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Patterns of year-round colony attendance by VHF radio-tagged Crested Auklets (*Aethia cristatella*) at their prototypical Aleutian breeding site

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ABSTRACT—Seabird colony attendance during their breeding seasons is driven by reproductive obligations of incubation and chick rearing, resulting in relatively predictable attendance patterns near breeding sites. Less is understood about patterns and function of activity ashore at colony sites outside the breeding season. We attempted to quantify year-round activity of crevice-nesting Crested Auklets (*Aethia cristatella*) at Gareloi Island, Alaska, a site with some of their largest colonies. In June and July 2013 and 2014, 94 Crested Auklets (92 adults and 2 subadults) were fitted with uniquely coded 1.0 g VHF radio-tags (0.6% of body mass) at 2 inland study plots in the southeast colony. Radio receiver–loggers remotely detected and recorded individuals present on the nearby colony site surface 24 h/d from date of tagging through autumn, winter, spring, and summer 2013–2015. Notably, we found Crested Auklets present in all months of the year, with half of our radio-tagged auklets ($n = 47$, 29 females, 10 males, 8 unknown sex) detected inland at the colony site during nonbreeding months (Sep–Mar). Visit duration for these individuals comprised about 0.4% of their total annual colony site activity; this is the first evidence of year-round Crested Auklet colony attendance that may be unique to Gareloi. Other findings included extreme individual variability and intersexual differences in colony attendance frequency, differences in attendance between breeding and nonbreeding birds, a lapse in surface activity prior to laying in May, and frequent nocturnal activity on the colony surface. Enhanced circannual patterns of Crested Auklet colony attendance at this island may relate to defense of nesting site and other social advantages, permitted by a nearby highly productive sea area with year-round foraging opportunities. *Received 7 September 2019. Accepted 18 August 2020.*

Key words: Alcidae, circannual activity, movement ecology, nonbreeding behavior, reproductive behavior.

Les schémas de la présence à la colonie toute l’année par les Stariques Cristatelles (*Aethia cristatella*) radiomarqués VHF à leur site prototypique de nidification aux Îles Aléoutiennes

RÉSUMÉ (French)—La présence d’oiseaux marins aux colonies pendant leurs saisons de reproduction est déterminée par les obligations reproductives d’incubation et d’élevage des poussins, ce qui entraîne des tendances de la présence relativement prévisibles à proximité des sites de nidification. On en comprend moins aux sujets des schémas et des fonctions de l’activité à terre aux sites de colonie en dehors de la saison de reproduction. Nous tentâmes de quantifier l’activité toute l’année des Stariques Cristatelles (*Aethia cristatella*) nichant dans les fissures sur l’île Gareloi, en Alaska, un site avec leurs plus grandes colonies. Pendant juin et juillet de 2013 et 2014, nous attachâmes les émetteurs radios VHF classiques à 94 Stariques Cristatelles (92 adultes et 2 juvéniles) aux deuz sites d’étude dans la colonie sud-est ; chaque émetteur radio était codé de façon unique et avait une masse de 1,0 g (0,6% de la masse corporelle). Les récepteurs détectèrent et enregistrèrent à distance des individus présents à terre dans la colonie proche pour 24h/24 à partir de la date de marquage tout au long de l’automne, l’hiver, le printemps, et l’été de 2013 à 2015. Notamment, nous trouvâmes des Stariques Cristatelles ce qui sont présentes tous les mois de l’année ; nous détectâmes la moitié de nos stariques radiomarquées ($n = 47$, 29 femelles, 10 mâles, 8 sexe inconnu) à l’intérieur des terres dans la colonie au cours de la saison d’hivernage (de septembre à mars). La durée des visites de ces individus constituait environ 0,4% de leur activité annuelle totale dans la colonie ; notre étude dévoile la première preuve de la présence à la colonie toute l’année par les Stariques Cristatelles, qui peut être unique à l’île Gareloi. Des autres résultats incluaient de la variabilité extrême des individus et des différences intersexuelles par rapport à la présence dans la colonie ; des différences de présence entre les oiseaux nicheurs et non-reproducteurs ; une halte de l’activité à terre avant la ponte en mai ; et des activités nocturnes et fréquentes à terre dans la colonie. L’augmentation des schémas circannuels de présence aux colonies par la Starique Cristatelle sur cette île peut être reliée à la défense du site de nidification et à d’autres avantages sociaux, permis par une région de mer très productive à proximité de la colonie avec des occasions de cherche de nourriture toute l’année.

Mots-clés: Alcidae, comportement migrateur, comportement reproducteur, écologie des déplacements, rythme circannuel.

Nelson’s (1980) introduction to seabird biology noted their relative (to other birds) independence from land, notwithstanding the requirement to return to terrestrial breeding sites for incubation and chick rearing (the ice shelf breeding Emperor Penguin [*Aptenodytes forsteri*] being the sole known exception; Kooyman 1993). Even so, year-round land visitations to breeding colony sites by some seabirds does occur, including some marine cormorants (Phalacrocoracidae) that forage near shore and routinely roost on land at their colony sites (Nelson 2005), and several penguins (Spheniscidae) that have year-round (or nearly so) colony attendance (Williams 1995). Among auks (Alcidae), colony attendance outside the breeding season is known for a few species, including Common Murres (*Uria aalge*; Harris and Wanless

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1989, Boekelheide et al. 1990), Whiskered Auklets (*Aethia pygmaea*; Schacter and Jones 2018), and Cassin's Auklets (*Ptychoramphus aleuticus*; Ainley and Boekelheide 1990); some non-colonial Marbled Murrelets (*Brachyramphus marmoratus*) visit inland breeding sites year-round (Naslund 1993, Naslund and O'Donnell 1995). With the exception of Whiskered Auklets, these species' attendance is intermittent rather than continuous in winter, usually pausing September–October following the breeding season.

Seabird land visiting outside the breeding season is interesting because it would appear to separate individuals from their food supplies offshore at a time of year with lowest prey abundance in a seasonal environment. In contrast, during seabirds' summer breeding seasons, individuals incubating eggs and raising nestlings are tied to their breeding colonies and subject to all the constraints of central place foraging (Elliott et al. 2009) and local prey depletion ("Ashmole's Halo"; Ashmole 1963). Nevertheless, off-season seabird colony attendance would be advantageous if there are social (including nest site territorial defense) and energetic (sheltered roosting) advantages of terrestrial activity (Schacter and Jones 2018) and if a reliable supply of food is available nearby all year. Recent technological advances have allowed remote measurement of annual movement and distribution at sea and how these differ between breeding and nonbreeding seasons (Ballance 2007, McKinnon et al. 2013, Gaston et al. 2017, Jaeger et al. 2017, Berg et al. 2019, Studholme et al. 2019; but see Vandenabeele et al. 2012).

Here, we applied some of this technology to year-round measurement of colony attendance of an abundant North Pacific pursuit diving planktivorous seabird, the Crested Auklet (*Aethia cristatella*), to better understand its biology and clarify its vulnerability to anthropogenic activities including fisheries by-catch (Dick and Donaldson 1978), marine pollution (Piatt and Ford 1996, Renner and Kuletz 2015), and depredation by invasive species (Ebbert and Byrd 2002, Williams et al. 2003, Major et al. 2006). We aimed to definitively quantify Crested Auklet activity on land using VHF radio-tags, expecting their colony attendance to be limited to the breeding season (Apr–Aug) as inferred from preexisting anecdotal information.

We were interested in male–female differences in attendance based on the unusual sexual dimorphism of this bird (Jones 1993a, Gaston and Jones 1998) and reported intersexual differences in parental care behavior (Fraser et al. 2002). Finally, we aimed to explore broader implications of our empirical results to ecology and conservation of this iconic bird at its biggest Aleutian colony. Specifically, the questions addressed by our study were, in relation to colony attendance, (1) What were the year-round, seasonal, and daily patterns of activity by Crested Auklets at Gareloi Island Alaska in 2013–2015? (2) Were there differences in colony attendance between males and females and breeding and nonbreeding birds? (3) Were there individual differences in colony attendance related to ornamental plumage? (4) How did our VHF radio-tag recorded activity patterns at Gareloi correspond to emerging information concerning Crested Auklet seasonal movements from light-based archival geolocation tags?

We further tested 4 hypotheses related to colony attendance during the breeding season: (1) visit duration depends on the purpose of colony attendance (i.e., reproductive obligations, nesting site prospecting) and thus will differ seasonally between breeding and nonbreeding auklets; (2) visit duration is the result of sex-specific parental roles and will thus differ seasonally between sexes; (3) visit duration is limited by individual condition as indexed by ornamental plumes and will thus vary with crest length for males and (4) mean auricular plume length for females (cf. Jones et al. 2000).

Methods

Study species

Crested Auklets are socially monogamous, crevice-nesting seabirds that copulate at sea only, nest synchronously, produce a clutch size of one egg, and rarely or never re-lay if the first egg is lost (Knudtson and Byrd 1982, Piatt et al. 1990a, 1990b; Jones 1993a, Fraser et al. 1999, Hunter and Jones 1999). Eggs are incubated by both pair members equally for about 36 d (shift changes at night), with hatchlings incapable of thermoregulation for several days and dependent on brooding provided mostly by males (Jones 1993a, Fraser et al. 2002, 2004), who may be better able to defend young chicks from conspecific and heterospecific attack (Fraser et al. 2002). Later in chick development, adults spend more time away,

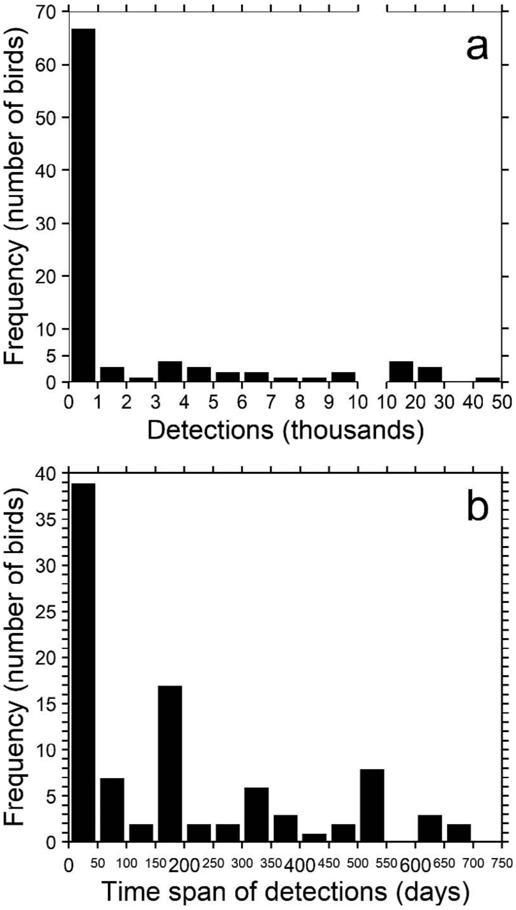

Figure 1. Detections of VHF radio-tagged Crested Auklets (292,875 detections, $n = 94$ birds tagged) at 2 study plots in the southeast colony, Gareloi Island, Alaska, during July 2013–July 2015: (a) number of detections by bird, (b) time span of detections by bird.

returning to the colony site only to provision chicks that fledge about 34 d after hatching (Fraser et al. 1999, 2002). Core breeding activities of a pair thus occupy a duration of about 70 d each year. In the Aleutians, Crested Auklets lay in late May–early June, their chicks hatch in late June–early July, and most chicks have fledged by early August (Jones 1993a, Fraser et al. 1999).

Crested Auklets exhibit "colony attendance," referring to visible standing on the surface of their colony sites, accompanied by flocks flying over and around the colony area, but not usually referring to invisible occupation of crevice breeding sites below by incubating and roosting birds (Byrd et al. 1983, Piatt 1990a, Jones 1992, 1993a; Harding et al. 2005). Auklets loiter on surface "display rocks" above nesting crevices and elsewhere on and near colony sites with individuals perching at multiple locations (Jones 1993a, Major et al. 2017). In the Aleutians (Buldir, Kiska, Gareloi, and Kasatochi Islands; Supplemental Fig. S1), visible colony attendance supposedly occurs in 2 daily periods, roughly 0800–1300 h and 2300–0000 h HADT (Hawaii-Aleutian Daylight Time), the colony surface otherwise deserted, with attendance petering out in mid- to late July as chick rearing is completed (Byrd et al. 1983, Jones 1993a, ILJ unpubl. data). Little colony attendance has been reported to occur during darkness, but Fraser et al. (2002) noted VHF-tagged breeding birds arriving and leaving their nesting crevices at night at Buldir. At islands with human habitation (Pribilof Islands and St. Lawrence Island, Alaska), auklets are not seen on land outside the May–August breeding season (Jones 1993a). Aleutian Crested Auklet breeding colony sites (located on remote and inaccessible islands uninhabited by humans) are rarely visited by researchers in autumn and winter, but birds apparently arrive in large numbers during April (6 weeks before laying begins) and commence courtship activities immediately (Jones 1993a, ILJ unpubl. acoustic monitoring data).

Emerging evidence from direct observations and light-based archival tags has shown that most Aleutian breeding Crested Auklets migrate northward into the northern Bering Sea and Chukchi Sea in mid-August immediately after breeding, turning southward to the Kuril Islands and Sea of Okhotsk in December where they remain until April before returning to their nesting colonies (Robinson and Jones 2013, 2014; Robbins and Jones 2015, Robbins et al. 2015, Robinson 2015). However, some tagged birds are present in the central Aleutians throughout autumn and winter (Robbins et al. 2015). Measurement errors up to 100 s of km on position estimates from light-based archival geolocation tags limit inference of precise locations (e.g., Welch and Eveson 1999, Schacter and Jones 2018), so here we used a large sample of short-range VHF radio-tags and a receiver antenna array with presence–absence logging within a major colony site to quantify colony attendance directly.

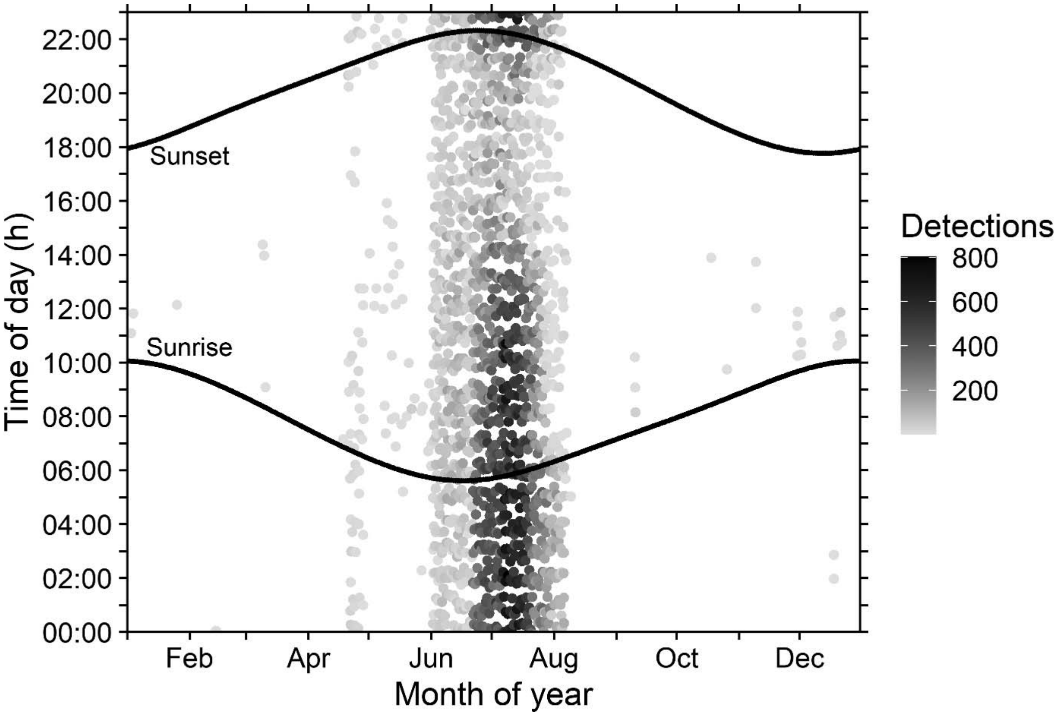

Figure 2. Detections (all data) of VHF radio-tagged Crested Auklets (292,875 detections, *n* = 94 birds tagged) at each hour (HADT) throughout the year at 2 study plots at the southeast colony, Gareloi Island, Alaska, during July 2013–July 2015. Nonbreeding season detections (Sep–Mar) consisted of 142 detections (0.04% of total detections).

Study site

We measured colony attendance at the "southeast colony" site at Gareloi Island, Alaska, USA (51°47′N, 178°47′W), Crested Auklets' prototypical breeding island, hosting the largest breeding numbers of this seabird (>500,000 pairs) anywhere in the Aleutian Islands and perhaps Alaska (Murie 1959, Sowls et al. 1978, Jones and Hart 2006, Major et al. 2017). Gareloi Island is located close to (23 km) a productive shallow pass between Unalga and Kavalga Islands that upwells zooplankton prey (Hunt et al. 1998).

Crested Auklets are widespread on this island, nesting at inland sites (lava flows), beach boulders, and associated eroding coastal cliffs (Sowls et al. 1978, Paragi 1996a, 1996b; Jones and Hart 2006, Major et al. 2017). The southeast colony corresponds closely to ~80 ha of the most recent lava flows and craters from 1930s era volcanic eruptions (Coats 1959; figure 2 in Jones and Hart 2006). Jones and Hart (2006) surveyed this site and estimated that the southeast colony supported about 230,175 pairs of Least (*A. pusilla*) and Crested auklets in 2006, with about half believed to be Crested Auklets. For the present research, we selected 2 high-density study plots, "Plot D" (51°45′14.4″N, 178°45′31.9″W) and "Tick Mountain" (51°45′14.1″N, 178°45′27.0″W), located about 300 m inland at an elevation of 40 m a.s.l., close to the geographic center of the southeast colony.

Auklet VHF radio-tagging

During the early incubation and hatching periods, we captured and attached VHF radio transmitter tags to 94 Crested Auklets (27 breeding adults and 2 nonbreeding adults in 2013; 33 breeding adults, 28 nonbreeding adults, 2 nonbreeding subadults, and 3 of unknown reproductive status in 2014 [one 2013 Crested Auklet was recaptured and issued a new tag in 2014]) by placing noose carpets on prominent social pads (flat-topped grassy lava extrusions used for social interactions) at Plot D (*n* = 39) and Tick Mountain (*n* = 55). Aiming to measure bird activity through

April–June of the following year (tag life ~1 year, see below), birds were tagged during 15–16 July 2013 and 1 June–6 July 2014.

This capture technique is believed to representatively sample birds attending the colony surface (Jones et al. 2000). After banding with a USFWS #4 aluminum band (used instead of stainless steel because of its lighter mass) on the right leg, a Darvic plastic (A.C. Hughes, Ltd., Hampton Hill, Middlesex, UK) band was placed above the aluminum band and a 1.0 g Lotek NTQB-4-2 coded VHF radio-tag (Lotek Wireless, St. John's, Newfoundland, Canada) that transmits a unique coded signal that is then detected remotely (Supplemental Fig. S2). Tags were 1.0 g mass (12 mm in length, 9 mm maximum width), had an internal antenna, and an advertised battery life of 400 d (Lotek Wireless).

Tags were attached using fast-curing marine epoxy and a clipped 75 mm plastic cable tie. In 2014, birds were fitted with 2 additional Darvic bands in a unique color combination on their left leg. The total mass of all materials attached to radio-tagged Crested Auklets was 1.5 g (0.6% of mean Crested Auklet body mass 260 g; Fraser et al. 1999), within the recommended 3% of body mass limit to reduce potential tag effects to individuals (Phillips et al. 2003; but see Vandenabeele et al. 2012, Robinson and Jones 2014, Schacter and Jones 2017 for an experimental assessment of tag effects on Crested Auklets). During processing, age class (i.e., adult or subadult, based on plumage characteristics; Pyle 2008), adults' sex (identified by bill size and shape; Jones 1993b), and standard measurements including crest and auricular plume lengths (Jones et al. 2000) were taken. We additionally assumed breeding status based on the presence of a complete vascularized brood patch or the presence of chick meal in the throat pouch, but did not attempt to locate the nest or tag the partner as our study plots were on active, densely nested sites of the colony. Tagged individuals were released after the epoxy had set, we ensured the Darvic band with attached VHF radio-tag could rotate freely around the leg, and the end of the cable tie was clipped with burrs removed.

Colony attendance of our radio-tagged Crested Auklets was measured using 2 Lotek SRX-DL radio receiver-loggers (one on each plot), each equipped with two 5-element Yagi antennae, with gain set at 65 dB giving an expected detection range of ~20 m. The radio receiver-logger sites were 88 m apart to minimize cross-detection. Radio-tags emitted uniquely coded signals (frequency 166.300 MHz) every 40 s (signal duration: 4.5–5.5 s). With these settings, the battery life of NTQB-4-2 VHF radio-tags was stated to be 400 d according to the manufacturer's specifications. Our radio receiver-loggers scanned for signals (continuously for 60 s followed by 60 s not scanning) and logged ID number, date, and time of detections (frequency and scanning intervals set to maximize battery life and probability of detection). All radio-tags were continuously monitored from attachment date in 2013 and 2014 through 13 July 2015 (about when colony attendance declined and detections ceased; Wails 2016). We anticipated that distance, bird position (flying, surface standing, underground), and weather would affect the probability of detection by the receiver-logger. Therefore, we a priori interpreted detection rate as a relative (minimum) measure not an absolute measure of colony attendance by Crested Auklets.

To measure detectability of the NTQB-4-2 tags, we conducted a series of 3 tests. First, at both plots, tags were handheld at varying distances from the receiver-loggers, both above and below (i.e., in crevices) the colony site surface, with the RealTime Monitoring function in the Lotek SRX-DL host program used to record detections. This same tag was carried throughout both breeding seasons as a mobile control (detections of this control tag allowing us to evaluate consistency in detection range). Second, we conducted watches (118 h) at study Plot D to resight birds wearing VHF radio-tags on the surface of the colony site, with resightings compared to the Lotek SRX-DL's log to measure detection rate of birds on the surface, and to measure rate of detections of birds when no tagged birds were visible (i.e., radio detection of birds underground). Third, on 30 June 2014 we placed a single fixed radio-tag as a static control near the radio receiver-logger at Plot D for the duration of the study (detections of this control tag allowing us to continuously evaluate system integrity on that plot).

Statistical analyses

Statistical analyses were performed in R 4.0.0 (R Development Core Team 2020). All summary statistics reported are means ± 95% confidence intervals, unless otherwise indicated.

Radio-tagging validation—We first validated our VHF radio-tagging method in quantifying Crested Auklet colony attendance activities. To understand the performance of our VHF radio-tagging method, we calculated Pearson's correlation coefficient between number of detections and tag life. For a static tag, we anticipated a positive correlation between tag detections and tag life; however, for tags placed on auklets, which are not continuously present at the colony, we expected no correlation between number of detections and tag life. We measured median time span of first to last detection (i.e., tag life). We calculated Pearson's correlation coefficient separately for tags applied to birds in 2013 and 2014 to account for an observed shortened tag life in 2013. Additionally, we ground-truthed our data by comparing resighting records to radio-tag detections and examining gaps (>60 s) in detection records for our 2 control tags.

Daily, seasonal, and circannual trends in colony activity—Using our full dataset of all detections from 2013 to 2015, we evaluated year-round trends 2 ways: (1) number of radio-tag detections and (2) number of unique radio-tagged auklets detected.

Visit duration—For known-sex adult auklets ($n = 82$), we defined visit duration based on consecutive detections of the same individual with ≤5 min between detections (duration being the time between first and last detection). We quantified mean visit duration per day and hourly for males and females separately.

Because we were unable to collect a complete set of all morphometric measures for each auklet, we used a reduced dataset to test our hypotheses related to breeding season colony attendance ($n = 62$ known-sex, radio-tagged auklets with all measures recorded). For comparative purposes, we defined reproductive stages of the breeding seasons at Gareloi based on crevice checks at the colony site (incubation: 1–26 Jun, hatching: 27 Jun–2 Jul, chick rearing: 3 Jul–1 Aug, fledging: Aug; Wails 2016). These periods overlapped somewhat, hatching and fledging dates both occurring over 2+ week periods; no difference was noted in timing between years.

We restricted this analysis to data collected in the same year individuals were tagged to account for observed tag life. We analyzed our reduced dataset using generalized linear mixed-effects models with a Gamma distribution and log link as our dependent variable, visit duration, is a continuous variable > 0. Individual radio-tag ID and year were included as random effects. Because our hypotheses are not mutually exclusive, we assessed hypotheses individually and considered statistical significance at $\alpha = 0.05$.

As we found no significant relationships for breeding season visit duration and our measures of ornamental plumes, we additionally examined Pearson's correlation coefficient between the number of radio-tag detections during the breeding season per individual and ornamental plume lengths. Because we had too few visits during the nonbreeding season, we also examined Pearson's correlation coefficient between the number of radio-tag detections during the nonbreeding season per individual and ornamental plume lengths.

Results

Among the 94 unique Crested Auklets that we radio-tagged, 92 were adults, one was a subadult, and one could not be aged based on Pyle's (2008) criteria. Among known-sex adults ($n = 82$; cf. Jones 1993b), 44 were female and 38 were male. One individual was captured in 2013 and recaptured in 2014 with a corroded VHF tag. We replaced the corroded VHF tag with a new tag in 2014.

Radio-tagging validation

Nearly all (92/94) radio-tagged auklets were detected at least once, one was detected once only, most (64/94) had less than 1,000 detections, 19 had less than 10,000 detections, and 8 auklets exceeded 10,000 detections—one of which was detected 41,387 times across 200 d (Fig. 1a). No cross-detections were recorded. Time span from first to last detection varied from 1 to 695 d, with 45 radio-tags (48%) with a span of <100 d, and 16 radio-tags (17%) with a detection time span of >400 d. The overall median detection time span was 146 d, less than half of the manufacturer's specified tag life (Lotek Wireless; Fig. 1b). While we could confirm 2 tag failures, we were otherwise unable to distinguish whether detection cessation

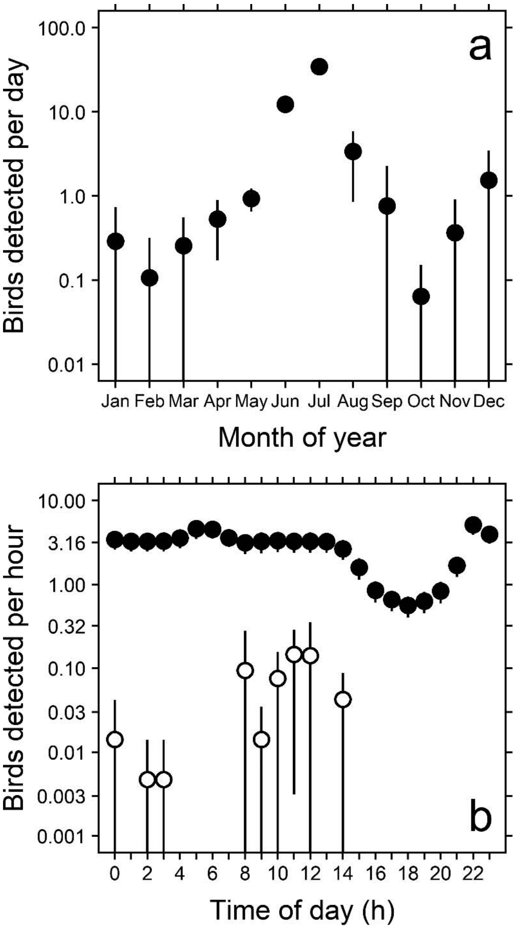

Figure 3. Mean (±95% CIs) number of VHF radio-tagged Crested Auklets (log10 scale, $n = 94$ birds tagged) detected (a) per day each month and (b) by time of day (HADT; filled points breeding season, unfilled points nonbreeding season), at 2 study plots at the southeast colony, Gareloi Island, Alaska, during July 2013–July 2015.

was the result of death (no deceased auklets found), emigration (no resighting elsewhere on colony), or tag failure—the southeast colony of Gareloi is >1 km^2 in area and has an estimated 230,000 pairs of Crested Auklets occupying a porous lava flow (Jones and Hart 2006).

Based on our handheld tag test, radio receiver-loggers had a 100% detection rate for tags on the colony site surface within a 20 m radius of the antennas and never detected tags placed in crevices. During 118 h of watches at Plot D (cf. Wails and Major 2017), we recorded 56 resights of 27 radio-tagged birds (54/56, 96% with a corresponding detection) in 2014 and 34 resights of 15 radio-tagged birds (34/35, 97% with a corresponding detection) in 2015. Detections indicated birds standing on the plot socializing and also arriving and departing from crevices. The receiver-logger took ~5–10 s to pick up a tag, indicating tags on birds flying over the plots were unlikely to be detected. However, one VHF radio-tag was detected at Tick Mountain on more than one occasion when no auklets were visible on the surface (as human observers were present), indicating subsurface detections were possible. Radio receiver-logger detection records for one static tag staked on Plot D (30 June 2014) were continuous with no lapses for 379 d with the exception of a 2 d lapse in power at the radio receiver-logger (444,365 detections, ceasing 16 Jul 2015 when radio-receiver-loggers were removed from the colony at the end of the study). Another hand-carried (dry continuously, no exposure to weather) VHF radio-tag activated 15 July 2013 was detected continuously when researchers were within detection range and lasted 731 d. One failed VHF radio-tag attached 16 July 2013 (with no detections after Aug 2013) was removed from its recaptured bird on 4 July 2014, inspected, and was corroded internally. No anomalous detection of any undeployed tag frequency was recorded, and we are unaware of any mechanism by which our equipment could log false detections. We found weak, nonsignificant correlations between total tag detections and tag life for auklets in 2013 (Pearson's $r = -0.23$, $P = 0.27$) and 2014 (Pearson's $r = -0.13$, $P = 0.31$).

Daily, seasonal, and circannual trends in colony activity

We detected surface activity of VHF radio-tagged Crested Auklets at the southeast colony of Gareloi Island in all months of the year, with half of our radio-tagged Crested Auklets detected at least once during the nonbreeding season ($n = 47$, 29 females, 10 males, 8 unknown sex; Fig. 2, 3a). We detected birds on 142 d (45.8%) during the breeding seasons (Apr–Aug) and 17 d (4.0%) during the nonbreeding seasons (Sep–Mar) of 2013–2015. The mean percent of individuals with live tags detected per day was greatest during the breeding season (intense activity commencing in Apr; Fig. 2), with peak attendance detected in July during chick rearing (26.0 ± 3.5% of radio-tagged individuals/d; Fig. 3a) and low during the nonbreeding season (1.4 ± 0.9% of radio-tagged individuals/d; Fig. 2). The lowest colony attendance during the breeding season occurred during August, as chicks fledged, with very low (but not zero) colony attendance during September and October (Fig. 2, 3a). Auklet colony attendance began to pick up again in November, with nonbreeding season attendance peaking in December around the winter solstice. During the breeding season, most detections occurred from 2200 h to 1300 h and fewer were detected between 1400 and 2100 h (Fig. 3b). Crested Auklets were detected 2.5 times more often during hours of darkness compared to daylight hours (estimated total time present: 43.6 h vs. 17.2 h). Detections during the nonbreeding season mostly occurred in the morning hours after sunrise (137 detections, 96.5%), with 5 (3.5%) middle of the night detections (Fig. 2, 3b). We did not find (for individuals) any correlation between the number of detections during the nonbreeding season and the breeding season (Pearson's $r = –0.06$, $P = 0.54$).

Visit duration

Annually, mean visit duration varied between months. Detections between January and March were single detections for all individuals (Fig. 2, 4a). Average visit duration for males increased in April (4.3 ± 2.3 min/visit), likely when males initiated courtship and social displays on the surface, but decreased in May (pre-laying "honeymoon" period; Fig. 2, 4b). Males spent the most time on the surface in June (incubation period: 78.3 ± 18.1 min/visit) and females spent the most time on the surface during August (chick rearing through fledging: 57.4 ± 26.6 min/visit; Fig. 4a). Following the breeding season, visit duration decreased drastically for both sexes (3.0 ± 1.5 min/visit; males: 4.6 ± 1.9 min/visit; Fig. 4a) with only single tag detections from October–November.

Some Crested Auklets made brief visits to the colony in December around winter solstice and visit duration during this time did not differ between sexes (females: 1.1 ± 0.9 min/visit; males: 1.9 ± 0.7 min/visit; Fig. 4a). When evaluating mean daily visit duration, visits varied by time of day and between sexes (Fig. 4b). Males consistently spent more time at the colony than females throughout the day except at 1900 h (Fig. 4b).

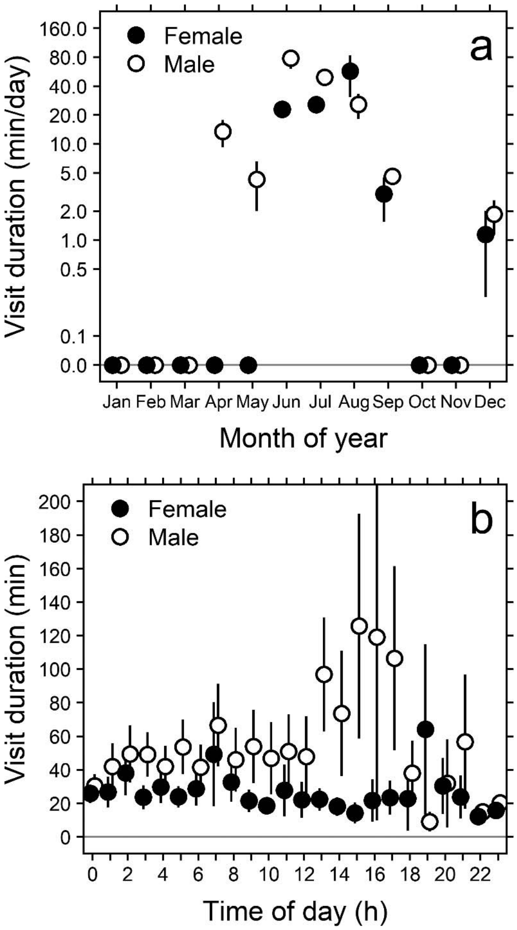

Figure 4. Mean visit duration (±95% CIs) made by VHF radio-tagged female ($n = 35$, filled points) and male ($n = 36$, open points) Crested Auklets by (a) month of year (log10 scale) and (b) time of day (HADT), at 2 study plots at the southeast colony, Gareloi Island, Alaska, during July 2013–July 2015.

Breeding season and reproductive stages—We found that visit duration during the breeding season for our subset of 62 auklets (30 female, 32 male) was best explained by individual breeding status and nesting chronology (Table 1). On average, duration of visits made by breeding auklets were consistently longer than that of nonbreeding auklets (breeding auklets: 52.6 ± 5.0 min/visit; nonbreeding auklets: 22.9 ± 2.6 min/visit) and the timing of peak visit duration also

Table 1. Results of the 4 generalized linear mixed-effects models (Gamma distribution, log link) evaluating visit durations of 62 Crested Auklets during the breeding season in which they were tagged. "×" indicates an interaction.

(a) Visit duration ~ Nesting period * Breeding status

Variable [Level]	*Coefficient*	*SE*	*T*	*P*
Intercept	2.66	0.30	8.98	<0.001
Period [hatching]	−0.25	0.12	−2.05	0.040
Period [chick rearing]	−0.43	0.11	−3.96	<0.001
Period [fledging]	0.35	0.18	2.02	0.043
Breeding status [nonbreeding]	−0.60	0.42	−1.43	0.15
Period [hatching] × Breeding status [nonbreeding]	0.05	0.16	0.32	0.75
Period [chick rearing] × Breeding status [nonbreeding]	0.40	0.14	2.79	0.005
Period [fledging] × Breeding status [nonbreeding]	−2.62	0.60	−4.38	<0.001

(b) Visit duration ~ Sex * Nesting period

Variable [Level]	*Coefficient*	*SE*	*T*	*P*
Intercept	1.98	0.41	4.88	<0.001
Sex [male]	0.62	0.39	1.58	0.11
Period [hatching]	−0.21	0.11	−2.02	0.043
Period [chick rearing]	−0.12	0.09	−1.36	0.17
Period [fledging]	1.29	0.22	5.92	<0.001
Sex [male] × Period [hatching]	−0.03	0.17	−0.18	0.85
Sex [male] × Period [chick rearing]	−0.26	0.15	−1.77	0.076
Sex [male] × Period [fledging]	−1.60	0.30	−5.34	<0.001

(c) Visit duration ~ Sex * Crest length

Variable [Level]	*Coefficient*	*SE*	*T*	*P*
Intercept	1.26	1.77	0.71	0.48
Sex [male]	0.09	2.89	0.03	0.98
Crest length	0.02	0.04	0.49	0.62
Sex [male] × Crest length	0.00	0.07	0.06	0.95

(d) Visit duration ~ Sex * Mean auricular plume length

Variable [Level]	*Coefficient*	*SE*	*T*	*P*
Intercept	0.44	1.91	0.23	0.82
Sex [male]	−1.05	3.66	−0.29	0.78
Mean auricular plume length	0.06	0.06	0.90	0.37
Sex [male] × Mean auricular plume length	0.04	0.12	0.36	0.72

* Sex [female], Period [incubation], and Breeding status [breeder] were set as reference levels.

differed. Mean visit duration for breeding auklets peaked during hatch (91.6 ± 21.6 min/visit) whereas nonbreeding auklets had the longest visit durations during chick rearing (25.8 ± 3.2 min/visit; Table 1a).

When considering sex-specific attendance, visit duration for males decreased significantly over the breeding season, with the longest visit durations during the incubation period (102.0 ± 37.5 min/visit) and shortest during fledging (28.8 ± 9.6 min/visit; Table 1b). Visit duration for females was shortest during chick rearing (25.2 ± 2.5 min/visit) but increased during fledging (60.5 ± 28.4 min/visit). We did not find evidence that visit duration during the breeding season was related to either crest length (Table 1c) or mean auricular length (Table 1d). Further, there were no statistically significant relationships between crest length and number of detections for either sex (female Pearson's $r = 0.04$, $P = 0.80$; male Pearson's $r = 0.12$, $P = 0.50$) or for mean auricular length and number of detections (female Pearson's $r = 0.27$, $P = 0.13$; male Pearson's $r = 0.15$, $P = 0.40$).

Nonbreeding season—During the nonbreeding seasons, we recorded 142 detections of 47 different auklets (28 female, 13 male, 7 unknown sex), with 7 spending time at the colony (12 visits total, mean visit duration: 2.4 ± 0.9 min/visit). There were no statistically significant relationships between crest length (cf. Jones et al. 2000) and detections during the nonbreeding season (Pearson's $r = -0.11$, $P = 0.91$) or for mean auricular length and number of detections (Pearson's $r = -0.28$, $P = 0.78$).

Discussion

Here, we used radio-tag detections to measure year-round patterns of colony attendance of a crevice-nesting seabird. Before considering interpretations of our data, it is important to assess limitations as well as strengths of our approach. Our study involved one colony site (Gareloi) with a short 2 year duration, for a species with a wide geographic breeding range and known variability in behavior (Jones 1993a), so we take extreme caution in generalizing to other locations and time periods. Our tagged individuals were mostly adults (92/94), so we are unable to evaluate behavior of immature birds in a species with prospecting subadults comprising a substantial proportion of visible activity (subadults' vagility made them poor candidates for short-range VHF monitoring; Jones 1992, 1993a; Major et al. 2017). Further, our radio-tagging approach inherently limited interpretations to tag detections on study plots—we were unable to distinguish cessation of tag transmissions among tag failure (e.g., due to battery exhaustion), bird death, and immigration, and we were unable to make inferences about survival, immigration, or movement. We did confirm tag breakdown due to battery failure related to saltwater intrusion (observed in 2 of 94 tags) and for 75 of 94 tags the detection period was less than manufacturer-specified tag life (Fig. 1b), reducing our sampling and suggesting in hindsight the need for more robust marine-grade coded VHF transmitters.

Despite these shortcomings, several aspects of our approach allowed valuable inferences about auklet behavior. Our measurements based on logged detections were year-round and their precision constant, verified by 3 experiments that indicated high detectability of tags for a representative sample (94 birds). Our antenna array and receiver-loggers detected tags when birds were present on the colony surface and in control tests, but not (with only one known exception) when they were underground, focusing our records on auklet surface activity (i.e., colony attendance), the subject of interest. Individually coded tag signals inherently precluded false positives (logging of tags when none were present). Mass and size of VHF radio-tags used was small (0.6% of body mass), suggesting results were not excessively interfered with by tag effect (based on previous experiments; Robinson and Jones 2014, Schacter and Jones 2017). Our data were from 2 representative plots within a major colony site at Gareloi Island, a nexus of this species in the Aleutians, and allowed us to directly quantify colony attendance through number of detections of individually identifiable birds. Because auklet colony attendance includes times of year (i.e., winter) and times of day (i.e., night) when direct observation was difficult or impossible on a remote island, our radio-tag approach produced a novel perspective on activities of this seabird.

Our most surprising result was detection of Crested Auklets near our inland capture sites on the surface of their colony site at Gareloi in all months of the year (Fig. 2). Previously, colony attendance of Crested Auklets during the nonbreeding season (Sep–Mar) was unknown (Jones 1993a). Furthermore, based on emerging results of light-based archival geolocation for Crested Auklets at Buldir and Gareloi Islands (Robinson and Jones 2014, Robbins and Jones 2015, Robbins et al. 2015, Robinson 2015, J Robinson and KF Robbins unpubl. data), we predicted that few or no Crested Auklets would be detected on land during the nonbreeding season because most (though not all) birds were far (>1,000 km) from Gareloi during September–March. However, some geolocation tagged birds from this colony site at Gareloi were present near the central Aleutians' Amchitka Pass-Delarof Islands area throughout autumn and winter 2013–2015 (Robbins et al. 2015).

Nevertheless, 50% of tagged individuals in our study ($n = 47$, 29 females, 10 males, 8 unknown sex) were detected inland at the colony site outside the breeding season and detections occurred in all months. The relatively low latitude of Gareloi (~52°N), consequent year-round mild temperatures, and lack of consistent snow cover at low elevations would appear to make winter colony attendance feasible. Equally important, presence of productive inter-island passes nearby (e.g., between Kavalga and Unalga Islands 24 km from Gareloi, known to be a preferred Crested Auklet foraging area, cf. figure 1 in Hunt et al. 1998) would also enhance the possibility of Crested Auklet year-round activity. Hunt et al. (1998) pointed to the constricted and shallow (12 km wide by 54 m deep) topography of this pass, and exchange of Bering Sea and North Pacific water through it, as factors concentrating *Aethia* auklet prey. Elsewhere in the Aleutians, Crested Auklets concentrate in winter at similarly active Unimak Pass (Renner and Kuletz 2015), where there are no nearby breeding sites (Jones 1993a).

A notable aspect of nonbreeding season colony attendance at Gareloi was its reduction during the mid-August through November period with a resurgence in December (Fig. 2). This may be explained by general seasonal movement of Aleutian Crested Auklets away northward en masse to the Bering Strait and Chukchi Sea at the conclusion of breeding in early August, to take advantage of productive foraging areas, and their later return southward in December when northern foraging areas ice up and become dark (Robinson and Jones 2013, Robbins and Jones 2015, Robbins et al. 2015, Robinson 2015, J Robinson, KF Robbins unpubl. data). Our Gareloi Crested Auklets likely resumed colony visitation when they returned to the Delarof Islands area after their late-autumn migration in December. The function of nonbreeding season colony attendance per se is unknown but presumably relates to territorial and mate selection factors similar to breeding season activity (Jones 1993a), as has been suggested for some other colonial seabirds (Hedd and Gales 2005).

An implication of our nonbreeding season detection data is that the number of Gareloi Crested Auklets with winter colony attendance was large (50% of adult birds in our sample), possibly involving ~500,000 birds from among those wintering in nearby passes (based on a 2006 island-wide Crested Auklet population estimate of ~500,000 pairs; Jones and Hart 2006). Although many Crested Auklets went ashore in winter, our data suggest time on the colony surface was brief, as demonstrated by a large number of single detections. The observed intermittent and mostly daytime detections in winter (Fig. 2) mirrored the breeding season morning activity period typical of this species (Jones 1993a). The few nighttime detections are more enigmatic; were these of birds entering or leaving crevices used for roosting as for Whiskered Auklets at Buldir Island (Schacter and Jones 2018)? Careful examination of wet–dry records of geolocation tagged Crested Auklets from Gareloi may provide an answer (KF Robbins unpubl. data).

Crested Auklets had intense late-April colony attendance followed by reduced activity in May (particularly late May, just prior to laying) in 2014 and 2015 (Fig. 2), likely a pre-laying exodus or “honeymoon period” in which birds spend more time at sea to build up reserves for egg production and incubation (Nelson 1980) and also mate (Hunter and Jones 1999). Our study is the first to quantify this pattern for an auklet species (*Aethia* sp.), even though this has been described for other seabird species, especially Procellariiformes (Warham 1990, Quillfeldt et al. 2019).

We found a clear, decreasing trend in visit duration through the breeding season with greatest visit duration occurring during the incubation period for both sexes and less time during chick rearing, as previously indicated by surface counts at various locations (Jones 1993a). Because of properties of our VHF radio-tags, our detections were entirely, or nearly so, from adults on the surface and not from incubating adults in crevices. If we had recorded detections from birds in crevices, we would have found visit durations upwards of 24 h, the normal incubation schedule of adults (Fraser et al. 1999). Although both pair members can sometimes be observed in the crevices simultaneously, for example at night (Jones 1993a, Fraser et al. 1999), incubation duties do not require both partners. This would permit one breeding pair member to socialize on the colony surface, as observed given we detected birds on ~50% of days during the breeding season. After chicks become older and no longer required brooding, parents were detected less frequently (cf. Fraser et al. 2002).

Peak circadian Crested Auklet colony site surface activity at Gareloi (indicated by VHF radio-tag detections) included all hours of darkness (Fig. 3b), somewhat of a surprise as standing birds are not normally observed after dark at Buldir or Kiska (ILJ pers. obs.). However, time-lapse camera images used to monitor auklet colony attendance at Gareloi during 2010–2015 showed auklets standing on the surface at night (Wails 2016, CNW and HLM unpubl. data, HLM, RT Buxton, CR Schacter, MG Connors, ILJ unpubl. data). Further, members of Crested Auklet breeding pairs are known to come and go from nesting crevices at all hours at Buldir (Fraser et al. 2002). Thus, we are confident that our nighttime tag detections represent previously undescribed nocturnal colony attendance. Such nocturnal activity may relate to predator avoidance, as has been observed in Procellariiformes (e.g., Mougeot and Bretagnolle 2000), as avian predators at Gareloi (gulls, eagles, falcons, and ravens) are less active at night and no owls are present to disrupt nocturnal colony attendance. The afternoon to early evening lull in detections between 1500 and 2100 h (Fig. 3b) was consistent with Crested Auklet colony attendance at other Alaskan colonies (Byrd et al. 1983, Piatt et al. 1990a, Jones 1993a). Our results did confirm a pattern observed in the Aleutians: that Crested Auklets at Buldir and Kasatochi (relatively small colonies) had shorter and better defined morning surface activity periods, while surface activity at Kiska and Gareloi (large colonies with relatively fewer avian predators) was more protracted into the afternoon (Jones 1993a, Bond et al. 2010, this study).

Another notable feature of our results was extreme individual variability in attendance (i.e., detectable surface activity) across our sampled birds. Counts (i.e., frequency) of detections varied across 4 orders of magnitude (10s, 100s, 1,000s, and 10,000s of detections among different individuals), indicating colony attendance varied from hours spent on the surface almost every day for some birds, to almost no surface activity in others. This pattern matched that observed at Buldir and Gareloi for resightings of color-marked Crested Auklets, where similarly some birds almost never appeared on the surface and others were resighted daily (Jones et al. 2004, Major et al. 2017, ILJ unpubl. data). Our tests of tag detectability confirmed that these differences reflected real natural variability in behavior and not a technological artifact. Moreover, this variability occurred within breeding adults, a population subset expected to be stable in behavior compared to prospecting nonbreeding adults and subadults. Our findings further underline hyper-variability of colony attendance as an inherent trait of *Aethia* auklets, at all individual, age, temporal (i.e., annual), and spatial (inter-colony) scales (Piatt et al. 1990a, 1990b; Jones 1992, 1993a; Gall 2004, Sheffield et al. 2006, Bond et al. 2012, Major et al. 2018). These results again indicate the need for caution in use of colony attendance measures for population monitoring.

In relation to intersexual differences, male colony attendance was consistently greater than females, except during the early evening (Fig. 4b). As predicted, after-hatch attendance was male-biased with females inclined toward food provisioning and males to nestling brooding. Crested Auklet chicks require brooding in the first week and are differentially brooded by males that are better equipped to defend chicks from conspecific attackers than are females (Fraser et al. 1999, 2002, 2004).

Our tag detections of nonbreeding Crested Auklets ($n = 17$) indicated lower levels of activity (Table 1), and also confirmed the presence of transient individuals that, although captured on our study plots, showed no site faithfulness. While nonbreeding birds of other seabird species engage in prospecting during chick rearing (e.g., Boulinier et al. 1996), subadult auklets attend earlier in the breeding season during the incubation period (Jones 1992). In contrast, our sample of nonbreeding Crested Auklets were adults (Pyle 2008 criteria), and our results indicated their longest visits were made during the chick rearing period. This suggests that colony attendance may differ with biological age as opposed to our simplified age class (i.e., subadult and adult), as well as other unidentified factors.

Our results showed that colony attendance was not related to ornamental plumes (i.e., crest and auricular plume lengths; Jones et al. 2000). We were unable to calculate a body condition index (Studentized residuals of mass on tarsus length, as used previously for this species; Jones 1993b) that was unbiased by capture date. Previous work by Jones et al. (2000) showed that crest length of males and auricular length of females correlated weakly with body condition.

Conservation implications of our study include Crested Auklet's vulnerability to anthropogenic mortality year-round near Gareloi Island. Vessel traffic close to breeding colonies with winter auklet colony attendance would likely increase mortality risk related to light attraction (Gaston and Jones 1998, ILJ pers. obs.). For example, in one event near Kodiak Island, Alaska, in January 1977, >6,000 Crested Auklets were attracted to lights of a moving fishing vessel and killed (Dick and Donaldson 1978). Occurrence near shore in winter may also place Crested Auklets at risk from oil spills due to vessel traffic near Aleutian passes (Morkill 2006, Renner and Kuletz 2015). Wildlife managers should consider risk to Crested Auklets of such events at or near their breeding colonies year-round. Moreover, Crested Auklet mortality related to predation by introduced Norway rats (*Rattus norvegicus*) at Sirius Point, Kiska Island, 251 km west of Gareloi Island and one of the largest auklet colonies in Alaska, has been assumed to be restricted to the breeding season (Bond et al. 2013). With colony attendance confirmed for all months of the year for Crested Auklets at Gareloi, the impact of rat predation can now be reassessed with the inclusion of possible mortality at the Kiska auklet colony site during the nonbreeding season.

Finally, ocean climate during our sampling period was likely to have influenced colony attendance by Crested Auklets at Gareloi, as for other auks (Gaston and Jones 1998). The Pacific Decadal Oscillation (PDO; Mantua et al. 1997, Mantua and Hare 2002) entered a strong "cool phase" in January 2014 (http://research.jisao.washington.edu/pdo/PDO.latest), continuing through 2015, so our activity data are coincident with a switch from "warm phase" to "cool phase" conditions (2013) and entirely "cool phase" conditions (2014–2015). Presenting in 2015, anomalously warm sea surface temperatures occurred throughout the western Bering Sea and northwest Pacific, extending along the west coast of North America in an unprecedented "marine heat wave" (Bond et al. 2015). This continued through 2018 with extreme effects on North Pacific seabirds (e.g., Jones et al. 2018, 2019). How our VHF-tagged birds interacted with this ocean climate event is beyond the scope of our study, but it seems likely that the growing heat wave began to affect colony attendance as early as 2015.

Taken together, our results indicate unexpected patterns of year-round colony attendance by Crested Auklets at one of their largest breeding colonies, with implications for our understanding of this species' biology and conservation. This underlines the need for more detailed study to quantify year-round seabird activity patterns at representative breeding colonies.

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