INTERSEASONAL MOVEMENTS AND NON-BREEDING LOCATIONS OF ALEUTIAN TERNS *ONYCHOPRION ALEUTICUS*

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ABSTRACT

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Few observations have been made of Aleutian Terns *Onychoprion aleuticus* outside of summer breeding colonies. We investigateed the non-breeding distribution of Aleutian Terns by collating published and unpublished records of observations during the migration and wintering periods, and by implementing a geolocator tracking study at the largest known breeding colony in North America (Yakutat, Alaska). We deployed 114 geolocator tags in 2010 and recovered six tags over the course of six years. Using light level data, we conducted spatial analysis of tern migration cycles from 2010 to 2013. Results revealed one of the longest distance terrestrial vertebrate migrations ever recorded, with a one-way migration distance of > 16 000 km between Alaska and the Southeast Asia/Oceania region. We found that core winter ranges occurred in coastal Thailand, the Philippines, three areas within Indonesia, and Papua New Guinea. Five of the six recovered geolocators contained data spanning multiple years and provided evidence of both wintering- and breeding-site fidelity. Our effort to more completely document the extent of the Aleutian Tern winter range is a foundational step toward understanding both the natural history and the ecological stressors that could affect this under-studied, locally-imperiled seabird.

Key words: Aleutian Tern, *Onychoprion aleuticus*, movements, migration, geolocator, Southeast Asia, Indonesia, Alaska

INTRODUCTION

The “brown-backed” terns *Onychoprion* are colonially-nesting seabirds having distributions spanning the tropical regions of the Pacific, Atlantic, and Indian oceans. Among them, the Aleutian Tern *Onychoprion aleuticus* stands out as being the sole congeneric to demonstrate peculiar annual migratory behavior between a subarctic breeding zone and tropical wintering areas in the South Pacific, heretofore inferred solely from a very small number of anecdotal records.

Aleutian Terns are also characterized by their rarity. Renner *et al*. (2015) estimated the current worldwide minimum breeding population at approximately 31 000 birds, with most colonies occurring in the Siberian region of Russia (25 602 birds in 89 colonies) and the remaining 18 % occurring in North America, exclusively within Alaska (5 529 birds in 111 colonies). The Alaskan population had a historical high of 13 000 birds (Sowls *et al*. 1978, Haney *et al*. 1991, USFWS 2006a, 2006b), but it has declined by an estimated 93 % since the 1960’s (Renner *et al*. 2015). Although coastal Alaska has yet to be systematically surveyed in its entirety, the geographic extent of decline includes several sub-regions: the Chukchi Sea and the Yukon-Kuskokwim River delta in the north; the Seward Peninsula, Alaska Peninsula, and the Aleutian Islands to the west; and the Kenai Peninsula, Copper River Delta, and Kodiak Archipelago in the more southern portions of the state (Renner *et al*. 2015). A possible exception to this trend is the largest known extant colony in the Yakutat forelands of southeastern Alaska, which has remained relatively stable since it was first documented in 1916 (Walker 1923).

An apparent decline in Alaskan breeding colonies prompted questions about the migration dynamics and wintering behavior of this species. Flyway and overwintering distributions have thus far been inferred from a small number of specimens collected from Honshu, Japan and the Philippines, as well as from anecdotal observations in coastal Hong Kong, Singapore, and Indonesia. This evidence indicates an East Asian migration route extending into Southeast Asia (Hill & Bishop 1999, North 2013). However, with scarce details, it remains unknown whether these records describe terns from Russian or North American cohorts, or both.

The possibility that Alaska-based Aleutian Terns winter in the East Asia region would be a particularly important scientific finding. Only a very small number of Charadriiformes breeding in Alaska appear to have a connection to East Asia, let alone Southeast Asia or Australasia (Winker *et al*. 2007). A wintering area in Southeast Asia would be of interest in relation to breeding population declines because this area is subject to ecological stresses from unregulated fishing, coastal development, and pollution (e.g., Hull 1996, Zhao *et al*. 2008). Moreover, adjacent avifaunas have been identified as a source of Influenza A, which is of concern to both birds and humans (e.g., Ferguson *et al*. 2005, Winker *et al*. 2007).

Herein, we elucidate Aleutian Tern migration patterns and identify both core winter ranges and the spatial extent of the winter distribution of this species. To this end, we 1) conducted outreach to collate published and unpublished records of flyway and winter locations, 2) affixed geolocator tags to nesting terns captured at colonies in Yakutat, Alaska, and 3) conducted recapture surveys for six years after the initial tagging effort. Given that Arctic Terns *Sterna paradisaea* exhibit strong nest-site fidelity (Egevang *et al*. 2010), we hypothesized that Aleutian terns would exhibit similar behavior. Therefore, we expected to have high success in tag recovery.

METHODS

Study area

We captured Aleutian Terns at breeding sites within the Yakutat Ranger District of the Tongass National Forest (USDA Forest Service). Nesting primarily occurred on sandy sites within a 10-km long, narrow (0.4-km) barrier beach that forms the boundary between the Situk River Estuary and the Gulf of Alaska. Interestingly, birds in this region also nested on a heavily vegetated boggy meadow located 15 km inland from the mouth of the Situk River. Commercial salmon fishing occurs near the mouth of the Situk River, and subsistence egg harvest of the Black Sand Spit colony has been observed. At these sites, Aleutian Terns may nest as a single species or in mixed colonies with Arctic Terns.

Geolocators

We used archival light-logging geolocators (Afanasyev 2004) to obtain two coarse-scale locations per day, from deployment until tag recovery or battery failure. Generally, we assumed the geolocators to have an accuracy between 160 and 185 km (Phillips *et al*. 2004, Fox 2009). Because sunrise and sunset times are estimated from thresholds in light curves, latitude was derived from overall day length, and longitude was derived from the time of local midday with respect to GMT and Julian day. We used two models of geolocators, MK14 (1.5 g; *n* = 104) and MK10 (1.0 g; *n* = 10), from British Antarctic Survey, Cambridge, UK. Because retrieval of movement data required physical recovery of the units, we deployed a relatively large number of tags to maximize the probability of recovery.

Geolocator deployment and recovery

In 2010, we trapped Aleutian Terns (*n* = 114) using standard walk-in traps and bow nets (Model TR190, Northwoods Falconry Ltd., Bend, Oregon). We then marked and recorded Aleutian Tern nest sites where

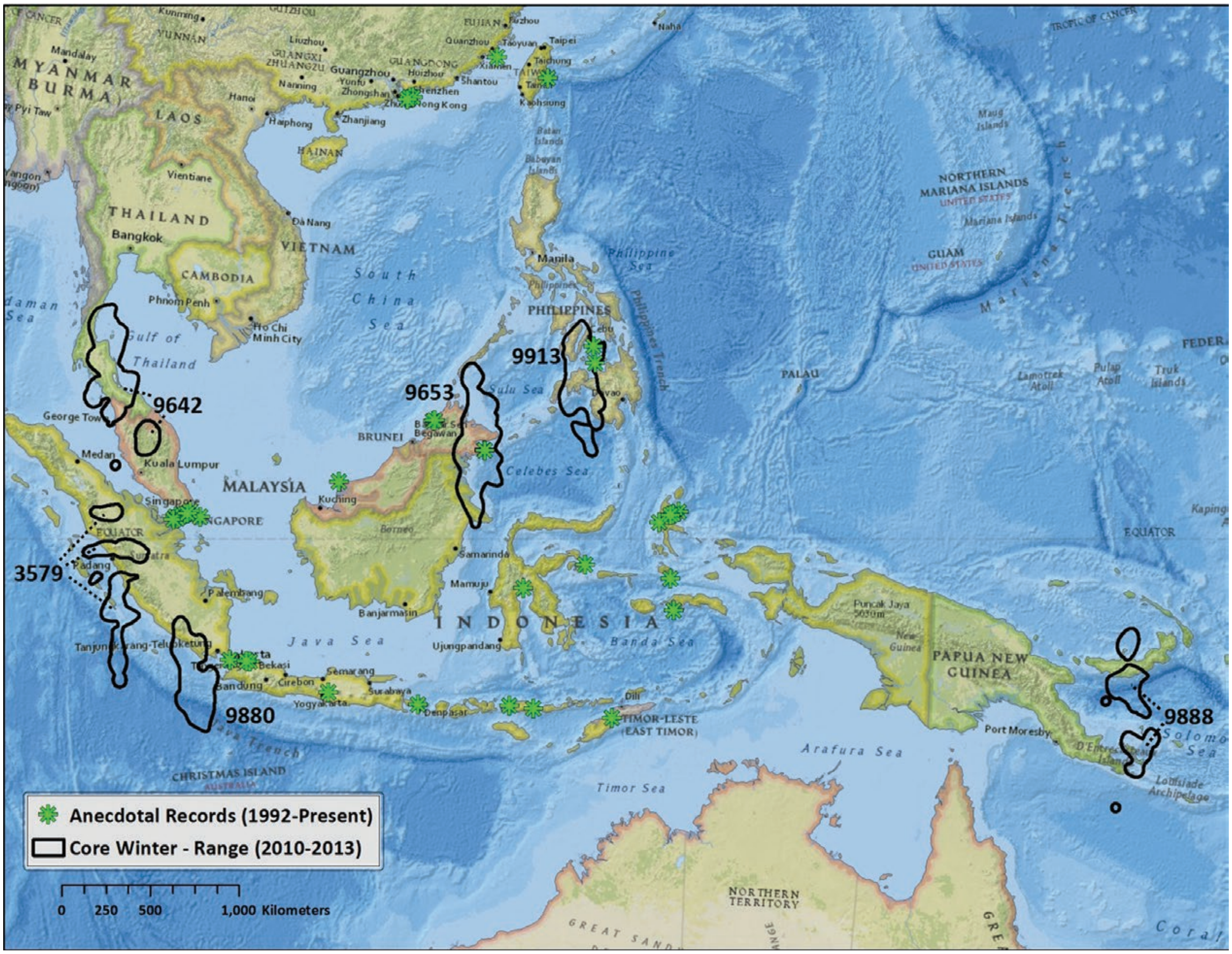

Fig. 1. The locations and boundaries of the core winter range, cumulatively across years (2010–2013) for six Aleutian Terns (individual tag numbers shown), relative to the locations of anecdotal records in Asia and Oceania.

trapping occurred with a ≤ 3 m accuracy differential GPS. We collected weight and morphological measurements (wingspan, wing chord, culmen, and cere). To each bird's right leg, we attached an aluminum numbered US Fish and Wildlife Service band and a yellow Darvic band (metal over yellow). On the left leg, we deployed a geolocator that was zip-tied to a rolled orange Darvic band, which was subsequently glued and heat-sealed after placement on the leg. All animal handling was completed under the University of Hawai'i's approved IACUC protocol #10-981-2, entitled *Aleutian Tern Migration Patterns*, and under banding permit #22833, issued to D. Irons (USFWS).

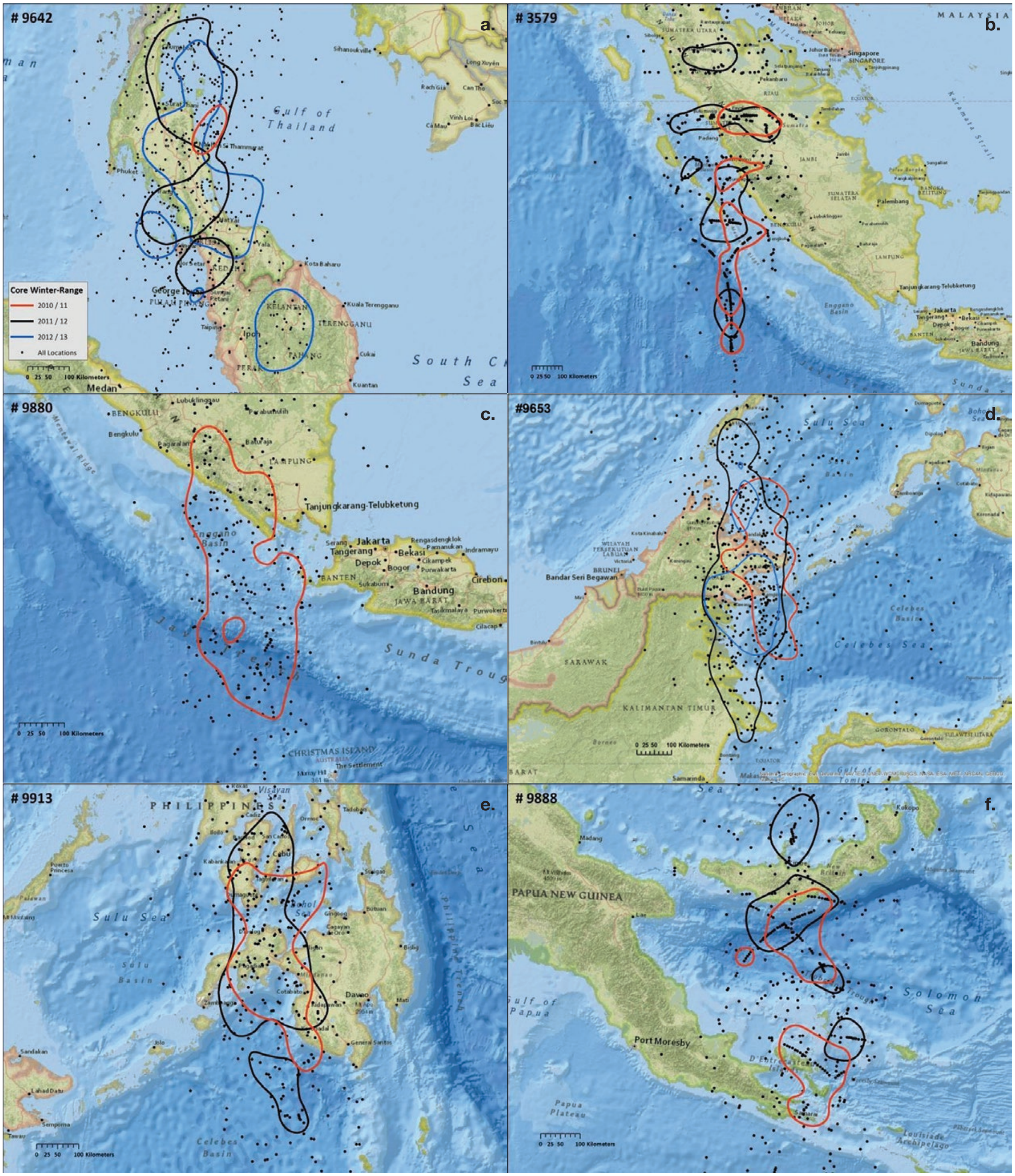

Fig. 2. The detailed locations and boundaries of annual core winter ranges for each of the six Aleutian Terns (individual tag numbers in upper left corner of maps) tracked in this study (2010–2013). The legend in panel A applies to all mapped ranges.

We conducted recapture surveys in Yakutat between 2011 and 2016 to recover the geolocators. We initially focused our re-trapping effort within 0.2 km of the original capture locations by glassing and trapping on nests near original capture sites. We then expanded our trapping effort across a broader area, and attempted to target trapping according to the methods of Duffy *et al*. (2013).

Data processing

We processed the raw geolocator data from recovered tags using Bastrak software v.7 and standard processing algorithms in the associated Geolocator manual v.7 (Fox 2009). The coordinates of each nest site where birds were captured were used as a reference to calculate local sun angles. For this calculation, date and time were gleaned from the first few readable light transitions collected during week one of tag logging (Hill 1994, McKnight *et al*. 2011, Bridge *et al*. 2013). The resultant sun angles for the region were ~ -3. Within the Bastak software (BioTrack, Wareham, UK), we subsequently used corresponding threshold values of 15.5–16.0 based on the calculated sun angles. Light level transitions were carefully inspected, and linear interpolation of the transitions were used to identify the timing of sunrise and sunset. Data filters were applied to remove biases due to short term diurnal shading, vernal and autumnal equinoxes, and noisy sunset/sunrise transitions. More specifically, after visual inspection of the location data, we chose a conservative approach to transition data filtering proximal to the equinoxes: data were deleted within ± 15 days of the equinox in each case. Although it can be informative to use the longitudinal data from each equinox period (Phillips *et al*. 2004), we deemed it acceptable to remove both latitudinal and longitudinal data within the equinox window (Bridge *et al*. 2013) because they were relatively unimportant to the primary aim of elucidating wintering grounds and assessing summer nest-site fidelity. The distances, bearings, and geographic areas of sequential locations were mapped and secondarily filtered to remove data points (< 3 %) that were obviously erroneous (e.g., unrealistic movements of 10 000 km/day). We also removed outliers such as single points in the incorrect hemisphere. Finally, we removed points that were highly suggestive of systematic measurement bias (e.g., when locations vacillated north and 180° directly south, or when locations were erratic near the end of the life cycle of the tracking devices).

Data analysis

We classified locations into preliminary groupings for analysis based on general phenology: breeding (15 May–07 July), post-breeding southbound (07 July–15 November), wintering (15 November–15 February), and return northbound (15 February–15 May). The boundaries of breeding and winter ranges for individual birds were initially delineated in GIS using 10 % kernel density estimates (KDE; 100-km kernel size). We then filtered locations in potential migratory phases to identify the dates when geographical "breaks" from breeding and winter ranges occurred. These dates were then used to derive more precise periods for each annual period and individual bird. We further analyzed and compared the timing of these different phases among years and individuals.

We mapped winter-phase locations and derived a 50 % KDE (100-km kernel size) to represent an annual core winter range for individual birds. We estimated the size of each core winter range and calculated % spatial overlap between returning years to infer the degree of site fidelity for each individual. Within these high-use zones, we estimated daily movement rates and distances of pelagic or inland movements from coasts.

For migration phase data, clusters of locations with low movement rates were treated as evidence that movements were more localized (e.g., foraging) and thus served as proxies for stopover or staging areas. Stopover potential was analyzed solely in the Eastern Hemisphere, and locations were pooled across individuals and migration cycles ($n = 960$ locations across six birds). Moran's I statistic was used as a global test of spatial autocorrelation between the density of locations and movement rates, and the Getis-Ord General G statistic was used as a global test of "low-value" or "coldspot" clustering (e.g., high densities of locations with relatively lower movement rates; ArcGIS, ESRI, Redlands, CA). The more specific Getis-Ord Gi statistic was then used to map these low-movement rate clusters and reveal where there was a high potential for stopover.

Finally, to guide future conservation and monitoring efforts, we evaluated the occurrence of possible migratory bottlenecks (i.e., areas that may be geographically constrained and concentrate movements across many individuals in a population (Crooks & Sanjayan 2006). We mapped movement routes during migration phases for individual birds, combined routes across the six birds, and mapped the kernel density (kernel size of 500 km) of cumulative routes. Similar to the criteria used to identify the core winter range, we then used a minimum 50 % KDE value to initially map geographic areas with possible evidence of migratory bottlenecks. We eliminated any kernels that arose from the movements of single birds to derive the final estimated boundaries of migratory bottlenecks.

TABLE 1
Estimates of the annual core winter range for each individual, and winter-site fidelity from geolocator tracking data of Aleutian Terns, 2010–2013

Bird ID Cycle	Area (km^2)	% Overlap, Prior Year
9642–1	5 991	–
9642–2	89 010	0.95
9642–3	98 704	0.47
3579–1	59 089	–
3579–2	83 060	0.55
9880–1	103 978	–
9913–1	69 921	–
9913–2	98 340	0.75
9888–1	58 823	–
9888–2	54 332	0.32
9653–1	65 054	–
9653–2	135 418	0.78
9653–3	52 227	0.39

TABLE 2
Previously documented winter records of Aleutian Terns

Locality	Region	Reference	Latitude	Longitude
Hong Kong	China	Hill & Bishop 1999	22.262891	114.190294
Hong Kong	China	BMT Asia Pacific 2009	22.287149	114.371255
Hong Kong	China	Kennish 2010	22.161768	114.090584
Hong Kong	China	Kennerly *et al*. 1993	22.297277	114.129248
Incheon	Korea	Moores 2004	37.767485	124.746363
Pamilican Island	Phillipines	Lee 1992	8.972408	124.235858
Bohol Island	Phillipines	Lee 1992	9.819492	124.148137
Taiwan west coast	Taiwan	S. Mulkeen, unpubl. data	24.493227	118.888851
Taiwan east coast	Taiwan	S. Mulkeen, unpubl. data	23.479532	121.722048
Singapore	Singapore	Ollington & Loh 1996	1.280403	103.890954
Singapore	Singapore	Hill & Bishop 1999	1.231203	103.986002
Karimun	Indonesia	Hill & Bishop 1999	1.059358	103.361295
Java	Indonesia	Hill & Bishop 1999	-7.65517	110.698577
Bali	Indonesia	Hill & Bishop 1999	-8.372299	115.190867
Sulawesi	Indonesia	Hill & Bishop 1999	-2.524379	120.585287
Halmahera	Indonesia	Lansley *et al*. 2011	1.360941	128.461198
Timor	Indonesia	Lansley *et al*. 2011	-9.139645	125.109985
Flores	Indonesia	Lansley *et al*. 2011	-8.653674	121.083451
Bintan Island	Indonesia	Lansley *et al*. 2011	1.061286	104.527078
Malucas	Indonesia	Lansley *et al*. 2011	-2.024803	128.031076
Straits of Malacca	Indonesia	Kennerley & Ollington 1998	0.97664	103.440092
Sunda Strait	Indonesia	Poole *et al*. 2011	-5.920518	105.885546
Jakarta Bay	Indonesia	Poole *et al*. 2011	-6.031643	106.841551
Singapore Straits	Singapore	Poole *et al*. 2011	1.179742	103.811939
Riau	Indonesia	Poole *et al*. 2014	0.921935	103.245228
Sabah	Malaysia	Wong 2009	4.520808	118.608851
Pulau Bruit	Malaysia	Kheng & Mizutani 2005	2.835227	111.313224
Ambon Bay	Indonesia	Birdtour Asia 2007	-3.645469	128.216122
Yellow Sea	South Korea	Robson 2014	37.585801	125.507765
Ambon Bay	Indonesia	Bird Tour Asia 2007	-3.636084	128.216028
Changi	Singapore	Singapore Bird Group 2014	1.312243	104.061019
Singapore Straits	Singapore	Singapore Bird Group 2014	1.226557	103.922962
Manukan Island	Malaysia	Barnes 2010	5.9721738	115.9998507
Kota Kinabalu	Malaysia	Kehoe 2009	5.983667	116.074667
Pulau Rambut	Indonesia	Mittermeier 2013	-5.998146	106.6807823
Salakan-Jorjoga Sea	Indonesia	Robson 2011	-1.329226	123.722534
Ternate Channel	Indonesia	Roberson *et al*. 2011	0.829851	127.461886
Ternate Channel	Indonesia	Robson 2013	0.829851	127.461886
Foli village	Indonesia	Swinnen 2008	1.250341	128.162513
Halmahera Sea	Indonesia	Szimuly 2006	1.207377	128.049087
Nusa Tenggara	Indonesia	Tizard 2016	-8.492896	119.836361
Semporna	Indonesia	Wong 2009	4.481667	118.615833

RESULTS

We recovered six of the 114 deployed geolocators during re-trapping efforts (2011 to 2016). Due to battery life, the six geolocators yielded data only from 2010 to 2013. The data for the six birds showed 13 migration cycles across the four-year period. Winter data were as follows: one bird for one winter, three birds for two winters, and two birds for three winters.

The six individual Aleutian Terns exhibited relatively distinct, non-overlapping ranges across a 6000-km span from Southeast Asia to Oceania in the following sub-regions: the Gulf of Thailand and Andaman Sea, southern Sumatra (Indonesia), the Sunda Strait between Sumatra and Java (Indonesia), northeastern Borneo and the Celebes Sea (Indonesia), the central Philippines and Bohol Sea, and the Bismarck Archipelago east of Papua New Guinea (Figs. 1, 2). The core winter range of individual birds in each annual migration cycle ranged from 5 991 km^2 to 135 418 km^2 and averaged 74 919 ± 31 892 km^2 (mean ± sd throughout results; Table 1). Among the five individuals for which we had data for consecutive winters, each bird returned to its respective wintering area, with a 60.1 % ± 22.9 % overlap in individual core winter ranges among years (Fig. 2a–f, except c).

Among all locations (n = 1 494) occurring strictly within core ranges, 66.5 % (n = 994) were marine-based locations occurring 61.8 ± 49.0 km from shore. The remaining locations occurred 35.7 ± 23.8 km inland, but only 9.8 % (n = 48) were far enough inland to exceed the geolocator error estimate of 100 km. Within core ranges, birds moved approximately 204.7 ± 166.5 km/d, or about 8.5 km/h.

Aleutian Terns arrived on their respective wintering range by about 25 September (range 28 August–22 October) and on their core wintering ranges by 2 October (n = 10 of 13 migration cycles). Birds stayed in wintering areas for 193 ± 50 d and departed by 16 March (range 18 February–23 April). Across years, at the individual level, four of five birds showed date-synchrony in their arrival (≤ 4 d) at winter ranges, and all five birds showed date-synchrony in their departure by a single day.

We compiled records of 44 Aleutian Tern sightings distributed across the Yellow Sea of East Asia, the Malaysian Peninsula, central Philippines, and southern and central Indonesia (Table 2, Fig. 1). All records but one were marine-based and occurred an average of 16.1 ± 18.2 km from shore. Two of the six sets of core winter ranges mapped in this study (Fig. 1) encompassed a small number (n = 3; 7 %) of these records. Overall, core ranges were relatively far (1 020.9 ± 1 173.1 km) from the closest record.

Migration routes in the Eastern Hemisphere extended from the Sea of Japan along the East Asian coastline. Five of six birds crossed the South China Sea, and one took an inland route over eastern China to core wintering ranges in west and central Southeast Asia. Birds moved southbound at 385.5 ± 199.1 km/d and northbound at 476.3 ± 67.1 km/d. On southbound routes in the Eastern Hemisphere, 76 % of locations (n = 460) were marine-based, occurring 211.9 ± 174.0 km from shore; the remaining locations occurred 64.9 ± 56.5 km inland. Corresponding northbound locations (n = 345) were also primarily marine (86 %), but were considerably more pelagic (850.7 ± 445.9 km from shore).

Birds arrived in the Eastern Hemisphere by about 20 July, and actively migrated southward by 8 August, after which time birds entered a transitional period prior to establishing their winter ranges. Conversely, birds began active migration northward on 15 April, migrated through Southeast Asia and eastern Asia for

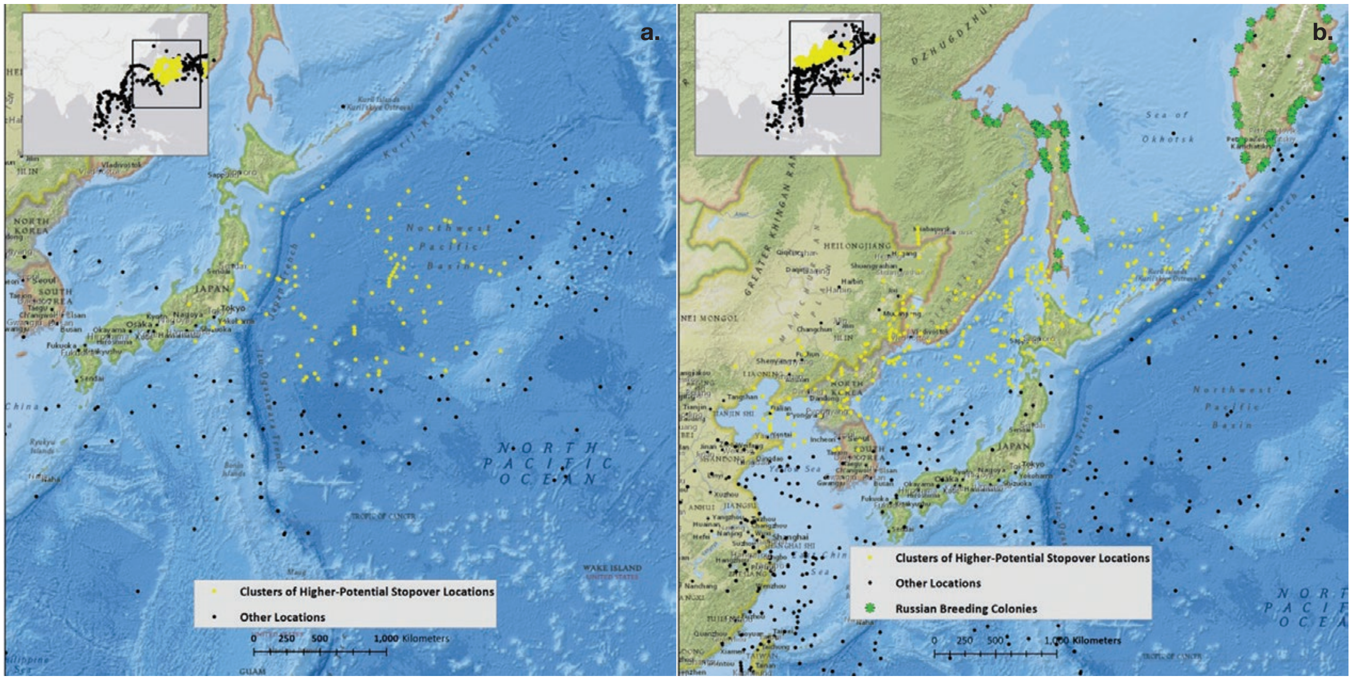

Fig. 3. Potential stopover or staging areas on the southbound (post-breeding) and northbound (pre-breeding) flyway segments in Asia, based on analysis of movement rates and the clustering of geolocation data from Aleutian Terns that breed in Alaska (2010–2012). Yellow locations are low-movement clusters composed of all six birds over all three years. The locations of Russian breeding colonies of Aleutian Terns are also shown for reference.

approximately two weeks, and left the Eastern Hemisphere by 29 April.

From a timing standpoint, Aleutian Terns spent 2.3–3.0 months migrating from breeding sites in southeast Alaska, stopping in several places before arriving in wintering areas in Indonesia and Oceania. They took approximately one month to return.

We found statistically significant evidence for possible stopover or staging areas along both southbound and northbound routes (Fig. 3a, b). Movement rates and location clusters in both the southbound and northbound routes were spatially auto-correlated (southbound: Moran's $I = 0.1389$, $z = 9.6454$, $P < 0.0001$ and northbound: Moran's $I = 0.5161$, $z = 23.0175$, $P < 0.0001$). The southbound migration route showed a particularly strong bias toward the clustering of locations with very low movement rates (Getis-Ord $G = 0.0000$, $z = 4.9172$, $P < 0.0001$), whereas among northbound routes this pattern of low-movement clustering was not as accentuated (Getis-Ord $G = 0.0000$, $z = 0.2301$, $P < 0.0001$).

The greatest potential for a southbound stopover was in the vicinity of the Sea of Japan; five of six birds, and nine of 13 southbound migration routes, occurred in this low movement-rate, high-density zone in all three years of the study (2010–2012) (Fig. 3a). The calendar-date range of locations across the three years was 4–27 August. Birds spent 11.75 ± 5.50 d (range 3–20 d) in the zone. Movement rates in this zone were 309.9 ± 199.1 km/d (slightly less than 13 km/h) compared to 477.9 ± 335.1 km/d outside of this zone. This potential stopover zone is close to the large majority (~ 85 %) of known Aleutian Tern breeding colonies (Fig. 3a) on Sakhalin Island and the Kamchatka Peninsula (Y. Artukhin, unpubl. data): 39 % of geolocator locations in this zone ($n = 292$) occurred within a day's movement (~ 300 km) of Russian colony locations. Fledging dates at Russian colonies in the last decade occurred in early August, with parental care lasting into September (Y. Artukhin, pers. comm.). Therefore, the peak timing of Alaskan migrants (~ second week of August) coincides spatially and temporally with Russian colony activity.

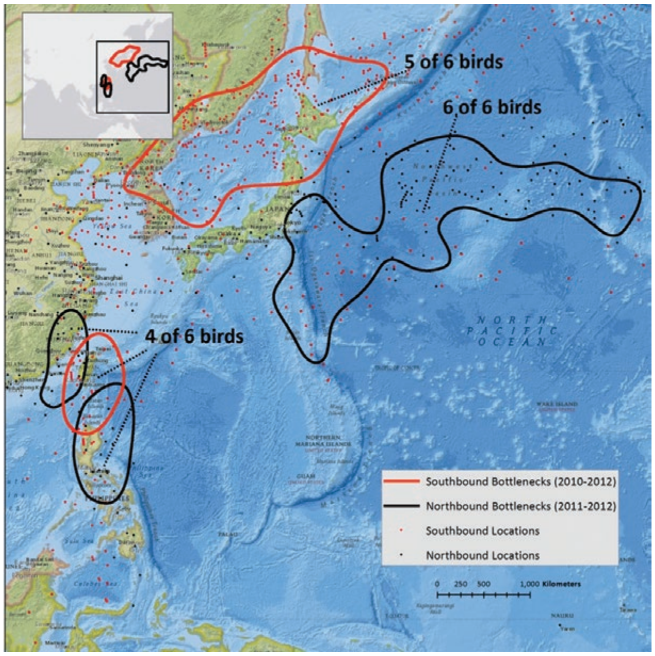

Fig. 4. Potential migratory bottlenecks on the southbound (post-breeding) and northbound (pre-breeding) migration segments in Asia, based on analysis of the density and coincidence of the movement routes (not shown) of Aleutian Terns that breed in Alaska (2010–2012). The locations from geolocator tracking devices are shown for reference.

On the northbound route, the analogous area was a more pelagic zone extending 1 500 km east of Japan in the Northwest Pacific Basin; this area was used by all six birds in both years that geolocator data were available (2011, 2012), during 10 of 11 northbound migration cycles (Fig. 3b). The date range across the two years was 15–30 April, with a duration of 6.5 ± 2.0 d (range 3–9 d). Movement rate patterns were similar to those in the southbound route described above, with average movement rates of 344.0 ± 294.2 km/d and 567.9 ± 450.5 km/d in and out, respectively, of this zone in the Eastern Hemisphere.

Areas with the highest densities of overlapping movement trajectories from multiple birds—what we identified as possible "bottlenecks" or "funneling zones"—were also distinct and apparent on both southbound and northbound flyways (Fig. 4). Potential bottlenecks on the southbound flyway of the Eastern Hemisphere occurred in a zone in the Sea of Japan (1 508 264 km^2; $n = 5$ birds), with a secondary zone near the Luzon Strait between southern Taiwan and Philippines (473 074 km^2; $n = 5$ birds). Potential northbound bottlenecks occurred offshore from Japan in the northwestern Pacific (2 364 236 km^2; $n = 6$ birds), in the Taiwan Banks near the Chinese mainland (329 978 km^2; $n = 5$ birds), and in the northern Philippines (627 191 km^2; $n = 5$ birds).

In the Western Hemisphere, movements to and from Alaska breeding sites ($n = 22$ migration trajectories total) occurred at roughly the same rate as in the Eastern Hemisphere (southbound 248 ± 67 km/d; northbound 458 ± 101 km/d); however, movements were more linear and of relatively short duration (southbound 14.6 ± 3.1 d; northbound 8.8 ± 4.0 d) compared to those in the Eastern Hemisphere. Fewer data, compounded by incomplete geolocator data for almost one-third of trajectories during spring equinox periods, limited inference about potential stopovers in or near Alaskan waters. However, a qualitative review of individual movement trajectories to and from Alaska breeding sites did indicate that during the post-breeding (southbound) migration phase all birds appeared to funnel through an area of the western Aleutians, starting near the Fox Islands. This was despite two slightly different trajectories from breeding sites: one along the arc of the southcentral Alaskan coast and Aleutian Archipelago (exhibited during nine migration cycles), and another farther south through the Gulf of Alaska (four migration cycles). In contrast, trajectories of all return migration routes ($n = 9$) occurred over more pelagic zones in the northeastern Pacific Ocean and the Gulf of Alaska.

DISCUSSION

Prior to our study, very little was known about Aleutian Tern migration and non-breeding distributions, apart from anecdotal evidence and a limited number of birder observations in Southeast Asia. Kessel & Gibson (1978) knew of no coastal or overland Aleutian Tern migration in Alaska. North *et al*. (2013) stated: "no data; probably pelagic migration." From six recovered geolocators (out of 114 deployed), we documented a migration pathway from

Alaska to the Philippines, Indonesia, and Papua New Guinea. Whereas migration is pelagic in some places and nearshore in others, it also likely occurs overland. Overland migration concurs with an inland record from Socheong Island, Incheon, Korea, where the species was detected but not photographed on 23 August 2004 (Chang-Yong Choi, pers. comm.). Our records confirmed movement overland in Korea from 16–26 August 2010, and again in 2011. This has conservation implications because terns passed over some of the most industrialized and polluted parts of China (Eleven 2006).

Interestingly, the results of this study show that Aleutian Terns from southeastern Alaska have one of the longest migrations ever recorded (e.g., compared to Croxall *et al*. 2005, Shaffer *et al*. 2006, Egevang *et al*. 2010). Regarding contributions to Aleutian Tern natural history, our study also shows that the known geographic extent of the species' wintering range is at least four times larger than was previously estimated, despite tag recovery from only six birds. We also show for the first time (based on our geolocation data) that Aleutian Terns show strong regional site fidelity during both winter and summer breeding periods. The terns we tracked made extensive use of tropical regions in Southeast Asia and Oceania, eastern and western Indonesia, the Philippines, and Papua New Guinea in winter. Based on the migration patterns and wintering ranges documented by our small sample size, we suggest that further research with improved technology is needed. In identifying the migration patterns and geographical sub-regions of interest, we can now begin to assess and identify conservation threats on species persistence. As baseline knowledge about the movement patterns of this species is illuminated by this study, we hope that this research will foster the ability to address conservation concerns and make informed recommendations for improved conservation management.

Unlike Arctic Terns in Prince William Sound, Alaska (Duffy *et al*. 2013), where birds re-nested within a meter of their original nest, the tagged Aleutian Terns did not exhibit nest-site fidelity. Instead, we observed a more regional nesting tendency, recovering three geolocators 3–20 km from their deployment locations.

Although we considered whether the low recovery rate of tags could be explained by the shedding of geolocators from the legs of birds, we found that the attachments of all six units that we recovered were in excellent condition. Furthermore, in the six years since affixing the geolocators, we had never observed or recaptured birds with color and metal bands on one leg but no geolocator on the other leg—this would have been a clear sign that their geolocator had been lost. We did not detect evidence of injury or stress from carrying geolocators; the recaptured birds appeared to be in excellent physical condition, and average weights before tagging (121.0 g, range 106.0–137.0, n = 111) and after tagging (118.0 g, range 111.0–123.0, n = 6) were similar. The total weight of the tracking device (including the attachment and Darvic band material) was below the 3–5 % unit-to-body weight guideline (Caccamise & Hedin 1985), although we understand that weight is not the only factor in determining the success of a bird carrying a device (Vandenabeele *et al*. 2012). Displacement of the colony due to disturbance from our research activities was not apparent: in the six years after tag deployment, similar numbers of birds bred annually in the greater Yakutat area as they did prior to the 2010 tagging effort.

It is possible that the remainder of the tagged Aleutian Terns dispersed farther than we anticipated. The resolution of our geolocation data was insufficient to determine if the terns prospect and breed within a greater "neighborhood" of colonies, but future research with lightweight satellite tags could address this. Bird mortality on the flyway or at the wintering sites identified in our study could also account for geolocator attrition. For instance, several anecdotal observations in Table 2 occurred near active fishing operations. In Jakarta Bay, Indonesia, Tirtaningtyas & Hennicke (2015) found several Christmas Island Frigatebirds *Fregata andrewsi* that had become accidentally entangled in fishing gear or had been directly captured (poisoned and shot), presumably to be eaten. We do not know how likely it is that tagged terns could have become entangled in fishing gear, nor do we know how many might have been eaten by locals in Southeast Asia. We do know from reports by Indonesian locals that Aleutian Terns are found closely associated with fishing operations in the Jakarta Bay and Sunda Straight areas of Indonesia.

The Indo-Pacific region, where all six birds overwintered, is a geographical zone of conservation concern. Foraging conditions in two important marine zones in which Aleutian Terns overwinter—the south China and Java Seas (Purwanto 2003, Sumaila & Cheung 2014, Christensen & Tull 2015, Teh *et al*. 2017)—may be drastically reduced by eutrophication, destruction of shoal areas through island creation, overfishing, and a lack of regulatory oversight. Tang *et al*. (2015) mentioned that sites of intense contamination and debris in the Yellow Sea resulted in reduced productivity. Several of our anecdotal observations (Table 1) identified Aleutian Terns sitting on debris in the water, often identified as human-made objects or trash. Heavy pollution levels may also lead to contaminant exposure. Other possible activities that could adversely affect Aleutian Terns include: market hunting for birds in their wintering areas and along the flyway; the numerous offshore wind farms that contribute directly to the mortality of seabirds and produce orientation issues due to electromagnetic noise (Engels *et al*. 2014); and the release of radioactive material into the Sea of Japan during the Fukushima reactor meltdown.

The results of our study, combined with the low tag return we experienced in the field, also raise compelling questions about the population structure and colony dynamics of Aleutian Terns. Although apparent regional fidelity exists in this species, whether cohorts of terns are philopatric to specific colonies, regions, or neighborhoods throughout their global range remains an open question. Comparative analyses of the broad population genetic structure of Aleutian Terns would help to elucidate the yet unknown population dynamics of this species, and future studies would benefit from being able to assess the extent of gene flow between populations and across localities. Conservation efforts should consider whether species-level protection (in the case of a low population genetic structure), or the protection of productive colonies like Yakutat (in the case of highly structured populations), would have the most efficacy. Finally, our low tag return in a large colony provides an important lesson for future studies: a higher recapture success may be achieved in colonies that are more condensed or smaller.

Given the enormous geographic range that we now know Aleutian Terns to occupy, the regional flyway bottlenecks that we have described herein, the threats to wildlife from pollution in Southeast Asia (Tang *et al*. 2015), the rapid declines in Alaskan breeding populations (Renner *et al*. 2015), and the uplisting of this species to globally vulnerable (BirdLife International 2017), we recommend that this species be included in future IUCN assessments to determine its international conservation priority. Without prior knowledge of the wintering habitats described in this study, this important recommendation would not be possible.

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