BREEDING SEASON MOVEMENTS OF ALEUTIAN TERNS *ONYCHOPRION ALEUTICUS*: IMPLICATIONS FOR POPULATION ASSESSMENT AND MONITORING

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ABSTRACT

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In 2017 and 2018, satellite transmitters were deployed ($n_{2017} = 13$, $n_{2018} = 14$) on Aleutian Terns *Onychoprion aleuticus* in two areas of Alaska, USA, to investigate breeding season movements and temporal patterns of colony activity. The effort was intended to aid in the development of a large-scale population-assessment framework. Across the two years, we observed dispersal to seven confirmed or potential (putative) colonies, none of which were previously documented, ranging in distance from 0.4 to 64.2 km from tag deployment sites. Although most terns did not associate with any known colonies during the breeding season, several individuals from the study area in western Alaska were sequentially associated with multiple colonies. Breeding season movements were usually within tens of kilometers of the capture location, but movements of several hundred kilometers were recorded occasionally. These results should be interpreted cautiously because we do not know the post-tagging nesting status of marked terns, nor were we able to determine whether there were tern behavioral changes related to capture and tagging. With this caution in mind and based on our findings, we recommend that future efforts to estimate total Aleutian Tern population sizes or trends consider the following: (1) estimates should not rely solely upon surveys of previously documented colonies; (2) estimation procedures should account for the potential movement of individual terns among colonies, the possible lack of association of a tern with any colony, the possible association of a tern with multiple colonies, and/or the possibility that adults do not attempt to breed each year; and (3) if necessary, studies should survey subsets of the Alaska breeding range in successive years to reduce the uncertainty around the size of the statewide tern population.

Key words: Alaska, Aleutian Tern, breeding season dispersal, colony dynamics, home range, population assessment, satellite telemetry

INTRODUCTION

Many seabird species nest in relatively stable, predator-free environments (e.g., offshore islands) and display both high colony-site fidelity and synchronous nesting at predictable times during their annual cycle (Hamer et al., 2001). For such species that are conspicuous nesters, such as those nesting on the ground in tight aggregations where there is sparse vegetation, population assessment and monitoring is comparatively straightforward (e.g., Bibby et al., 2000). Given adequate resources and an understanding of the locations of most breeding-colony sites, annual surveys can be planned and executed using suitable species-specific methods, and accurate estimates of population abundance can be achieved. For seabird species that nest in environments that experience frequent disturbance due to severe weather, predation, or other factors (e.g., human disturbance), the capacity for dispersal to other colonies, the initiation of new colonies, asynchronous and variable breeding phenology, and crypsis are common (e.g., Heath et al., 2009; North, 2013). For such species, including Aleutian Terns *Onychoprion aleuticus*, estimating abundance at both the colony and population levels can be challenging due to variable, but relatively higher, rates of colony failure, within-season breeding dispersal, and intermittent nesting across years (i.e., ‘skipped breeding’ or breeding propensity < 1).

The Aleutian Tern is a seabird with a small global population, with breeding restricted to Alaska (USA) and the Russian Far East (North, 2013). It is the only subarctic/temperate-breeding *Onychoprion* species, the other three having tropical/subtropical breeding distributions (Harrison et al., 2021). It is the only member of the genus that nests on the continental mainland; the other *Onychoprion* species nest strictly on oceanic islands and islets. The Alaskan breeding range of Aleutian Terns covers a large portion of the state’s coastline, with colonies documented as far north and west as Kasegaluk Lagoon on the Chukchi Sea coast, throughout the Aleutian Islands, and as far south and east as Glacier Bay National Park (Renner et al., 2015). Aleutian Tern colonies are discrete groupings of nesting terns, generally with substantial unoccupied areas between colony pairs, although there are exceptions to this pattern. Breeding ecology and movements during the breeding season are poorly known, but study results indicate breeding-habitat plasticity, variability in colony attendance within and among years, and potential for high inter-colony movement (Corcoran, 2012;

Goldstein et al., 2019; North, 2013). Nesting often occurs at low densities and in obscuring vegetation, which can make many traditional methods for estimating abundance (e.g., Bibby et al., 2000) unsuitable, as is true of other seabirds that nest in similar circumstances. An assessment of Aleutian Tern conservation status in Alaska indicated significant population declines at known colonies (Renner et al., 2015), but it is unclear if this trend is consistent across the region because there is a poor understanding of this species' natural history and fine-scale distribution. Thus, a better understanding of Aleutian Tern breeding season movements and within-season colony dynamics could improve interpretation of current and historical abundance data. Such additional information would also improve study designs for future estimations of Aleutian Tern abundance and population trends in Alaska at both local and statewide scales.

Previous individual-based studies of the movement behavior of terns have depended on using relatively small archival tags or bands, due to weight limitations (e.g., body mass 110–140 g). In a study at Black Sand Spit near Yakutat, Alaska, Aleutian Terns equipped with geolocator tags moved among known colonies up to 20 km apart. The results of that study, however, were based on recapture of only six individuals (Goldstein et al., 2019), thus potentially underestimating movement probability and distances. Small-mass (*ca*. 2 g) satellite transmitters (Doppler-effect Platform Transmitter Terminals or PTTs) that have become available in recent years offer significant promise to aid in understanding the movements of small seabirds (e.g., most Sternidae species). These PTTs allow investigation of movements during the breeding season, potentially detecting previously undocumented colonies of Aleutian Terns without requiring the re-encounter and recapture of tagged individuals, such as is necessary with geolocator tags. Measures of breeding season movement (e.g., probability of dispersal, number of colonies visited, home-range size) will be useful for evaluating assumptions associated with population estimation procedures and models and for adapting methods to more closely reflect Aleutian Tern biology, thus minimizing bias and increasing precision of estimates.

The objective of our study was to characterize the breeding season movements and dispersal patterns of Aleutian Terns in two regions of Alaska, to help better design population estimation and monitoring efforts. In particular, we were interested in (1) determining the geographic scale of movements, (2) documenting within-breeding-season dispersal (i.e., movement away from the capture or breeding location with no return during that breeding season), (3) identifying previously undocumented areas of nesting, and (4) determining patterns of colony association (i.e., what proportion of a tern's locations were close to a single colony) and home-range sizes across the breeding season.

METHODS

Study areas

We chose two geographically separated areas to conduct our study: the Dillingham area (western Alaska) and the Yakutat area (southeastern Alaska) (Figs. 1, 2). Our Dillingham capture site was at Lily Pond (59°02′34.80″N, 158°28′26.40″W), approximately 0.55 km inland from the northwestern portion of Nushagak Bay, near the outfalls of the Wood and Nushagak rivers. This area is part of Bristol Bay, the southeastern extension of the Bering Sea. The habitat used by Aleutian Terns at this site is primarily a freshwater tundra marsh with hummocks interspersed throughout (KN, personal observation). Unlike the Yakutat area, where there were several known colonies within 20 km of one another, only five known or suspected (putative) colony locations had been documented within 100 km of Dillingham: Lily Pond, Grassy Island, Cape Constantine, Naknek, Johnston Hill (Alaska Center for Conservation Science, 2020; M. Cady, personal communication, May 2018; Renner et al., 2015). Between 1969 and 2017, data from these locations had been collected only one to three times per colony. The sparseness of data surrounding the Dillingham study area provided an opportunity to fill an information gap on Aleutian Terns in this region.

At the Yakutat study area, the colony is located primarily at the western end of Black Sand Spit (59°26′16.70″N, 139°34′50.80″W), a coastal barrier spit (or island) formed by the drainage of the Situk and Dangerous rivers into the Gulf of Alaska. The colony area is primarily sand with sparse herbaceous ground cover and scattered driftwood. Aleutian Tern presence and nesting in the Yakutat region was reported as of 1916 for colonies at the Situk River and Black Sand Spit (Walker, 1923), with the site used annually for nesting through the present, as documented by local reports, periodic published accounts, and annual monitoring since 2001 (Andres & Browne, 2004; Oehlers, 2018; Pyare et al., 2013). Additionally, a conservation status assessment concluded that the Black Sand Spit colony was much larger than any other known Aleutian Tern colony in Alaska (Renner et al., 2015). Monitoring efforts in recent years—including during this study—have documented high among-year variability in colony attendance, in addition to high rates of nest predation (e.g., by Coyotes *Canis latrans*, Northern Ravens *Corvus corax*, Bald Eagles *Haliaeetus leucocephalus*), frequent colony abandonment, and low breeding success (Oehlers, 2017, 2018; S. Oehlers, unpublished data; Pyare et al., 2013). There are also smaller known Aleutian Tern colonies in the region (Fig. 2).

Both study areas were located near small human communities in coastal Alaska. Small villages were present within the larger study areas but were more common in the Dillingham region (e.g., Clark's Point, Naknek) than in the Yakutat region. Commercial fishing is important in both areas, but there were no fisheries that targeted small forage fish (and consequently competed directly with terns for food). Subsistence harvesting of wildlife resources, including collecting Aleutian Tern eggs (Dillingham area only) and setting nearshore gillnets, is also an important source of food for community residents (e.g., Naves, 2018; Naves et al., 2021). Sport fishing is also a common summer activity in both areas, and it occurs not only in the marine environment via commercial guides and individuals but also along rivers (e.g., Nushagak [Dillingham area] and Situk [Yakutat area] rivers). Other shore-related activities that could affect nesting terns include the presence of commercial and subsistence-related fish camps, use of off-road vehicles, and recreational activities (e.g., beach combing, dog walking). Human activities are likely more common near communities but can be widely dispersed.

Field methods

In 2017 and 2018, we deployed 27 solar-recharging Argos Doppler-effect PTTs (mean mass 2.33 g; Microwave Telemetry Inc., Columbia, USA) on Aleutian Terns. These PTTs did not operate on a set duty cycle, but instead transmitted locations as battery

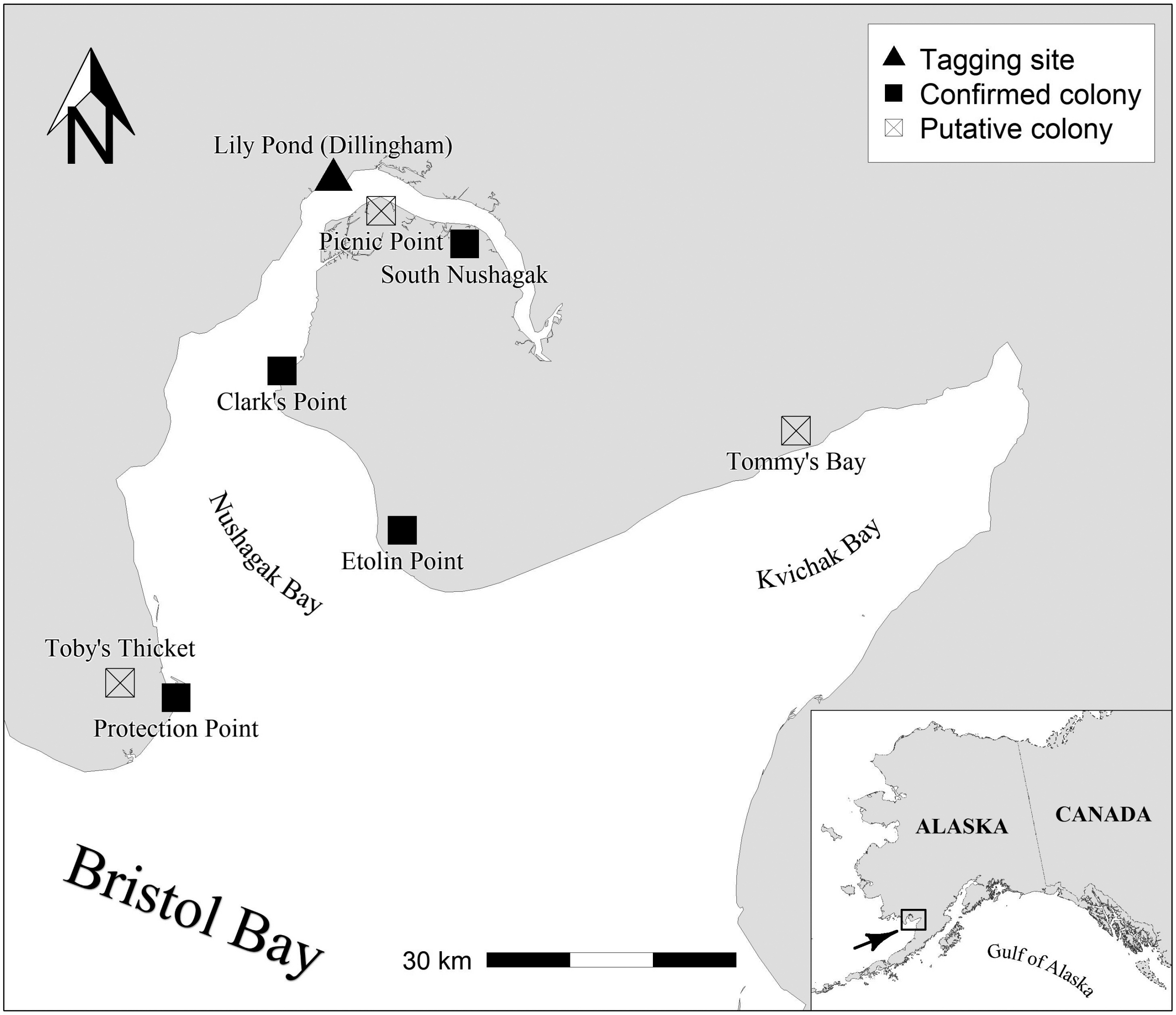

Fig. 1. Dillingham, Alaska, USA, study area for the Aleutian Tern *Onychoprion aleuticus* satellite transmitter study. The tagging site and confirmed and putative colonies are shown.

voltage allowed. Bow nets were used to capture both nesting and non-nesting adult terns. Depending on colony-specific nesting phenology, bow nets were placed either on active nests or at non-nest ground sites where conspecific playbacks and decoys were used to attract non-nesting terns. PTTs were attached using a leg-loop harness and Teflon ribbon (Thaxter et al., 2014). PTT-tagged terns averaged 122 g (standard deviation (SD) = 9). Research was conducted under Bird Banding Laboratory Permit #22395 from the U.S. Geological Survey as well as Institutional Animal Care and Use Committee protocols #0006-2017-06 and #0006-2018-06 from the Alaska Department of Fish and Game. All applicable ethical guidelines for the use of birds in research were followed, including those set out by the Ornithological Council (Fair et al., 2010).

Breeding season dispersal and identification of previously undocumented nesting areas for Aleutian Terns were first investigated using mapped Argos Location Class (ALC) 1 to 3 transmissions (ALC 1 accuracy < 1,500 m, ALC 2 < 500 m, ALC 3 < 250 m; Collecte Localisation Satellite, 2016). Visually determined clusters of mapped ALC 2 and 3 locations were used to direct visits by observers to high-use areas from June through August 2017 and from May through August 2018. When possible, multiple ground-based surveys (range = 1–12) were conducted each year. Each area was searched for Aleutian Tern adults, and researchers recorded nesting (i.e., presence of nests with eggs or flightless chicks) and reproductive success (i.e., presence of fledglings). Due to limited access sometimes resulting in incomplete coverage of the site, we could not conclusively rule out successful nesting or fledging even at sites where neither was observed during ground surveys. Thus, we defined all location clusters with tern activity as "dispersal areas" and further classified them as "confirmed" or "putative" colonies based on whether we confirmed active nesting or not, respectively. The area around concentrated tern activity (i.e., colony extents) were recorded in the field using handheld Global Positioning System units; these colony extents were used in subsequent spatial analyses.

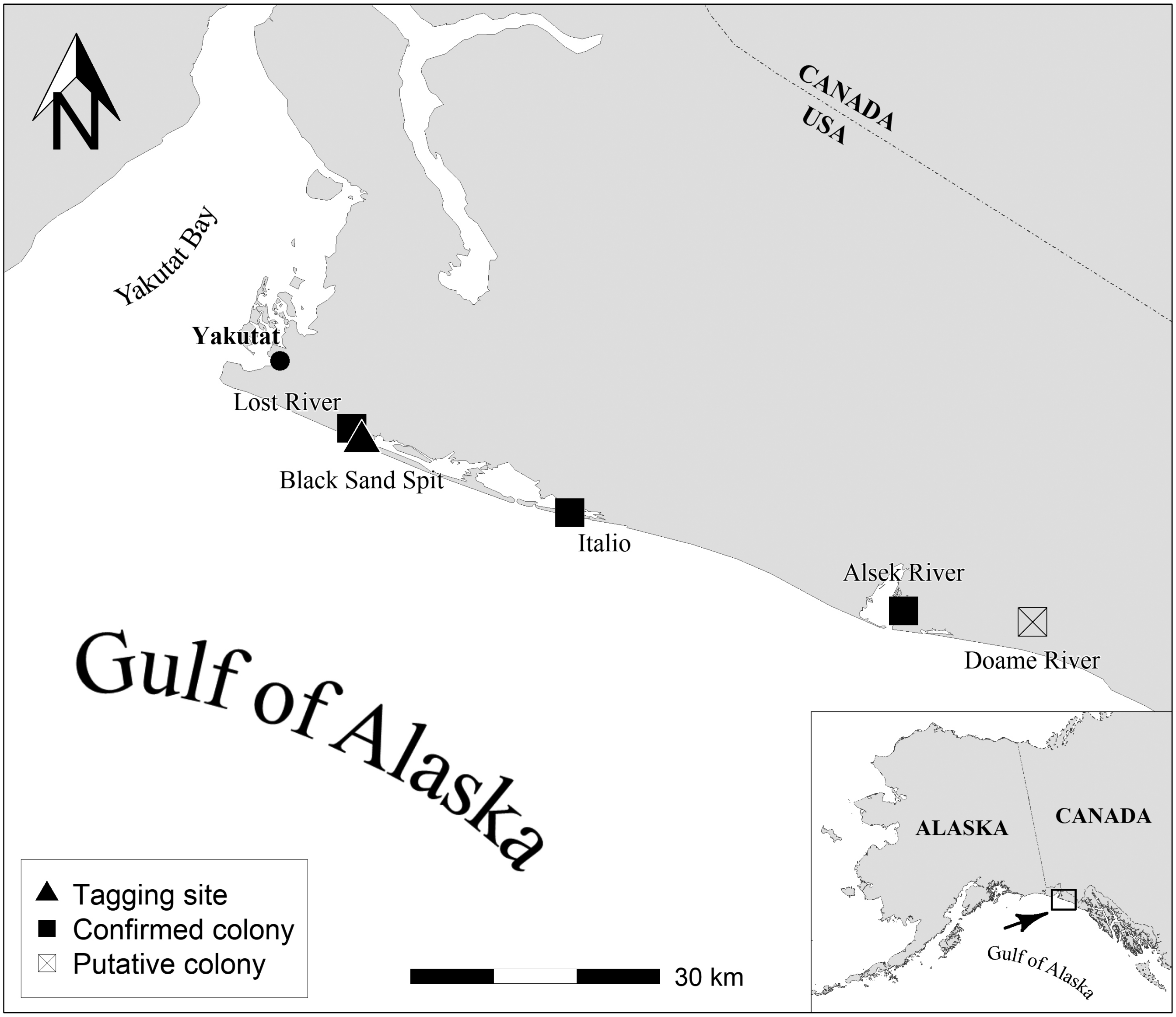

Fig. 2. Yakutat, Alaska, USA, study area for the Aleutian Tern *Onychoprion aleuticus* satellite transmitter study. The tagging site and confirmed and putative colonies are shown.

Data analysis

Summary data on PTT performance, including the duration of deployment, were compiled for each year using filtered Argos location data. Only ALC 1 through 3 locations from the breeding season were used; classes 1, 0 A, B, and Z were also recorded but not used here. Migratory and overwinter locations were removed; the start of migration was determined by a sharp increase in distance from the banding location and movement to locations far beyond those observed during the breeding season. The geographic scale of movement was investigated using kernel density estimates (KDEs) produced with the *kernelUD* function of the "adehabitatHR" package in R (Calenge, 2006; R Development Core Team, 2014; Worton, 1995). For each PTT-tagged Aleutian Tern with sufficient data (i.e., > 100 locations; range = 113–527), we calculated the maximum distance from the deployment site to the furthest point of each 50% and 95% breeding-season KDE; breeding-season home-range size was calculated from 50% KDEs, a measure that is more robust to outliers and likely provides a better metric for comparing core-use areas across individuals (Anderson, 1982).

We used a multi-step process to estimate the association between individual terns and one or more colonies (both confirmed and putative). For each tern location, we calculated a circular bivariate normal probability distribution (BNPD) with the standard deviation, which determines the area of the distribution, equal to the location error radius reported by Argos. The tails of the BNPDs were truncated at five standard deviations. As a measure of each point's association (i.e., single-point association) with one or more colonies, we then calculated the proportion of the BNPD volume (i.e., probability) that overlapped with each colony's mapped extent. We calculated a tern's association with a colony during non-overlapping, five-day intervals (i.e., colony association) as the variance-weighted average of all single-point associations with a colony during each five-day interval of the breeding season; weights were based on the inverse square of the error radius. We did not estimate colony associations when data were not available for an entire five-day interval.

This approach for estimating colony association allowed us to consider location certainty. Low-quality points, with their larger error radii, were more likely to overlap a colony extent, but their more-diffuse probability densities resulted in lower contributions to estimates of colony association. With this approach, PTT locations with higher precision and locations that were closer to a colony contributed more to estimates of colony association. We categorized an individual as having "high colony association" in a five-day interval if the weighted-average colony association was > 0.30. This breakpoint was chosen after we reviewed a histogram of the data and observed a distinct inflection in the association frequency distribution at this value. We report colony associations for each study area, along with the number of tagged Aleutian Terns exhibiting high colony associations during a breeding season and the duration of high colony association. We would also have liked to have known whether movement patterns, including colony association, varied between terns captured on active nests and those captured away from a nest. Nesting status, however, was potentially confounded with study area and year (i.e., movement patterns could differ by location and year). Consequently, evaluation of the effect of nest status on movement patterns can be made only within location/year combinations to eliminate the effects of other, likely unknown, factors that could affect movement and that vary among locations and years. Because we had small samples within each location/year combination, our ability to investigate the effect of nest status on movement patterns was weak.

The same intervals used to calculate colony associations were also used to calculate five-day core home-range sizes (50% KDEs). We used generalized mixed linear models (GLMM, lognormal errors; Littell et al., 2006) to examine how the five-day core home-range size varied within each study area with respect to the categorical predictor variables year, start of five-day interval (date), and whether the tern had a high colony association (i.e., association > 0.30) for that interval. We included individual tern as a random effect to account for the repeated measures of five-day home ranges within individuals (Littell et al., 2006). We selected the most-supported model of those considered based on the sample-size-adjusted Akaike's Information Criteria (AICc) weights (Burnham & Anderson, 2002). From the GLMM, we estimated marginal means (Littell et al., 2006) for the effects of interest and back-transformed them to produce estimated geometric means and 95% confidence intervals; geometric means were appropriate for these data that exhibited distributions with long right-hand tails.

RESULTS

PTT transmission and performance

All but four of the 27 PTTs deployed transmitted for > 70 days (*n* = 15 in 2017 and *n* = 12 in 2018; Fig. 3). Three of these four PTTs did not transmit sufficient data to be useful, resulting in data from 24 individual Aleutian Terns being used for the movement analyses. Transmission frequency for ALC 1 through 3 (i.e., Argos location precision < 1,500 m) comprised 23% of all transmissions in 2017 and 26% in 2018. In both years, < 6% of all transmissions were in ALC 2 or 3 (Argos location precision < 500 m; Table 1); there generally were no more than two ALC 2 or 3 transmissions in a single day. The maximum number of ALC 1 transmissions received in a single day was four.

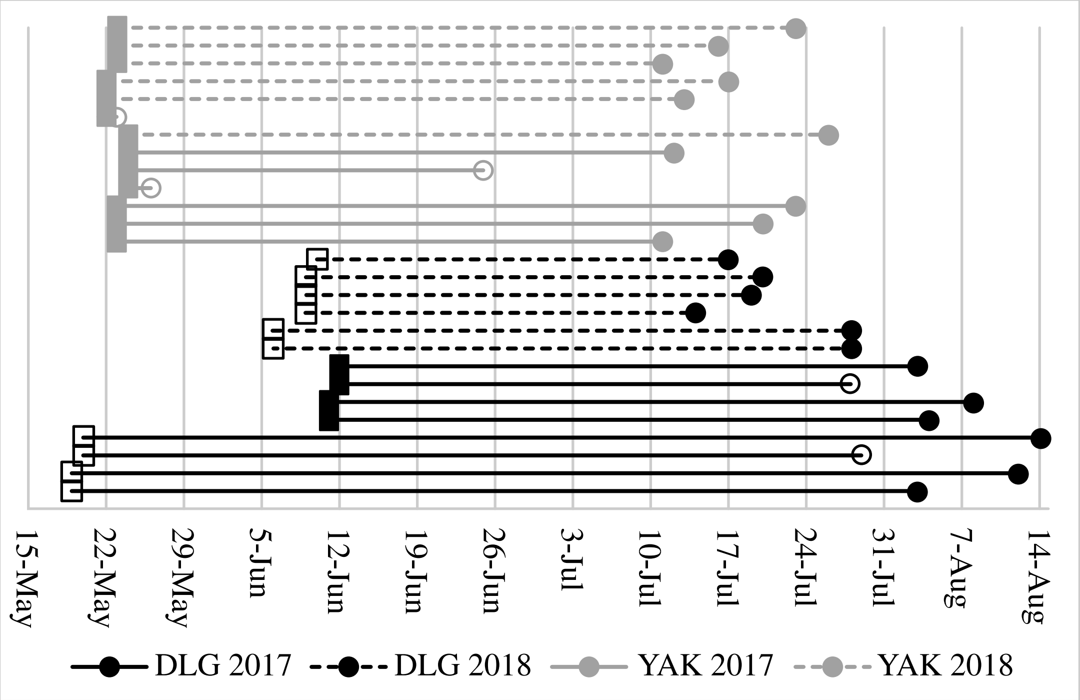

Fig. 3. Aleutian Tern *Onychoprion aleuticus* satellite transmitter (Platform Transmitter Terminals, PTT) deployment dates and extent of breeding-season PTT transmissions in 2017 and 2018 in Dillingham (DLG; black lines and symbols) and Yakutat (YAK; gray lines and symbols), Alaska, USA. Each line represents one PTT deployment, with squares marking deployment dates and circles marking migration date (filled) or loss of signal from the PTT (open). Filled squares signify nesting captures and open squares signify non-nesting captures.

TABLE 1
Argos Location Class transmission summaries for satellite transmitters deployed on Aleutian Terns *Onychoprion aleuticus* in 2017 and 2018 in Dillingham and Yakutat, Alaska, USA

	2017		2018	
Location Class[a]	**Location transmissions**[b]	**Percent location transmission**	**Location transmissions**[c]	**Percent location transmission**
Z	35	0.2	32	0.2
B	6909	31.6	5930	35.7
A	2723	12.5	1998	12.0
0	7197	32.9	4407	26.5
1	3794	17.4	3574	21.5
2	845	3.9	590	3.5
3	361	1.7	100	0.6

[a] Location Class accuracy: 3 < 250 m; 2 < 500 m; 1 < 1,500 m; 0 > 1,500 m; A, B, and Z unspecified accuracy but generally decreasing across A, B, and Z.

[b] 2017: $n = 15$; 1,485 transmission days

[c] 2018: $n = 12$; 1,095 transmission days

Geographic scale of breeding season movements

Dillingham study area

In 2017, breeding season movements were primarily at the local scale (i.e., < 300 km from capture site), with no long movements documented before fall migration commenced (Table 2). The maximum distance for all tagged Aleutian Terns between the deployment site and the farthest point of the 95% KDEs was 214 km. In 2017, core breeding-season home ranges based on 50% KDEs ranged from 146 to 2,615 km^2. In contrast, 2018 core breeding-season home ranges ranged from 1,938 to 7,962 km^2, with corresponding larger maximum movement distances from the deployment site for the 50% and 95% KDEs (Table 2).

Yakutat study area

For both years, all tagged individuals in Yakutat displayed movements on a local scale only (< 300 km from deployment site). Maximum movement distances from the deployment site for tagged Aleutian Terns were estimated at 251 km in 2017 and 190 km in 2018. Core breeding-season home ranges based on 50% KDEs ranged from 1925 to 4509 km^2 for both years combined (Table 2).

Nest status

Based on terns from Dillingham in 2017, terns tagged on active nests had slightly smaller median home ranges and shorter median movement distances than terns tagged away from nests (Table 2). There was broad overlap in individual movement measures between terns with differing capture status, suggesting no evidence of a systematic difference.

BREEDING SEASON DISPERSAL AND IDENTIFICATION OF PREVIOUSLY UNDOCUMENTED COLONIES

Dillingham study area

Over the two breeding seasons, we identified seven previously undocumented Aleutian Tern dispersal areas (Fig. 1). Of these seven, four were confirmed colonies (i.e., reproduction observed) and three were classified as putative colonies (Fig. 1). The distances from the deployment site to the seven dispersal areas ranged from 5.8 to 64.2 km.

TABLE 2
Core breeding-season home range (50% kernel density estimates (KDE)) and scale-of-movement data for Aleutian Terns *Onychoprion aleuticus* (ALTE) with satellite transmitter deployments in Dillingham and Yakutat, Alaska, USA, in 2017 and 2018[a]

Study area	**Year**	**Status**[b]	**ALTE (n)**	**Core home range (km^2)**	**50% KDE maximum distance (km)**	**95% KDE maximum distance (km)**
Dillingham	2017	A	8	503 (146–2,615)	29 (21–86)	96 (41–214)
		N	4	450 (146–567)	26 (21–33)	57 (41–214)
		O	4	693 (437–2,614)	33 (29–86)	108 (86–140)
	2018	O	6	2,528 (1,938–7,962)	86 (84–119)	159 (101–333)
Yakutat	2017	N	5	3,467 (3,148–4,509)	77 (601–96)	179 (104–251)
	2018	N	5	2,577 (1,925–3,466)	55 (42–76)	126 (102–190)

[a] Values are medians and ranges across individuals.

[b] Status at capture: A = all, N = on a nest, O = non-nest location

Yakutat study area

In 2017, we observed that PTT locations overlapped a previously known colony at Lost River Marsh. Furthermore, nesting and hatching were confirmed at this site in 2017, but no fledglings were observed. The Lost River Marsh colony is < 1 km from the PTT deployment site (Black Sand Spit colony) and, given the accuracy of the PTT data, dispersal distances between Lost River Marsh and Black Sand Spit were less than the typical measurement error of the Argos data. To be conservative, we did not include Lost River Marsh as a dispersal area in our results.

In 2017, PTT data from Aleutian Terns tagged at Black Sand Spit indicated movement to two dispersal areas. These included the known Alsek River/Dry Bay colony and a previously undocumented location near the Doame River (Fig. 2). One aerial survey was conducted over these areas on 27 June 2017. A total of 10 terns (species undetermined) were observed from the flight in the Doame River area, but no nesting aggregations were observed. No terns were observed at the Alsek River site. Due to lack of visual confirmation of the presence of a possible breeding colony, we did not include these as dispersal areas in our analyses in 2017. In 2018, nesting was confirmed by observers visiting the Alsek River site on 28 June, but PTT data suggested that tagged Aleutian Terns did not use the Alsek or Doame River areas in that year. Because the Alsek River colony was active, it was included in our 2018 analyses.

Colony associations

For the 24 Aleutian Terns tagged in 2017 and 2018, a total of 254 five-day intervals during the breeding season were analyzed for colony association. Tagged individuals produced sufficient data to determine breeding season colony associations for 6–17 five-day intervals each year (median = 10). The general breeding-season pattern across both years and study areas was that most tagged terns did not display high colony association with confirmed or putative colonies; only 8 of 24 tagged terns and 29 out of all 254 five-day intervals assessed indicated high colony associations. There was some variation in the number of associated terns for each study area and year, with more terns exhibiting high colony associations in Dillingham than in Yakutat and in 2017 than in 2018 (Fig. 4, Table 3).

Dillingham study area

For 2017, data from 101 five-day intervals were analyzed and 21 had high colony associations. In contrast, only 49 five-day intervals were analyzed for 2018 and six of those were designated as having a high colony association. One confirmed colony (South Nushagak) had multiple terns associated simultaneously in 2017, and three of eight terns had high association with > 1 colony, but never with > 1 colony within a single five-day interval. Dillingham colony associations peaked after 13 June (Table 3).

Yakutat study area

Given their proximity to each other (< 1 km), the Black Sand Spit and Lost River Marsh colonies were combined to determine colony associations. Data from 51 five-day intervals were analyzed for 2017 and data from 52 five-day intervals were analyzed for 2018. Only two out of 103 five-day intervals analyzed over the two years indicated high colony associations (2%, Table 3). All tagged Aleutian Terns in this area were nesting captures and 80% were never found to have high colony association, while 20% had high colony association with Black Sand Spit/Lost River Marsh. All five-day intervals indicated that high colony association occurred before 18 June.

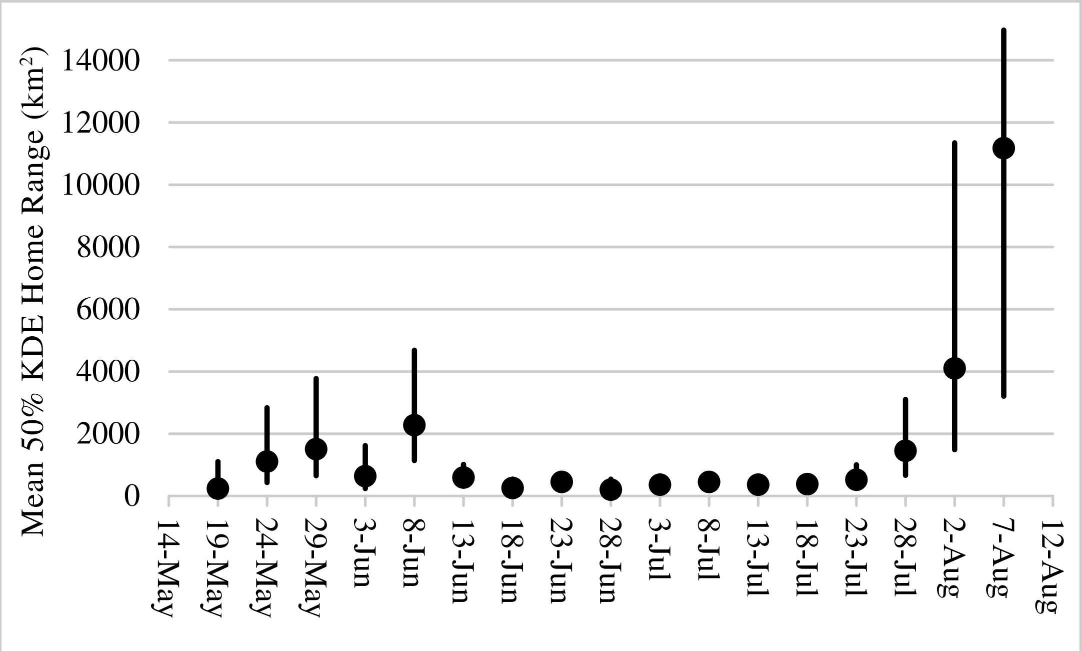

Fig. 4. Model-predicted geometric mean (with 95% confidence intervals) of 50% kernel density estimates (KDE) core home ranges (km^2) by five-day interval for satellite-tagged Aleutian Terns *Onychoprion aleuticus* during 2017 and 2018 in the Dillingham, Alaska, USA, study area. Means are adjusted for association weighted means and year.

TABLE 3

Five-day colony association weighted means from location data received by satellite transmitters (Platform Transmitter Terminals, PTTs) deployed on Aleutian Terns *Onychoprion aleuticus* at Dillingham and Yakutat, Alaska, USA, in 2017 and 2018[a]

				Association weighted mean by five-day intervals																
Study area	**Year**	**PTT ID**	**19-May**	**24-May**	**29-May**	**03-Jun**	**08-Jun**	**13-Jun**	**18-Jun**	**23-Jun**	**28-Jun**	**03-Jul**	**08-Jul**	**13-Jul**	**18-Jul**	**23-Jul**	**28-Jul**	**02-Aug**	**07-Aug**
Dillingham	2017	790	0.00	0.00	0.00	0.03	**0.37C**[d]	**0.46C**[d]	**0.42C**[d]	**0.58C**[d]	**0.56C**[d]	0.16	0.05	**0.57D**[d]	0.00	0.00	0.00	.	.
		791	0.01	0.00	0.00	0.00	0.00	0.01	0.26	0.00	0.02	0.00	0.04	0.01	0.10	0.00	0.01	0.00	0.00
		792	.	0.00	0.00	0.00	0.00	0.00	0.13	0.14	0.24	0.09	0.02	0.28	0.01	0.00	.	.	.
		793	.	0.00	0.00	0.19	**0.66A**[c]	**0.66D**[d]	**0.89D**[d]	**0.92D**[d]	**0.74D**[d]	0.21	0.04	0.01	0.26	0.05	0.00	0.04	0.06
		794[b]	.	.	.	.	.	0.19	0.23	0.15	0.00	0.00	0.01	0.02	0.16	0.01	0.00	.	.
		795[b]	.	.	.	.	.	0.13	**0.46B**	**0.63B**	**0.75B**	**0.65B**	0.00	0.08	0.15	0.29	0.00	0.00	.
		796[b]	.	.	.	.	.	0.01	**0.52D**[d]	0.25	0.14	0.23	**0.38C**[d]	0.03	0.17	0.13	0.04	.	.
		797[b]	.	.	.	.	.	0.00	**0.52D**[d]	**0.67D**[d]	0.15	**0.67D**[d]	0.09	**0.37D**[d]	0.01	0.00	.	.	.
	2018	690	.	.	.	.	0.00	0.01	0.00	0.00	0.04	0.15	0.00	0.00	0.01	0.00	.	.	.
		691	.	.	.	.	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.	.	.
		692	.	.	.	.	.	0.10	0.04	0.07	0.17	0.05	0.01	0.00	.	.	.	.	.
		693	.	.	.	.	.	**0.67F**	**0.50F**	**0.55F**	0.03	**0.35G**	**0.52G**	**0.68G**	0.00	0.00	.	.	.
		694	.	.	.	.	.	0.06	0.00	0.00	0.00	0.05	0.00	0.00	.	.	.	.	.
		695	.	.	.	.	.	0.00	0.00	0.00	0.15	0.00	0.22	.	.	.	.	.	.
Yakutat	2017	798[b]	.	0.00	0.00	0.03	0.27	**0.41E**[c]	0.07	0.00	0.00	0.00	.	.	.	.	.	.	.
		799[b]	.	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.	.	.	.	.
		800[b]	.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.	.	.	.	.
		802[b]	.	0.00	**0.42E**[c]	0.29	0.00	0.00	0.00	0.00	0.00	.	.	.	.	.	.	.	.
		804[b]	.	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.	.	.	.
	2018	752[b]	.	0.00	0.02	0.01	0.00	0.00	0.03	0.00	0.00	0.00	.	.	.	.	.	.	.
		754[b]	.	0.00	0.00	0.00	0.10	0.04	0.00	0.00	0.00	0.00	0.00	0.11	.	.	.	.	.
		755[b]	.	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	.	.	.	.	.	.
		756[b]	.	0.24	0.09	0.01	0.00	0.00	0.09	0.00	0.00	0.00	0.00	.	.	.	.	.	.
		757[b]	.	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.04	0.01	0.01	.	.	.	.

[a] Bold values represent high colony association (five-day colony association > 0.30). Letters denote the associated colony (A = Lily Pond, B = Picnic Point, C = Clark's Point [successful fledging], D = South Nushagak, E = Black Sand Spit/Lost River Marsh, F = Tommy's Bay, G = Etolin Point). A dot (.) represents intervals with insufficient data for estimation.

[b] Nesting capture

[c] Telemetry deployment site

[d] Colony with successful fledging

Nest status

Based on our limited data from Dillingham in 2017 ($n = 8$, four for each nest status; Fig. 3), terns tagged on nests had similar colony-association patterns as terns tagged elsewhere (Table 3). Three of four terns tagged at nests had associations with a colony, while two of four terns tagged away from nests had colony associations. Terns tagged in either situation that had a colony association were associated with one or two colonies.

Colony associations and five-day core home-range analyses

Dillingham study area

The most-supported model relating five-day core home-range sizes (50% KDEs) to colony association, year, and date was an additive model with all three main effects (AICc weight = 0.48, Table 4). Geometric-mean core home ranges of terns not associated with colonies were 2.25 times larger than those of terns that were highly associated with a colony (Table 5). Geometric-mean core home ranges were also much larger (4.87 times) in 2018 than in 2017, possibly a function of stronger associations in 2017, although the model including association × year had lower AICc weight and was less supported (Table 4). Geometric-mean core home-range sizes were largest early and, especially, late in the season with small core home ranges when strong associations were most common (Fig. 4).

Yakutat study area

There was no support for relationships between core home-range sizes at five-day intervals and any of the predictors (Table 4). The geometric-mean core home-range area was 1,782 km^2 (Table 5).

DISCUSSION

We recognize that this study was based on a small sample of Aleutian Terns during only two breeding seasons and, thus, our results should be interpreted cautiously. In addition, we had no way of knowing the post-tagging nesting status of tagged terns, which potentially could affect movement patterns. Also of concern is the invasive nature of satellite transmitter deployments that could have affected results (e.g., Massey et al., 1988). We cannot separate any deployment effects from naturally low proportions of birds associated with colonies, apparently low breeding propensities in the Dillingham study area, or terns switching between colonies during a single breeding season. Note, however, that low nesting success was reported widely for marine birds in Alaska during our study period (Arimitsu et al., 2021; Romano et al., 2020).

Our efforts to capture and outfit Aleutians Terns with PTT tags provided us with new insights about Aleutian Tern movements during the breeding season. This new information included documentation of previously unknown colonies, documentation of within-season dispersal to multiple colonies, and indications that some individuals may not associate with any colony for significant portions of the breeding season. Additionally, differences in breeding season phenology were observed between the two study areas in western and southeastern Alaska.

TABLE 4
Model selection results (Akaike's Information Criteria weights, adjusted for sample size) for predicting Aleutian Tern *Onychoprion aleuticus* five-day core home-range area (50% kernel density estimates, km^2) from satellite transmitter deployments in Dillingham and Yakutat, Alaska, USA, during 2017 and 2018[a]

	AICc weights by study area	
Model	**Dillingham**	**Yakutat**
Null	0	**0.54**
HCA	0	0.19
Year	0	0.19
Date[b]	0	0.01
HCA, Year	0	0.07
HCA, Date	0	0
Year, Date	0	0
HCA, Year, Date	**0.48**	0
HCA, Year × Date	0	0
HCA × Date, Year	0.18	0
HCA × Year, Date	0.34	0

[a] Bold values indicate the most-supported model. Predictor variables included in the models were *High Colony Association* (HCA; colony association > 0.30), *Year*, *Date*, and interactions (×) between variables.

[b] Date was included as day-of-the-year for the start of a five-day interval

Scale of movements

In our study, a majority of the home ranges suggested only local-scale movements of tagged Aleutian Terns, with a few birds showing larger-scale movements of up to 332.5 km from the deployment colony during the breeding season. The general scale of observed movement was comparable to those of breeding (i.e., non-migrating) Sooty Terns *Onychoprion fuscatus*, an ecologically distinct tropical congener of the Aleutian Tern (Huang et al., 2017; Soanes et al., 2015; Fig. 1).

Colony association

Actively nesting terns are central-place foragers (North, 2013). We would expect that terns have a relatively high association with the nesting colony while they have an active nest or chicks, with a home range that is as small as possible, conditional on food availability. Higher colony association, shorter movements, and smaller foraging ranges should be especially pronounced during the middle part of the breeding season. Terns without an active nest or dependent chicks would have fewer constraints on movement without the need to return to a single location. Estimates from our data met some of the predictions for central-place foragers, but not others. We more often observed higher colony association and smaller home ranges during the middle part of the breeding season, relative to early or late in the season, in the Dillingham study area during 2017 (Fig. 4; Tables 2, 3). However, we found strong evidence that these patterns were not universal (Tables 4, 5). Almost no terns in Dillingham in 2018 or in Yakutat in either year had a high association with any colony, and correspondingly, they had much larger movement ranges. Presumably, home-range size and travel distances are associated with food availability, as has been

TABLE 5
Predicted geometric mean of five-day core home ranges (50% kernel density estimates, km^2) and 95% confidence intervals (CI). Values are given in association with each level of the variables *High Colony Association* (HCA; colony association > 0.30) and *Year* for Aleutian Terns *Onychoprion aleuticus* tracked using satellite transmitters in Dillingham and Yakutat, Alaska, USA, during 2017 and 2018[a]

		Dillingham		Yakutat
Predictor	**Level**	**Geometric mean (95% CI, km^2)**	**Relative size (95% CI)**	**Geometric mean (95% CI, km^2)**
Null		—	—	1,782 (1,483–2,141)
HCA	no	1,432 (1,159–1,769)	2.25 (1.17–3.86)	—
	yes	441 (289–671)	—	—
Year	2017	328 (257–417)	—	—
	2018	1,924 (1,332–2,781)	4.87 (3.23–7.16)	—

[a] Predicted geometric-mean estimates of core home range by date for the Dillingham study area are shown in Fig. 4.

reported for Sooty Terns (Neumann et al., 2018), as well as colony size (function of intraspecific competition; Furness & Birkhead, 1984). Terns not associated with a colony and without a nest, would be free to move more widely in search of food; low food abundance could necessitate abandoning a colony to improve chances for survival at the expense of reproduction (Neumann et al., 2018).

Food web anomalies

Although we do not know the nesting status of our marked terns after tagging, the low association values (Dillingham in 2018, Yakutat in both years), large home ranges (Dillingham in 2018, Yakutat in both years), and early colony abandonment (Yakutat in both years) suggests our tagged terns in these areas no longer had active nests or chicks. This pattern (i.e., low association values, large home ranges, early colony abandonment) could have been caused by low food availability resulting from factors that brought anomalously warm ocean temperatures in both study areas. Aleutian Tern life-history traits (e.g., short breeding season, effects during the breeding season, relatively short foraging range) would not make them immune to ocean anomalies that are known to affect seabirds that have more conservative strategies (Woehler & Hobday, 2024). The Bering Sea, of which Bristol Bay is a part and which is adjacent to the Dillingham study area, was anomalously warm during 2017–2019; the factors bringing these warm conditions likely changed forage fish abundance and composition, which in turn resulted in widespread seabird mortality and expanded foraging ranges (Duffy-Anderson et al., 2019; Jones et al., 2019, 2024; Osborne et al., 2020; Romano et al., 2020; Will et al., 2020; Yasumiishi et al., 2020). We do not know why we saw stronger effects (e.g., weaker associations, larger home ranges) on Aleutian Terns in 2018 compared to 2017.

A particularly strong oceanographic anomaly in the form of a marine heat wave existed in the Gulf of Alaska, including the area adjacent to the Yakutat study area, during 2014–2016, and this apparently continued during 2018–2019. This heat wave and continuing warm conditions also caused widespread seabird die-offs and low nest success, and it affected other species groups as well (Arimitsu et al., 2021; Hastings et al., 2023; Oehlers, 2017, 2018; Piatt et al., 2020; Suryan et al., 2021). In addition, nest loss due to predation was common at the main Aleutian Tern colony in the Yakutat study area during the study and might have been a contributing factor to early colony abandonment in both years (Oehlers, 2017, 2018).

Estimation of population abundance and trends

The data currently available for estimating Aleutian Tern population sizes in Alaska are counts of terns from a convenience sample (i.e., not a probability-selected sample) of tern colonies (Renner et al., 2015). The number of count surveys per colony has varied widely both within and among years, as have the survey protocols and seasonal timing (see Renner et al., 2015). To obtain an unbiased abundance estimate of the tern population size (e.g., the sum of the counts from the surveyed colonies) from these data requires the assumption that all tern colonies are known and surveyed. Unbiased estimates of population trend would require the assumption that the surveyed colonies are representative of all colonies, whether known or unknown. Other key assumptions for unbiased abundance estimates are that all terns were available when the surveys occurred (i.e., the probability that an adult tern was at the colony during a survey was equal to 1), that detection of the terns was perfect (i.e., the probability that a tern present at a colony when the survey occurred was counted was equal to 1), and, for trend estimates, that availability and detection probabilities were constant if they were < 1. These assumptions can be relaxed by using a probability-based sample of colonies (i.e., not all colonies would need to be known in advance; McDonald et al., 2022a, 2022b) and by estimating availability probability, potentially from tagged birds (Nichols et al., 2009). In the Dillingham study area, we found seven previously undocumented colonies with four of these confirmed to have successfully fledged young. These previously undocumented colonies represent a substantial increase in the number of known and potential Aleutian Tern colony locations in the Dillingham area. We also observed that most of the tagged terns were not associated with colonies during the breeding season (i.e., were rarely or never present at a colony) and that terns with the lowest association scores had much larger home ranges. These patterns likely will greatly reduce the probability that all terns would be available to be counted during colony surveys. Also, variability in the length of time that individuals were associated with colonies would complicate efforts to estimate availability. If not accounted for in estimation procedures, the unknown colonies and low availability will result in negatively biased estimates of tern abundance if abundance is based solely on counts at previously known colonies. Trend estimation, which often requires weaker assumptions than abundance estimation, can still be affected when availability for counting during surveys is < 1 (Barker & Sauer, 1992).

With terns moving among colonies, individual colonies contain different proportions of the population among years, which could be one source of variation in availability when not all colonies are surveyed annually. Multiple distinct colonies were documented within 0.4–64.2 km from deployment sites; inter-colony distance was > 5 km for all but one pair of colonies (Black Sand Spit and Lost River Marsh). These findings suggest that surveys may need to be conducted at larger geographic scales (e.g., aerial surveys), rather than at the individual colony level, to correctly estimate Aleutian Tern abundance (e.g., McDonald et al., 2022a, 2022b). However, region-level analyses would still need to consider that some terns were not associated with any colony and others were associated with more than one colony within a single breeding season, potentially resulting in some terns never being counted and others being double counted. However, the effects of movements on estimates would depend on the timing of individual colony surveys and indicate a need for surveys among colonies to be as synchronous as possible. However, the possibility of colonies developing late in the nesting season should be considered.

Tag performance

The small solar-powered PTTs performed consistently during the two years of deployment, in terms of both the duration of operation and the number of high-quality transmissions (i.e., ALC 2 and 3). Given the typical precision error associated with these highly miniaturized Doppler-effect tags and the irregular timing of received locations (i.e., low number of high-quality transmissions and lack of a fixed PTT duty cycle), these data were not sufficient to describe fine-scale movements (e.g., < 5–10 km movements within hours or shorter time periods); however, they were sufficient to assess the general scale of movements, the birds' dispersal to confirmed or putative colonies within the breeding season, and the intensities of colony association; our data are the most precise movement data available for the species and one of the few PTT-based studies on an *Onychoprion* species (e.g., Huang et al., 2017). One potential drawback of our study was that our deployment of PTT tags was possible only after terns arrived within the breeding range in the spring. This made it impossible to assess effects of captures, of PTT-tagging, and of how these experiences may have altered breeding and potential associations with a colony or colonies.

CONCLUSION

In summary, the most appropriate geographical scale for estimating Aleutian Tern abundance and trends may be at a local or regional scale (e.g., 10s or 100s of kilometers of coastline) instead of the single-colony scale (e.g., McDonald et al., 2022a, 2022b). Furthermore, the potential for Aleutian Terns to disperse to and associate with more than one colony in a season suggests that within-season abundance estimates need to incorporate within-breeding-season movements. Equally important, if a substantial number of birds do not associate with any colony, they are likely unavailable to be counted. This unknown level of availability could be a source of bias and uncertainty in current abundance and trend estimates. If not accounted for, low and variable availability, especially from low or variable breeding propensity, will weaken our understanding of the relationships between colony-based counts and estimates of the nesting population or total population of adult Aleutian Terns.

Further research would be helpful to confirm or expand on our results. We found previously undocumented colonies in the Dillingham study area, but not in Yakutat. Renner et al. (2015) suggest that movement of terns to undocumented colonies is unlikely to be sufficient to account for historical declines at known colonies, but additional studies such as ours are needed to assess the likelihood of undocumented colonies in other areas of Alaska. We also found low levels of association with colonies, even for Aleutian Terns tagged after they had initiated nesting (although we do not know their post-tagging nesting status), and potentially low breeding propensity in the Dillingham study area. Additional study of tagged Aleutian Terns will also help determine if our low association/availability estimates are anomalous. Both intermittent breeding (i.e., breeding propensity < 1) and predator avoidance via colony abandonment are well-documented behaviors for long-lived seabirds (Bibby et al., 2000), but the causes and frequency of these behaviors in Aleutian Terns are unknown. We suggest more directed study on these two aspects of Aleutian Tern breeding ecology, including estimates of breeding propensity and how much it varies among years, along with what factors cause the annual variation. Such studies likely will involve intensive observational studies of individually identifiable terns, through either external marking or genetics (e.g., Hillary et al., 2018). Again, such studies will need to be carefully designed to separate tagging or observation effects from the phenomenon of interest.

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AUTHOR CONTRIBUTIONS

KN: project conception and administration, animal capture, field data collection, data curation, manuscript writing. GWP: field data collection, data analysis, manuscript writing. JPS: field data collection, data analysis, manuscript writing. SO: animal capture, field data collection, manuscript review and editing. JM: animal capture, data curation. DEL: project conception, animal capture.

REFERENCES

Alaska Center for Conservation Science (2020, May 25). *Wildlife data portal*. https://biotics.aknhp.axds.co/

Anderson, D. J. (1982). The home range: A new nonparametric estimation technique. *Ecology, 63*(1), 103–112. https://doi.org/10.2307/1937036

Andres, B. A., & Browne, B. T. (2004). *The birds of Yakutat, Alaska.* General Technical Report R10-TP-131. U.S. Forest Service, Alaska Region.

Arimitsu, M. L., Piat, J. F., Hatch, S., Suryan, R. M., Batten S., Bishop, M. A., Campbell, R. W., Coletti H., Cushing, D., Gorman, K., Hopcroft, R. R., Kuletz, K. J., Marsteller, C., McKinstry, C., McGowan, D., Moran, J., Pegau, S., Schaefer, A., Schoen, S., … Von Biela, V. R. (2021). Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. *Global Change Biology, 27*(9), 1859–1878. https://doi.org/10.1111/gcb.15556

Barker, R. J., & Sauer, J. R. (1992). Modelling population change from time series data. In D. R. Mccullough & R. H. Barrett (Eds.), *Wildlife 2001: Populations* (pp. 182–194). Elsevier Applied Science. https://doi.org/10.1007/978-94-011-2868-1_17

Bibby, C. J., Burgess, N. D., Hill, D. A., & Mustoe, S. H. (2000). *Bird Census Techniques* (2nd ed.). Academic Press.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and inference: A practical information-theoretic approach* (2nd ed.). Springer New York. https://doi.org/10.1007/b97636

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*(3–4), 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Collecte Localisation Satellite. (2016). *Argos user's manual*. https://www.argos-system.org/wp-content/uploads/2023/01/CLS-Argos-System-User-Manual.pdf

Corcoran, R. M. (2012). *Aleutian Tern counts from seabird colony and nearshore marine bird surveys in the Kodiak Archipelago, Alaska 1975–2012* [Unpublished report 01-12]. U.S. Department of the Interior, Fish and Wildlife Service, Kodiak National Wildlife Refuge.

Duffy-Anderson, J. T., Stabeno, P., Andrews, A. G., III, Cieciel, K., Deary, A., Farley, E., Fugate, C., Harpold, C., Heintz, R., Kimmel, D., Kuletz, K., Lamb, J., Paquin, M., Porter, S., Rogers, L., Spear, A., Yasumiishi, E. (2019). Responses of the northern Bering Sea and southeastern Bering Sea pelagic ecosystems following record-breaking low winter sea ice. *Geophysical Research 46*(16), 9833–9842. https://doi.org/10.1029/2019GL083396

Fair, J., Paul, E., & Jones, J. (Eds.). (2010). *Guidelines to the use of wild birds in research* (3rd ed.). Ornithological Council.

Furness, R. W., & Birkhead, T. R. (1984). Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature, 311*, 655–656. https://doi.org/10.1038/311655a0

Goldstein, M. I., Duffy, D. C., Oehlers, S., Catterson, N., Frederick, J., & Pyare, S. (2019). Interseasonal movements and non-breeding locations of Aleutian Terns *Onychoprion aleuticus*. *Marine Ornithology, 47*(1), 67–76. http://doi.org/10.5038/2074-1235.47.1.1294

Hamer, K. C., Schreiber, E. A., & Burger, J. (2001). Breeding biology, life histories, and life history-environment interactions in seabirds. In E. A. Schreiber & J. Burger (Eds.), *Biology of Marine Birds* (pp. 217–261). CRC Press.

Harrison, P., Perrow, M., & Larsson, H. (2021). *Seabirds: The new identification guide*. Lynx Edicions.

Hastings, K. K., Gelatt, T. S., Maniscalco, J. M., Jemison, L. A., Towell, R., Pendleton, G. W., & Johnson, D. S. (2023). Reduced survival of Steller sea lions in the Gulf of Alaska following marine heatwave. *Frontiers of Marine Science, 10*, Article 1127013. https://doi.org/10.3389/fmars.2023.1127013

Heath, S. R., Dunn, E. H., & Agro, D. J. (2009). Black Tern (*Chlidonias niger*), version 2.0. In A. F. Poole (Ed.), *The Birds of North America*. Cornell Lab of Ornithology. https://doi.org/10.2173/bna.147

Hillary, R. G, Bravington, M. V., Patterson, T. A., Grewe, P., Bradford, R., Feutry, P., Gunasekera, R., Peddemors, V., Werry, J., Francis, M. P., Duffy, C. A. J., & Bruce B. D. (2018). Genetic relatedness reveals total population size of white sharks in eastern Australia and New Zealand. *Scientific Reports, 8,* Article 2661. https://doi.org/10.1038/s41598-018-20593-w

Huang, R. M., Bass, O. L., Jr., & Pimm, S. L. 2017. Sooty tern (*Onychoprion fuscatus*) survival, oil spills, shrimp fisheries, and hurricanes. *PeerJ, 5*, Article e3287. https://doi.org/10.7717/peerj.3287

Jones, T., Divine, L. M., Renner, H., Knowles, S., Lefebvre, K. A., Burgess, H. K., Wright, C., & Parrish, J. K. (2019). Unusual mortality of Tufted Puffins (*Fratercula cirrhata*) in the eastern Bering Sea. *PLoS ONE, 14*(5), Article e0216532. https://doi.org/10.1371/journal.pone.0216532

Jones, T., Parrish, J. K., Lindsey, J., Wright, C., Burgess, H. K., Dolliver, J., Divine, L., Kaler, R., Bradley, D., Sorenson, G., Torrenta, R., Backensto, S., Coletti, H. A., Harvey, J. T., Nevins, H. M., Donnelly-Greenan, E., Sherer, D. L., Roletto, J., & Lindquist, K. (2024). Marine bird mass mortality events as an indicator of the impacts of ocean warming. *Marine Ecology Progress Series, 737*: 161–181. https://doi.org/10.3354/meps14330

Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. D., & Schabenberger, O. (2006). *SAS for mixed models* (2nd ed.). SAS Institute Inc.

Massey, B. W., Keane, K., & Boardman, C. (1988). Adverse effects of radio transmitters on the behavior of nesting Least Terns. *The Condor, 90*(4), 945–947. https://doi.org/10.2307/1368856

McDonald, T., Kaler, R., Oehlers, S., Goldstein, M. I., Boldenow, M., Renner, H., Corcoran, R., Larsen Tempel, J., Lyons, D., Cooper, E., Renner, M., Szczys, P., Catterson, N., Zeller, T., & Pepin., D. (2022a). *Aleutian Tern surveys in northeast Bristol Bay, 2021 field season.* McDonald Data Sciences report to the Aleutian Tern Technical Committee, U.S. Fish & Wildlife Service.

McDonald, T., Kaler, R., Oehlers, S., Goldstein, M. I., Boldenow, M., Renner, H., Corcoran, R., Larsen Tempel, J., Lyons, D., Renner, M., Szczys, P., Catterson, N., Williams, A., Curl, J., Welfelt, J., & Pepin, D. (2022b). *Aleutian Tern surveys in northeast Bristol Bay, 2022 field season*. McDonald Data Sciences report to the Aleutian Tern Technical Committee, U.S. Fish & Wildlife Service.

Naves, L.C. (2018). Geographic and seasonal patterns of seabird subsistence harvest in Alaska. *Polar Biology, 41*(6), 1217–1236. https://doi.org/10.1007/s00300-018-2279-4

Naves, L. C., Mengak, L. F., & Keating, J. M. (2021). *Alaska subsistence harvest of birds and eggs, 2019–2020, Alaska Migratory Bird Co-Management Council.* Technical Paper No. 479, Alaska Department of Fish and Game Division of Subsistence. https://www.adfg.alaska.gov/static/home/subsistence/pdfs/Naves_et_al_2021_AMBCC_harvest_report_2019-2020_TP479.pdf

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*(1), 11–18. http://doi.org/10.5038/2074-1235.46.1.1242

Nichols, J. D., Thomas, L., & Conn, P. B. (2009). Inferences about landbird abundance from count data: Recent advances and future directions. In D. L. Thompson, E. G. Cooch, & M. J. Conroy (Eds.), *Environmental and Ecological Statistics: Vol. 3. Modeling demographic processes in marked populations* (pp. 201–235). Springer. https://doi.org/10.1007/978-0-387-78151-8_9

North, M. R. (2013). Aleutian Tern (*Onychoprion aleuticus*), version 2.0. In A. F. Poole (Ed.), *The Birds of North America*. Cornell Lab of Ornithology. https://doi.org/10.2173/bna.291

Oehlers, S. O. (2017). *Summary of Yakutat Area 2017 Aleutian Tern monitoring* [Unpublished report]. U.S. Department of Agriculture, Forest Service.

Oehlers, S. O. (2018). *Summary of Yakutat Area 2018 Aleutian Tern monitoring* [Unpublished report]. U.S. Department of Agriculture, Forest Service.

Osborne, O. E., O'Hara, P. D., Whelan, S., Zandbergen, P., Hatch, S. A., & Elliott, K. H. (2020). Breeding seabirds increase foraging range in response to an extreme marine heatwave. *Marine Ecology Progress Series, 646*, 161–173. https://doi.org/10.3354/meps13392

Piatt, J. F., Parrish, J. K., Renner, H. M., Schoen, S. K., Jones, T. T., Arimitsu, M. L., Kuletz, K. J., Bodenstein, B., García-Reyes, M., Duerr, R. S., Corcoran, R. M., Kaler, R. S. A., McChesney, G. J., Golightly, R. T., Coletti, H. A., Suryan, R. M., Burgess, H. K., Lindsey, J., Lindquist, K., … Sydeman, W. J. (2020). Extreme mortality and reproductive failure of Common Murres resulting from the northeast Pacific marine heatwave of 2014–2016. *PLoS ONE, 15*(1), Article e0226087. https://doi.org/10.1371/journal.pone.0226087

Pyare, S., Goldstein, M., Duffy, D., Oehlers, S., Catterson, N., & Frederick, J. (2013). *Aleutian Tern (*Onychoprion aleuticus*) research in Alaska: Survey methodology, migration, and statewide coordination* [Unpublished report]. State Wildlife Grant Project T-9-1-3. Alaska Department of Fish and Game.

R Development Core Team. (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Renner, H. M., Romano, M. D., Renner, M., Pyare, S., Goldstein, M. I., & Arthukin, Y. (2015). Assessing the breeding distribution and population trends of the Aleutian Tern *Onychoprion aleuticus*. *Marine Ornithology, 43*(2), 179–187. http://doi.org/10.5038/2074-1235.43.2.1129

Romano, M. D., Renner, H. M., Kuletz, K. J., Parrish, J. K., Jones, T., Burgess, H. K., Cushing, D. A., & Causey, D. (2020). Die–offs, reproductive failure, and changing at–sea abundance of murres in the Bering and Chukchi Seas in 2018. *Deep Sea Research Part II, 181–182*, Article 104877. https://doi.org/10.1016/j.dsr2.2020.104877

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*(2), 235–239. http://doi.org/10.5038/2074-1235.43.2.1136

Suryan, R. M., Arimitsu, M. L., Coletti, H. A., Hopcroft, R. R., Lindeberg, M. R., Barbeaux, S. J., Batten, S. D., Burt, W. J., Bishop, M. A., Bodkin, J. L., Brenner, R., Campbell, R. W., Cushing, D. A., Danielson, S. L., Dorn, M. W., Drummond, B., Esler, D., Gelatt, T., Hanselman, D. A., … Zador, S. G. (2021). Ecosystem response persists after a prolonged marine heatwave. *Scientific Reports, 11*, Article 6235. https://doi.org/10.1038/s41598-021-83818-5

Thaxter, C. B., Ross-Smith, V. H., Clark, J. A., (2014). A trial of three harness attachment methods and their suitability for long-term use on Lesser Black-backed Gulls and Great Skuas. *Ringing & Migration, 29*(2), 65–76. https://doi.org/10.1080/03078698.2014.995546

Walker, E. P. (1923). Definite breeding record for the Aleutian Tern in southern Alaska. *The Condor, 25*(4), 113–117. https://doi.org/10.2307/1362550

Will, A., Takahashi, A., Thiebot, J.-B., Martinez, A., Kitaiskaia, E., Britt, L. , Nichol, D., Murphy, J., Dimond, A., Tsukamoto, S., Nishizawa, B., Niizuma, Y., & Kitaysky, A. (2020). The breeding seabird community reveals that recent sea ice loss in the Pacific Arctic does not benefit piscivores and is detrimental to planktivores. *Deep Sea Research Part II*, *181–182*(December), Article 104902. https://doi.org/10.1016/j.dsr2.2020.104902

Woehler, E. J., & Hobday, A. J. (2024). Impacts of marine heatwaves may be mediated by seabird life history strategies. *Marine Ecology Progress Series, 737*, 9–23. https://doi.org/10.3354/meps14333

Worton, B. J. (1995). Using Monte Carlo simulation to evaluate kernel-based home range estimators. *The Journal of Wildlife Management, 59*(4), 794–800. https://doi.org/10.2307/3801959

Yasumiishi, E. M., Cieciel, K., Andrews, A. G., Murphy, J., & Dimond, J. A. (2020). Climate-related changes in the biomass and distribution of small pelagic fishes in the eastern Bering Sea during late summer, 2002–2018. *Deep Sea Research Part II, 181–182*(December), Article 104907. https://doi.org/10.1016/j.dsr2.2020.104907