currently feeding nestlings. Therefore, in addition to dawn surveys, evening surveys could be used to pinpoint the locations of active nests.

Marbled murrelet nestlings were fed up to 5 times a day in this study and up to 8 times a day elsewhere (P. H. Jones, pers. comm.). The timing of feedings at dawn (a less narrow arrival period than during incubation) and the number of feedings per day may be influenced by the time associated with catching prey for nestlings. The relatively large fish fed to chicks are thought to be less abundant and more difficult to locate than the smaller fish generally consumed by adults (Carter 1984, Carter and Sealy 1990, Mahon et al. 1992). On many days, 2 feeding visits occurred at both dawn and dusk indicating that each adult carried a fish to the chick at least twice daily. The relatively synchronous timing of these visits suggests that pairs forage together. This hypothesis is supported by at-sea studies that have found murrelets frequently foraging in pairs during the breeding season (Sealy 1975b, Carter and Sealy 1990, Strong 1995). However, both birds rarely arrived at the nest at the same time. The rarity of simultaneous arrivals may be related to minor differences in time of prey capture, adults holding fish for some period of time on the ocean before flying inland (Carter and Sealy 1987a), or an attempt to minimize attraction of predators.

Murrelets (not necessarily the same individuals) are known to return to the same forest stands in successive years (Divoky and Horton 1995), and sometimes use the same nest platform or tree in subsequent years (N = 7 nests; Naslund et al. 1995; Singer et al. 1995; T. E. Hamer, pers. comm.; P. H. Jones, pers. comm.). In Oregon, 1 nest platform was reused and birds used different nest platforms in the same tree for nesting in successive yrs (N = 3 trees, including 1 found subsequent to this study). Most alcids are known to have high colony and nest-site fidelity (see De Santo and Nelson 1995), but are more likely to return to the same site if they were successful in the previous year (Nettleship and Birkhead 1985). However, at 2 murrelet nest sites, 1 in California (Singer et al. 1995) and 1 in Oregon (this study), birds returned to the same tree in the year following a suspected failure. Breeding-site fidelity can provide benefits in increased breeding success and overall fitness for relatively long-lived species by reducing the need to locate suitable nest sites or mates each year and allowing species to develop a familiarity with their environment (Nettleship and Birkhead 1985).

Flight Patterns

Individual marbled murrelets consistently used the same flight paths when they approached and exited nest sites. Because murrelets used similar flight paths on a daily basis, observations of birds flying in repetitive patterns in suitable habitat are probably indicative of nearby nesting. Surveys in forests could be designed to focus on flight paths to document stand use and locate nests.

Flight paths in this and other studies were often associated with openings in the forest canopy (Manley and Kelson 1995, Naslund et al. 1995, Singer et al. 1995). However, data on the characteristics of flight paths may be biased because most nests have been found near edges of stands where observation of the canopy is easiest. Therefore caution should be used when attempting to interpret the characteristics of flight paths. Only data from an unbiased sample of nests and information on the association between nest placement and nest success will provide accurate details on characteristics of flight paths and their importance to murrelets.

Vocalizations

Limited information is available on marbled murrelet vocalizations and the context in which the calls are given. However, chicks and adults frequently uttered soft calls from the nest limb, and adults gave loud vocalizations in flight. Although nestling vocalizations were not always heard, our video and tape recordings, coupled with observations at nests elsewhere (T. E. Hamer, pers. comm.), suggest that nestlings regularly call in the presence of an adult with food. The frequency of soft calls by both adults and chicks, and rarity of loud vocalizations on active nests corresponds with observations at other murrelet nests (Singer et al. 1991; Naslund 1993; T. E. Hamer, pers. comm; P. H. Jones, pers. comm.). Soft vocalizations at nests probably decrease the chances of being detected by avian predators.

Murrelets may have the ability to recognize individuals by their vocalizations, as is the case with other seabirds (Beer 1970, Brooke 1978). Incubating adults and chicks were observed to change behavior or vocalize on the nest limb just prior to arrival of the (other) adult. These observations suggest that birds on these nests were aware of the impending arrival of their mate or parent by recognizing a call. Alternatively, they could have seen their mate or parent fly by the nest tree prior to their arrival on the nest branch.

Predator Avoidance Behavior

Marbled murrelets exhibit specific behavioral patterns and morphological characteristics that appear to minimize their chances of being discovered by avian predators. For example, the plumage of both nesting adults and chicks includes cryptic colors and patterns, and nestlings do not molt into their juvenal plumage until just prior to leaving the nest (Simons 1980, Nelson and Hamer 1995a). Breeding birds fly rapidly, directly and generally silently to the nest branch during low light levels (near sunrise or sunset, or later on cloudy days). In addition, interactions between a mated pair occur for only a few minutes and most vocalizations from the nest are muted. These secretive behaviors have also been observed at nests and in nesting stands in California, Washington, and British Columbia (Manley et al. 1992; Rodway et al. 1991; Singer et al. 1991, 1995; Naslund 1993; Nelson and Hamer 1995a; O'Donnell et al. 1995). Other alcid species also exhibit behavioral patterns and morphological characteristics for minimizing detection by predators (Ainley and Lewis 1974, Birkhead 1985, Wittenberger and Hunt 1985, Gaston 1992).

Despite the behaviors used by marbled murrelets to avoid predation, 56% of nests (18 of 32 with known outcomes) were thought to have been depredated (Nelson and Hamer 1995b). Predators observed to destroy eggs, or kill chicks and adults at nests include common ravens (*Corvus corax*), Steller's jays (*Cyanocitta stelleri*), and sharp-shinned hawks (*Accipiter striatus*) (Marks and Naslund 1994, Nelson and Hamer 1995b). Rates of predation on bird nests could be related to habitat fragmentation and increased amount of edge as many predator species, especially corvids, are thought to be more successful at foraging or more abundant near edges than within intact forests (Yahner and Scott 1988, Paton 1994, Bryant 1994). Although the interaction between marbled murrelets, habitat fragmentation, and nest predation has not been studied, if changes in the landscape have made murrelet nests more vulnerable to predation, then the impacts of a changed landscape on murrelet nesting success may be significant. The effects of habitat fragmentation on murrelet fitness components and on coexisting species needs further evaluation.

CONCLUSIONS

Prior to 1980, little was known about the behavior of murrelets at nests. This was primarily due to the limited number of nests found and limited efforts at documenting their behavior. With increased searching efforts in recent years, more than 65 tree nests have been located and detailed information is now available on their nesting behavior. This paper, in addition to others (Simons 1980; Hirsch et al. 1981; Singer et al. 1991, 1995; Nelson and Hamer 1995a), has provided information on the timing, frequency, and patterns of activity at nests that will be useful in designing future research projects and developing survey methods for locating nests. However, additional information on murrelet nesting behavior is needed to refine our knowledge. Future studies of murrelet behavior should focus on individuals, identifying specific interactions of males and females, determining the degree of nest and site fidelity, and exploring the relationship between individual nesting birds and the groups of murrelets observed in forests. These data will provide more details on their social interactions and habitat use and are needed to enact adequate conservation and management strategies. Because the murrelet is listed as threatened, the urgency in obtaining this information has never been greater.

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