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RESEARCH ARTICLE

Confirmed year-round residence and land roosting of Whiskered Auklets (*Aethia pygmaea*) at Buldir Island, Alaska

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ABSTRACT

Most seabirds are constrained to forage near breeding sites when incubating and provisioning offspring but at other times are free to migrate to more favorable foraging habitat. Auklets (*Aethia* and *Ptychoramphus* spp., family Alcidae) are considered to be highly mobile during the nonbreeding season, except for one species, the Whiskered Auklet (*Aethia pygmaea*), which anecdotal evidence indicates remains close to breeding colonies year round. To clarify Whiskered Auklet year-round whereabouts, we deployed light-based archival geolocation "tags" onto breeding adults in 2013 and 2014. To quantify activity on land we used wet–dry logs from the tags and automated digital sound recording of vocalizations at Buldir Island, Aleutian Islands, Alaska, during 2014–2015. Tagged Whiskered Auklets ($n = 17$) breeding at Buldir remained close to the island all year (mean distance from Buldir 199 km in latitude, 49 km in longitude, which is comparable to measurement error of bird-borne tags recorded in other studies). Audio recordings confirmed presence of vocalizing birds on land from March to October and wet–dry data indicated roosting on land between sunset and sunrise year-round (including more than 14 hr of each 24 hr period in December), except for nocturnal trips to sea during full moons. Our results quantified the extraordinary year-round residency and land roosting of Whiskered Auklets at Buldir. Although it is impossible to generalize from our single study, if typical across this species' range, this places Whiskered Auklets well outside the behavior of all other auks and most seabirds. Year-round residence near breeding sites and land roosting may be behavioral adaptations that interact with the use of near-shore tide rip foraging habitat in a tradeoff of metabolic costs against foraging success.

Keywords: Aethia pygmaea, auklet, geolocation, migration, residence, seabird, tracking

Confirmation de la résidence à l'année et du repos en milieu terrestre d'*Aethia pygmaea* sur l'île Buldir, en Alaska

RÉSUMÉ

La plupart des oiseaux marins sont contraints de rechercher leur nourriture près des sites de reproduction lorsqu'ils couvent ou nourrissent leurs jeunes mais ils sont libres de migrer vers des habitats d'alimentation plus favorables en d'autres temps. On considère qu'*Aethia* spp. et *Ptychoramphus* spp. (famille des Alcidés) sont très mobiles en dehors de la saison de reproduction, à l'exception d'une espèce, *Aethia pygmaea*, pour laquelle des preuves anecdotiques indiquent qu'elle reste près des colonies de reproduction toute l'année. Afin de vérifier les allées et venues d'*A. pygmaea* au cours de l'année, nous avons installé des balises archives de géolocation par la lumière sur des adultes nicheurs en 2013 et 2014. Pour quantifier l'activité terrestre, nous avons utilisé les enregistreurs d'humidité (sec/humide) des balises et un enregistrement numérique automatisé des vocalisations sur l'île Buldir, dans les Aléoutiennes, en Alaska, en 2014-2015. Les individus marqués (n = 17) se reproduisant sur Buldir sont demeurés dans les environs de l'île toute l'année (distance moyenne de Buldir de 199 km en latitude et de 49 km en longitude, ce qui est comparable aux erreurs de mesure des balises portées par des oiseaux dans d'autres études). Les enregistrements audio ont confirmé la présence d'oiseaux vocalisant sur terre entre mars et octobre et les données des enregistreurs d'humidité ont confirmé le repos en milieu terrestre entre le coucher du soleil et le lever du soleil tout au long de l'année (incluant plus de 14 heures pour chaque période de 24 heures en décembre), sauf pour les déplacements nocturnes vers la mer lors des pleines lunes. Nos résultats ont permis de quantifier l'extraordinaire résidence à l'année et le repos en milieu terrestre d'*A. pygmaea* sur Buldir. Bien qu'il soit impossible de généraliser à partir de notre étude seulement, ce comportement, s'il est typique à l'ensemble de l'aire de répartition de l'espèce, est bien différent de celui des autres pingouins et de la plupart des oiseaux marins. La résidence à l'année près des sites de reproduction et le repos en milieu terrestre peuvent être des adaptations comportementales qui interagissent avec l'utilisation de l'habitat d'alimentation associé aux remous de marée près du rivage, pour un compromis entre les coûts métaboliques et le succès d'alimentation.

Mots-clés: géolocalisation, suivi, oiseau de mer, résidence, migration, *Aethia pygmaea*

INTRODUCTION

Whiskered Auklets (*Aethia pygmaea*) are small, planktivorous, highly ornamented, and otherwise unusual members of the auk family (Alcidae; Byrd and Williams 1993, Hunter et al. 2002, Jones et al. 2007, Seneviratne and Jones 2008). Among their most enigmatic traits is their possible year-round resident status near breeding sites (Byrd and Gibson 1980, Gaston and Jones 1998, Williams et al. 2003) and land-roosting after the breeding season (Zubakin and Konyukhov 2001). True seabirds are generally considered to be independent of land, except during the breeding season, when they are constrained to roam within foraging range of the breeding site by the need to incubate and provision offspring (Nelson 1980), while during the nonbreeding season they are free to migrate to ideal foraging habitat (e.g., Arctic Tern [*Sterna paradisaea*]; Egevang et al. 2010). Uniform year-round residence at breeding sites by seabirds is rare, with some exceptions, including land-roosting marine cormorants that typically forage near shore (Nelson 2005) and several penguins with year-round residence near their breeding colonies (Williams 1995). Nevertheless, such behavior would be expected to be favored if a reliable supply of food is available locally all year, and/or if there are territorial advantages to regular year-round visits to the colony. Although resident seabird species avoid the costs associated with migration, they would incur possible metabolic costs from remaining in seasonally less favorable habitat, and/or expending more energy foraging for lower-quality prey (Garthe et al. 2012).

Among auks, nearly year-round occurrence at breeding colonies has been documented for a few species, including Common Murre (*Uria aalge*; Harris and Wanless 1990) and Cassin's Auklet (*Ptychoramphus aleuticus*; Ainley and Boekelheide 1990), at a few sites, but for these species attendance lapses following the breeding season (i.e. September–October) and is sporadic rather than daily in winter. Whiskered Auklets are small (mean mass ~120 g), planktivorous alcids endemic to the Aleutian, Commander, and Kuril islands (Byrd and Williams 1993, Gaston and Jones 1998, Zubakin and Konyukhov 2001, Hunter et al. 2002; Figure 1). They have mainly nocturnal colony attendance throughout the Aleutian and Commander islands (52–54°N; Knudtson and Byrd 1982, Byrd and Williams 1993, Zubakin and Konyukhov 2001). However, in the Sea of Okhotsk (at least at Iona Island, 56°N; Figure 1), breeding activity is apparently diurnal, with minimal activity in darkness (Andreev et al. 2012). Colonies in the Sea of Okhotsk also differ from all other parts of Whiskered Auklets' range, in that breeding islands are icebound during winter, lying well within the region of continuous ice cover every year (e.g., Figure 1, and figure 1a in Nihashi et al. 2009), cautioning against drawing inference about the entire species from data from one population.

Only vague anecdotal information has been published concerning Whiskered Auklets' nonbreeding-season activities. For example, Stejneger (1885), based on the discovery of one bird aboard ship sheltering in a sail fold, stated, "This would indicate that they pass the night in holes as long as they are near land." Murie (1959) noted that, "According to the natives, this species also winters in the Aleutian Islands and, as is the habit of the Least Auklet, it enters the rocky crevices to roost," it being unclear whether this refers to winter roosting or simply to nesting in rock crevices during summer. Byrd and Gibson (1980) suggested that the large concentration of birds wintering in narrow passes in the Andreanof Islands might breed elsewhere (i.e. in the Islands of Four Mountains, 430 km to the east), inconsistent with residency near their breeding sites. Finally, Zubakin and Konyukhov (2001) observed nightly nocturnal land roosting by juveniles 6 weeks after fledging (September) at a Whiskered Auklet colony site at Buldir Island, Alaska—the only unequivocal evidence of colony attendance and land roosting outside the breeding season. Sparse data from ship-based surveys suggest that Whiskered Auklets' at-sea winter distribution is restricted to areas within a few kilometers of the Aleutian Islands, close to known or suspected breeding areas (Byrd and Gibson 1980, Byrd and Williams 1993, Renner et al. 2008, Piatt and Drew 2015). Analyses of long-term monitoring data have shown that Whiskered Auklet productivity and annual adult survival at Buldir Island depend mainly on local conditions the previous winter and spring (Jones et al. 2007, Bond et al. 2011a), consistent with individual Whiskered Auklets wintering near their breeding sites, but no direct evidence exists to test this hypothesis. Due to lack of visits to breeding colony sites in winter, and lack of individual tracking data, it remains unconfirmed whether this species is sedentary year-round or if birds disperse along and/or beyond the Aleutian Islands chain outside the breeding season, and whether land-roosting at night is continuous or sporadic.

The development of small, lightweight geolocation devices now allows tagging of Whiskered Auklets for the first time (Bridge et al. 2011, Wilson and Vandenabeele 2012). We had 3 objectives for this study: (1) using geolocation devices, test the hypothesis that Whiskered Auklets are year-round residents near their breeding sites at Buldir Island, Alaska; (2) using wet–dry sensors from these tags, test whether Whiskered Auklets roost continuously or sporadically on land in winter; and (3) further examine Whiskered Auklet year-round activity on land using automated digital audio recording devices placed near breeding sites at Buldir.

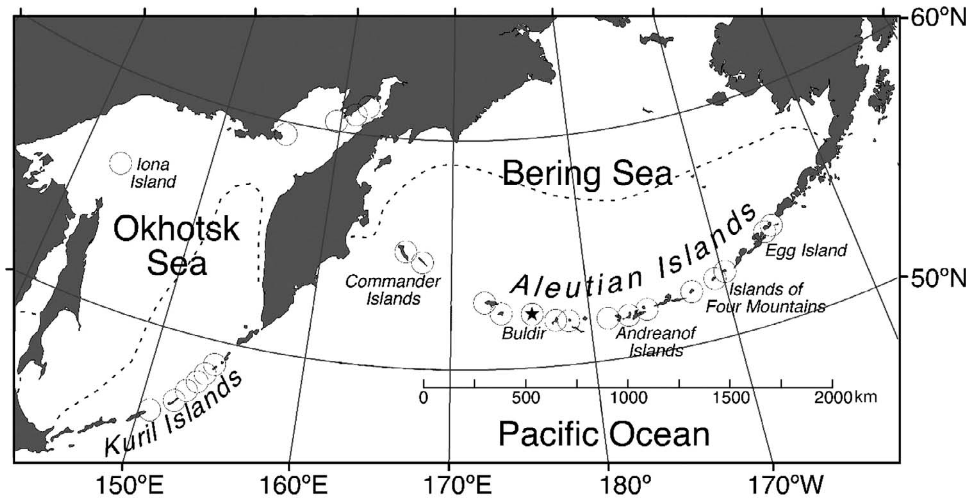

FIGURE 1. World breeding range of Whiskered Auklet showing location of Buldir Island (starred) and places named in the text. Known breeding areas (Gaston and Jones 1998) are circled. Approximate average annual maximum limit of sea ice indicated with a dashed line.

METHODS

Study Area

Our study was conducted at Buldir Island, Aleutian Islands, Alaska (52.36905°N, 175.88150°E), part of the Alaska Maritime National Wildlife Refuge. Buldir is located at approximately the geographic center of this species' world range (Gaston and Jones 1998; Figure 1) and Whiskered Auklet biology has been intensively researched at this location (Knudtson and Byrd 1982, Byrd and Williams 1993, Zubakin and Konyukhov 2001, Hunter et al. 2002, Jones et al. 2007, Seneviratne and Jones 2008, Bond et al. 2011b). Breeding sites (crevices and burrows) used were concentrated at Main Talus, Northwest Ridge, and elsewhere along the rocky cliffs of Buldir's northern shore (see site descriptions in Knudtson and Byrd 1982, Jones et al. 2001). These sites were spread across a variety of habitats (e.g., rocky talus slopes, vegetated hillsides) representative of most Whiskered Auklet breeding habitat at Buldir.

Device Attachment

We attached 1 g light-based archival geolocation devices (hereafter "tags"; Intigeo C65, 14 × 8 × 6 mm, Migrate Technology, Cambridge, UK; total attachment mass 2 g, averaging 1.8% of body mass) to 23 Whiskered Auklets in 2013 (14 female, 9 male) and 25 in 2014 (10 female, 15 male). Adults were removed from breeding sites in June while they brooded chicks, because handling does not cause nest abandonment at this stage (Schacter and Jones 2017). Birds were captured by hand or pulled out using a blunt metal crook placed around the tarsus/tibia. We gave each adult a numbered USGS aluminum band and a custom-made Darvic color band with a flattened side to which tags were attached with a 2-part marine epoxy and further secured with a cable tie. We compared the breeding success and return rates of tagged birds to undisturbed control birds to assess potential negative effects of tags on reproduction and return rates (Schacter and Jones 2017). We collected breast feathers for genetic sex determination (Fridolfsson and Ellegren 1999) of tagged individuals at the Genomics and Proteomics Facility at Memorial University of Newfoundland.

Tracking Data Processing

We deployed 5 tags for 13 days in June 2014 on a hilltop near the colony as an open-sky calibration to determine an appropriate elevation angle for this region to use as a parameter when estimating location from the sunrise/sunset data recorded by the tags (Lisovski et al. 2012). The resulting elevation angle (–5.6, threshold = 2) was evaluated for each tagged bird using breeding season data (birds known to be near the colony location), and was found to be acceptable in most cases. For a few tagged individuals this angle resulted in a distribution of points that did not overlap with Buldir Island at all (skewed too far south), and in these cases we shifted the angle until the breeding season data overlapped with the known location of the birds (Lisovski et al. 2012). We used IntiProc 1.03 (Migrate Technology, Cambridge, UK) software (based on the GeoLight 2.0 R package; Lisovski and Hahn 2012) to process the raw light curves provided by the geolocation tags. We scored each sunrise/sunset event based on the amount of shading apparent in the light curve, which corresponds with error in location estimates. These errors were especially prevalent during the breeding season when birds are in and out of their breeding crevices (Lisovski and Hahn 2012). We then mapped the individual points.

Obvious outliers that were also associated with a low score due to tag shading were removed a priori, as were points during the equinoxes (September 9–October 18, February 24–April 4) when day lengths around the planet are too similar for reliable estimates of latitude (Hill and Braun 2001). We smoothed the data twice (Phillips et al. 2004), using a running average including the points immediately before and after, with fixed origin points at the beginning and end of each track and of equinox exclusion periods (Hedd et al. 2012). To map the resulting location points, we created a kernel density estimation surface in Geospatial Modelling Environment (Beyer 2015), using the plug-in method for bandwidth selection (Sheather and Jones 1991, Jones et al. 1996) and a cell size of 1 km. We then calculated percent volume contours representing 25%, 50%, and 80% of locations for display purposes. As a control to evaluate the accuracy of the tags, we deployed 5 tags on a pole 1 m above the ground at 52.36905°N, 175.88150°E from August 2013 to May 2014 (~11 mo) near where birds were tagged. Data from these control tags were processed in the same way as the bird-borne tags.

Immersion Data

In order to quantify time spent dry (assumed to indicate roosting on land or flying; see Discussion), C65 tags on auklets were programmed to record whether or not the tag was wet (immersed in salt water) every 30 s using a conductivity sensor (Fox 2015). Using R 3.1.1 (R Core Team 2014; script adapted from Hedd et al. 2014), we processed the data from each individual to determine the percent of time spent dry during each day or night period (based on the sunrise/sunset times recorded by the tags). We then calculated an average across all birds for each period and plotted the pattern of percent of time dry across the 11 mo deployment.

Audio Recordings

In order to further quantify Whiskered Auklets' year-round activity near their breeding sites, we made and analyzed automated nocturnal sound recordings for the entire nonbreeding season. Whiskered Auklets are highly vocal at Buldir at night during the breeding season (May–July; Byrd and Williams 1993, Seneviratne et al. 2009), so we inferred that vocal activity might indicate colony attendance at other times of year. We deployed 2 Song Meter SM2 recording units (Wildlife Acoustics, Maynard, Massachusetts, USA) from July 2014 to May 2015 at sheltered areas of high Whiskered Auklet breeding site density at Main Talus, Buldir Island. Song Meters were programmed to record every 5 days throughout the nonbreeding season, and recordings were made in six 5-min bouts during times of peak Whiskered Auklet nocturnal surface activity (3 at 30-min intervals leading up to sunrise, and 3 at 1-hr intervals after sunset). We scored each 5-min recording for background noise (from wind and waves) on a scale of 0–6, and calculated the average noise score for each night. Recordings ranged from being almost completely free of noise (score of 0) to being completely unusable due to static from high winds and precipitation (score of 6). We confirmed the presence of Whiskered Auklet vocalizations in recordings by reviewing spectrograms using Song Scope 4.1.3A (Wildlife Acoustics, Maynard, Massachusetts, USA), and listening to all potential vocalizations for verification. We then gave each day a presence score (0–6) based on how many of the 6 recordings that day contained Whiskered Auklet calls, which was then plotted alongside noise scores for context.

RESULTS

We recovered tags from 17 Whiskered Auklets (2013–2014: 7 females and 5 males; 2014–2015: 3 females and 2 males). Tag recovery rate was significantly lower for 2014–2015 (20%) compared to 2013–2014 (52%; Fisher's Exact test, $P = 0.03$), with no difference in recovery rate between sexes ($P = 0.6$). We arrived late at Buldir in 2015 due to weather delays (first tag retrieval June 3, 2015, compared to May 30, 2014), and some of the disparity in tag recovery rate between years was caused by missed recapture opportunities for birds whose nesting attempt failed early in the incubation phase (see more detailed discussion below and in Schacter and Jones 2017).

Tracking Data

Whiskered Auklet tracking data (Figure 2A) form an elliptical distribution similar to that of stationary control tags (Figure 2B), but with greater spread due to more variable shading (Phillips et al. 2004). Recorded positions of stationary control tags were, on average, 120 km (coefficient of variation CV = 0.96, n = 2,217) from the known location (113 km in latitude, CV = 1.04, n = 2,217; 24 km in longitude, CV = 0.77, n = 2,217). Whiskered Auklet positions averaged 212 km (CV = 0.88, n = 8,049) from the colony (199 km in latitude, CV = 0.95, n = 8,049; 49 km in longitude, CV = 0.99, n = 8,049).

Immersion Data

Our immersion data show that Whiskered Auklets were at sea during the day for most of the year (Figure 3). Virtually all nighttime readings showed that the tags were continuously dry at night, indicating nocturnal land roosting year-round, with increases in daytime dry readings during the breeding season (Figure 3), peaking during incubation (May/June) and tapering off during chick-rearing (June/July). Tagged birds were dry at night, with the exception of regularly spaced spikes in wet readings, coinciding with the timing of full moons (Figure 4A). These trips to sea at night are more evident in a plot

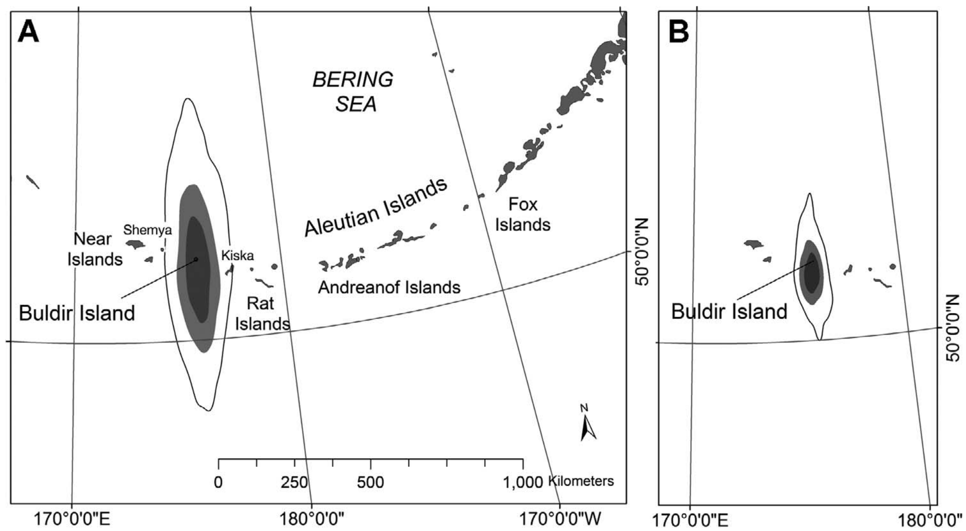

FIGURE 2. Year-round position data from Intigeo C65 light-based archival geolocation tags from Buldir Island Alaska during 2013–2015: (**A**) Whiskered Auklets ($n = 17$); (**B**) stationary control tags ($n = 5$). Percent volume contours displayed for 25% (dark gray), 50% (light gray), and 80% (black outline) of points. Tag position error in latitude is inherently ~5× larger than for longitude.

overlaying all individual data (Figure 4A) than in the averages (Figure 3), because there was a lot of variation among individuals in the timing and occurrence of these trips. At the height of winter, Whiskered Auklets averaged up to 14 hr/night on land (Figure 4B).

Audio Recordings

One of the Song Meters failed. The second produced 251 individual recordings totaling 1,255 min from July 29, 2014, to April 1, 2015. The predominant call types detected were "beedoo" calls (Seneviratne et al. 2009). The latest date at which we could confirm the presence of adult Whiskered Auklets at this part of the colony using vocalizations was October 9, 2014, and the earliest March 8, 2015. Most calls were detected in dawn recordings in summer/fall (91%) and in dusk recordings in spring (71%) (Figure 5). Even during the breeding season, when Whiskered Auklets were known to be present in the area, only 43% of recordings contained identifiable calls.

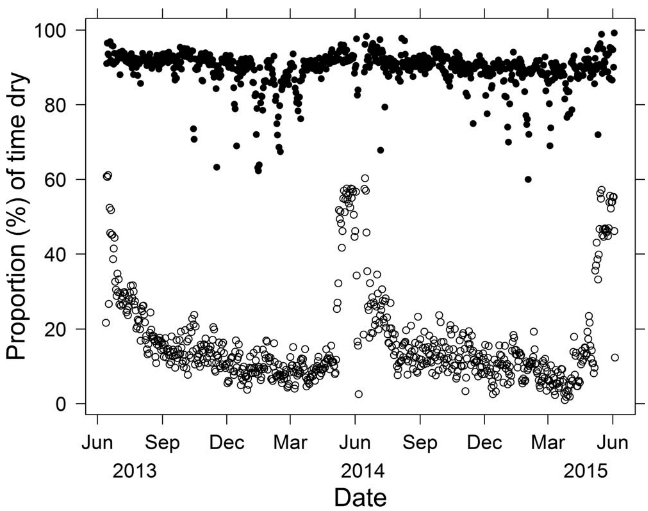

FIGURE 3. Daily proportion (%) of time spent dry (not immersed in seawater) for Whiskered Auklets equipped with Intigeo C65 tags at Buldir Island, Alaska, averaged across all individuals (2013–2014: $n = 12$; 2014–2015: $n = 5$), separated into day (○ = local sunrise to sunset) and night (• = local sunset to sunrise) periods. Note: data from the 2 years of the study are from different individuals.

DISCUSSION

Data from our 17 tracking tags showed that Whiskered Auklets breeding at Buldir were distributed close to the island throughout 2013–2015, including the nonbreeding season. The birds' leg-mounted tags were dry at night year-round, except for occasional nighttime wet records during full moon periods. We infer from this pattern that our tagged birds from Buldir roosted on land at night every night year-round with no departures except for nocturnal foraging trips during full moons when there was sufficient ambient light and/or stronger tidal currents. Similar lunar-assisted nocturnal foraging has been documented for albatrosses (Phalan et al. 2007) and other auks (Thick-billed Murres [*Uria lomvia*]: Jones et al. 2002, Paredes et al. 2008; Common Murres: Regular et al. 2011). That birds from which we recovered tags roosted on land at Buldir Island was indicated by the distribution of the geolocation data, which excludes the location of the nearest land on other islands (Kiska, 104 km to the east, and Shemya, 125 km to the west). Audio recordings confirmed their presence at the colony site close to where the birds were

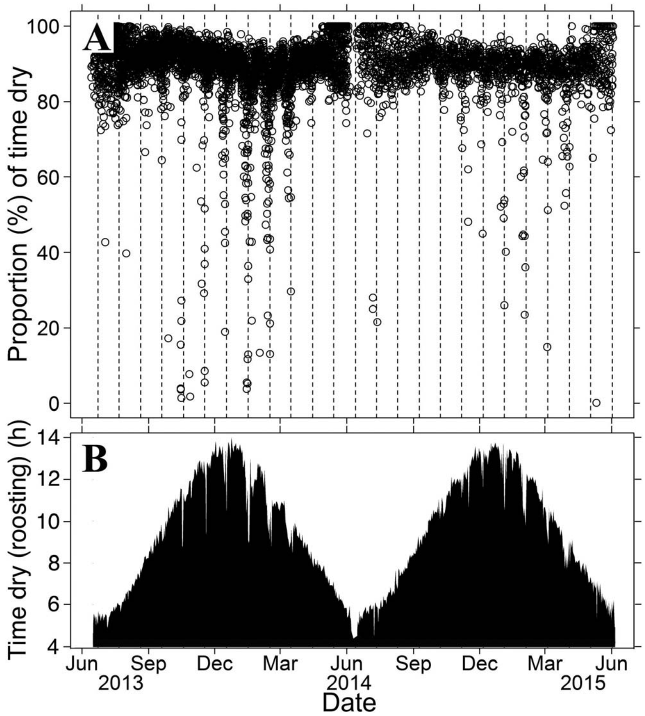

FIGURE 4. (**A**) Daily proportion (%) of time spent dry (not immersed in seawater) at night for Whiskered Auklets equipped with Intigeo C65 tags at Buldir Island, Alaska, plotted for all individuals (2013–2014: $n = 12$; 2014–2015: $n = 5$). Dashed vertical lines represent timing of full moons. (**B**) Daily total hours of time spent dry at night (assumed to indicate nocturnal roosting on land) inferred from the same data. Note: data from the 2 years of the study are from different individuals.

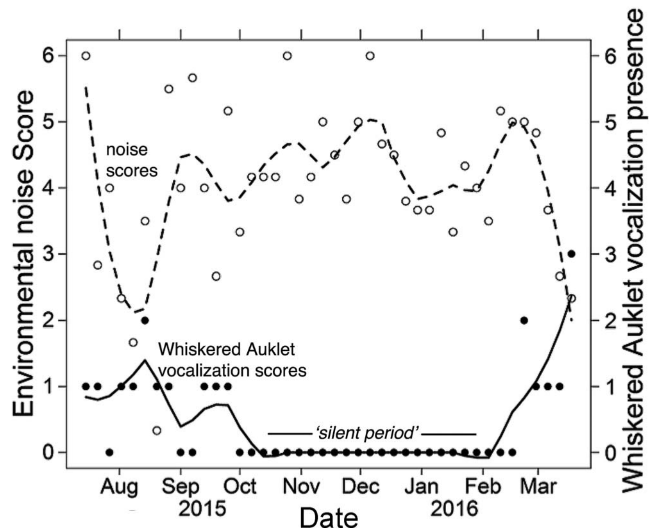

FIGURE 5. Daily scores of Whiskered Auklet vocalization presence in nighttime audio recordings from Buldir Island, Alaska during July 2014 to April 2015 (filled circles, solid line; score of 0–6 indicating how many of the recordings on that day contained at least one identifiable call), plotted alongside background surf/wind noise scores (empty circles, dashed line; noise score 0–6 averaged across the 6 recordings from each day). Curves created using loess smoothing function (span = 0.25).

tagged from at least early March to mid-October. Taken together, our data provide strong evidence that Whiskered Auklets from this colony are nonmigratory, remaining resident at Buldir Island during the nonbreeding season and roosting on land.

Our tracking data were somewhat limited by the low precision of geolocators relative to other types of tracking tags (Wakefield et al. 2009). However, the average distance recorded of 212 km from the colony is within the range of error (169–400 km) reported for similar bird-borne tags in other studies (Phillips et al. 2004, Shaffer et al. 2005), and is consistent with little or no movement away from Buldir. The longitudinal error of geolocation tags is inherently lower than their latitudinal error (resulting in a north–south elliptical distribution; Hill and Braun 2001), and is sufficient to reject the alternative hypothesis that Whiskered Auklets from this colony dispersed east–west along the Aleutian Islands chain. As Whiskered Auklets prefer shallow water and active tide-rips as foraging areas year-round (Byrd and Williams 1993), significant north–south movement from Buldir into deep basin waters is highly unlikely.

As with any tracking study based on attached devices, it is essential to consider potential effects that tag attachment could have on the behavior of interest (Vandenabeele et al. 2011, Robinson and Jones 2014). A comparison of tagged and control Whiskered Auklets at Buldir showed minor decreases in chick growth, and much lower adult return rates in one of two years studied (Schacter and Jones 2017), and so we cannot rule out the possibility that behavior recorded may differ from that occurring naturally in untagged individuals. However, we believe that our lower tag recovery rate in the second year of the study was at least partially related to our delayed arrival at Buldir (due to logistical issues) and consequent missed captures of birds whose nests failed early in incubation, not wholly due to the tags themselves. Compared to highly migratory species like Crested Auklet (*Aethia cristatella*; Robinson and Jones 2014), Whiskered Auklets' sedentary nature would be expected to render them less susceptible to tag effects as the birds did not make costly long-distance movements (for more detailed discussion of tag effects, see Schacter and Jones 2017).

We concluded that long bouts of dry readings recorded nightly for virtually the entire year resulted from birds roosting nocturnally on land at Buldir Island, if not necessarily near the breeding sites themselves. Given how close Whiskered Auklets remained to Buldir (Figure 2A), it is unlikely they were undertaking sustained continuous flight that would produce the observed dry pattern

(Figures 3 and 4). Dry readings can occur when seabirds tuck their legs out of the water while afloat (e.g., murres: Fifield et al. 2009, Atlantic Puffins [*Fratercula arctica*]: Harris et al. 2010). However, leg-tucking behavior, although commonly observed in captive Horned Puffins (*Fratercula corniculata*) and Thick-billed Murres, is rare in captive Parakeet Auklets (*Aethia psittacula*; D. Zombeck, Curator of Birds, North Carolina Zoo, personal communication), and is unlikely to be responsible for dry readings in our closely related Whiskered Auklets, given their small size, the turbulent nature of the sea surface near Buldir Island, field observations of birds on the water with their legs submerged, the tendency of C65 tags to rotate on the tarsus to a position away from body feathering (I. L. J. personal observation), and the observed pattern of continuous unbroken dry records at night only (Figure 3). Parakeet and Crested auklets monitored at sea far from land with the same wet–dry sensors showed a high frequency of wet readings at night when they were resting on the sea surface (Schacter 2017). It was not possible to tell whether Whiskered Auklets were roosting in the open on cliff ledges, within crevices away from their breeding sites, or at their breeding sites in winter (as they do in summer; C. R. S. and I. L. J. personal observations). However, large deposits of weathered excrement within and just outside some breeding sites (C. R. S. and I. L. J. personal observation) might have resulted from the birds taking shelter underground in or near their nests. Blockage of some sites by snow may occur (e.g., at Main Talus), but low elevations at Buldir receive little snow in most years and snow is unlikely to accumulate in the steep terrain of most Whiskered Auklet breeding habitat and adjacent cliffs. We suggest that their roosting behavior may be a behavioral adaptation to reduce metabolic costs by avoiding cold water when not foraging, and also avoiding activity during times of day when darkness would render foraging unprofitable. Future work could use wet–dry data to examine swimming/roosting patterns of individuals in more detail.

Our sound recordings from breeding areas at Buldir suggest a lack of Whiskered Auklet vocalizing near the recording device during November–February (4 winter months), where birds vocalized March–October. The nature of Whiskered Auklet habitat (cliffs and steep slopes overlooking rocky shoreline) made it difficult to deploy automated recording devices in a suitably sheltered location, so many recordings were too noisy due to surf and wind to detect birds, even during the breeding season when large numbers were known to be present. Therefore we believe that our recordings could have missed some calling birds, and so lack of detections does not definitively indicate absence. However, our results were also consistent with Whiskered Auklets not vocalizing much, if at all, on land during the nonbreeding season, for example, if they underwent torpor (Schleucher 2004) to conserve energy. Alternatively, it is equally likely that the 4-mo vocalization gap resulted from birds in the winter roosting on cliffs or otherwise away from the breeding site area that we monitored. Whiskered Auklets are routinely observed in summer at night roosting on cliff ledges not directly connected to breeding crevices at Buldir (I. L. J. personal observation) and also at Egg Island in the eastern Aleutian Islands (Jones and Seneviratne 2005). There was nothing in the immersion or tracking data to suggest that the absence of calls in our recordings between November and February represents an actual departure from the island, although the full-moon trips to sea were most noticeable during this period (Figures 3 and 4). Exactly where on Buldir Whiskered Auklets roost during November–February could be verified using VHF radio tags and a year-round VHF logging system as used by Wails (2016) at Gareloi Island for Crested Auklets.

We cannot generalize about the species as a whole based on data from one colony. Whiskered Auklets differ in size, ornamentation, and behavior across their range (Byrd and Williams 1993, Zubakin and Konyukhov 2001, Jones et al. 2002), so our results indicating sedentary behavior should be interpreted cautiously. However, Whiskered Auklets across the Aleutians have been shown to be similar in many ways. Breeding season observations of nocturnal activities at several colonies, including Egg Island, Ulak Island (Andreanof Islands), Kanaga Island, Gareloi Island, and Kiska Island (Gaston and Jones 1998, Jones and Seneviratne 2005) are consistent with behavioral observations at Buldir. Additionally, all recorded Aleutian sightings of Whiskered Auklets at sea have been concentrated close to land and near known or suspected breeding sites (Byrd and Williams 1993, Piatt and Drew 2015). A range-wide pattern of residence near breeding colonies without long-distance movement (leading to a lack of mixing among populations) would be consistent with the high levels of genetic divergence in Whiskered Auklets recently described by Pshenichnikova et al. (2017). Nevertheless, some variability in movement activity across the species' breeding range is expected because breeding islands in the Okhotsk Sea (Iony Island and Penzhina Bay; Figure 1) are surrounded by heavy pack ice cover in winter (Nihashi et al. 2009). Migration to and from these sites would appear to be inevitable, although these birds could still roost on land at nearby ice-free locations such as the Kurile Islands, part of the species' breeding range (Gaston and Jones 1998; Figure 1). Okhotsk Whiskered Auklets also differ from Aleutian populations in morphology (larger body size and ornaments; Pshenichnikova et al. 2017) and colony attendance (diurnal instead of nocturnal; Andreev et al. 2012).

Further research is required to determine whether winter residence is the norm for Whiskered Auklets at other colonies, as seems likely in the rest of their Aleutian range. However, undertaking a similar study at other colonies will be challenging. Successful tag deployment and recovery for Whiskered Auklets requires opportunities to capture and reliably recapture individuals from breeding sites (rock crevices, mostly on cliffs), limiting opportunities to carry out work on other islands as these are largely inaccessible. Nevertheless, Iona Island (priority) in the Okhotsk Sea, Gareloi Island, and sites in the Andreanof Islands near Little Tanaga Island, in the Aleutian Islands, are likely viable candidates for future work. Whiskered Auklets' inactivity during long hours of nocturnal roosting (e.g., at Buldir up to 14 hr per night in December) also merits an investigation of whether they use torpor (Schleucher 2004) to conserve energy.

Whiskered Auklets are vulnerable to fatal nocturnal attraction to artificial lights on vessels (Byrd and Williams 1993, Gaston and Jones 1998, I. L. J. personal observation.). For example, in one event at the Islands of Four Mountains in November 1964, an estimated 1,140 Whiskered Auklets were attracted to the lights of an anchored fishing vessel and killed (Dick and Donaldson 1978), the number of dead recovered representing a substantial proportion of the estimated population at Buldir Island at that time (1,000–1,500 pairs; Byrd and Day 1986). The presence of this species near shore may also place them at greater risk from oil spills due to shipping traffic through Aleutian passes (Renner and Kuletz 2015). Our results underline the imperative for wildlife managers to consider the risk to Whiskered Auklets of such events at or near their breeding colonies year-round. Our conclusions regarding extensive roosting on land also highlight the conservation concern outlined by Williams et al. (2003) about Whiskered Auklets' increased vulnerability to introduced mammalian predators like foxes, especially during the winter when few other prey species remain accessible on land.

The Whiskered Auklet may provide us with a rare example of a nonmigratory seabird, and its year-round use of land stretches the definition of "seabird" as a concept. When combined with its congeners, which fall along a continuum including dispersive and long-distance migrations (Robinson and Jones 2014, Robinson 2015, Schacter 2017), this system has the potential for interesting future investigations into the topic of migration.

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Author contributions: I. L. J. conceived the study. C. R. S. and I. L. J. designed the methods, collected data, and conducted the research. C. R. S. analyzed the data. C. R. S. and I. L. J. led in writing the paper. I. L. J. and C. R. S. contributed substantial resources.

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