AT-SEA DISTRIBUTION AND MOVEMENTS OF NESTING AND NON-NESTING MARBLED MURRELETS *BRACHYRAMPHUS MARMORATUS* IN NORTHERN CALIFORNIA

PERCY N. HÉBERT[1] & RICHARD T. GOLIGHTLY

Department of Wildlife, Humboldt State University, Arcata, California, 95521, USA
(phebert@tru.ca)
[1]Current address: Department of Biological Sciences, Thompson Rivers University, Kamloops, British Columbia, V2C 5N3, Canada

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SUMMARY

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Marbled Murrelets *Brachyramphus marmoratus* feed entirely at sea. However, little is known of their distribution within the marine environment. Such knowledge would allow agencies to identify critical foraging and loafing areas that could be protected, especially relative to nesting habitats. The purpose of the present study was to examine the at-sea locations of radio-marked Marbled Murrelets during the breeding season relative to: (1) the shoreline and old-growth forest, (2) the maximum extent of alongshore travel during the breeding season, and (3) home range size on the ocean. For each of these measures, we also stratified the analyses by sex and nesting status (nested after capture or did not nest after capture). Using aircraft telemetry, we followed 102 Marbled Murrelets in the coastal waters of northern California between 2001 and 2003. Over the three years, murrelets were detected 1.4 ± 0.1 km (n = 93; mean ± standard error) from shore regardless of sex or nesting status. Murrelets traveled a maximum of 99.1 ± 9.5 km (n = 94) alongshore (north–south direction). Male murrelets tended to travel a greater distance than did females, and male murrelets that did not nest traveled significantly more alongshore than did male murrelets that nested after capture. Average home range size (minimum convex polygon) was 505 ± 75 km^2 (n = 94) and was larger for males than females. Home range size was larger for non-nesting murrelets than for nesting murrelets. When the data were stratified by sex and nesting status, home range size was larger for non-nesting males than for nesting males. However, home range size was similar for non-nesting and nesting female murrelets. Our data suggest that Marbled Murrelets in northern California occupied nearshore waters, and traveled less than 50 km away from the mouth of Redwood Creek, CA, the prominent watershed where most nesting occurred. However, the data also suggest that non-nesting males can make long-distance movements, perhaps in search of mates or nesting habitat.

Key words: At-sea locations, *Brachyramphus marmoratus,* home range size, Marbled Murrelet

INTRODUCTION

During the breeding season, incubating Marbled Murrelets *Brachyramphus marmoratus* alternate 24-hour incubation bouts with 24-hour periods at sea (Singer *et al.* 1991, Naslund 1993, Nelson & Peck 1995). Non-nesting murrelets in that season typically spend most of their time at sea, with the exception of a few hours around sunrise, when they may fly inland (Nelson 1997, Whitworth *et al.* 2000). Adults tending chicks fly inland with food during the morning and evening twilight hours (Sealy 1974, Carter & Sealy 1990), and only rarely during daylight hours (Carter & Sealy 1990, Nelson 1997). During the non-breeding season, Marbled Murrelets spend most of their time at sea, but may fly inland to visit nesting areas during the early morning hours (Naslund 1993).

At-sea surveys consistently detect Marbled Murrelets in coastal waters within 2 km of shore (e.g. Burger 1995, Ralph & Miller 1995, Strachan *et al.* 1995, Strong *et al.* 1995). Censuses have also shown a strong relationship between at-sea distribution of Marbled Murrelets and nearby nesting habitat (Meyer *et al.* 2002). Despite these observations, little is known of the extent of movement by Marbled Murrelets in their marine environment. It is not known if male and female Marbled Murrelets occupy similar areas at sea, or if nesting and non-nesting Marbled Murrelets occupy similar areas at sea. Also, a recent study (Bradley *et al.* 2002) observed that male Marbled Murrelets may be more active during the breeding season (chick feeding). If the latter observation is true, then nesting male Marbled Murrelets, as compared with nesting females and non-nesting Marbled Murrelets, may expand their home range to help meet the increased food demand.

Knowledge of the at-sea distribution of Marbled Murrelets will help agencies to identify critical foraging and loafing areas, which can be protected as necessary (e.g. Carter & Kuletz 1995), especially relative to the known nesting habitat. The purpose of the present study was to examine the at-sea locations of Marbled Murrelets during the breeding season relative to

- the shoreline and adjacent old growth forest,
- the extent of alongshore travel during the breeding season, and
- home range size on the ocean.

Given that at-sea movements could be affected by sex and breeding status, we stratified the data by sex and nesting status (i.e. did or did not nest after capture, hereafter denoted as nesting or non-nesting murrelets).

METHODS

Capture

We captured Marbled Murrelets in northern California coastal waters near the mouth of Redwood Creek, between 41.186°N, 124.135°W and 41.388°N, 124.062°W in 2001–2003 and in Trinidad Bay (41.069°N, 124.171°W) in 2002. Capture occurred between 21h00 and 04h00, using the night-lighting and dip-net technique (Whitworth *et al.* 1997). Each murrelet captured received a US Geological Survey stainless steel leg band and was fitted with a 2-g radio transmitter having a unique frequency (Model BD-2G: Holohil Systems Ltd., Carp, Ontario, Canada), following the procedure described by Mauser and Jarvis (1991) and Newman *et al.* (1999). Radio-marked murrelets were transported back to the area of capture and hand-released onto the water. All birds exhibited normal behavior (flying, diving, preening) when released.

Telemetry

Beginning the morning after the first capture, we determined the locations of radio-marked murrelets, both at sea and in forests, using a global positioning system and aircraft telemetry (Gilmer *et al.* 1981, Whitworth *et al.* 2000). We located murrelets from fixed-wing aircraft (Cessna 182, 185) equipped with a receiver (model R4000: Advanced Telemetry Systems, Isanti, MN, USA) and either a 4-element H-antenna or a single-element omnidirectional antenna. Flights were conducted between 08h00 and 20h00. Survey time and length of the aircraft flight depended on the weather, location of birds, and number of birds to be located.

Telemetry flights began over the ocean. If a bird was not detected at sea, then the plane flew inland over adjacent areas with old-growth forest to determine the location of the bird. Flights typically occurred over coastal waters and adjacent old-growth forests between Eureka, California (40.783°N, 124.150°W), to the south, and Crescent City (41.966°N, 124.166°W) to the north. If a bird was not detected in this area, the search was expanded to the coastal waters and adjacent old growth south to Humboldt Redwoods State Park (40.316°N, 123.916°W) and north to Brookings, Oregon (42.066°N, 124.266°W).

At-sea distribution and movements

We analyzed the locations, range of movements, and home range size [minimum convex polygon estimator (MCP)] of radio-marked Marbled Murrelets using the Animal Movement extension (Hooge & Eichenlaub 2000) for ArcView (version 3.3: Environmental Systems Research Institute, Redlands, CA, USA). For each bird, we calculated the average distance to nearest shore, the maximum extent of alongshore movements (distance between the two locations farthest apart in the north–south direction), the mean distance that each bird traveled north or south of where Redwood Creek enters the ocean (which was adjacent to the nest sites), and home range size (square kilometers, MCP). For each polygon, we removed the furthest 5% of the outliers from the MCP (Hooge *et al.* 2001) to minimize the consequence of rare movements. If a polygon included land mass, that portion of the polygon was removed using the Erase function in the X-Tools extension of ArcView (version 3.3). For these analyses, we used data for only the Marbled Murrelets with radios that were active for at least 10 days and for which we obtained a minimum of five detections.

Statistical analyses

Statistical analyses were performed using the SPSS software (version 11.5: SPSS, Chicago, IL, USA). For each year (2001–2003), we used analysis of variance (ANOVA) to compare average distance to shore, maximum extent of alongshore movement, and home range size between male and female Marbled Murrelets, and between nesting and non-nesting murrelets. If warranted, post-hoc analyses were made using a least significant difference multi-comparison test. To minimize inter-year differences in the dependent variables, we standardized the data by subtracting the yearly mean of the dependent variable from each observation and dividing the result by the yearly standard deviation (Perrins & McCleery 1985). The resulting standardized data for each dependent variable were then analyzed using two-factor analysis of variance (sex, nesting status). Unless otherwise noted, two-way interactions were statistically nonsignificant. Although analyses were performed on standardized data, we present descriptive statistics using raw values for illustrative purposes. Measures of central tendency are expressed as the mean ± standard error.

TABLE 1
Aircraft flight dates, number of flights, radio detectability, and mean number of days that all Marbled Murrelet *Brachyramphus marmoratus* transmitters were functional in northern California, 2001–2003

	2001	2002	2003
Aircraft flight dates			
First flight	13 Apr	13 Apr	17 Apr
Last flight	19 Aug	26 Aug	6 Aug
Detections from aircraft			
Aircraft flights (n)	94	103	72
Radio detectability[a] (%)	92.7	90.9	83
Total detections (n)	918	2021	886
Range of n (functioning transmitters)	1–19	1–42	1–30
Mean radio transmission (±SE)			
Period	13 Apr–12 Aug	13 Apr–26 Aug	17 Apr–6 Aug
All birds, with early failures excluded[b] (n)	64.6±6.3	66.8±3.5	50.4±4.2
Days (n)	20	42	32

[a] Number of birds detected per aircraft flight divided by number of birds with functioning transmitters.
[b] Data for eight murrelets were excluded because of radio failure, mortality, or fewer than five detections.

RESULTS

We radio-marked 102 Marbled Murrelets between April and May of 2001–2003. We exclude data from eight birds because of early radio failure (n = 4), death within 10 days of release (n = 2), or because we obtained fewer than five detections (n = 2). The number of flights, period of flights, and number of days radios transmitted varied from year to year (Table 1).

At-sea distribution and movements

Distance from shore

Mean distance to shore did not differ significantly between the years (ANOVA: $F_{2,91}$ = 1.2, P = 0.33; Table 2). When the data were combined across years, Marbled Murrelets were located, on average, 1.4 ± 0.1 km (n = 94) from shore. Male and female murrelets were located at similar standardized distances from shore (ANOVA: $F_{1,85}$ = 0.001, P > 0.95; Table 3). Likewise, non-nesting and nesting Marbled Murrelets were detected at a similar distances from shore (ANOVA: $F_{1,85}$ = 0.12, P > 0.7; Table 3).

Alongshore movements

The mean maximum movements alongshore (north–south distance) traveled tended to differ between the years (ANOVA: $F_{2,91}$ = 2.68, P = 0.074; Table 2). When the data were combined across years, the mean maximum alongshore distance was 99.1 ± 9.5 km (n = 94). The mean standardized maximum alongshore distance traveled tended to be greater for male than for female murrelets (ANOVA: $F_{1,85}$ = 3.8, P = 0.055; Table 3). The mean standardized maximum alongshore distance traveled by nesting murrelets was significantly less than that of non-nesting murrelets (ANOVA: $F_{1,85}$ = 4.99, P = 0.03; Table 3). Furthermore, the standardized maximum alongshore distance traveled by non-nesting male murrelets tended to be greater than that of nesting male murrelets (ANOVA: $F_{1,42}$ = 3.7, P = 0.062; Table 3). In contrast, the standardized maximum alongshore distance traveled by non-nesting female murrelets was similar to that of nesting female murrelets (ANOVA: $F_{1,43}$ = 1.49, P = 0.23; Table 3).

When the data were combined across years, murrelets traveled 16.7 ± 0.4 km (1840 detections) south of Redwood Creek and 22.3 ± 0.8 km (1780 detections) north of Redwood Creek. The maximum distance any bird travelled south of Redwood Creek was 119.9 km (Cape Mendocino, CA), and the maximum distance any bird travelled north of Redwood Creek was 724.5 km (Port Johnson, WA). Overall, six detections occurred more than 100 km south of Redwood Creek, representing two male and one female murrelet, and 26 detections occurred more than 100 km north of Redwood Creek, representing nine male and three female murrelets.

Home range size

Home range size was similar between years (ANOVA: $F_{2,91}$ = 1.89, P = 0.16; Table 2). Overall, the mean standardized home range of male Marbled Murrelets was significantly larger than that of females (ANOVA: $F_{1,85}$ = 3.98, P = 0.049; Table 3). Standardized

TABLE 2
Annual mean distance from shore, distance traveled alongshore, and home range size of Marbled Murrelets *Brachyramphus marmoratus* located in nearshore waters in northern California, 2001–2003

	2001		2002		2003	
	X̄±SE	n	X̄±SE	n	X̄±SE	n
Distance from shore (km)	1.5±0.1	20	1.4±0.1	42	1.2±0.1	32
Alongshore movement (km)	69.7±8.1	20	92.1±10.4	42	126.7±23.2	32
Home range size (km^2)	330±85	20	442±85	42	697±179	32

SE = standard error.

TABLE 3
Distance to shore, distance traveled alongshore, and home ranges of Marbled Murrelets *Brachyramphus marmoratus* located in nearshore waters of northern California stratified by sex and nesting status, 2001–2003

	Distance to shore (km)		Alongshore movement (km)		Home range size (km^2)	
	X̄±SE	n	X̄±SE	n	X̄±SE	n
Sex[a]						
Male	1.3±0.1	44	120±19	44	682±148	44
Female	1.4±0.1	45	79±6	45	344±48	45
Nesting status						
Non-nesters	1.4±0.1	60	114±14	60	655±111	60
Nesters	1.3±0.1	34	72±7	34	240±38	34
Sex and nesting status						
Male non-nesters	1.3±0.1	25	152±31	25	1018±238	25
Female non-nesters	1.4±0.1	32	83±7	32	375±60	32
Male nesters	1.3±0.1	19	78±9	19	239±46	19
Female nesters	1.4±0.1	13	69±11	13	269±74	13

[a] Sex could not be ascertained for five birds.
SE = standard error.

home range size for non-nesting murrelets was significantly larger (ANOVA: $F_{1,85}$ = 8.59, P = 0.004) than that for nesting murrelets (Table 3). The interaction between sex and nesting status was also significant (ANOVA: $F_{1,85}$ = 4.84, P = 0.031). Standardized mean home range size for non-nesting male murrelets was significantly larger (ANOVA: $F_{1,42}$ = 7.92, P = 0.007) than that for nesting male murrelets (Table 3, Fig. 1). In contrast, standardized home range size was similar for non-nesting and nesting female murrelets (ANOVA: $F_{1,43}$ = 0.72, P = 0.40; Table 3, Fig. 2). Finally, non-nesting male murrelets had a significantly larger standardized home range than did non-nesting females (ANOVA: $F_{1,55}$ = 8.67, P = 0.005; Table 3), whereas standardized home range size was similar for nesting male and female murrelets (ANOVA: $F_{1,30}$ = 0.08, P = 0.78; Table 3).

DISCUSSION

Marbled Murrelets frequent shallow marine habitats with upwelling, underwater sills, and tidal rips (Sealy 1975a; Ainley *et al.* 1995). Such sites likely concentrate prey in a spatially predictable manner (Carter & Sealy 1990). In northern California, the coastline is relatively devoid of bays and promontories. The continental shelf is narrow (<35 km) over much of the area, with the exception of Eureka (*c.* 40 km to the south of our study area), where it broadens, but remains <50 km wide (Briggs *et al.* 1987). Together, these characteristics would tend to standardize the location of upwellings and the breadth of surface and subsurface currents along the coast of northern California, so that murrelet prey are likely to occur at a relatively predictable distance from shore throughout much of our study area.

The distance to shore that we recorded for radio-marked Marbled Murrelets (1.2–1.6 km) was similar to that observed in previous at-sea surveys off the coast of northern California (Ralph & Miller 1995) and Oregon (Strong *et al.* 1995). However, Lougheed (2000) observed that Marbled Murrelets nesting in British Columbia foraged closer to shore than non-nesting murrelets and argued that this behavior occurred to minimize travel distance to the nest to feed a chick. In comparison, non-nesting murrelets may be less constrained by foraging efficiency, and thus may occupy safer and less productive waters more distant from shore (Lougheed 2000). In our study, the distance from shore at which murrelets were detected did not vary with nesting status. Considering that murrelets in British Columbia (Desolation Sound) nested an average of 39 km from their foraging grounds, foraging closer to shore may allow for some energy savings by reducing travel time (Hull *et al.* 2001). In northern California, radio-marked murrelets usually nested within 10 km of the coast and usually foraged within 1.6 km of shore. Thus relative economies gained by foraging closer to shore would be proportionally small.

Other studies on alcids and other seabirds have detected sex differences in areas of the ocean used for foraging, particularly

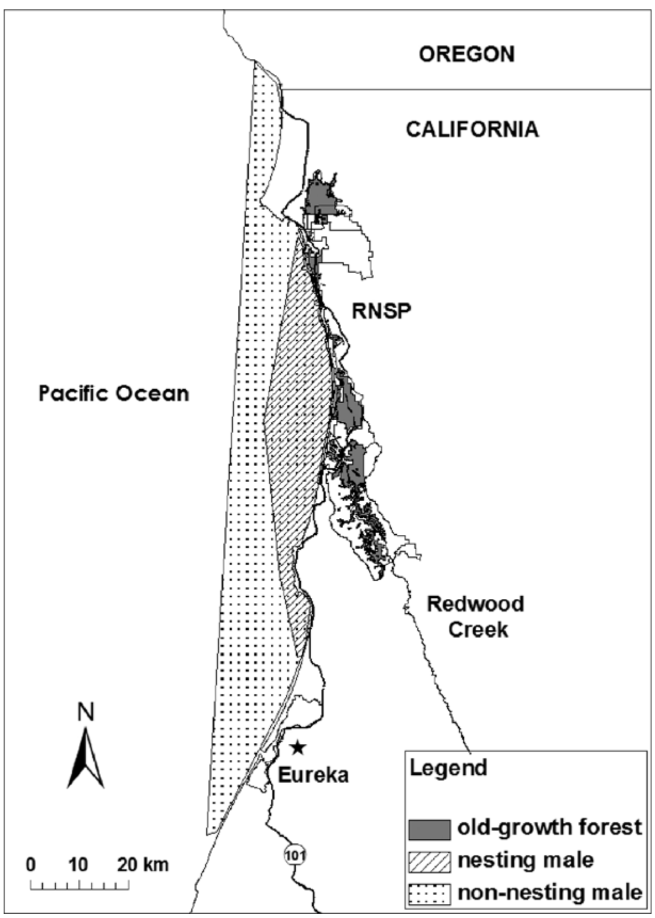

Fig. 1. Home ranges (minimum convex polygons) of nesting and non-nesting male Marbled Murrelets *Brachyramphus marmoratus* in Humboldt County, northern California.

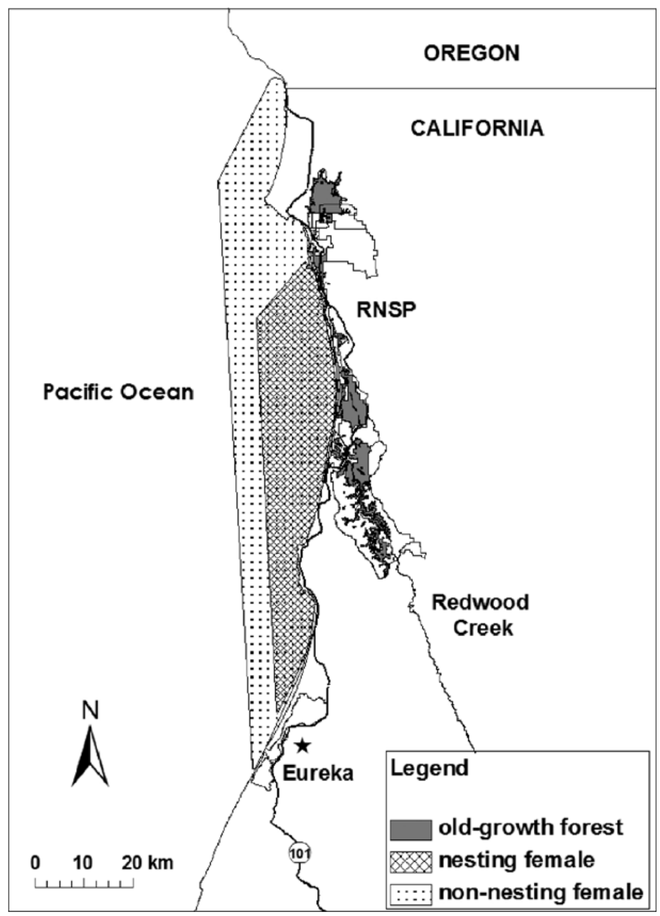

Fig. 2. Home ranges (minimum convex polygons) of nesting and non-nesting female Marbled Murrelets *Brachyramphus marmoratus* in Humboldt County, northern California.

among nesting birds (e.g. Cassins Auklets *Ptychoramphus aleuticus,* Adams *et al.* 2004; Wedge-tailed Shearwaters *Puffinus pacificus,* Peck & Congdon 2006). In contrast, we found no difference in the distance from shore at which male and female Marbled Murrelets were located. Again, the structure of the coastline within our study area likely dictated the location of prey such that murrelets, regardless of sex, foraged at a predictable distance from shore.

We did, however, observe that non-nesting male Marbled Murrelets traveled farther alongshore than did nesting male murrelets and female murrelets (Table 3). Home range size also differed in a manner similar to maximum alongshore distance traveled (Table 3). That is, non-nesting male murrelets had a larger home range as compared with nesting male murrelets and female murrelets. These results suggest that prey searching probably consisted of alongshore movements tied to particular substrates (R.T. Golightly & P.N. Hébert unpubl. data) rather than distance from shore.

Larger home range sizes in non-nesting males could reflect any of several influences, including foraging efficiency, constraints on travel to nest sites, and reproductive opportunities. First, as in other seabirds (e.g. Burger 1987, Williams *et al.* 1992), non-nesting males may be younger and less experienced at foraging and thus may travel greater distances to find appropriate foraging areas. However, a similar argument could be made for non-nesting females. Because non-nesting female murrelets had significantly smaller home ranges as compared with non-nesting males, lack of foraging experience does not wholly explain the larger home range size of non-nesting males.

Second, non-nesting males may be less constrained spatially because they do not have to commute to a nest site every other day during incubation or every day during the chick period. This situation would allow non-nesting males to track profitable prey patches without incurring added travel costs. In agreement with this hypothesis, maximum alongshore distance traveled tended to be greater ($P = 0.062$) in non-nesting males than in nesting males, and the mean home range of non-nesting males was significantly larger than that of nesting males. Again, however, it would be expected that non-nesting females would also be less constrained by energy costs associated with traveling to a nest. Because non-nesting female murrelets had significantly smaller home ranges than did non-nesting males and home ranges similar to those of nesting females, energy constraints associated with nesting cannot account for the difference in home range between non-nesting males and either nesting males or non-nesting females.

Finally, larger home range size in non-nesting males may reflect behavior associated with habitat selection or mate-selection and courtship (or both). For instance, non-nesting males may visit multiple "staging" (e.g. Sealy 1976) or foraging areas (e.g. Carter & Sealy 1990) in search of potential mates or perhaps to obtain extra-pair copulations on the water (see Strachan *et al.* 1995) or at inland sites (Nelson 1997). Also, because many of the non-nesting males had a brood patch at capture, it may be inferred that they were failed breeders. Studies of other seabirds have noted a tendency to divorce after a failed breeding attempt (Ainley *et al.* 2002), and thus male murrelets that we classified as non-nesters may have been failed breeders seeking new mates. In some instances, loss of a mate or divorce is followed by a change in nest site (Butler & Buckley 2002). Therefore, in addition to increasing encounter rates with potential mates, visitation of different staging areas may provide non-nesting murrelets with cues relevant to habitat selection.

Movement patterns of radio-marked murrelets during this study are consistent with recent population genetics analyses. Work by Friesen *et al.* (2005) suggests that the Marbled Murrelet population of northern California is distinct from the central California population. Although murrelets off the coast of northern California did not move great distances from Redwood Creek (the main outflow from adjacent nesting habitat), three birds ventured more than 100 km south, and 12 birds ventured more than 100 km north. Thus, northern California birds were more likely to move north than south, which contributes to the isolation of central California murrelets.

To summarize, the at-sea distribution of Marbled Murrelets in northern California is likely influenced by several factors. The topography and associated bathymetric characteristics differ little along the coastal region of our study area (Briggs *et al.* 1987), appearing to concentrate Marbled Murrelets, regardless of sex or reproductive status, at a fairly predictable distance from shore (Tables 2 and 3). However, male Marbled Murrelets classified as non-nesters tended to forage over a greater area than do nesting male murrelets. This suggests that nesting reduces energy expenditure by minimizing the distance between nest and foraging grounds. However, non-nesting male murrelets traveled greater distances during summer than did nesters, which we interpret as possibly a search for mates or nest sites.

Finally, most murrelets captured near Redwood Creek traveled less than 25 km either north or south during this study. The maximum extent of foraging habitat for breeding Marbled Murrelets in northern California was ±36 km from the mouth of the watershed containing their nests. Murrelets, especially non-nesting males, that ranged more widely (up to ±76 km from the mouth of the watershed containing nests) were likely future breeders. Regardless of the reasons for variation by sex and nesting status, managers should consider our findings in identifying, protecting, and managing marine use areas of Marbled Murrelets.

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