



Research Article

Low Breeding Propensity and Wide-Ranging Movements by Marbled Murrelets in Washington

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ABSTRACT The marbled murrelet (*Brachyramphus marmoratus*) is a threatened seabird that forages in nearshore marine waters but nests inland, commonly in older coniferous forests. Information on ranging behavior and breeding propensity can be useful for informing management, especially when comparisons can be made between declining or threatened populations and more stable, unthreatened populations. Over 5 years, we measured ranging behavior and breeding propensity of marbled murrelets in Washington, USA where murrelets are considered threatened. Our primary objective was to compare space use and breeding by murrelets in Washington with those from other regions and where the species is not considered threatened. We radio tracked 157 murrelets from 2004 to 2008. Median marine 95% kernel ranges were 487 km² ($\bar{x} = 938 \pm 1,348$ [SD]) and larger than those reported for non-threatened populations in Alaska, USA in other studies. Ranges computed from minimum convex polygons (MCPs; median = 404 km²; $\bar{x} = 708 \pm 847$) were on average similar to those reported for threatened populations in California, USA, although larger than those reported for Alaska. Distances traveled between consecutive marine telemetry locations were greater than reported previously in Alaska. Variation in movements in our study were not associated with oceanographic conditions although appeared greater for murrelets captured along the Pacific Coast compared to those occupying interior marine waters in the Salish Sea. Twenty individuals (12.7%) attempted to breed in our study, and we estimated breeding propensity was 13.1–20.0%. This is the lowest breeding propensity reported for a population of murrelets to date. For breeders, nest-sea commuting distances were greater than reported previously, with 4 breeders traveling farther than the previously reported maximum of 125 km. The low breeding propensity, large marine ranges, and long nest-sea commutes in this study may point to poor-quality marine habitat in Washington compared to other parts of the murrelet's range. In combination with reported declines in terrestrial nesting habitat from other studies, this indicates that additional management is needed to improve murrelet breeding habitat in Washington. Future management actions should focus on improving both terrestrial and marine habitat. © 2016 The Wildlife Society.

KEY WORDS *Brachyramphus marmoratus*, marbled murrelet, old growth forest, Salish Sea, sea surface temperature, space use, upwelling index, Washington.

Information on space use and movements of wildlife is important for guiding management decisions. Although many factors influence animal behavior and movements, space use often, at least partially, reflects the underlying quality of habitat used by animals (Brown and Orians 1970).

Exceptionally long movements compared to the norm may indicate poor quality habitats in which individuals must traverse large areas to meet their basic needs.

Marbled murrelets (*Brachyramphus marmoratus*) are seabirds in the family Alcidae that nest in coastal, old-growth forests in the Pacific Northwest. They are listed as threatened species from British Columbia south to California (U.S. Fish and Wildlife Service 1992, Committee on the Status of Endangered Wildlife in Canada 2012). Thus, marbled murrelets have been the focus of numerous

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space use studies. These studies have measured marine range size (Hebert and Golightly 2008, Barbaree et al. 2015), marine movements (Kuletz 2005, Hebert and Golightly 2008, Peery et al. 2009), and nest-sea commuting distances (Whitworth et al. 2000, Hull et al. 2001, Kuletz 2005, Barbaree et al. 2015) to identify important factors for sustaining populations. Notably, however, there have been no published studies on space use by murrelets in Washington, where declines have been observed (Miller et al. 2012, Falxa and Raphael 2016). Past published studies of space use in marbled murrelets have occurred in Alaska, USA (Whitworth et al. 2000; Kuletz 2005; Barbaree et al. 2014, 2015), British Columbia, Canada (Hull et al. 2001, Bradley 2002, Bertram et al. 2015), and California, USA (Hebert and Golightly 2008, Peery et al. 2009), which are different from Washington with respect to murrelet population dynamics and available habitat (Falxa and Raphael 2016).

To address this information gap, we undertook a study of breeding season space use by marbled murrelets in Washington. We were interested in comparing ranges, movements, and breeding in the Washington population with those from other regions to understand factors that may be associated with population declines. Our objectives were to quantify nest-sea commuting distances and marine movements and ranges. We also estimated breeding propensity (i.e., proportion of individuals of both sexes for which we detected breeding) and nesting success (i.e., proportion of breeders that fledged a young) for each year. During the years of our study, a shift in climate patterns resulted in a widespread delayed oceanic upwelling in the California current (Schwing et al. 2006, Barth et al. 2007, Dorman et al. 2011), which can affect marine productivity in coastal Washington (Hickey and Banas 2003). The upwelling event enabled us to also explore the possible effects of large-scale oceanic processes on murrelet movements in Washington.

STUDY AREA

We conducted this study in northwestern Washington ($\sim 47^{\circ} 48' \text{ N}$, $123^{\circ} 40' \text{ W}$) and captured murrelets on 3 areas (Fig. 1). Our Coast study site occurred along the Pacific coast of Washington (i.e., west side of the Olympic Peninsula) and we expected it was most influenced by large-scale ocean processes, particularly upwellings associated with the California Current. Our Strait study site included marine waters within the Strait of Juan de Fuca (i.e., north side of the Olympic Peninsula) and we expected it to be less influenced by upwellings and more by tidal flows within the Salish Sea. Our third study site, Hood Canal, was a narrow, deep channel on the east side of the Olympic Peninsula and was most heavily influenced by tidal flows and by terrestrial runoff, with less immediate impact from ocean upwellings compared to the other study sites.

The climate within our study area is best described as a wet, maritime oceanic or temperate climate, and is characterized by mild, rainy weather year-round, except for a mild, dry

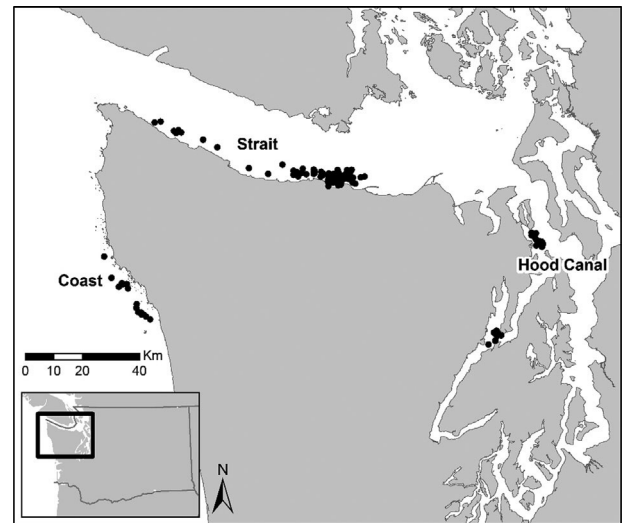


Figure 1. Three capture sites used for capturing marbled murrelets in northwestern Washington, USA, 2004–2008. Black dots show capture sites for individual murrelets.

period in mid- to late summer. Forests used for nesting by murrelets in this region are generally temperate coastal rainforests dominated by western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), and western red cedar (*Thuja plicata*).

METHODS

Field Data Collection

We used radio-telemetry to examine space use by marbled murrelets. We captured murrelets by using night-lighting and long-handled dipnets (Whitworth et al. 1997) from April to July 2004–2008. With the exception of a few individuals that were released without transmitters because of concerns over handling stress, we fit captured birds with a very high frequency (VHF) 3.3-g transmitter (<2% of body weight; Advanced Telemetry Systems, Isanti, MN, USA) using a subcutaneous anchor following Newman et al. (1999) except we did not use anesthesia or sutures. We also collected a small sample of blood from the brachial vein of each murrelet to determine sex. We released murrelets at the site of capture within 1 hour. All handling was in accordance with the United States Fish and Wildlife Service Endangered Species 10a1a permit (Permit no. TE-070589-2) and in compliance with Ornithological Council guidelines (Fair et al. 2010).

We estimated transmitter battery life was 80 days. We located radio-tagged murrelets primarily by aerial tracking from fixed wing aircraft and we used ground-based telemetry for pinpointing the exact location of nest sites, and for monitoring nests. We initiated aerial tracking searches within 3 days after the first murrelet was tagged in each year. We ended searches after the last identified nest had fledged or failed and when significant numbers of transmitters were no longer detectable within our study area, indicating post-breeding dispersal or transmitter battery failure.

Weather permitting, we conducted tracking flights daily. Tracking flights lasted ≤ 5 hours until either all birds had been located or the aircraft needed refueling. Aerial searches included marine foraging areas and terrestrial nesting areas. If we did not locate an individual murrelet at sea or on an inland nest for 2–3 consecutive days, we expanded our search area to find the missing bird and generally focused on areas beyond the location that the missing murrelet was last detected. When pilots detected a murrelet's radio signal from the air, they circled over the transmitter and used a global positioning system (GPS) unit to mark the location from which they heard the loudest signal. Our tests with stationary transmitters on land indicated that GPS location accuracy from aircraft was 385 m on average (± 230 , range = 93–685 m). We attempted to conduct tests with stationary transmitters attached to buoys in water, but ocean currents caused the buoys to move before test flights could be conducted, precluding an assessment of location accuracy.

Because most telemetry flights occurred over marine areas, we typically first detected breeding activity when radio-tagged murrelets exhibited the characteristic on-off nest attendance pattern indicative of incubation (Bradley et al. 2004). When the on-off pattern was observed for a murrelet, we conducted aerial telemetry search over potential nesting habitat until we detected the tagged bird. We then visited the area on foot and located the nest by homing to the murrelet's radio signal. At a subset of nests ($n = 4$), we set video cameras (Sandpiper Technologies, Manteca, CA, USA) to record continuous footage while the nest was active.

We estimated breeding propensity as the proportion of radio-tagged adults of both sexes that were detected attempting to nest. We computed an uncorrected breeding propensity as the ratio of tagged murrelets for which we observed breeding, compared to all tagged murrelets. This uncorrected breeding propensity may underestimate breeding if murrelets are radio-tagged after they have initiated but failed in their nesting attempts. To account for this possibility, we also computed a corrected breeding propensity including only murrelets that were captured before or during the median range of nest initiation dates. We computed the median range of nest initiation dates for this population using all observations of fish-holding murrelets during boat-based surveys conducted in this region from 1998 to 2012 (Havron 2012). To estimate a range of dates that nesting could have occurred, we considered that fish-holding murrelets could be either at the beginning or end of the nestling phase and subtracted 58 days (for early initiated chicks) or 30 days (for late initiated chicks) from the median fish-holding date following recommendations by McFarlane Tranquilla et al. (2005). We used these 2 dates to compute the median range of nest initiation, and excluded murrelets captured after those dates from our corrected estimate of breeding propensity.

For known breeders, we determined nest success by video monitoring, radio-telemetry monitoring, or viewing nest contents after the nesting season. Once we had detected an on-off pattern at sea that indicated birds were incubating (rather than prospecting for nest sites), we determined nests

were successful if we observed fledging on video, if the length of time an adult visited a nest indicated nest attendance for approximately 30-day incubation and nestling periods, or if we observed a large fecal ring in the nest after the nesting season (Nelson 1997). We classified nests as unsuccessful if video showed the nest failed, if the timing of adult visits was too short for successful nesting based on known dates of nest initiation ($< \sim 60$ days; Nelson and Hamer 1995, McFarlane Tranquilla et al. 2005), there was an underdeveloped fecal ring at the nest site, or a broken egg or dead chick was at or near the nest site after the nesting season (Nelson and Hamer 1995, Nelson 1997).

Marine Ranges

We estimated marine range size for radio-tagged murrelets using 5 methods to compare with past research studies. We first estimated 95% kernel ranges using Geospatial Modeling Environment (Geospatial Modeling Environment Version 0.7.1.0) and used 2 different bandwidth estimators. We computed 95% kernels using least squares cross-validation (LSCV) as a bandwidth estimator for direct comparison with Barbaree et al. (2015). However, we found that these kernels were heavily influenced by 1 or a few outlier points, such that single points far from the majority of point locations would result in an unrealistically large range. Such kernels often contained areas never used by murrelets, such as pelagic environments > 30 km from shore (murrelets were not detected > 10.9 km offshore in the course of our study). Thus, we also computed 95% kernels using the plugin bandwidth estimator; this method was less subject to range expansion with a few distant telemetry relocations. We viewed these 95% plugin kernels as more accurate representations of range size and used them in all analyses. We then computed a range core area using the 50% contour of the utilization distribution (UD) for LSCV and plugin kernels. For all kernels, we removed portions of the range that included land using the erase tool in ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA, USA).

Last, for comparison with Hebert and Golightly (2008), we computed 95% minimum convex polygons (MCP). We computed 95% MCPs using *adehabitatHR* in R version 3.1.1 (R Core Development Team, R Foundation for Statistical Computing, Vienna, Austria), which computes 95% MCPs by removing 5% of relocations farthest away from the home range centroid, estimated with the arithmetic mean of relocations (Calenge 2015). Similar to kernel ranges, we removed parts of each murrelet's MCP composed of land. Although this method was useful for comparing ranges directly to Hebert and Golightly (2008), we did not view these ranges as especially representative of murrelet space use in our study because they included large amounts of unused areas, and somewhat simplistically truncated the range boundary at the outermost telemetry locations.

Previous research indicated that murrelets travel overwater except when prospecting for or attending nest sites (Barbaree et al. 2015). For murrelets that traveled around large land masses like the Olympic Peninsula, we constructed MCPs

using marine least cost paths (see section below on LCP Analysis—Marine) converted to points to ensure that the MCP was not split into 2 separate MCPs after removing land. This was necessary for birds that moved between the Coast and Strait or Hood Canal study areas but were not detected en route (e.g., they were detected on the Coast and the next day in the Strait or Hood Canal). By using LCPs instead of telemetry relocations, the MCP then included all of the coastline that would have been traveled by the murrelet, rather than only the coastline near the points where we detected the murrelet.

We constructed ranges using only marine locations even for breeders that used terrestrial areas for nesting because we were specifically interested in measuring marine space use. For constructing ranges, we assumed that consecutive marine telemetry relocations were spatially and temporally independent because they were obtained on different days. We compiled area observation curves (Odum and Kuenzler 1955) for 95% plugin kernels of 10 randomly selected murrelets and found that all ranges reached an asymptote near 15 point relocations. This is similar to the cut-off of 12 point locations used by Barbaree et al. (2015) for summarizing range size for murrelets in Alaska. Therefore, we estimated ranges only for individuals with ≥ 15 point locations.

LCP Analysis—Marine

We computed least cost paths (LCPs; Wang et al. 2009, Sawyer et al. 2011, LaPoint et al. 2013) to estimate the minimum distances likely traveled between consecutive marine locations for individual murrelets. Similar to our construction of MCP ranges, we assumed that murrelets preferred to travel via water, rather than overland, and also preferentially traveled in nearshore waters, rather than far offshore or in pelagic waters (Kuletz 2005, Burger et al. 2008). We defined nearshore waters as those within 3,061 m

of the shoreline, which represented the 95th percentile of all murrelet telemetry locations from this study. We then used a cost-weighted path analysis in R, where costs were imposed on each possible step for traveling via land (user assigned value of 10) or over open water (user assigned value of 2). Nearshore marine areas (areas within 3,061 m of coastline) had the least cost imposed for travel (user assigned value of 1). We then computed the distance in kilometers for the path (i.e., LCP) that minimized the cost of traveling between 2 consecutive telemetry relocations. This approach resulted in murrelet marine LCPs that were generally restricted to the nearshore waters, although open water could be crossed when necessary to move between different nearshore regions (Fig. 2). Our user-assigned values had no direct effect on the distance estimated for each LCP. They simply restricted the murrelets' traveled pathways to nearshore marine areas in most cases. As noted below, this method is analogous to the pivot-point procedure used to compute nest-marine commuting distances by Barbaree et al. (2015). This approach best reflected what is currently known of the spatial ecology of marbled murrelets, which restrict their marine movements to nearshore regions, and which are generally thought to travel over land only while nesting or prospecting for nest sites. Importantly, however, these paths do not represent the actual routes that murrelets traveled because we only visited each individual at most once daily. Rather, they represent a minimum distance likely traveled between consecutive marine telemetry relocations.

LCP Analysis—Nest to Sea

For breeding murrelets with active nests, we computed the distance between consecutive nest and marine relocations also by constructing LCPs. We assumed that both distance and elevation constituted a cost for murrelets traveling to inland nest sites (Barbaree et al. 2015). For the overland portion of paths, we used a digital elevation model (DEM) to

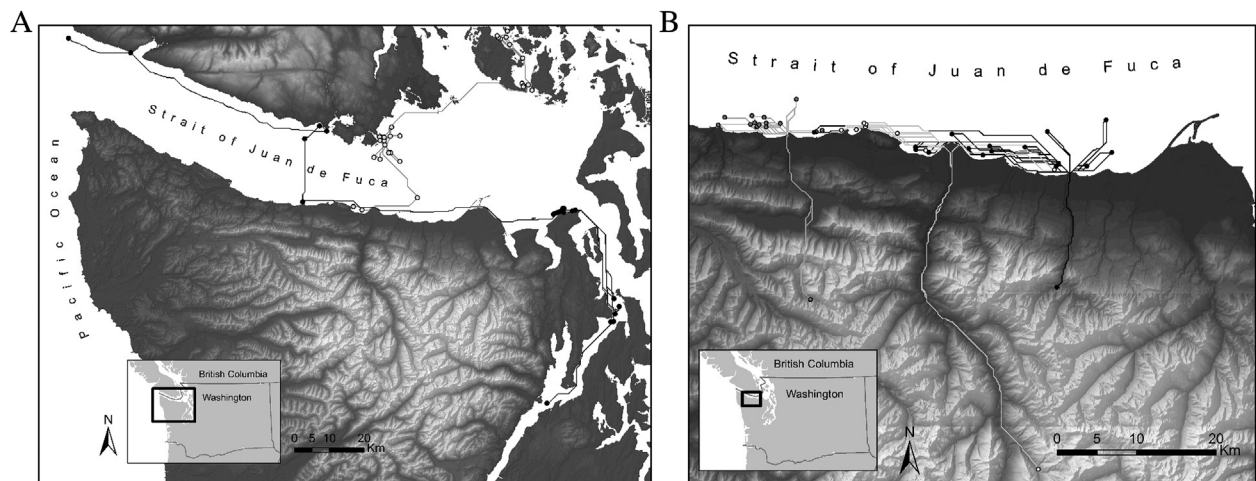


Figure 2. Example of cost-weighted paths computed for marbled murrelets in northwest Washington, USA, and southwest British Columbia, Canada, 2004–2008, between consecutive marine locations (A; marine least-cost paths [LCPs]) and terrestrial nest sites and marine telemetry relocations (B; nest-sea LCPs). For LCPs in A, black and gray circles and lines indicate computed paths for 2 different non-breeding radio-tagged murrelets. For nest-sea LCPs in B, dark gray, white, and black circles and lines indicate computed paths for 3 different breeding radio-tagged murrelets. Once we constructed paths, we estimated the length of each path in kilometers.

represent elevational costs, and the computed paths minimized the distance and elevational costs between nest and marine locations. For the marine portion of the commute, similar to the marine LCP analysis, we assumed murrelets preferentially traveled in nearshore waters and we similarly defined nearshore waters as those within 3,061 m of the shoreline (user assigned value of 0, compared to areas >3,061 m from shore with a user assigned value of 1).

This method assumes that murrelets commute overland between nest and marine locations by traveling along river valleys (e.g., the lowest elevation path), unless it is less costly to traverse narrow or low ridgelines (Fig. 2). These assumptions are supported by observations of murrelets predominately using river valleys for travel to nests in past studies, although minor ridgelines may occasionally be traversed (Hull et al. 2001, Bradley 2002, Barbaree et al. 2015). It is analogous to the pivot-point procedure used to compute nest-marine commuting distances by Barbaree et al. (2015) but uses elevation rather than human-derived pivot points to direct the path. Following Barbaree et al. (2015), we separately computed distances commuted over land and over marine areas.

We calculated nest-sea LCPs only for days in which we knew a murrelet's location on the water and during the active nesting period. We determined whether nests were active using an individual murrelet's marine on-off pattern (Bradley et al. 2004), by observing murrelets at their nest sites, or by back-counting from known hatch or fledging dates. We assumed that murrelets visited their nest at least once daily during the nestling period and once every-other day during the incubation period, unless we detected an individual with telemetry visiting its nest more or less often.

Oceanographic Conditions

The second year of our study (2005) had an anomalously delayed upwelling in the California Current. This delayed upwelling had widespread effects on many marine taxa. To examine whether this unusual upwelling event influenced marbled murrelet movements, we modeled the influence of several oceanographic conditions on murrelet paths (see Analysis for modeling procedure), including upwelling conditions, sea surface temperature, and chlorophyll-*a*.

We characterized upwelling conditions for our study site using estimates of the Bakun Upwelling Index obtained from the National Oceanic and Atmospheric Administration's Pacific Fisheries Environmental Laboratory (PFEL) website (www.pfel.noaa.gov) for 125° W 45' N, which is off-shore northwestern Washington. This index is an estimate of the offshore Ekman transport derived from surface pressure fields (Perez-Brunius et al. 2007) and is measured as $\text{m}^3/\text{s}/100\text{m}$. We characterized upwelling conditions using 2 methods: the monthly upwelling anomaly and the daily cumulative upwelling index from the PFEL website. We downloaded monthly upwelling anomalies for the months and years of our study directly from the PFEL website, and they represented the difference in between mean monthly upwelling values for each month of our study versus the 20-year average from 1948–1967. We computed a daily cumulative upwelling index (CUI) as the cumulative sum

of the daily upwelling index beginning on the average date of physical spring transition (i.e., date of min. upwelling index value for year) for this location (ordinal day 103, or ~Apr 13) and ending on the last date of murrelet tracking for this study (ordinal day 223, or ~Aug 10) for the years of our study (2004–2008) following Schwing et al. (2006).

Upwellings are thought to improve forage conditions for top predators like seabirds primarily by bringing cool and nutrient-rich waters to the sea surface. We expected that a higher CUI would be associated with increased prey availability and therefore shorter paths in murrelets, because murrelets would be able to find prey while traveling shorter distances overwater. However, it is possible that murrelet movements would be better modeled directly by sea surface temperature (SST) and chlorophyll-*a* concentrations, rather than the CUI. If this was the case, we expected that low SST and high concentrations chlorophyll-*a* would be associated with shorter marine LCPs in murrelets (Becker and Beissinger 2003, Barrett 2008, Raphael et al. 2015). We obtained spatially explicit satellite derived data on SST (°C) and chlorophyll-*a* concentrations (mg/m^3) for each month and year of our study from the National Oceanic and Atmospheric Administration (NOAA 2007) Aqua MODIS (Moderate Resolution Imaging Spectroradiometer) at a resolution of 1 km, similar to Raphael et al. (2015). We considered the effect of current- and previous-month SST and chlorophyll-*a* on murrelets to account for possible time lags between changes in these factors and responses of the murrelet's prey.

Analysis

We used 2-tailed *t*-tests to compare 95% plugin kernel marine range size between males and females and breeders and non-breeders. For breeders, we looked for differences in marine LCPs by breeding stage (i.e., pre-nesting, incubation, nestling, post-nesting) using a repeated measures analysis of variance (ANOVA), treating individual birds as random replicates on each of the 4 breeding stages. We modeled repeated measurements with an autoregressive lag-1 covariance structure to capture covariation among daily measurements for each bird. We used 2-way ANOVA to compare marine range size among years and sites, and included an interaction term for year and site. For all of these analyses, we log transformed marine range size and marine LCPs to better meet assumptions of normality, and report Type 3 effects when overall *F* tests indicated statistical significance at $\alpha = 0.05$.

To assess the potential influence of delayed upwellings on murrelet movements, we used an information-theoretic approach (Burnham and Anderson 2002) where we compared support for a set of 11 *a priori* models. We developed models that considered results of past research, and our expectations of murrelet movements following changes in ocean conditions, based on modeling recommendations by Johnson and Omland (2004). We treated marine LCPs as the response variable. Similar to the preceding analysis with marine ranges, we log transformed marine LCPs to better meet assumptions of normality. We used marine LCPs rather than marine ranges to

represent murrelet movements in this analysis for 3 reasons. First, marine LCPs were typically measured daily (median time between consecutive points was 1.04 days), rather than yearly. This allowed us to examine within-year variation in movements, and led to a more robust sample size ($n = 4,932$ LCPs; and $\bar{x} = 32.32 \pm 14.51$ /bird) compared to using ranges ($n = 137$ marine ranges total, and 1/bird). Second, they allowed for an examination of effects at finer spatial resolution (i.e., point data, rather than 500–1,000 km² ranges). Third, LCPs were a less subjective measure of murrelet movements because the computation of ranges has its own set of inherent assumptions (Harris et al. 1990, Kernohan et al. 2001, Laver and Kelly 2010). As noted below, different methods for constructing ranges resulted in range sizes that varied by a factor of 2 to 3 in some individual cases, and ranges were not necessarily correlated with each other (i.e., correlation coefficient for ranges using different estimation methods averaged 0.831 and ranged 0.640–0.978; Table S1, available online in Supporting Information). Marine LCPs simply represented the minimum distance traveled between consecutive telemetry relocation points and did not vary numerically based on the method used to compute them.

We included CUI, capture site, and spatially explicit SST and chlorophyll-*a* as explanatory variables. Because each marine LCP was composed of 2 consecutive telemetry locations, we estimated SST and chlorophyll-*a* from the first point comprising each LCP. We expected that CUI, SST, and chlorophyll-*a* at each location would influence a murrelet's decision to move to the next consecutive location; higher CUI (Becker and Beissinger 2003, Peery et al. 2009), lower SST (Becker and Beissinger 2003, Day et al. 2003, Barrett 2008, Raphael et al. 2015, Lorenz et al. 2016), or higher chlorophyll-*a* (Peterson et al. 2010) would be associated with shorter marine LCPs if murrelets would be more likely to find prey in cooler, more nutrient rich waters and thus less prone to travel great distances to the next location. We included a term for both current- and previous-month SST (cSST and pSST, respectively) and chlorophyll-*a* (cchl_{or} and pchl_{or}) to account for possible time lags between changes in those factors and responses by murrelets (Raphael et al. 2015).

To reduce problems caused by pairwise collinearity among predictor variables, prior to building our models we looked for correlations between pairwise combinations of covariates with the intention of removing covariates if their coefficient was >0.60 (Dormann et al. 2013). However, we did not find any correlations >0.60 and therefore included all covariates. We did not include sex or breeding status as explanatory variables in this analysis because we did not observe differences between males and females or breeders and non-breeders (see Results).

Waters within the Salish Sea mix at different rates with those on the coast (Sutherland et al. 2011, Yang and Wang 2013), and we expected that the short-term effects of upwelling on distance may vary by capture site or by an individual's location at any given time. Murrelets captured or occurring on the Coast may be more influenced by upwellings than those in the Strait or Hood Canal. We

therefore included an interaction term for CUI with both capture site and point site (i.e., categorical variable for study area each telemetry relocation occurred in) in all models that included CUI as a factor.

We included a random effect for individual (bird ID) to account for multiple marine LCPs by individual murrelets. To account for temporal autocorrelation, we treated ordinal day as a repeated factor (using a random statement in Proc GLIMMIX; SAS Institute, Cary, NC, USA). We attempted multiple covariance structures, including a spatial power covariance structure to account for covariance within birds. We found that the only viable covariance structure was compound symmetry; no other structure could achieve starting values to begin the fitting process. We therefore used a compound symmetry structure, which assumes that all observations over time for the same bird have a common covariance with all other observations for that bird.

We ranked candidate models based on Akaike's Information Criterion corrected for small sample sizes (AIC_c) and Akaike weights (Burnham and Anderson 2002), where we considered models with lower AIC_c and higher weights better supported than other models. We used maximum likelihood estimation for computing AIC_c . We used restricted maximum likelihood (REML) for estimating model parameters for our best-supported model. We looked for violations of model assumptions using standard diagnostic plots. We assessed model fit for our best-supported model using k -fold cross-validation. We randomly removed 25% of observations as test data and fit the model with the remaining observations (i.e., training data). We then computed a predicted value of the response variable (LCP) for each observation in the test data based on the training model. We calculated root mean square error (RMSE), and the simple correlation coefficient (r) between actual and predicted values. We also computed the R^2 of the regression line fitted between the actual and predicted values. We completed 10 iterations (10-folds) of this process and averaged r , RMSE, and R^2 across iterations.

We used R for computing marine LCPs, nest-sea LCPs, and marine MCPs as described above, and SAS version 9.4 statistical software (SAS Institute) for statistical tests and models. For statistical tests, we considered results significant at $\alpha = 0.05$ and reported effect sizes in addition to test statistics. Throughout the results, we report means ($\pm$ SD) unless otherwise noted.

RESULTS

We captured and radio-tagged 157 marbled murrelets from 2004–2008. We captured 72% in the Strait of Juan de Fuca, 18% in Hood Canal, and 10% on the Pacific Coast. In general, capture rates were similar among sites. For days in which weather was conducive to capture, on average we captured 1.4, 1.5, and 1.6 murrelets/night ($n = 85$ nights) in the Strait, Hood Canal, and Coast sites, respectively. However, the Coast and Hood Canal sites were farther from our field center or more difficult to access, and therefore we captured fewer birds there. For logistical reasons, we did

Table 1. Proportion breeders, successful breeders, and the average date of egg-laying among 157 marbled murrelets radio-tracked 2004–2008 in Washington, USA, and British Columbia, Canada.

Year	No. murrelets radio-tagged	No. breeders	Proportion breeders	No. successful breeders among all tagged murrelets (proportion among those attempting nesting)	Average ordinal day for laying
2004	27	3	0.11	1 (0.33)	148
2005	40	8	0.20	1 (0.13)	143
2006	40	2	0.05	1 (0.50)	137
2007	32	5	0.16	0 (0.00)	145
2008	18	2	0.11	1 (0.50)	162

not attempt to capture murrelets on the Coast in 2004 and 2008.

We conducted telemetry tracking flights 76 ± 14 days each year, for 381 days of aerial telemetry tracking. Tracking flights occurred predominately from May to August and so we restricted our analyses only to points that were collected during this time period. During this period, flights did not occur on an average of 10.2 ± 10.6 days each year. We obtained 5,388 diurnal marine telemetry tracking relocations on murrelets from May to August 2004–2008, most of them during telemetry tracking flights. Mean number of marine relocations/individual during this period was 34.3 ± 15.3 (range = 1–71).

Murrelets captured in different study areas differed in their fidelity to their capture site. Few Hood Canal (0%) and Strait (9%) birds ever visited the Coast study site, but all Coast birds (100%) visited the Strait or Hood Canal at some point during the May to August tracking period. Consequently, Coast birds showed lower fidelity to their capture area, with 48% of coastal birds' point relocations occurring on the Coast ($\bar{x} = 44\%$ points/bird for Coast-captured birds; the remainder were in the Strait or Hood Canal). In contrast, 71% and 79% of Hood Canal and Strait birds' telemetry relocations occurred within their respective capture site. Thus, in

combination with the high number of birds captured on the Strait relative to Coast, interior waters were used far more commonly than coastal waters by radio-tagged murrelets; 4% of all telemetry points occurred in the Coast study site compared to 96% in interior waters (i.e., Strait and Hood Canal combined).

The San Juan Islands in the northeastern part of the Strait of Juan de Fuca were unusual because they were used by murrelets from all study areas even though only 2 individuals (1%) were ever captured there. The San Juan Islands were used more heavily by tagged murrelets in 2005 and 2007. Collectively, 17% of telemetry relocations occurred in the San Juan Islands in those 2 years. Across all years, 37% of murrelets visited the San Juan Islands (58% and 66% of individuals in 2005 and 2007, respectively).

We detected breeding for 20 murrelets (12.7%), and located 19 nest sites. One nest site in a tree was not found before the nest failed (Wilk et al. 2016). Four murrelets successfully fledged young (Table 1). We detected no breeding by Coast murrelets, compared to 17 Strait murrelets and 3 Hood Canal murrelets. The year 2005 had the highest percentage of radio-tagged breeders (20%), whereas 2006 had the lowest proportion with only 5% of tagged birds attempting to breed.

Table 2. Mean, standard deviation, median, and range for kernel and minimum convex polygon (MCP) marine ranges of 138 marbled murrelets radio tracked 2004–2008 in Washington, USA, and British Columbia, Canada. We computed kernels using plugin and least squares cross validation (LSCV) bandwidth estimators.

	95% plugin kernel (km ²)				95% LSCV kernel (km ²)				95% MCP (km ²)			
	$\bar{x}$	SD	Median	Range	$\bar{x}$	SD	Median	Range	$\bar{x}$	SD	Median	Range
F ($n = 78$)	979	1,248	555	23–7,835	1,708	2,065	1,000	24–12,071	705	801	417	11–3,738
M ($n = 60$)	890	1,487	257	31–8,749	1,484	2,227	602	43–11,613	723	916	391	18–3,534
Breeders ($n = 20$)	686	640	508	31–2,711	1,203	1,042	1,162	43–4,548	664	592	516	20–2,202
Non-breeders ($n = 118$)	981	1,429	492	22–8,749	1,677	2,251	899	24–12,071	716	884	391	11–3,738
Coast ($n = 12$)	3,378	2,706	2,538	336–8,749	5,700	3,699	5,055	516–12,071	1,826	1,381	1,470	91–3,738
Hood Canal ($n = 27$)	903	1,003	747	37–5,073	1,490	1,880	1,039	45–5,936	637	647	472	18–2,937
Strait ($n = 99$)	938	1,346	322	22–4,187	1,145	1,416	666	24–8,444	592	714	313	11–3,213
2004 ($n = 20$)	793	1,425	182	31–5,073	1,130	1,963	262	43–6,459	338	683	76	20–2,937
2005 ($n = 37$)	1,084	1,052	787	58–4,283	1,959	1,880	1,424	75–8,444	1,000	907	842	46–3,738
2006 ($n = 35$)	740	1,088	239	23–5,293	1,313	1,944	564	24–9,485	422	583	199	11–3,008
2007 ($n = 30$)	1,358	2,009	863	42–8,749	2,281	2,905	1,698	55–12,071	1,104	1,033	804	25–3,534
2008 ($n = 16$)	446	301	336	47–942	780	678	528	50–2,011	379	373	268	27–1,408
All birds ($n = 138$)	938	1,348	487	22–8,749	1,608	2,123	891	24–12,071	708	847	404	11–3,738

The median date of fish-holding for murrelets on surveys in our study area was ordinal day 202.5 (~Jul 20). Thus, we estimated that nest initiation ranged between 24 May (subtracting 58 days for early nesters) to 21 June (subtracting 30 days for later nesters) for our study population. This is within the range of nest initiation dates estimated by Nelson and Hamer (1995) for murrelets in Washington (~18 Apr to 1 Aug, with a median of ~15 Jun). After correcting for missed breeders (i.e., subtracting murrelets that were captured after the median range of nest initiation dates), our corrected estimate of breeding prosperity ranged from 13.1% if we assume median nest initiation occurred on June 21, or 20.0% if we assume median nest initiation occurred on May 24 for this population.

Marine Ranges

Mean number of marine telemetry locations/bird was 34.3 ± 15.3 (range = 2–71), and we obtained ≥ 15 marine telemetry locations for 138 murrelets for computing ranges (19 murrelets had < 15 locations and were not included in range analysis). The number of telemetry locations was not correlated with 95% plugin kernel size ($r = -0.025$) or 50% kernel plugin kernel size ($r = -0.041$). Median marine 95%

plugin kernels were 487 km^2 ($\bar{x} = 938 \text{ km}^2 \pm 1,348 \text{ km}^2$), and median 95% MCPs kernels were 404 km^2 ($\bar{x} = 708 \text{ km}^2 \pm 847 \text{ km}^2$; Table 2).

Ninety-five percent plugin kernels did not differ between females and males ($t_{137} = 1.17$; $P = 0.243$) or breeders and non-breeders ($t_{137} = -0.17$; $P = 0.865$; Table 2). Although we observed a significant overall ANOVA ($F_{7, 131} = 6.46$, $P < 0.001$) for variation among years and capture sites (Table 2), Type 3 effects indicated that range size varied only by capture site ($F = 25.62$, $P < 0.001$) and not by year ($F = 1.73$, $P = 0.146$). Plugin kernels were larger for birds captured on the Coast ($\bar{x} = 3,378 \pm 2,706$) than for Strait ($\bar{x} = 938 \pm 1,346$) or Hood Canal birds ($\bar{x} = 903 \pm 1,003$; Table 2).

We assumed that 50% kernels (Table S1) represented core areas, similar to Barbaree et al. (2015). Differences in core areas among groups mirrored those for 95% plugin kernels, with the only significant differences occurring by capture site, where again coastal birds had significantly larger core areas ($F_{12, 126} = 19.51$, $P < 0.001$). There were no significant differences by sex ($t_{137} = 1.04$; $P = 0.300$), breeding status ($t_{137} = 0.03$; $P = 0.974$), or year ($F_{12, 126} = 1.30$, $P = 0.274$).

Table 3. Mean, standard deviation, and range of distances (km) between inland nests and sea, nest-sea commuting distances (from least cost path analysis), and nest fate for 20 breeding, radio-tagged marbled murrelets in Washington, USA and British Columbia, Canada, 2004–2008. Distances represent 1-way travel.

Bird (<i>n</i>) ^a	Sex	Straight-line distance from nest to sea	Total nest-sea commute (terrestrial and marine)			Terrestrial portion of nest-sea commute ^b	Marine portion of nest-sea commute			Nest fate
			$\bar{x}$	SD	Range		$\bar{x}$	SD	Range	
2004										
021 (63)	M	14.6	20.5	3.6	17.4–29.2	16.8	3.7	3.6	0.6–12.4	Successful
562 (31)	M	14.0	27.1	8.7	16.8–49.4	15.0	12.1	8.7	1.8–34.4	Failed—nestling
983 (9)	F	17.7	35.1	7.8	25.1–46.6	23.8	11.3	7.8	1.3–22.8	Failed—incubation
2005										
070 (2)	M	22.7	86.9	60.8	43.9–129.9	29.0	57.8	60.8	14.9–100.8	Failed—incubation
141 (26)	M	9.9	63.6	4.0	60.0–75.5	11.8	51.7	4.0	48.1–63.7	Failed—incubation
212 (20)	F	4.7	89.0	15.7	45.9–138.3	5.1	83.9	15.7	40.7–133.1	Failed—incubation
302 (20)	F	37.7	71.9	11.2	45.2–79.7	61.2 (43.4–65.6)	10.7	3.5	1.8–14.1	Failed—nestling
619 (31)	M	18.9	86.2	23.3	41.3–103.6	21.8	64.4	23.3	19.5–81.8	Failed—nestling
844 (59)	F	8.2	37.2	5.9	18.2–48.3	10.4	26.8	5.9	7.8–37.9	Failed—nestling
853 (16)	F	36.7	57.6	3.5	49.7–61.3	47.4	10.3	3.5	2.4–14.0	Failed—incubation
932 (60)	M	30.7	69.2	29.2	40.4–127.0	40.4	28.9	29.2	0.5–86.7	Successful
2006										
122 (27)	M	12.7	48.9	5.3	40.5–58.0	21.5	27.3	5.3	19.0–36.4	Failed—nestling
232 (61)	F	7.0	47.6	16.9	21.7–78.0	8.6	38.9	16.9	13.0–69.3	Successful
2007										
161 (18)	M	20.4	42.7	7.4	34.2–53.0	33.6	9.0	7.4	0.6–19.4	Failed—incubation
211 (8)	M	14.2	74.8	29.1	28.0–97.0	19.1	55.7	29.1	8.9–77.9	Failed—incubation
295 (24)	M	24.1	39.3	9.3	29.3–60.2	28.0	11.4	9.3	1.3–32.2	Failed—incubation
382 (27)	M	3.9	51.9	13.8	25.3–62.7	4.1	47.9	13.8	21.3–58.7	Failed—incubation
520 (66)	M	21.6	53.9	18.7	33.2–93.8	31.3	22.6	18.7	1.8–62.5	Failed—nestling
2008										
258 (27)	M	57.9	124.4	7.1	117.9–145.3	84.3	40.1	7.1	33.6–61.0	Successful
346 (28)	M	20.3	27.1	1.8	24.3–31.7	22.5	4.6	1.8	1.8–9.2	Failed—nestling
All birds (623)		19.9 ± 12.5	53.1	28.4	16.8–145.3	24.9 ± 19.6 (4.1–84.3)	28.1	24.6	0.5–133.1	

^a *n* is sample size of commutes for each individual. We only computed it when individuals were located on the water, which was not always possible. Thus *n* varies even for birds with similar nest fates.

^b For all but 1 individual, nest-sea commuting distance did not vary because the same terrestrial path was presumably taken on every commute. One individual (bird 302) that nested in the interior of the Olympic Peninsula foraged both in the Pacific Ocean (to the west) and in the Strait of Juan de Fuca (to the north) and thus had 2 different terrestrial paths estimated.

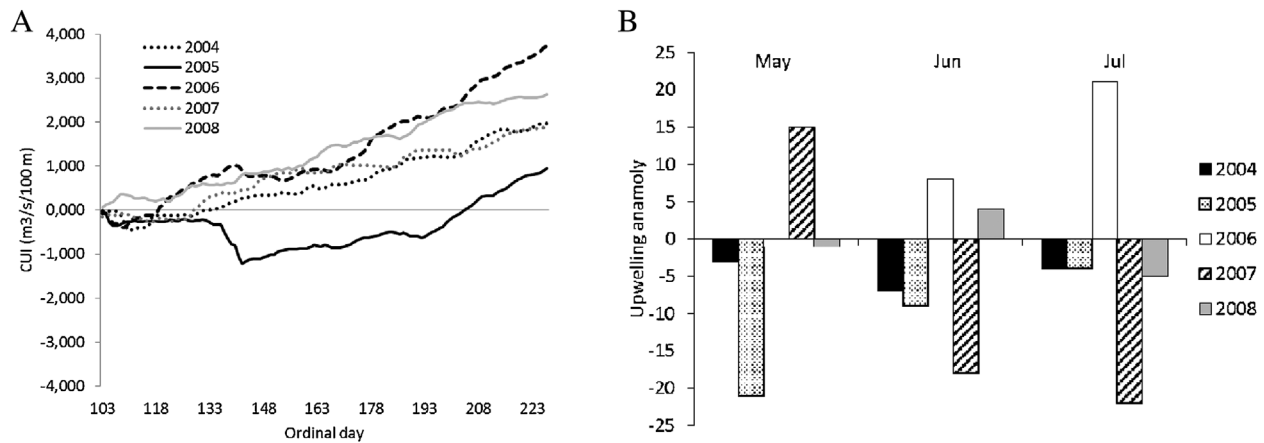


Figure 3. Cumulative upwelling index ($\text{m}^3/\text{s}/100 \text{ m}$; A) and upwelling anomalies (B) for northwestern Washington, USA, ($125^\circ \text{ W } 45' \text{ N}$; www.pfel.noaa.gov) during the months and years (Apr–Aug 2004–2008) that we radio-tracked marbled murrelets in northwestern Washington and southwestern British Columbia. Cumulative upwelling index (CUI) is shown beginning on the mean day of spring transition for this location, estimated from the date of the minimum CUI in each year, 1967–2013.

LCP Analysis—Nest to Sea

Among 20 breeding murrelets, the mean nest-sea commuting distance (i.e., nest-sea LCP) was $53.5 \pm 28.4 \text{ km}$ (Table 3) and ranged from 16.8–145.3 km. The straight-line distance from nest to sea was on average 19.9 km ($\pm 12.5 \text{ km}$; range = 3.9–57.9 km), or 5.0 km shorter on average than the terrestrial portion of the nest-sea commute distance calculated by our LCP analysis (Table 3).

The marine portion of the nest-sea commute ($\bar{x} = 28.1 \pm 24.6 \text{ km}$; median = 21.4 km) was similar to the terrestrial portion ($\bar{x} = 24.9 \pm 19.6 \text{ km}$; median = 22.5 km), although this varied by individual. The longest terrestrial commute of 84.3 km occurred for murrelet number 258, which nested within the Cascade Range and foraged in

Puget Sound. This individual successfully fledged his young with an average nest-sea commute of 124.4 km (Table 3).

The longest marine commute of 133.1 km occurred for a failed breeder, murrelet number 212 (Table 3), which nested 4.7 km from shore on Vancouver Island, Canada but foraged at times in the San Juan Islands (total 1-way commute of 138.3 km). Four other individuals with long marine commutes ($>60 \text{ km}$ 1-way) due to foraging trips to the San Juan Islands included bird 932 (in 2005; successful), bird 619 (in 2005, failed), bird 211 (in 2007; failed), and bird 520 (2007; failed). These 4 individuals nested on the Olympic Peninsula. Other long marine commutes were associated with foraging in Admiralty Inlet by birds that nested in the eastern Olympic Mountains (birds 080 in 2005 and 141 in 2005; Table 3).

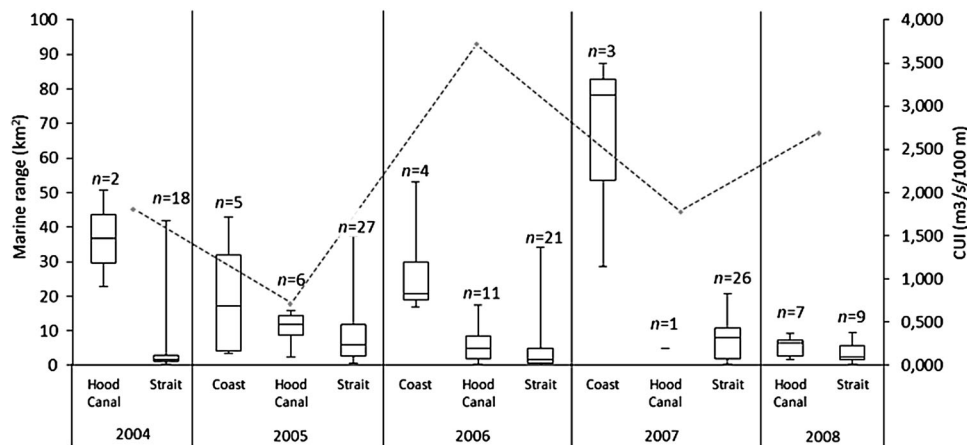


Figure 4. Comparison of 95% plugin kernels for marine ranges by year and capture site (Pacific Coast [Coast], Hood Canal, and Strait of Juan de Fuca [Strait]) for 138 radio-tracked marbled murrelets (boxplots) plotted against the cumulative upwelling index (CUI; $\text{m}^3/\text{s}/100 \text{ m}$) at the end date of each field season ($\sim$ ordinal day 223; gray dotted line), 2004–2008, northwestern Washington, USA. Box plots show maximum (top whisker), minimum (bottom whisker), first and third quartiles (top and bottom line of box), and median (center line of box). Sample sizes of murrelets by year and capture site, for which we estimated 95% plugin kernels, are indicated above each plot.

Table 4. Marine least-cost path (LCP) distance (km) between consecutive marine locations (usually obtained daily) for marbled murrelets that were detected attempting to breed in northwestern Washington, USA and southwestern British Columbia, Canada, 2004–2008. Shown are means ($\pm$ SD), with sample sizes of LCPs and murrelets in parenthesis for the pre-breeding, incubation, nesting, and post-breeding stages, followed by non-breeding (includes incubation and post-breeding stage) and breeding (includes incubation and nesting stage). Note that in 2004 and 2006 no breeders were tracked during the post-breeding period.

	2004		2005		2006		2007		2008		All years	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Pre-breeding	7.40 ($n_{LCP}=31$, $n_{birds}=2$)	4.7	10.00 ($n_{LCP}=109$, $n_{birds}=7$)	15.00	15.12 ($n_{LCP}=20$, $n_{birds}=2$)	12.1	12.17 ($n_{LCP}=72$, $n_{birds}=4$)	16.1	4.70 ($n_{LCP}=36$, $n_{birds}=2$)	3.27	9.95 ($n_{LCP}=268$, $n_{birds}=17$)	13.48
Incubation	8.48 ($n_{LCP}=17$, $n_{birds}=2$)	5.9	12.7 ($n_{LCP}=73$, $n_{birds}=8$)	30.18	10.76 ($n_{LCP}=23$, $n_{birds}=2$)	9.57	10.96 ($n_{LCP}=125$, $n_{birds}=5$)	17.1	9.91 ($n_{LCP}=23$, $n_{birds}=2$)	13.7	11.19 ($n_{LCP}=261$, $n_{birds}=19$)	20.46
Nesting	4.95 ($n_{LCP}=37$, $n_{birds}=2$)	5.1	16.17 ($n_{LCP}=58$, $n_{birds}=4$)	33.88	11.94 ($n_{LCP}=22$, $n_{birds}=2$)	12.1	16.78 ($n_{LCP}=16$, $n_{birds}=1$)	8.46	7.33 ($n_{LCP}=7$, $n_{birds}=2$)	8.22	12.17 ($n_{LCP}=140$, $n_{birds}=11$)	23.11
Post-breeding			21.00 ($n_{LCP}=66$, $n_{birds}=5$)	29.69			25.10 ($n_{LCP}=16$, $n_{birds}=3$)	34.2	15.40 ($n_{LCP}=5$, $n_{birds}=1$)	16	21.43 ($n_{LCP}=87$, $n_{birds}=9$)	29.73
Non-breeding	7.40 ($n_{LCP}=31$, $n_{birds}=2$)	4.7	14.15 ($n_{LCP}=175$, $n_{birds}=8$)	22.31	15.12 ($n_{LCP}=20$, $n_{birds}=2$)	12.1	14.52 ($n_{LCP}=88$, $n_{birds}=4$)	20.9	6.01 ($n_{LCP}=41$, $n_{birds}=2$)	6.89	12.76 ($n_{LCP}=355$, $n_{birds}=18$)	19.42
Breeding	6.06 ($n_{LCP}=54$, $n_{birds}=3$)	5.6	14.26 ($n_{LCP}=131$, $n_{birds}=8$)	31.79	11.34 ($n_{LCP}=45$, $n_{birds}=2$)	10.8	11.62 ($n_{LCP}=141$, $n_{birds}=5$)	16.4	9.31 ($n_{LCP}=30$, $n_{birds}=2$)	12.6	11.53 ($n_{LCP}=401$, $n_{birds}=20$)	21.4

Oceanographic Effects

In 2005, the date of physical spring transition (date of min. upwelling index value for year), which generally corresponds to the beginning of the upwelling season, was delayed by 39 days and occurred on ordinal day 142 (~May 22) compared to the 49-year mean of ordinal day 103 (~Apr 13) off the coast of Washington. Thus, the CUI in 2005 continuously lagged behind the CUI for other years of this study, even in June and July (Fig. 3). The upwelling anomaly was also pronounced in 2005 (Fig. 3), with the strongest negative effects occurring in May. Upwelling anomalies indicated that 2007 was also an unusual year, with relatively strong negative anomalies in June and July. The year 2006 showed strong positive anomalies (e.g., increased upwelling) compared to other years (Fig. 3).

As noted above, 2006 with the strongest positive anomalies had the lowest proportion of breeders (5%). Conversely, 2005 and 2007, in which large negative upwelling anomalies were observed, were years in which the highest proportion of murrelets attempted to breed in our study (20% in 2005 and 16% in 2007; Table 1). The years 2005 and 2007 were also associated with larger murrelet range sizes, when pooling all murrelets together (Table 2). However, this effect was somewhat confounded by unequal sampling effort, because murrelets on the Coast, which consistently had larger ranges than murrelets in the Strait and Canal, were only tracked from 2005–2007. When considering yearly variation in range size by capture site (Table S1), there was no clear pattern of range size increasing in months and years of upwelling anomalies. Murrelets on the Coast had large ranges in May and June 2005, corresponding to upwelling anomalies in those months and years, but not in June and July 2007 (Table S1). Murrelets radio-tagged in the Strait of Juan de Fuca had consistently small ranges across all months and years of study compared to Coast birds (Fig. 4).

LCP Analysis—Marine

We computed marine LCPs for all marine locations and for all murrelets with ≥ 2 telemetry points recorded ($n=153$). We eliminated 14 marine LCPs that were separated by >8 days. Among the remaining 4,932 marine LCPs, the median time between consecutive points was 1.04 days ($\bar{x}=1.39 \pm 0.96$; range = 0.11–8.33 days) and LCP distance was not correlated with the minutes between points ($r=0.0679$). On average we obtained 32.32 marine LCPs/bird (± 14.51 ; median = 33.00, range = 3–68). Median marine LCP distance was 4.18 km ($\bar{x}=10.43 \pm 16.93$; range = 0.00–224 km).

We did not observe differences in marine LCPs between females ($\bar{x}=13.3 \pm 9.6$ km) and males ($\bar{x}=11.5 \pm 8.2$ km; $t_{137}=1.14$; $P=0.257$), or breeders ($\bar{x}=12.3 \pm 6.0$ km) and non-breeders ($\bar{x}=12.6 \pm 9.5$ km; $t_{137}=-0.56$; $P=0.580$). We separately computed the mean marine LCP for breeding murrelets during different stages of their nesting cycle (Table 4). Marine LCPs did not differ by nesting stage ($F_{3,33}=1.97$, $P=0.14$; Fig. 5). Least squared means ($\pm$ SE) for LCPs were 8.37 ± 0.15 km ($n=17$ murrelets), 8.42 ± 0.15 km ($n=19$ murrelets), 8.67 ± 0.20 km ($n=11$

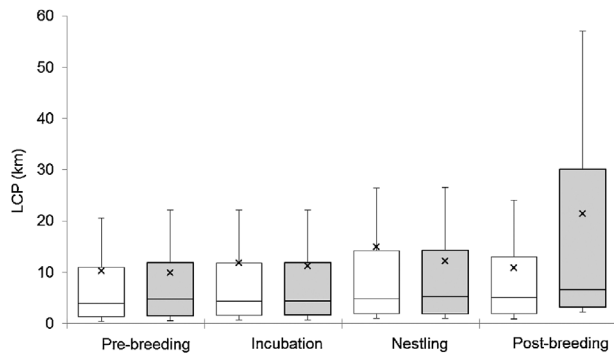


Figure 5. Comparison of distance between consecutive marine telemetry relocations (usually obtained daily, and computed from least-cost path [LCP] analysis) for non-breeding (white boxes) and breeding (gray boxes) radio-tagged marbled murrelets during the pre-breeding, incubation, nestling, and post-breeding period, in northwestern Washington, USA, and southwestern British Columbia, Canada, 2004–2008. Box plots show the interquartile range $\times$ 1.5 (whiskers), first and third quartiles (top and bottom line of box), median (center line of box), and mean ($\times$ symbol).

murrelets), and 8.96 ± 0.25 km ($n = 9$ murrelets) for the pre-breeding, incubation, nestling, and post-breeding stages, respectively. We did not have a large enough sample of breeders each year to look at among-year differences in marine LCPs by breeders.

The best-supported model explaining variation in marine LCPs from among those we considered was the global model (Table 5). Parameter estimates that did not overlap 0 (i.e., significant parameter estimates) included 1 continuous variable, cSST, and 4 indicator variables: Coast capture site, Hood Canal capture site, Strait capture site, and Coast point site (Table 6). Our analysis indicated that holding all other parameters constant, a 1-degree increase in cSST corresponded to a 1.08-km increase in distance traveled by murrelets between consecutive marine locations. Interpretation of categorical variables was more complicated.

Significant parameter estimates for Hood Canal and Strait indicated that model fit would be improved if separate models with separate intercepts were fit for those groups; given results from a 2-way ANOVA that showed home ranges differed by capture site, this suggests that movements may differ by capture site. Significant and positive parameter estimates for Coast capture site and Coast point site (Table 6) indicate that movements of murrelets increase when on the coast, regardless of an individual's capture site, but are also greater for individuals that were trapped on the coast.

Residuals plots indicated that the model assumptions were not violated. However, measures of goodness of fit indicated somewhat poor model performance. There was little correlation between predicted and actual values on average ($r = 0.215$). The RMSE, an indication of the standard deviation between predicted and actual values, was 24.5 km. Thus, although the global model ranked higher than others that we considered, variation in marine LCPs by murrelets could be largely associated with factors we did not measure.

DISCUSSION

Murrelet Breeding Propensity

The breeding propensity of radio-tagged marbled murrelets in this study (0.131–0.200) is the lowest reported in a murrelet population that we are aware of. Across 6 past studies that we reviewed, breeding propensity from radio-tagged murrelets ranged from 0.23 in Clayoquot Sound, British Columbia (McFarlane Tranquilla et al. 2005) to 0.58–0.65 in Alaska (Hull et al. 2001, Bradley et al. 2004). In Peery et al. (2004), breeding propensity was 11% in 1 year but rebounded to 50% in the following year. In contrast, over the 5 years of our study, the proportion of breeders was never higher than 16% in a given year, suggesting low rates of breeding were not a 1- or 2-year response to temporarily poor ocean conditions. In our study, the year 2006 had the lowest

Table 5. Support for models explaining variation in marine least-cost path (distance between consecutive marine locations [usually obtained daily]) for marbled murrelets in Washington, USA, and British Columbia, Canada, 2004–2008.

Model ^a	AIC _c ^b	Δ_i ^c	w_i ^d
Global (pSST, cSST, pchlor, cchlor, CUI, capturesite, CUI $\times$ capturesite, pointsite, CUI $\times$ pointsite)	17,517.43	0	0.779
pSST, cSST, pchlor, cchlor, CUI, capturesite, CUI $\times$ capturesite	17,521.78	4.35	0.089
cSST, cchlor, CUI, capturesite, CUI $\times$ capturesite	17,521.79	4.36	0.088
cSST, CUI, capturesite, CUI $\times$ capturesite	17,523.41	5.98	0.039
Capturesite, cSST	17,527.68	10.25	0.005
Pointsite	17,542.57	25.14	<0.001
CUI, pointsite, CUI $\times$ pointsite	17,543.76	26.33	<0.001
cSST	17,546.62	29.19	<0.001
CUI, capturesite, CUI $\times$ capturesite	17,552.13	34.70	<0.001
CUI, capturesite, CUI $\times$ capturesite, cchlor	17,552.85	35.42	<0.001
Capturesite	17,554.23	36.80	<0.001

^a cSST = sea surface temperature ($^{\circ}$ C) measured at each location in the current month; capturesite = categorical variable for whether a murrelet was captured in the Coast, Strait, or Hood Canal study site; CUI = daily cumulative upwelling index ($\text{m}^3/\text{s}/100 \text{ m}$); cchlor = concentration of chlorophyll-*a* (mg/m^3) at each location in the current month; pSST = sea surface temperature ($^{\circ}$ C) measured at each location in the previous month; pchlor = concentration of chlorophyll-*a* (mg/m^3) at each location in the previous month; pointsite = categorical variable for whether a telemetry relocation occurred in the Coast, Strait, or Hood Canal study site.

^b AIC_c = Akaike's Information Criterion corrected for small sample sizes.

^c Δ_i = Akaike's Information Criterion relative to the highest ranked model.

^d w_i = Akaike weight.

Table 6. Parameter estimates and 95% confidence intervals for the best-supported model explaining variation in marine least-cost path (LCP) distance (km) between consecutive locations (usually obtained daily) for marbled murrelets in northwestern Washington, USA, and southwestern British Columbia, Canada, 2004–2008.

Parameter ^a	Estimate	Lower CI	Upper CI
Coast capture site	8.079	7.578	8.581
Hood Canal capture site	7.702	7.246	8.158
Strait capture site	7.646	7.209	8.082
pSST	−0.003	−0.043	0.038
cSST	0.084	0.047	0.121
pchlor	−0.001	−0.002	0.000
cchlor	−0.001	−0.003	0.000
CUI	0.000	−0.001	0.002
Coast capture site × CUI	0.002	−0.001	0.006
Hood Canal capture site × CUI	−0.003	−0.005	0.000
Strait capture site × CUI	0.001	−0.001	0.003
Coast point site	0.409	0.132	0.685
Hood Canal point site	−0.130	−0.370	0.111
Coast point site × CUI	0.001	−0.003	0.005
Hood Canal point site × CUI	0.000	−0.003	0.004
Strait point site × CUI	−0.001	−0.002	0.001

^a pSST = sea surface temperature (°C) measured at each location in the previous month; cSST = sea surface temperature (°C) measured at each location in the current month; pchlor = concentration of chlorophyll-*a* (mg/m³) at each location in the previous month; cchlor = concentration of chlorophyll-*a* (mg/m³) at each location in the current month; CUI = daily cumulative upwelling index (m³/s/100 m).

rate of breeding, with only 5% of murrelets attempting breeding in that year.

Breeding propensity in our study possibly was higher than detected by radio-telemetry. There are 2 reasons proposed in past studies that transmitters may underestimate breeding propensity. First, radio-tracking may be initiated after adults had started, but failed in their nesting attempts. McFarlane Tranquilla et al. (2005) reported that radio-telemetry missed breeding attempts in Clayoquot Sound, British Columbia, because murrelets could not be effectively captured during the early breeding stages. If this is the case, successful nesting is rare in our population because birds that nested earlier should have been feeding nestlings during the early parts of our tracking period. However, we feel it is unlikely that we missed breeding because observations of fish-holding murrelets during 14 years of surveys in our study area indicate that nest initiation fell within the time frame of our telemetry tracking. In our study area, fish-holding was observed by surveyors from 8 June to 13 August 1998–2012, which equates to nest initiation from 24 May to 21 July. This corresponds to the peak of our telemetry tracking effort.

A second possibility is that the process of capturing and radio-tagging murrelets negatively affected breeding (Bradley et al. 2004). Without measuring blood vitellogenin (Vanderkist et al. 2000, McFarlane Tranquilla et al. 2003b), most past telemetry studies have not been able to compare breeding propensity of tagged and non-tagged murrelets because nests of untagged murrelets are difficult to locate in large numbers, and other cues such as brood patches, fish-holding behavior, and pairing status on the water have inherent biases (McFarlane Tranquilla et al. 2003a, c).

Survival estimates from Peery et al. (2006) suggest that tags may negatively affect murrelet survival and thus tags may also affect breeding propensity. However, with the exception of 1 study (Hebert and Golightly 2006, 2008) the methods used in our study to capture and tag murrelets were similar to those in the aforementioned telemetry studies that reported higher breeding propensity. Thus, it seems unlikely that murrelets were negatively affected by handling in our study compared to other studies that used telemetry to estimate breeding propensity. Yet another consideration is that transmitter weight negatively affected murrelet breeding propensity because transmitters in our study were 0.3–1.4 g heavier (3.3 g total) than those used in past studies (transmitter weight range = 1.9–3.0 g; Hull et al. 2001, Bradley et al. 2004, Kuletz 2005, McFarlane Tranquilla et al. 2005, Hebert and Golightly 2008, Peery et al. 2009, Barbaree et al. 2014). Vandenabeele et al. (2012) theorized that transmitter weight may disproportionately negatively affect alcids compared to other seabirds. However, we feel this explanation for low breeding propensity is also unlikely because the transmitters used in our study were 1.1–1.9% of body mass ($\bar{x}$ = 1.5%), which is below the 3–5% mass limit tested by Vandenabeele et al. (2012).

If the breeding propensity we documented with radio-transmitters reflects actual breeding propensity in this population, additional studies are needed to identify the cause. Losses in nesting habitat over the last century may have contributed to or caused low breeding propensity. Although long-term survival data are lacking, murrelets are considered long-lived birds (Peery et al. 2004, Gutowsky et al. 2009). Therefore, individuals hatched many years ago may have lost nesting habitat for breeding, but are still persisting in the population. Poor marine conditions may also enable adults to survive but with insufficient energy reserves to attempt or succeed at breeding, as was found by Peery et al. (2004) in some years in central California. For the region encompassing our study area in Washington, such conclusions are supported by stable isotope analyses by Norris et al. (2007) and Gutowsky et al. (2009), which show murrelet diet and productivity have declined in the last 100 years throughout the Salish Sea.

Nest-Sea Commuting

Breeding murrelets in our study generally commuted greater distances between nest and at-sea locations than those in other studies, indicating that despite the aforementioned possible effects of transmitters on breeding propensity, transmitters did not limit murrelet movements. Past studies have reported maximum, 1-way nest-sea commuting distances of approximately 111 km (Burns et al. 1994), 124 km (Whitworth et al. 2000), 60 km (Kuletz 2005), 102.3 km (Hull et al. 2001), and 94.2 km (Barbaree et al. 2015), compared to the maximum of 145.3 km in our study. Four of 20 breeders in our study traveled greater distances than the previous reported maximum distance (124 km) from nests to sea.

Nesting habitat is reportedly much reduced in our study area compared to pre-1900 levels (Perry 1995) and this likely contributes some to long commutes. However, reductions in

nesting habitat should only lead to long terrestrial commutes, whereas murrelets in this study traveled equally long distances over water. It follows that if longer than average terrestrial commutes indicate degraded nesting habitat that force murrelets to travel far to nesting habitat (Ralph et al. 1995), long marine commutes may indicate poor foraging habitat. Thirteen of 20 breeders traveled greater distances over water than over land at some point during their nesting cycle, sometimes far greater distances over water (e.g., murrelet with the longest marine commute of 133.1 km that nested within 4.7 km of the sea). This collectively may point to poor marine habitat in this region, or at least marine habitat that is less productive than other parts of the murrelet's range. It corroborates conclusions from Norris et al. (2007) and Gutowsky et al. (2009) that present-day marine productivity within the Salish Sea is poor, and has negatively affected marbled murrelet populations. It is further supported by data showing that the number of murrelets/ha of nesting habitat is >10 times lower in Washington than in southeastern Alaska, and is lower than in California and Oregon (M. G. Raphael, Forest Service, unpublished data).

Marine Ranges and Movements

Like marine commuting distances of breeding murrelets, marine ranges of murrelets for breeding and nonbreeding murrelets were greater in our study than reported previously. Barbaree et al. (2015) reported mean LSCV kernel ranges of 127 km² for murrelets in Alaska, which was almost an order of magnitude smaller than the mean plugin kernel ranges of 938 km² for murrelets in this study. Hebert and Golightly (2008) reported mean MCP ranges of 505 km² in northern California, compared to 708 km² for our study. Our estimates are also much larger than the marine MCPs of 143 km² (computed using slightly different methods) by Kuletz (2005) for murrelets in Alaska. Some caution should be exercised when comparing ranges among studies because small differences in methodology or software can result in differences in range size (Laver and Kelly 2010). Nevertheless, nest-sea commuting distances and LCPs were also greater in our study than in past studies. Because these measures should be less affected by methodological or software differences, they are more directly comparable across studies. All the factors we measured (nest-sea commuting distance, marine kernels, and marine MCPs) were greater in our study than previously reported. Thus, numerous lines of evidence indicate that murrelets in Washington are moving greater distances in the marine environment than murrelets in other populations, even if the magnitude of the difference is difficult to quantify.

Building on observations discussed in the preceding section, these large marine ranges suggest subpar marine conditions within our study area. Habitat quality and food availability are influential factors in animal ranging behavior, and larger ranges often occur in poorer habitat because animals are required to traverse larger areas to locate food (Brown and Orians 1970). Although this hypothesis has not been specifically tested for marbled murrelets and factors other than prey availability can affect murrelet space use

(Burger et al. 2008), coupled with the low breeding propensity (13%), low nest success (1.5%), and long marine commutes by breeders (up to 133 km), the large marine ranges in our study indicate that marine conditions may be poor for murrelets in this population, in addition to declines in terrestrial habitat noted in many past studies. If this is the case, murrelets may be forced to travel greater distances than other populations to locate food for sustaining themselves or raising young during the breeding season, in addition to the large travel distances overland required to find nesting sites.

Oceanographic Effects

Many past studies have explored a hypothesis that oceanographic conditions that influence prey availability (e.g., SST, upwelling conditions, and chlorophyll-*a*) can be used to understand seabird movements and breeding (Bertram et al. 2002, Gjerdrum et al. 2003, Ronconi and Burger 2008, Borstad et al. 2011). In this study, we modeled daily marine movements by murrelets as a function of SST, cumulative upwelling index (CUI), and chlorophyll-*a* but found no strong associations. We found some indication that murrelet movements were shorter in cooler waters, indicating that cooler water may provide higher abundances of prey, similar to some past studies (Barrett 2008). It also appears that murrelets have greater movements when in the Pacific Coast study site, suggesting that the Pacific Coast may have more sparsely distributed prey, or poorer foraging conditions than the interior study areas. Future studies on prey occurrence are needed to verify if this is the case.

The absence of any CUI effect was somewhat surprising because of a strongly delayed upwelling in 2005 and a moderately delayed upwelling in 2007. During this unusual upwelling event, other studies reported that the delayed upwelling negatively affected many marine processes such as recruitment of intertidal organisms (Dorman et al. 2011), anchovy larval growth (Takahashi et al. 2012), and Cassin's auklet (*Ptychoramphus aleuticus*) breeding (Sydeman et al. 2006). For the marbled murrelet specifically, Ronconi and Burger (2008) reported reduced productivity in southwest Vancouver Island, as measured from ratios of adults to juveniles at sea, which they linked to this delayed upwelling.

Although our modeling analysis only considered the effect of ocean conditions on movements, the limited information that we have on breeding propensity and nest success also suggests that delayed upwelling did not substantially affect breeding by murrelets in our study. The year 2005 had the numerically highest rate of breeding propensity for our tagged murrelets. Nest success was consistently low in all years of this study, and ranged from a low of 0 in 2007 to 0.05 in 2008. Murrelets possibly compensated for the change in ocean conditions by switching prey, similar to observations of common murre (*Uria aalge*) in this region (Schrimpf et al. 2012), and this did not require changes in the overall amount of space used or breeding behavior. The lack of any upwelling effects may also be partially explained by the heavy use of tidally driven, more interior marine waters (i.e., Strait of Juan de Fuca and Hood Canal) by murrelets in our study, where effects of upwelling may have been mitigated by factors such

as runoff from terrestrial sources. However, even for birds that were captured on the coast, we found no evidence of CUI effects on movements or ranges. Our sample size of murrelets on the Coast may have been too small ($n = 12$) to document effects due to upwelling. Also, oceanographic predictors may have performed poorly because murrelets were foraging several trophic levels above the phytoplankton that would have been directly influenced by changes in SST or chlorophyll. Murrelets may have been buffered against some of the direct effects of changing ocean conditions (Schwing et al. 2006), and the prey used by murrelets may not have been affected by the upwelling event in the areas where they foraged. To assess these possibilities, future studies are needed that directly measure forage fish used by murrelets in Washington, and their abundance and responses to variable ocean conditions. Such direct measures of murrelet prey may better explain variation in murrelet space use and breeding in this region.

MANAGEMENT IMPLICATIONS

We encourage additional studies to more thoroughly test whether marine areas in Washington are poorer in quality than those used by other murrelet populations, and suggest 3 information gaps on which additional research is needed: 1) identification of specific prey species and differential use of these prey by murrelets in different parts of our study area and in different times of year, especially by successful breeders; 2) measures of the abundance and distribution of these prey; and 3) models of how these prey respond to changes in ocean conditions. Although past stable isotope and hydroacoustic studies have advanced our knowledge in many important dimensions, they are generally too coarse to track fine-scale among-year (Bertram et al. 1991, 2002; Hedd et al. 2006; Schrimpf et al. 2012), among-site (Bertram et al. 2002), or among-individual (Golet et al. 2000) differences in foraging that have been found in seabirds and that can affect breeding success.

Until such research is conducted, our results suggest that efforts to improve the health of marine food webs in the Salish Sea and along the Pacific Coast would benefit murrelets in this region. Given the relatively long over-land commutes by breeding murrelets in our study, we also encourage measures to protect and enhance terrestrial nesting habitat closer to sea. This will require protecting nesting habitat on state and private lands, because the federal lands in Washington are already protected under the Northwest Forest Plan. Without improvements to both marine and terrestrial habitat, the low reproductive output of this population may continue and contribute to further declines of marbled murrelets in this region.

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