ASSESSING THE UTILITY OF SATELLITE TRANSMITTERS FOR IDENTIFYING NEST LOCATIONS AND FORAGING BEHAVIOR OF THE THREATENED MARBLED MURRELET *BRACHYRAMPHUS MARMORATUS*

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ABSTRACT

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Understanding movements of small seabirds has been particularly challenging due to limitations in tracking technology. As tracking devices become smaller and more powerful, and are deployed on smaller bird species, they need to be evaluated. We assessed whether small, platform terminal transmitters (PTTs; 5 g) could be used to study the nesting, movement, and foraging behaviors of the Threatened Marbled Murrelet *Brachyramphus marmoratus* in Oregon, US. We attached PTTs that transmitted locations and temperature measurements through the Argos satellite system to seven adult murrelets. We fit continuous-time correlated random-walk models to location data to examine coarse movement patterns and determine whether murrelets were moving inland to potential nesting habitat. We used temperature measurements from the PTTs to examine murrelet diving patterns, indicative of foraging. Sixteen independent movements appeared to be consistent with inland movements. However, the PTT-tagged murrelets appeared to be on the ocean during nearly all of these movements, based on concurrent temperature readings. To further assess the utility of PTTs in locating murrelet nests, we deployed 3 PTTs in trees within suitable nesting habitat. Naive observers required 2–9 d to attain sufficient high-quality locations to attempt to locate these PTTs, and 4–13 h of searching to locate the exact trees. The PTTs we tested can be useful for describing coarse patterns of movement and foraging, but are not an improvement over VHF transmitters for locating nests. All of the tagged murrelets ceased movement during the course of the study. Three were found dead, and the rest were unrecoverable. We suspect that tagging negatively affected welfare of these birds. We recommend waiting for future versions of these tags that weigh less and include GPS technology before deploying them on small diving seabirds such as the Marbled Murrelet.

Key words: animal tracking, Argos, movement ecology, nesting ecology, platform terminal transmitter, seabird

INTRODUCTION

On-animal tracking devices are critical tools for research and conservation of wild animals (Hussey *et al.* 2015, Kays *et al.* 2015). These devices, often paired with auxiliary sensors (e.g., temperature loggers), provide detailed information on a range of behavioral (Louzao *et al.* 2014) and physiological (Andrews & Enstipp 2016) processes. Although tracking devices have been deployed most frequently on large-bodied animals, advances in recent years have led to smaller, lighter, and more powerful technology, which is being used for a growing list of species and applications (Robinson *et al.* 2010, Kays *et al.* 2015).

Avian ecology and conservation have been revolutionized by these modern tracking technologies. Geolocators and solar-powered satellite transmitters provide enhanced understanding of long-distance bird migrations (Egevang *et al.* 2010, Trierweiler *et al.* 2014), while global positioning system (GPS) tags provide detailed information on foraging behavior (Louzao *et al.* 2014) and space-use patterns at large spatial scales (Young *et al.* 2015). Tracking technology provides great promise for understanding the ecology of seabirds, in particular, since these birds spend much of the non-breeding period in areas that are difficult or impossible to access for direct observation. To date, most applications of tracking technology in seabird research and conservation have been on larger-bodied species, such as the Wandering Albatross *Diomedea exulans* and Brown Booby *Sula leucogaster,* in which welfare is less likely to be affected by tracking tags, due to their size (Burger & Shaffer 2008). Animal tracking technology has advanced sufficiently, however, that tags are now small enough to be deployed on small seabirds (<300 g), offering new opportunities for studying their ecology and movements (e.g., Soanes *et al.* 2015, Neuman *et al.* 2018). With the rise of these new capabilities, there is growing need for assessments of the utility of these tracking devices.

The Marbled Murrelet *Brachyramphus marmoratus* (hereafter murrelet) is a small alcid seabird listed as Endangered on the IUCN Red List (http://www.iucnredlist.org/details/22694870/0) and Threatened in the conterminous United States under the *Endangered Species Act* (United States Fish & Wildlife Service 1997) and in Canada under the *Species at Risk Act* (Committee on the Status of Endangered Wildlife in Canada 2013). Unlike most seabirds, murrelets move large distances between at-sea foraging locations and inland nesting sites (sometimes >100 km; Nelson &

Hamer 1995, Whitworth *et al.* 2000, Lorenz *et al.* 2016a), where they typically nest in trees in mature and old-growth forest stands (Nelson 1997). Some murrelet populations are currently in decline, which may be due to decreases of at-sea prey (Norris *et al.* 2007). Other primary contemporary threats to murrelet populations appear to be loss of inland nesting habitat (Raphael & Falxa 2016) and low recruitment due to high levels of nest predation (Peery *et al.* 2004). Therefore, finding and monitoring nests is critical for understanding population trends and developing recovery plans for the species.

Finding murrelet nests is difficult, however. Indeed, the first murrelet nest was not discovered until 1974 (Binford *et al.* 1975), and few nests have been monitored (Nelson 1997). Thus far, the most effective means of finding nests has been through tagging birds at sea with very high frequency (VHF) transmitters and conducting intensive aerial telemetry to locate stands in which birds are nesting, followed by ground visits to find the actual nest (Bradley *et al.* 2004, Barbaree *et al.* 2014). Because murrelets may nest over a large area and farther than 50 km inland, this approach is labor-intensive, so new on-animal tracking devices that relay locations via satellites could offer time and cost savings. In addition, population dynamics and reproductive success can be influenced by at-sea conditions that influence forage availability (Becker & Beissinger 2003, Peery *et al.* 2006). Thus, identifying at-sea habitat selection, movement patterns, and foraging behavior are also important topics for murrelet conservation that could be addressed using tracking devices.

Satellite transmitters that are small enough to deploy on murrelets have been available only in recent years, and there has been only a single study published on their use in this species (Bertram *et al.* 2016). That study examined long-distance movements of murrelets but was restricted to assessing space use of marine habitats, which does not require the same accuracy needed to locate nests in forests. To date, no study has assessed the use of satellite tags in identifying murrelet nests or in evaluating fine-scale foraging behavior. In this study, we assessed the utility of using platform terminal transmitter (PTT) satellite tags to characterize the behavior of murrelets during the breeding season. Specifically, we addressed the following questions: (1) Can satellite tags be used to determine inland movements of murrelets, and, if so, can they be used to identify nest locations? (2) Can satellite tags be used to assess foraging behavior and daily movement patterns of murrelets?

METHODS

Murrelet capture and tagging

During 2–12 May 2016, we captured murrelets in the nearshore marine environment off the coast of central Oregon, between the towns of Newport and Lincoln City (Fig. 1). On four nights, a three-person crew captured murrelets using night-lighting from an inflatable boat (Zodiac), deployed from a fishing vessel (Whitworth *et al.* 1997) and transported captured murrelets to the fishing vessel in protective carriers. On board, we banded each individual bird with a standard US Geological Survey (USGS) leg band, took standard morphological measurements, and collected blood and feather samples as part of a related research project. Birds weighing >220 g were fitted with a 5 g solar-powered platform terminal transmitter (PTT-100, Microwave Telemetry, Inc., Columbia, MD, US) that was 24 mm long, 14 mm wide, had a 21-cm antenna, and sat 7.5 mm high off each bird's back; PTTs were equipped with an internal temperature sensor. We attached PTTs to the upper back using four subcutaneous sutures following Bertram *et al.* (2016) before releasing birds, all within 1 h of capture.

The PTTs were programmed to transmit locations through the Argos system once per minute during 10 h on-periods, followed by 48 h off-time, but were able to transmit longer if a sufficient charge was gained in the intervening time periods. We also monitored each murrelet several times each week from the ground using a handheld direction finder (RXG-134, CLS America, Inc., Lanham, MD, USA) and accompanying goniometer antenna (ACG-134, CLS America, Inc.). Further, we reviewed the transmitted locations and temperature readings from each tag daily to determine whether the tag had ceased moving (changes in temperature that tracked ambient temperatures, combined with apparent cessation of movement). All procedures followed an Animal Care and Use Protocol approved by the Institutional Animal Care and Use Committee (IACUC) at Oregon State University.

Data filtering and estimation of location uncertainty

Telemetry devices using the Argos system provide estimates of animal locations using the Doppler effect via receiving satellites passing overhead in polar orbit. Satellite fixes estimated in this manner can have large associated errors (Lopez *et al.* 2014), substantially larger than those from GPS transmitters. Thus, some degree of data filtering, correction, and estimation of uncertainty is needed to use these data to examine patterns of movement and breeding behavior in murrelets. With the Argos system, each fix is assigned a class based on the likely error associated with the reported location (Table 1). In turn, these error classes are used to filter the data or are included in models to estimate the true location of the animal at a given time with associated uncertainty (Johnson *et al.* 2008). More recently, Argos has reported error ellipses associated with each satellite fix, which provide more accurate estimates of location-specific error, as opposed to broad classifications (Lopez *et al.* 2014). Several modeling approaches are available to address Argos location error (e.g., Jonsen *et al.* 2005, Johnson *et al.* 2008, McClintock *et al.* 2015). However, recent statistical advances allow error ellipses to be incorporated into models used for estimating true locations and complete tracks (the complete and continuous path of the animal from tag deployment through recovery) of tagged animals, along with associated uncertainty (McClintock *et al.* 2015, Johnson 2016). In our study, we used the continuous-time correlated random-walk model (hereafter, random-walk model) described by Johnson *et al.* (2008) to estimate locations and tracks of the tagged murrelets. The random-walk model offers three distinct advantages over other forms of location estimation: (1) the model can account for the complex errors associated with Argos satellite fixes, including incorporating error ellipses; (2) the underlying model has been coded into a format for use in the R statistical software (the 'crawl' package; Johnson 2016) by non-statisticians; and (3) there are online resources that describe the procedural details of model-fitting (https://cran.r-project.org/web/packages/crawl/vignettes/crawl_intro.html).

Before fitting the random-walk models, we removed locations that were clear outliers, i.e., those in which the calculated speed (distance/time between locations) from the previous location exceeded the flight speed of murrelets (approximately 22 m sec^{-1}; Elliott *et al.* 2004). We eliminated 3% of the fixes through this procedure. Using the remaining data, we fit the random-walk model to the data from each individual in the R statistical software using the error ellipses to estimate uncertainty. Following model fitting, we obtained estimates of the mean and variance of the predicted locations at the times matching each fix reported by Argos and produced realizations (estimates based on random draws from a distribution) of the entire track of each animal.

Assessment of inland movements

To identify potential inland movements of murrelets, we first estimated the probability that a murrelet was over land during each of the transmitted satellite fixes. Using all data, regardless of error class, we used the estimated mean and variance for the murrelet's location at the time of each recorded fix to produce 10 000 realizations of the location process from a multivariate normal distribution (i.e., we conducted 10 000 random draws from this distribution to produce a group of estimated locations). We then calculated the proportion of these realizations that fell over land for each location. Next, we visually examined each location for which the probability of being over land was >0.5 in ArcMap 10.3 (Environmental Systems Research Institute, Redlands, CA) to

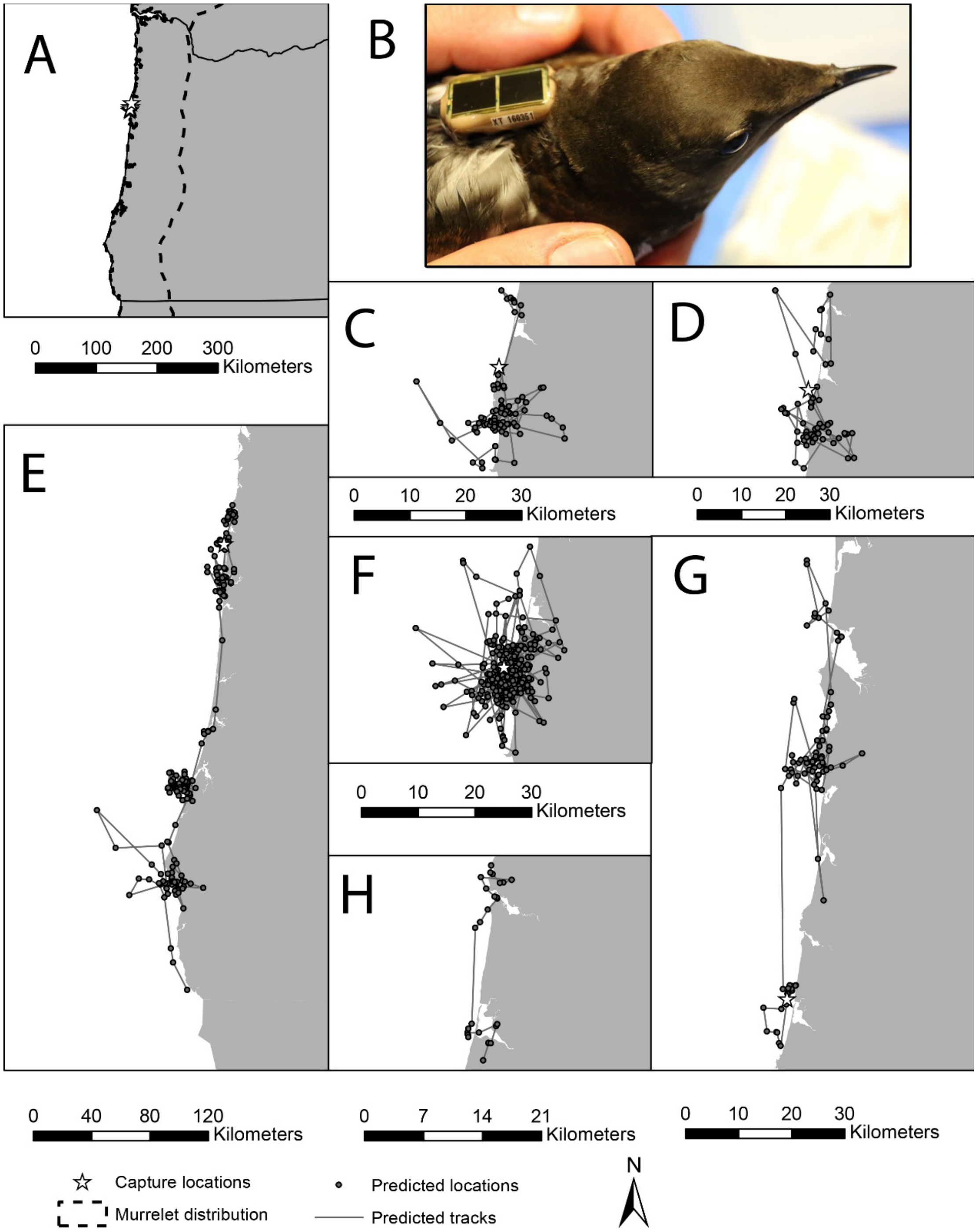

Fig. 1. (A) General capture area for Marbled Murrelets along the central Oregon coast and capture locations; (B) Marbled Murrelet with PTT attached, and (C–H) mean locations and tracks estimated from a continuous-time correlated random-walk model fit to data from PTTs for Marbled Murrelet with PTT ID (see Table 2) 160348 (C), 160349 (D), 160350 (E), 150351 (F), 160354 (G), and 160352 (H).

assess whether it was a part of a potential inland movement “bout” (i.e., a group of movements). We determined this by evaluating the timing and location of the preceding and subsequent fixes to determine whether the focal location appeared to be an outlier. We classified a location as an outlier if both the previous and subsequent locations appeared to be at-sea locations. Following this classification procedure, we examined whether murrelets were likely to be engaged in diving activity, which is indicative of foraging, during the potential inland movements, based on PTT temperature data (see below).

In addition to evaluating PTTs on live birds, we undertook an additional test to determine whether these tags could be used to identify the location of murrelet nests. We deployed three PTTs in separate conifer stands in the Oregon Coast Range that had characteristics similar to those used by nesting murrelets (see Hamer & Nelson 1995). We mounted each PTT to a 600 mL plastic water bottle to mimic the conductance of an actual bird, and placed each in a large conifer tree. Bottles were turned on their sides in an area with ample sun with the PTT facing upward to mimic the position of a nesting murrelet. Ground crews with no prior knowledge of the PTT locations used transmitted satellite fixes to identify the approximate location of PTTs within each stand. Next, they used a handheld antenna to locate the tree in which each tag was placed, mimicking conditions under which researchers would attempt to identify murrelet nests associated with a PTT-tagged bird.

Assessing movement patterns and foraging behavior

Using the results of the random-walk models, we produced 10 000 complete tracks for each individual (see https://cran.r-project.org/web/packages/crawl/vignettes/crawl_intro.html for a discussion of this procedure) to estimate the mean and standard deviation of the total distance moved (i.e., sum of all movements during the entire time period that the bird was tagged) and daily distance moved (total divided by the number of days a bird was monitored) for each murrelet. We also calculated the net-squared displacement (a measure of the distance between the first location of the animal and all subsequent locations; Turchin 1998) from each bird’s capture location to understand whether individuals dispersed from the capture location or remained close to a centralized area. We also calculated the hourly rate of movement of each murrelet to assess temporal movement patterns. This rate was the number of kilometers moved per hour of location data, calculated by measuring the straight-line distance between locations, dividing by the intervening time, and standardizing to an hourly rate and averaging. Locations with large error radii could inflate movement estimates, so we repeated the estimation of daily and hourly movements twice, once censoring all locations classified as A or B, and again censoring all locations classified as A, B or 0 (these are the location classes with the largest errors; see Table 1), while keeping locations classified as 3, 2, or 1. We noted that removing locations reduces movement estimates, so we conducted this sensitivity analysis to obtain a range of plausible measures of movement distances.

During each communication with the Argos satellite system, the PTTs send information on the temperature of the tag. Because murrelets pursue prey exclusively underwater, where PTTs do not transmit, changes in tag temperature can provide information regarding the timing of foraging. To evaluate the utility of temperature data, we first censored readings that were <0 °C or >40 °C as likely erroneous (3.2% of n = 2 752 readings). Because our temperature data displayed clear bimodality (Fig. 2), we fit a finite mixture model to the data to identify a breakpoint. We fit the model using the ‘depmix’ package in R (Visser & Speekenbrink 2010), specifying that there were two distributions from which the data arise. The model fit in this manner is a statistical clustering procedure that estimates the probability that each data point falls into one of two distributions, while simultaneously estimating the parameters associated with the distributions. In our application, the state characterized by the lower mean temperature was most likely to represent diving; thus, we used that state to indicate diving locations. Of note, the lower bound of the temperature data appeared to be similar to the average sea-surface temperature near Newport, Oregon, where our tagging efforts were carried out (https://www.nodc.noaa.gov/dsdt/cwtg/npac.html). This provided anecdotal confirmation that the low temperature readings did indeed correspond to diving behavior.

We further assessed diving behavior by examining changes in temperature between messages assigned to the same location. Different messages assigned to the same fix represent communication between the PTT and different satellites. These messages can be several minutes apart, and, thus, any changes in temperature

TABLE 1
Distances between the true location of platform terminal transmitters (PTT) and locations estimated by the Argos system by error class for three PTTs placed in trees in Marbled Murrelet nesting habitat in Oregon, US

Error class	PTT 1		PTT 2		PTT3	
	Mean (SD)	Range (m)	Mean (SD)	Range (m)	Mean (SD)	Range (m)
3	544 (433)	49–1 231	330 (320)	100–696	472 (290)	131–1 079
2	1 014 (1 261)	128–4 887	973 (631)	164–1 678	853 (672)	32–2 706
1	1 437 (1 582)	64–6 975	1 697 (1 643)	338–6 274	1 515 (1 981)	45–8 064
0	1 534 (7 037)	1 534–24 957	8 446 (9 529)	623–32 370	3 928 (3 838)	128–12 843
A	12 951 (36 803)	46–178 775	4 063 (5 447)	66–19 620	1 361 (2 116)	112–11 872
B	12 347 (15 089)	74–61 370	11 590 (13 473)	139–65 174	6 635 (12 022)	122–67 754
Z	188 (–)	–	–	–	–	–
All	8 915 (18 258)	46–178 775	8 527 (11 682)	66–65 174	3 721 (8 530)	32–67 754

between messages may indicate changing environmental conditions, such as whether the tag was recently submerged. We classified fixes for which there was a >2 °C change in temperature among messages as 'likely diving' behavior. To test the sensitivity of this approach to different temperature thresholds, we repeated these analyses using different temperature change thresholds (3 °C, 4 °C and 5 °C) for classifying dives to assess the sensitivity of our results to different thresholds. We then examined patterns of diving in relation to time of day. In addition, for each individual and for all data combined, we fit a logistic regression model to the diving data; the response variable was whether diving occurred (i.e., diving/non-diving), with the mean estimated movement speeds from the random-walk model as an independent variable. For all of the data combined, we fit models with random intercepts (i.e., intercepts varying by individual). This model tested whether there was any relationship between diving and estimated movement speed.

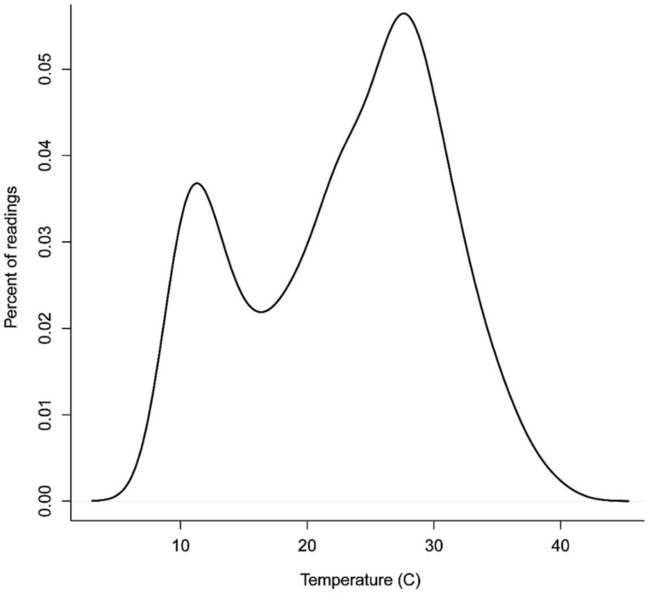

Fig. 2. Distribution of temperature measurements reported by PTTs attached to 7 Marbled Murrelets on the central Oregon coast.

RESULTS

Data, space use, and movements

We captured 11 murrelets, of which seven were of sufficient size to be fitted with a PTT. All tagged birds were alert and either flew or dove upon release from the side of the boat. The PTTs transmitted for an average of approximately 9 d (range: 1–25; Table 2), providing an average of 120 fixes (range: 7–358). We eliminated fixes collected after the PTTs ceased to move for all analyses. All tagged birds appeared to cease movement during our study, and we attempted to make visual contact to determine whether this cessation was due to bird mortality or to suture failure. Coastal topography and access issues precluded obtaining data on the fate of four PTT-tagged murrelets. Of the remaining three birds, two appeared to have been killed and/or scavenged by a raptor (e.g., Peregrine Falcon *Falco peregrinus*), and one individual was recovered intact. The latter individual underwent necropsy by the Veterinary Diagnostic Laboratory at Oregon State University and was found to be in poor body condition and determined to have yolk peritonitis.

We fit the random-walk model to the data from six individuals; one PTT transmitted too few fixes for use in the model and was thus excluded in all movement analyses. Using the tracks from the random walk model, we estimated that tagged murrelets traveled, on average, 60 km d^{-1} (95% confidence interval [CI] 54.3–67.3 km); however, our estimates varied widely depending on whether location data in the A, B, or 0 classes were included (Table 2). Four individuals stayed close to their capture locations, whereas one individual moved >90 km north and a second individual moved >300 km south of their respective capture locations (Fig. 1). The net-squared displacement analysis mirrored these results and further indicated that one individual, for which more data were available, displayed spatially restricted behavior around a centralized area (Appendix 1, available on the website). It appeared that there was a peak in hourly movement speeds in the early morning for most individuals (Appendix 2, available on the website); however, there was substantial uncertainty around the estimates of movement speeds.

Assessment of inland movements

We identified potential inland movements for all six of the individuals for which we obtained transmitted fixes for more than a day, with

TABLE 2
Summary transmission data for Marbled Murrelets fitted with platform terminal transmitters (PTTs) along the central coast of Oregon

					Daily distance (95% CI)		
PTT ID	**Days transmitting**	**Number of fixes**	**Mean number of fixes/d**	**Cumulative distance (95% CI)**	**All Argos error classes included**	**Excluding Argos error classes A and B**	**Excluding Argos error classes A, B, and 0**
160348	9.3	100	10.7	355 (316–401)	38 (34–43)	13 (12–16)	10 (9–12)
160349	4.7	61	13.0	366 (313–435)	78 (67–93)	50 (42–59)	15 (13–16)
160350	17.5	202	11.5	1692 (1594–1807)	97 (91–103)	52 (48–57)	30 (29–32)
160351	25.6	358	14	1660 (1575–1753)	65 (61–68)	35 (33–37)	19 (18–20)
160352	2.3	26	11.3	486 (407–660)	21 (18–29)	NA[a]	NA[a]
160354	8.5	89	10.4	516 (469–574)	61 (55–67)	37 (24–32)	21 (19–23)

[a] There were too few remaining locations from this individual to fit these models.

the maximum distance inland estimated at 16 km. We identified 16 movements that may have represented inland forays (one to four per individual). There was evidence from PTT temperature data that the tagged murrelet was diving during 14 of these 16 apparent inland movements, however, indicating that they were unlikely to represent inland forays to prospective nest sites. The remaining two movements occurred during times when murrelets are unlikely to be flying inland except during chick-rearing (11h00–16h00 and 18h45–21h52), yet our study took place in early May, when murrelets would be expected to be incubating eggs.

We found that it took 2–9 d to obtain an adequate number of fixes of sufficient accuracy before ground crews could attempt to locate the PTTs deployed in trees to mimic a nesting murrelet. This duration was due to the duty cycle (i.e., the schedule of location transmission) of the PTTs, which restricted the number of reported locations. Once the general location of a deployed PTT was identified, it took an additional 4–13 h of intensive ground-based searching to identify the tree in which the PTT had been placed. However, this is a conservative estimate because our field crew detected supporting rope lines in two of the three trees when narrowing their search. For two PTTs, search time was split between 2 d, while for the third it was split among 6 d. The need to split search effort across days was due to duty-cycle constraints (i.e., the tags ceased to transmit during times of insufficient solar charging). The satellite fixes were generally close to the location of the PTT, but some locations that initially appeared to have high accuracy based on the error class and ellipse radius turned out to have a high associated error (Table 1; Appendix 3, available on the website).

Assessment of foraging behavior

The latent-state model predicted an approximate breakpoint in the temperature data of 15 °C, below which readings were likely indicative of diving; however, based on changes in temperature readings between messages, birds also apparently dived when the tag was much warmer (Fig. 3). There appeared to be a peak in diving activity at dawn, yet most individuals dived throughout the day (Appendix 4, available on the website). We found no strong evidence that murrelets were diving at night, but the tags rarely transmitted during this time, precluding a robust assessment of nighttime diving. Logistic regression models indicated no significant relationship between diving and movement speed predicted from the random-walk models (Appendix 4).

DISCUSSION

The objective of our study was to assess whether we could use small satellite tags to study the movement and breeding behavior of a small alcid, the Marbled Murrelet. Transmitters that are small enough to be affixed to birds of this size have become available only recently, and, thus, it is important to test their utility prior to large-scale deployments. Using PTTs, we identified several inland movements that at first appeared consistent with the behavior of nesting murrelets, but, on closer examination, we found this to be erroneous. Using combined temperature and location data, we were able to identify coarse patterns of murrelet movements and foraging. Importantly, we could not rule out the possibility that the tags led to mortality of all birds in the study, discussed below.

Despite using a state-of-the-art modeling framework that relied on error ellipses and the movement behavior of murrelets to improve location accuracy, all of the potential inland movements that we identified appeared to be erroneous. Large errors in animal locations reported by the Argos system are well known (Lopez *et al.* 2014). We had intended to use the satellite fixes as a first step towards identifying behavior indicative of nesting (i.e., inland movements), then to narrow down the location of a potential nest, followed by ground investigation to locate the nest tree itself. Our results indicate that PTTs are likely to be less effective and efficient than VHF transmitters and aerial telemetry for this purpose, for several reasons. First, considering the large errors associated with the satellite fixes in our study, some nests are likely to be too close to the ocean to distinguish between fixes taken from the nest and fixes obtained on the water (Hamer & Nelson 1995). Second, in our efforts to locate PTTs deployed in trees, it took many days to narrow down the transmitter location to a sufficiently small area to initiate ground search efforts. If researchers wish to conduct nest monitoring to estimate nest survival, this period is likely too long to allow for robust estimates. If nest survival rates are low, nests could fail before they can be identified for monitoring. This issue is exacerbated by bi-parental incubation by murrelets, where each parent spends about 24 h on the nest before being relieved by its mate (Singer *et al.* 1991, Nelson & Peck 1995). If only one adult in each breeding pair is marked, half of the locations obtained from a tagged bird will not be from the nest, doubling the time needed

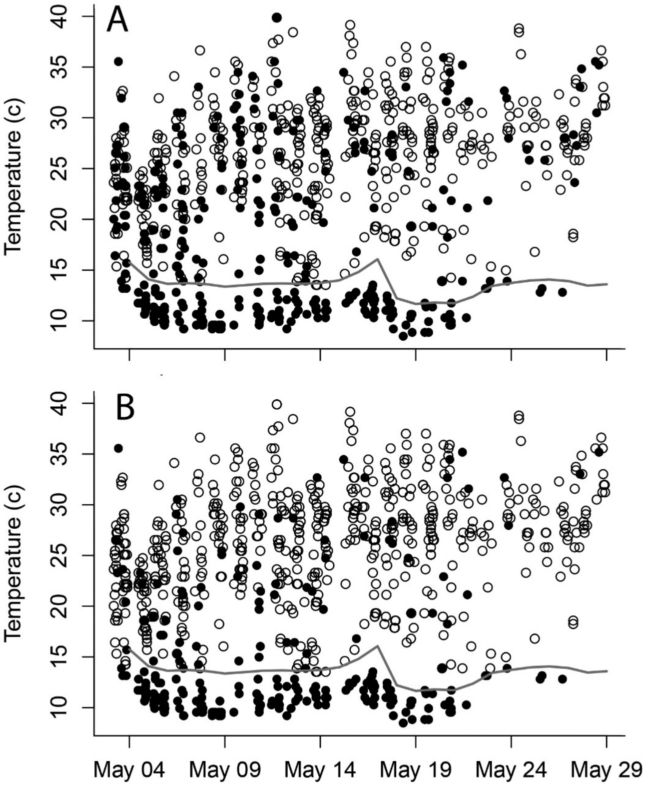

Fig. 3. Temperature measurements reported by PTTs attached to seven Marbled Murrelets on the central Oregon coast, by date. Open circles represent readings during which the murrelet was considered not to be diving. Closed circles represent readings during which murrelets were considered to be diving using temperature between messages within a fix as a threshold for determining diving (A) threshold 2 °C change in temperature and (B) threshold 5 °C. The gray line represents average sea-surface temperature off Newport, Oregon.

to obtain a sufficient number of accurate fixes to initiate ground searches for the nest tree and potentially causing major biases in nest survival estimates. Third, we found that the goniometer we employed to locate nests from the ground was unable to provide consistently accurate azimuths in the rugged topography of the Oregon Coast Range, thus limiting its use for determining fine-scale locations of tagged birds in this terrain.

Although the PTTs used in our study are unlikely to provide an advantage over VHF telemetry, our results could represent a somewhat pessimistic outlook on the utility of the PTTs to locate murrelet nests. First, because the PTTs deployed in trees were stationary, we could not use the random-walk model to refine location estimates. Although nesting murrelets are also stationary, data collected during movements can help to improve estimates. Doing so could shorten the time required to locate the stand in which murrelets were nesting. Second, if none of our tagged murrelets attempted to nest, our results regarding the capacity to identify murrelet nesting behavior would be biased toward the negative. Lastly, this work took place during mild El Niño conditions, which are typically associated with lower prey availability and lower propensity for reproduction in murrelets (Becker & Beissinger 2003), which could have driven atypical behavior. Regardless of these caveats, the erroneous identification of inland movements and the extended times to identify stationary PTTs in trees support our main conclusion that tag improvements are needed before PTTs prove useful in locating murrelet nests.

We were, however, able to characterize the timing of murrelet diving. Previous studies have assessed the diving behavior of this species with intensive VHF telemetry (Jodice & Collopy 1999, Henkel *et al.* 2004, Peery *et al.* 2009) or direct observation (Ronconi & Burger 2008, Pontius & Kirchhoff 2009) to quantify patterns. Although there was substantial uncertainty in our PTT data, our results indicate a general peak in foraging behavior at dawn for most individuals, along with intermittent foraging throughout the daylight hours. We did not find any evidence of nocturnal diving, although we note there were few readings transmitted at night. Our results match those of previous studies regarding the timing of foraging (Ronconi & Burger 2008, Pontius & Kirchhoff 2009), so PTT tags could be used to quantify the timing of foraging behavior. A key constraint is the duty cycle of the PTT tag, which limited temperature data collection to times when data were transmitted and made it impossible to collect data in a standardized manner. Thus, researchers using PTTs in their current format can only address questions related to coarse foraging patterns, such as whether there are differences among years or individuals of different status (e.g., breeders versus non-breeders). Having more detailed information might be especially useful for understanding how foraging behavior changes with ocean conditions over time (e.g., typical conditions versus El Niño conditions). In addition, while the temperature readings from locations classified as at-sea appeared to follow the general pattern of sea-surface temperatures (Fig. 3), further work is needed to assess the validity of the classification procedure that we employed. Lastly, we tagged only birds above a certain weight limit, which could bias results if larger birds behave differently than smaller birds.

In the only other study to use Argos satellite tags on murrelets, Bertram *et al*. (2016) delineated coarse space-use patterns in British Columbia to assess overlap with shipping routes. The results of our movement analyses provide further evidence that PTTs can be useful for inferring general space use for small seabirds. Although admittedly coarse, these data provide valuable information for the ecology and conservation of murrelets. Similar to Bertram *et al*. (2016), we identified marked variation in space use and movement patterns among the individuals we tagged; some individuals appeared to have centralized space use, whereas others traveled long distances along the coast. Of particular interest was our documentation of two individual murrelets that engaged in relatively long-distance movements during the breeding season, including one individual that traveled >300 km in only a few days. This finding is relevant to murrelet conservation because at-sea surveys are undertaken during the breeding season using distance-sampling techniques for estimating populations and their change over time (Raphael *et al.* 2007). To make valid estimates of population size, these methods assume that individual birds are not counted more than once, or at least that the number of double-counted individuals is small relative to the population. If the large-scale movements we documented are common, this assumption may be violated. This violation may be most relevant for population survey results during years of sparse food (which our study encompassed), when many individuals may forgo nesting and use larger foraging areas. To overcome this issue, the timing of surveys relative to bird movement among sample units could be structured to mitigate the effects of long-distance movements (e.g., surveys conducted simultaneously in multiple sampling units). In addition, recent analyses indicate that population dynamics of murrelets are strongly influenced by the distribution of nesting habitat on shore close to monitored transects (Raphael *et al.* 2015, Lorenz *et al.* 2016b). The large movements we documented in this study suggest that the spatial relationship between murrelet at-sea distributions and nesting habitat are likely more complex than previously considered. Therefore, further research on the movements of murrelets during the breeding season are needed to better understand the relationship between at-sea distribution and nesting habitat.

All or most of the birds we tagged appeared to have died during the course of our study. Combined with sparse food, the shape and weight of the PTT could have influenced the ability of tagged murrelets to undertake normal behaviors. The centralized space use observed for some tagged birds may have reflected their inability to move longer distances. Birds that moved farther may have been searching for areas with easier access to forage fish. Peery *et al.* (2006) also reported reduced survival of radio-tagged birds relative to birds receiving only a leg band; annual survival of untagged birds was around 0.8, but around 0.5 for radio-tagged birds. Further, Ackerman *et al.* (2004) reported that tagging had impacts on reproductive success of Cassin's Auklets *Ptychoramphus aleuticus*. Although our sample size was small, our apparent survival rates were substantially lower than those previously reported. While we were unable to assess the actual impacts of the PTTs on our tagged murrelets, we recommend that improvements be made to PTTs, especially reducing drag and improving location accuracy, and we caution other researchers that great care is necessary in deploying these devices on other small diving birds.

Tracking technology has revolutionized research on the ecology and conservation of seabirds (Burger & Shaffer 2008). Although new and improving technologies have the potential to provide much-needed data in such effort, this study indicates that PTT technology is unable to provide the detailed information required to assess fine-scale space use (within a day) and nesting behavior of the Marbled Murrelet. Our results indicate that these tags are useful for studying murrelet movements at coarse scales (i.e., daily movement distances and diving patterns), identifying long distance movements (see also Bertram *et al*. 2016), and delineating time periods when murrelets were likely foraging. Given how far technology has advanced in recent decades, we are hopeful that further progress will allow researchers to obtain fine-scale movement and space-use data for the Marbled Murrelet to delineate key nesting and foraging areas and to improve conservation of this species. Specifically, the development of GPS transmitters small enough to be deployed on murrelets would provide highly accurate nesting and at-sea locations, while obviating the need for costly and hazardous telemetry flights (Bradley *et al*. 2004, Lorenz *et al*. 2016a).

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REFERENCES

ACKERMAN, J.T., ADAMS, J., TAKEKAWA, J.Y., CARTER, H.R. *et al*. 2004. Effects of Radiotransmitters on the Reproductive Performance of Cassin's Auklets. *Wildlife Society Bulletin* (1973–2006) 32: 1229-1241.

ANDREWS, R.D. & ENSTIPP, M.R. 2016. Diving physiology of seabirds and marine mammals: Relevance, challenges and some solutions for field studies. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 202: 38-52.

BARBAREE, B.A., NELSON, S.K., DUGGER, B.D., ET AL. 2014. Nesting ecology of Marbled Murrelets at a remote mainland fjord in southeast Alaska. *Condor* 116: 173-184.

BECKER, B.H. & BEISSINGER, S.R. 2003. Scale-dependent habitat selection by a nearshore seabird, the Marbled Murrelet, in a highly dynamic upwelling system. *Marine Ecology Progress Series* 256: 243-255.

BERTRAM, D.F., MacDONALD, C.A., O'HARA, P.D., ET AL. 2016. Marbled Murrelet *Brachyramphus marmoratus* movements and marine habitat use near propsed tanker routes to Kitimat, BC, Canada. *Marine Ornithology* 44: 3-9.

BINFORD, L.C., ELLIOTT, B.G. & SINGER, W.W. 1975. Discovery of a nest and the downy young of the Marbled Murrelet. *Wilson Bulletin* 87: 303-319.

BRADLEY, R.W., COOKE, F., LOUGHEED, L.W. & BOYD, W.S. 2004. Inferring breeding success through radiotelemetry in the marbled murrelet. *Journal of Wildlife Management* 68: 318-331.

BURGER, A.E. & SHAFFER, S.A. 2008. Perspectives in ornithology application of tracking and data-logging technology in research and conservation of seabirds. *Auk* 125: 253-264.

COMMITTEE ON THE STAUTS OF ENDANGERED WILDLIFE IN CANADA. 2013. Assessment and Status Report on the Marbled Murrelet *Brachyramphus marmoratus* in Canada. Ottawa, ON: Environment and Climate Change Canada,. p. 94.

EGEVANG, C., STENHOUSE, I.J., PHILLIPS, R.A., ET AL. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences* 107: 2078-2081.

ELLIOTT, K.H., HEWETT, M., KAISER, G.W. & BLAKE, R.W. 2004. Flight energetics of the Marbled Murrelet, *Brachyramphus marmoratus*. *Canadian Journal of Zoology* 82: 644-652.

HAMER, T.E. & NELSON, S.K. 1995. Characteristics of Marbled Murrelet nest trees and nesting stands. In: RALPH, C.J., HUNT, G.L. JR., RAPHAEL, M.G. & PIATT, J.F. (Eds.) *Ecology and Conservation of the Marbled Murrelet*. Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture. pp. 151-161.

HENKEL, L.A., BURKETT, E.E. & TAKEKAWA, J.Y. 2004. At-sea activity and diving behavior of a radio-tagged Marbled Murrelet in Central California. *Waterbirds* 27: 9-12.

HUSSEY, N.E., KESSEL, S.T., AARESTRUP, K., ET AL. 2015. Aquatic animal telemetry: a panoramic window into the underwater world. *Science* 348. doi:10.1126/science.1255642.

JODICE, P.G.R. & COLLOPY, M.W. 1999. Diving and foraging patterns of Marbled Murrelets (*Brachyramphus marmoratus*): testing predictions from optimal-breathing models. *Canadian Journal of Zoology* 77: 1409-1418.

JOHNSON, D.S. 2016. crawl: fit continuous-time correlated random walk models to animal movement data. R Package version 2.0. [Available online at: https://CRAN.R-project.org/package=crawl. Accessed 7 February 2018.]

JOHNSON, D.S., LONDON, J.M., LEA, M.A. & DURBAN, J.W. 2008. Continuous-time correlated random walk model for animal telemetry data. *Ecology* 89: 1208-1215.

JONSEN, I.D., FLEMMING, J.M. & MYERS, R.A. 2005. Robust state-space modeling of animal movement data. *Ecology* 86: 2874-2880.

KAYS, R., CROFOOT, M.C., JETZ, W. & WIKELSKI, M. 2015. Terrestrial animal tracking as an eye on life and planet. *Science* 348, doi:10.1126/*science*.aaa2478.

LOPEZ, R., MALARDE, J.P., ROYER, F. & GASPAR, P. 2014. Improving Argos doppler location using multiple-model Kalman filtering. *IEEE Transactions on Geoscience and Remote Sensing* 52: 4744-4755.

LORENZ, T.J., RAPHAEL, M.G., BLOXTON, T.D. & CUNNINGHAM, P.G. 2016a. Low breeding propensity and wide-ranging movements by marbled murrelets in Washington. *Journal of Wildlife Management* 81: 306-321.

LORENZ, T.J., RAPHAEL, M.G. & BLOXTON, T.D. 2016b. Marine habitat selection by Marbled Murrelets (*Brachyramphus marmoratus*) during the breeding season. *PloS One* 11: e0162670.

LOUZAO, M., WIEGAND, T., BARTUMEUS, F. & WEIMERSKIRCH, H. 2014. Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. *Movement Ecology* 2(1): 8. doi:10.1186/2051-3933-2-8.

McCLINTOCK, B.T., LONDON, J.M., CAMERON, M.F. & BOVENG, P.L. 2015. Modelling animal movement using the Argos satellite telemetry location error ellipse. *Methods in Ecology and Evolution* 6: 266-277.

NELSON, S. 1997. Marbled murrelet (*Brachyramphus marmoratus*). In: POOLE, A. (Ed.). *The Birds of North America Online*, No. 185. Ithaca, NY: Cornell Laboratory of Ornithology. [Available online at: http://bna.birds.cornell. edu/bna/species/276. Accessed 7 February 2018.]

NELSON, S.K. & HAMER, T.E. 1995. Nest success and the effects of predation on marbled murrelets. In: RALPH, C.J., HUNT, G.L. Jr., RAPHAEL, M.G. & PIATT, J.F. (Eds.) *Ecology and Conservation of the Marbled Murrelet*. Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture. pp. 89-97.

NELSON, S.K. & PECK, R.W. 1995. Behavior of Marbled Murrelets at nine nest sites in Oregon. *Northwestern Naturalist* 76: 43-53.

NEUMANN, J.L., LAROSE, C.S., BRODIN, G. & FEARE, C.J. 2018. Foraging ranges of incubating Sooty Terns *Onychoprion fuscatus* on Bird Island, Seychelles, during a transition from food plenty to scarcity, as revealed by GPS loggers. *Marine Ornithology* 46: 11-18.

NORRIS, D.R., ARCESE, P., PREIKSHOT, D., ET AL. 2007. Diet reconstruction and historic population dynamics in a threatened seabird. *Journal of Applied Ecology* 44: 875-884.

PEERY, M.Z., BEISSINGER, S.R., BURKETT, E., ET AL. 2006. Local survival of Marbled Murrelets in central California: roles of oceanographic processes, sex, and radiotagging. *Journal of Wildlife Management* 70: 78-88.

PEERY, M.Z., BEISSINGER, S.R., NEWMAN, S.H., ET AL. 2004. Applying the declining population paradigm: diagnosing causes of poor reproduction in the marbled murrelet. *Conservation Biology* 18: 1088-1098.

PEERY, M.Z., NEWMAN, S.H., STORLAZZI, C.D. & BEISSINGER, S.R. 2009. Meeting reproductive demands in a dynamic upwelling system: foraging strategies of a pursuit-diving seabird, the Marbled Murrelet. *Condor* 111: 120-134.

PONTIUS, K.E. & KIRCHHOFF, M.D. 2009. Prey-capture by Marbled Murrelets in Southeast Alaska. *Northwestern Naturalist* 90: 151-155.

RAPHAEL, M.G., BALDWIN, J., FALXA, G.A., ET AL. 2007. *Regional population monitoring of the Marbled Murrelet: field and analytical methods.* General Technical Report PNW-GTR-716. Albany, CA Pacific Northwest Research Station, Forest Service, US Department of Agriculture.

RAPHAEL, M.G., & FALXA, G.A. 2016. *Northwest Forest Plan—the first 20 years (1994–2013): status and trend of marbled murrelet populations and nesting habitat.* Portland, OR: Pacific Northwest Research Station, Forest Service, US Department of Agriculture.

RAPHAEL, M.G., SHIRK, A.J., FALXA, G.A. & PEARSON, S.F. 2015. Habitat associations of marbled murrelets during the nesting season in nearshore waters along the Washington to California coast. *Journal of Marine Systems* 146: 17-25.

ROBINSON, W.D., BOWLIN, M.S., BISSON, I., ET AL. 2010. Integrating concepts and technologies to advance the study of bird migration. *Frontiers in Ecology and the Environment* 8: 354-361.

RONCONI, R.A. & BURGER, A.E. 2008. Limited foraging flexibility: increased foraging effort by a marine predator does not buffer against scarce prey. *Marine Ecology Progress Series* 366: 245-258.

SINGER, S.W., NASLUND, N.L., SINGER, S.A. & RALPH, C.J. 1991. Discovery and observations of two tree nests of the Marbled Murrelet. *Condor* 93: 330-339.

SOANES, L.M., BRIGHT, J.A., BRODIN, G., MUKHIDA, F. & GREEN, J.A. 2015. Tracking a small seabird: First records of foraging behaviour in the Sooty Tern *Onychoprion fuscatus*. *Marine Ornithology* 43: 235–239.

TRIERWEILER, C., KLAASSEN, R.H., DRENT, R.H., ET AL. 2014. Migratory connectivity and population-specific migration routes in a long-distance migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences* 281 (1778): 20132897-1-20132897-9.

TURCHIN, P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Plants and Animals*. Sunderland, MA: Sinauer Associates.

UNITED STATES FISH AND WILDLIFE SERVICE. 1997. *Recovery plan for the threatened Marbled Murrelet* (Brachyramphus marmoratus) *in Washington, Oregon, and California.* Portland, OR: USFWS.

VISSER, I., & SPEEKENBRINK, M. 2010. depmixS4: An R-package for fitting mixture models on mixed multivariate data with Markov dependencies. [Available online at: https://r-forge.r-project.org. Accessed 8 February 2018.]

WHITWORTH, D.L., NELSON, S.K., NEWMAN, S.H., ET AL. 2000. Foraging distances of radio-marked Marbled Murrelets from inland areas in southeast Alaska. *Condor* 102: 452-456.

WHITWORTH, D.L., TAKEKAWA, J.Y., CARTER, H.R. & MCIVER, W.R. 1997. A night-lighting technique for at-sea capture of Xantus' Murrelets. *Colonial Waterbirds* 20: 525-531.

YOUNG, H.S., MAXWELL, S.M., CONNERS, M.G. & SHAFFER, S.A. 2015. Pelagic marine protected areas protect foraging habitat for multiple breeding seabirds in the central Pacific. *Biological Conservation* 181: 226-235.