



Northward migration, molting locations, and winter residency of California breeding pigeon guillemots *Cepphus columba*

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ABSTRACT: Pigeon guillemots *Cepphus columba* are ubiquitous along the coasts of the eastern North Pacific, yet little is known about their winter migration patterns, habitat needs, and potential threats faced during the non-breeding period. We used 3 seasons of year-long light level data from tagged individuals to estimate the migration timing and winter residency of pigeon guillemots breeding on Southeast Farallon Island in California (USA). Light level data were combined with a movement model to estimate positions of tagged animals, revealing that individuals from this population undertook a coordinated coastal migration north in the fall, stopping at sites near Haida Gwaii in British Columbia (Canada), presumably during a flightless prebasic molt, before continuing north to stationary overwintering sites in coastal British Columbia and Southeast Alaska. Birds then made an uninterrupted migration south in the spring, returning to waters around Southeast Farallon in late March and early April. Wet/dry data indicated nocturnal resting on land during the breeding season and likely on the water throughout the non-breeding months. This is the first study to confirm the migratory patterns of pigeon guillemots from California, and highlights the importance of the waters of British Columbia and Southeast Alaska for the studied population and possibly other major populations of this species.

KEY WORDS: Colonial seabirds · Alcidae · Geolocator · Farallon Islands · Tracking

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1. INTRODUCTION

Colonial seabirds can be vulnerable to population-wide disturbance during the breeding season when reproductively active individuals remain close to the colony while in incubation and chick-provisioning phases. Much of the annual mortality measured for seabirds in temperate and polar climates, however, occurs during the non-breeding winter months when resources become more scarce and storms more severe (Barbraud & Weimerskirch 2003, Fort et al. 2009, Harding et al. 2011). Effective management thus requires a year-long assessment of habitat needs and potential threats that encompass both

the breeding and non-breeding periods, which for migratory species can span entire ocean basins. The application of tracking technology has been used to slowly fill gaps in our understanding of the post-breeding dispersal patterns of seabirds, providing a tool for establishing connectivity between non-breeding and breeding locations, identifying important migratory corridors, and studying the dynamics between sub-populations.

For species with high wing-loading, such as those in the family Alcidae, the benefits of long-distance movements post-breeding must be weighed against the energetic demands of flight (Elliott et al. 2014). Benefits of migration include reduced competition,

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escaping adverse winter weather, and seeking regions with improved foraging conditions (Newton 2008). Wing morphology of the Alcidae has evolved to maximize the compromise of underwater pursuit diving. Because of this, members of the Alcidae skirt the physical limitations of flight and require more wing beats than traditional migrants like shearwaters (Shaffer et al. 2006) and terns (Egevang et al. 2010) to stay aloft, making migration energetically more demanding for alcids compared to those in other taxonomic groups.

Wing morphology may limit the migratory potential of Alcidae, but several species are known to make substantial movements (2 to >6 km away from the colony) after breeding. These dispersal movements tend to be more variable and less predictable (facultative) than the obligate migrations of many species of waterfowl, raptors, and songbirds that move between lower latitudes and higher latitudes as part of their annual cycle (Newton 2008, 2012). Some Alcidae that breed in higher latitudes move south in the fall and winter, such as Atlantic puffins *Fratercula arctica* that breed in Greenland (Burnham et al. 2021) and thick-billed murres *Uria lomvia* from St. Lawrence Island in the northern Bering Sea (Takahashi et al. 2021). Ancient murrelets *Synthliboramphus antiquus* from British Columbia (Canada) move north and west to the Aleutian Islands, Bering Sea, and the north Asian coasts primarily for post-breeding molt (Gaston et al. 2017, Miller et al. 2020). Rhinoceros auklets *Cerorhinca monocerata* from Alaska and British Columbia disperse widely throughout the Gulf of Alaska and as far south as offshore of southern California, presumably in search of favorable foraging habitat (Hipfner et al. 2020). For those species where suitable forage resources are available year-round, migration is less pronounced. For example Cassin's auklets *Ptychoramphus aleuticus* that breed in the productive upwelling region of central California (Johns et al. 2020b) and whiskered auklets *Aethia pygmaea* that breed in productive tidal regions in the western Aleutian Islands (Schacter & Jones 2018) remain near their respective breeding colonies throughout the year.

Pigeon guillemots *Cepphus columba* belong to the family Alcidae, and, despite their ubiquitous presence on North Pacific coasts, little is known about their winter movement patterns and foraging ecology (Ewins 2020). Breeding occurs coastally from the southern Chukchi Sea in the north including throughout the Bering Sea (except the Pribilof Islands), along the Aleutian Islands and the Kamchatka Peninsula, to southern California in the east-

ern North Pacific and the Kuril Islands in the western North Pacific (Ewins 2020). Breeding pairs utilize crevices and burrows on predator-free islands and cavities inaccessible to predators on mainland shorelines throughout their range, with major colonies of more than 1500 individuals at sites in Siberia, Russia; Prince William Sound, Alaska; Puget Sound in Washington State; and central California (Johns et al. 2020a, Hyrenbach et al. 2022). The diet of pigeon guillemots consists of a diversity of demersal fish such as sculpins (Cottidae), gunnels (Pholidae), flatfish (Bothidae, Pleuronectidae), and juvenile rockfish (Sebastidae), along with invertebrates, the assemblage of which varies depending on location (Golet et al. 2000, Robinette et al. 2007, Bishop et al. 2016, Johns et al. 2020a). Given this diet, pigeon guillemots are considered shallow benthic foragers. They likely do not spend substantial time foraging or traveling beyond the continental shelf at any point in their annual cycle (Clowater & Burger 1994).

Southeast Farallon Island (SEFI) off the coast of central California supports one of the largest colonies of pigeon guillemots range-wide. The island is part of the Farallon Islands National Wildlife Refuge and lies within the Gulf of the Farallones National Marine Sanctuary. Population monitoring and banding of fledglings have been conducted by Point Blue Conservation Science on SEFI since the early 1970s. Birds occupy the loosely consolidated granitic slopes and surrounding waters of the island from March through September, with an annual SEFI breeding population estimate that has fluctuated between 2000 and 5000 individuals over the past 50 yr (Nelson 1987, Johns et al. 2020a). A possible coastal migration northward post breeding has been suggested, as the birds are absent from central California from October through February. The species has been noted traveling north off Grays Harbor in Washington State in the fall and moving southwards in the spring, with few detected offshore (Wahl & Tweit 2000). Recoveries of individuals banded on SEFI have occurred as far north as Washington and British Columbia.

Pigeon guillemots likely undergo a prealternate molt from January through March prior to the breeding season, and a prebasic molt from August through October post breeding (Pyle 2009). Based on their similarity to the congeneric black guillemot *C. grylle*, it is assumed that pigeon guillemots experience a flightless period of roughly 4 wk while simultaneously replacing their flight feathers during the prebasic molt (Ewins & Kirk 1988). This may explain why guillemots from SEFI are not observed off the coast of

California post breeding during the fall and winter months, as the exposed coastline provides little shelter from storms and major swells that could interfere with foraging. This could be particularly problematic during the flightless period of the prebasic molt when reliable and easily accessible prey might be limited.

In this multi-year tagging study, we provide new information on the migratory behavior and movement patterns of pigeon guillemots from one of their largest colonies, filling previous data gaps necessary for identifying potential risks faced by this population during the non-breeding period. Our primary objectives were to (1) identify important molting and overwintering locations, (2) determine the timing and consistency of arrival and departure dates from SEFI and at different latitudes throughout their proposed range, and (3) describe the non-breeding behavior of individuals on migration and at their overwintering sites.

2. MATERIALS AND METHODS

2.1. Field methods

Approximately 95 natural crevices and artificial nest boxes were monitored for hatching success (HS) and fledging success (FS) throughout the duration of the tagging study, as part of a long-term monitoring project on SEFI that began in 1971. Individuals breeding at these monitored sites were selected for tag deployment to maximize successful tag recovery and to test for potential impacts of handling breeding adult pigeon guillemots. A total of 90 Migrate Technology Intigeo-C65 geolocators were deployed on breeding adults during the summers of 2017–2019 (30 in each year). Adults were extracted from breeding sites by hand during the incubation and early chick-rearing periods. Geolocators were mounted to plastic leg bands with a UV stable cable tie and glue, which were then secured to the tarsus. Total mass of each tag including the band was ~1.5 g, which represents ~0.3% of a conservative average adult mass of 450 g (Ewins 2020). All tagged individuals were given a numerically engraved stainless-steel band on the opposing leg for future identification. Recoveries were attempted during the following summer, and in some cases, birds were recaptured more than 1 yr after deployment, resulting in up to 2 yr of recorded light data. In instances where birds evaded recapture by departing the crevice or nest box upon researcher arrival at the site, a small noose carpet was placed at

the entrance of the breeding site to snare the leg of the tagged bird when it returned. Recaptures using this method were most successful between 08:00 and 11:00 h local time when birds made frequent chick-provisioning visits to the site.

2.2. Assessing handling effects

Randomization tests were performed to examine whether annual observed differences in mean HS and FS between the treatment group (handled for tagging) and control group (unhandled) were the results of chance or were statistically significant. For each year of the study, the following steps were performed. (1) The observed differences in mean HS and FS between the treatment and control groups were calculated. (2) Data for tagged and untagged individuals were pooled, and a random draw equal to the sample size of tagged individuals from that year was assigned to the treatment group and the remaining assigned to the control group. (3) Differences in mean HS and FS between the resampled treatment and control groups were calculated. Steps 2 and 3 were repeated 10 000 times to generate lists of randomized differences in HS and FS. The number of instances when randomized differences from these lists were either equal to or less than the observed difference was divided by 10 000 to calculate a probability of the observed difference for HS and FS. If the observed difference was positive (handled birds had higher HS or FS compared to unhandled), then the number of instances when the randomized differences were either equal to or greater than the positive difference was used. Observed differences were considered statistically significant if the probability was <0.025 (2-tailed test with an alpha of 0.05), indicating the likelihood that the observed difference in HS or FS in that year occurred beyond chance alone.

2.3. Processing light data

Devices were programmed to summarize maximum light levels every 5 min to capture twilight events (sunrise and sunset) used for geolocation. We used the function 'preprocessLight' in the package 'TwGeos' version 0.1.2 in R version 4.0.2 (R Core Team 2020) to visually inspect twilight events, with a light intensity threshold of 1. Twilight events defined during periods of heavy shading or that were substantially different from pre- and post-twilight events were manually removed. These

annotated twilight events were then used to estimate latitude and longitude every 12 h with the R package 'FLightR' version 0.5.0 (Rakhimberdiev et al. 2017). The template fit method was applied using pre- and post-calibration periods when an individual was at the breeding colony to establish a linear relationship between known and theoretical light levels. A particle filter in 'FLightR' combined calibration information and annotated raw twilight data to estimate a probability of space use at each time step within a spatial boundary of longitudes 140° W, 115° W and latitudes 30° N, 65° N. Priors acting on the movement model included a conservative maximum distance of 1000 km between consecutive twilight events based on an assumed maximum flight speed of 90 km h⁻¹ (Blake & Chan 2006), and a lower probability of movements beyond 200 km from shore and 100 km inland. The spatial mask for confining possible locations within 200 km offshore and 100 km inland was chosen based on the shallow foraging ecology of this species and several preliminary model runs without a spatial mask.

2.4. Defining migration

Migratory patterns were characterized by areas of residency and the timing of movements across defined lines of latitude. The function 'stationary.migration.summary' in 'FLightR' was used to estimate the likelihood of stationary behavior that lasted greater than 4 d with a probability cutoff of 0.01 (presumed movement between t and $t + 1$ if 1% of particles moved >25 km) between the months of August and March. This function produced point locations for stationary periods throughout the non-breeding period, with the possibility of multiple stationary locations per individual. We assumed these residency periods represented molting locations if they overlapped with the period of expected prebasic molt (August through October) or non-breeding feeding locations if they occurred between November and February. Benchmark lines of latitude were defined based on physical features and clustering of stationary locations to describe the timing of migration to and from SEFI (38° N), and across the entrance to Puget Sound (48.22° N), Queen Charlotte Sound (51.15° N), Dixon Entrance on the north end of Haida Gwaii (54.45° N), and Admiralty Island (57.7° N). The function 'find.times.distribution' in 'FLightR' generated estimated median dates when birds crossed these lines of latitude during the fall migration north and spring migration south.

2.5. Non-breeding behavior

In addition to light level data, the 2017 tags collected wet/dry data, allowing examination of non-breeding behavioral patterns. The total number of 30 s periods where the tag was immersed in water was summarized every hour (capped by the manufacturer at 7 min, or 14 periods of 30 s for each hour, presumably to preserve data storage potential). Any hour that contained no wet readings was characterized as dry, either because the bird was on land or in flight, or the tagged leg was entirely tucked (Fifield et al. 2009, Harris et al. 2010) while the bird rested on water for the full hour. Twilight events identified from light level data were used to assign day or night to each hour, correcting for latitudinal changes in the diurnal period. Hourly wet vs. dry classifications were summarized across all birds to achieve mean proportion of time spent out of the water during the day and night, and mean hourly proportion of time spent out of water for the sample population. These results were compared to migration timing estimates and empirical egg-laying and fledging dates to look for patterns in activity budgets across different stages of the year (breeding, molting, migration, and winter residency).

2.6. Core non-breeding locations

Monthly utilization distributions (UDs) were generated to characterize the spatial use patterns of pigeon guillemots throughout the non-breeding period. Location estimates were pooled across all individuals and years for the month of September to show the extent of presumed molting habitat, November and January separately to show the extent of winter residency, and March to show the beginning of the southern migration back to SEFI. The function 'kernelUD' in the R package 'adehabitatHR' version 0.4.19 (Calenge 2006) was used to produce population-level UD for each focal month, using the 'href' reference bandwidth projected on a 0.1° × 0.1° grid.

3. RESULTS

A total of 67 of the 90 tags deployed were recovered across all 3 years of the study, and 86% of tags recovered ($n = 58$) successfully recorded at least 12 mo of usable light-level data (Table 1). Tag recovery was most successful from birds breeding in artificial nest boxes, which tended to remain at the site

Table 1. Summary of total tags deployed and recovered by year, and number of recovered tags that successfully recorded usable data from pigeon guillemots over a complete non-breeding period (August to April). The success rate represents the proportion of tags recovered, including tags that failed to collect data

Year	Deployed	Recovered	Success rate (%)	Data
2017	30	26	86.7	24
2018	30	23	76.7	19
2019	30	18	60.0	15

when approached compared to birds in more open natural crevices that would leave the site when adjacent nesting western gulls *Larus occidentalis* alerted them to our presence. A single individual was resighted with a geolocator but never retrieved. All of the 68 tagged birds that returned to breed and could be identified by their metal band number or color band combination retained an intact geolocator; there were no instances of lost devices or failure of the plastic bands. A total of 22 geolocator tagged birds were never resighted. Randomization tests indicated there were no statistical differences in mean hatching success or fledging success between tagged and untagged birds (Table 2), except for a significant 0.297 decrease in hatching success for tagged birds compared to untagged birds in 2019 (probability of random chance was 0.004).

On average and across all years, individuals used roughly 2 stationary locations (mean \pm SD = 1.94 \pm 1.46) during the non-breeding period. Individuals with multiple stationary locations arrived at their first stationary site in late August and early September (3 September \pm 18 d), where they spent on average 45 \pm 32 d. Most of these initial stationary sites were near the Haida Gwaii archipelago (\sim 53.3°N) in British

Table 2. Randomization test results for the probability (Prob.) of the observed differences (Diff.) in mean hatching success (HS) and fledging success (FS) of pigeon guillemots between the treatment group (tagged birds) and control group (untagged birds) for each year of the study. **Bold** font indicates a statistical difference between groups; differences were considered statistically significant if the probability was <0.025 (2-tailed test with an alpha of 0.05)

Year	HS		FS	
	Diff.	Prob.	Diff.	Prob.
2017	-0.083	0.222	-0.088	0.246
2018	-0.106	0.172	0.033	0.394
2019	-0.297	0.004	0.095	0.279
2020	-0.009	0.518	0.085	0.179

Columbia (Fig. 1). Birds arrived at their longer winter residency locations in October and November (15 October \pm 19 d) and stayed an average of 131 \pm 37 d, with a maximum record of 211 d. These locations clustered approximately between latitudes 48.8 and 58.9°N in British Columbia and southeast Alaska (Fig. 1).

Migration timing was variable and less coordinated in the fall when birds were flying north to their respective molting and overwintering locations compared to a more synchronized migration in the spring when birds were moving south back to SEFI (Fig. 2a). On average and across all years, birds departed SEFI on 26 August (\pm 8 d) and returned on 30 March (\pm 11 d). Haida Gwaii represented a temporary stationary location for some individuals, resulting in a longer delay of 27 d between the average elapsed time for crossing latitudes 51 and 54.5°N during the fall migration north as opposed to a shorter delay of 14 d during the spring migration south. Both the stationary behavior and timing across benchmark latitudes shows that the southern migration back to the breeding colony occurs in a single movement event while the fall northern migration contains periods where guillemots temporarily pause before making a final movement to their northern overwintering locations.

Guillemots spent on average approximately 75 to 80% of nocturnal hours and roughly 25% of daylight hours out of the water during the chick-provisioning period in July (Fig. 2). Birds are often observed at the colony roosting near their breeding sites during the night and throughout the late morning hours during this time, so we can assume these dry periods represent resting on land and not leg-tucking behavior while resting at sea. Both night and day proportions of dry periods dropped sharply once chicks had fledged by the end of July as parents departed the colony and formed large rafts on the water near the island. Once fall migration began in August, there was a slight increase in the amount of time spent out of water during the day, particularly in the morning hours, likely representing periods of time when the birds were in flight and moving. There was an increase in the amount of time dry in the evening before sunset in September and October, coinciding with the period when birds were presumed to be in a flightless stage during the prebasic molt. This also coincides with the longer stationary periods observed around Haida Gwaii. There was a baseline rate of roughly 15% dry at night during the overwintering residency locations from November through February, with virtually no time spent out of the water during the day in these months (Fig. 2). For the

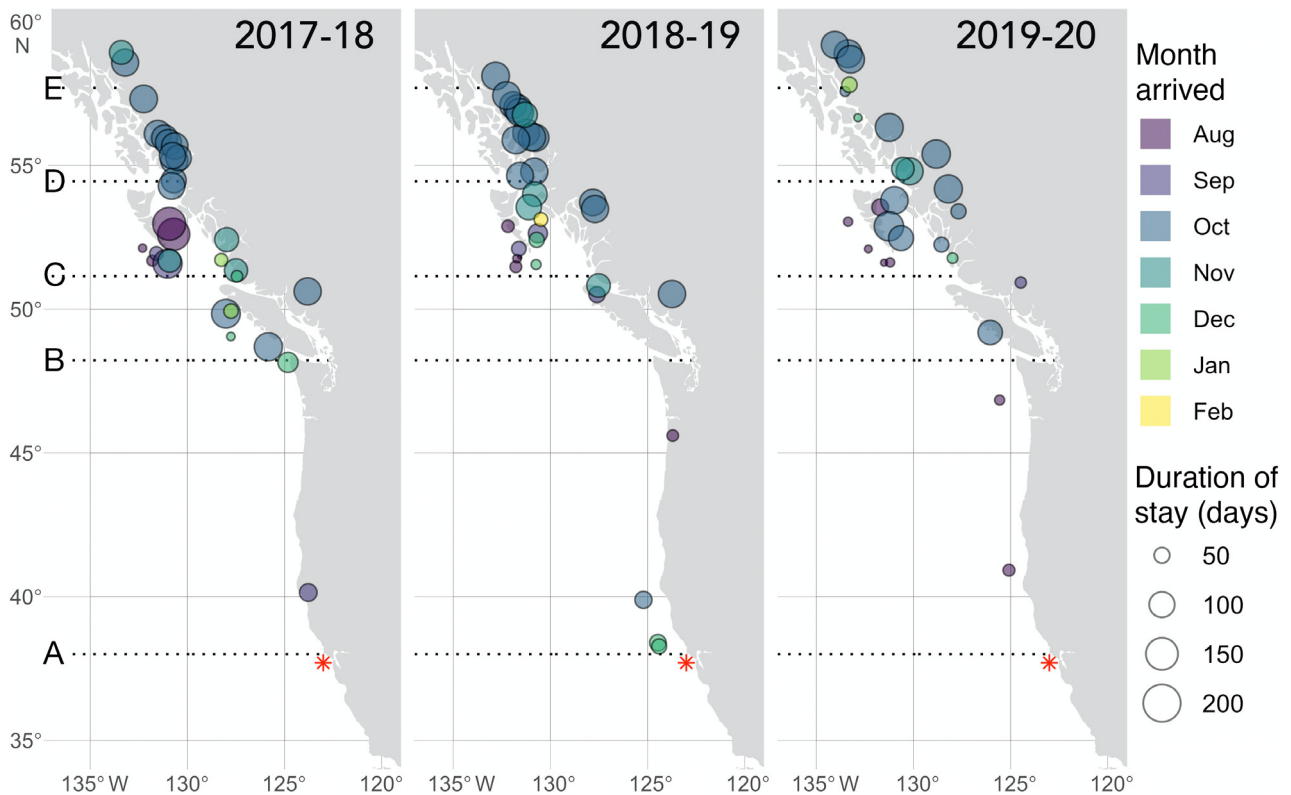


Fig. 1. Stationary periods (probability of no movement greater than 25 km for at least 4 d) of all tagged pigeon guillemots separated by each winter of deployment (2017–18, 2018–19, or 2019–20). The center of each circle represents the stationary location, the size of the circle shows the total number of days spent at each location, and circles are colored by the month the bird arrived at each stationary location. Dashed lines show benchmark latitudes used to estimate timing of migration from (A) Southeast Farallon Island (SEFI; 38°N), (B) entrance to Puget Sound (48.22°N), (C) Queen Charlotte Sound (51.15°N), (D) Dixon Entrance (54.45°N), and (E) Admiralty Island (57.7°N). Red star is the location of the breeding colony at SEFI. Basemap created using the R package ‘rnatualearth’ version 0.1.0 (South 2017)

spring migration, the data show a short period with a slight increase in time out of the water during the day in mid-March when birds would be traveling south, with a steady increase in time out of the water once birds arrived back at SEFI in late March and early April to reestablish breeding site locations.

The temporal pattern of locations used during the non-breeding season is summarized in Fig. 3. Birds departing SEFI in late August and early September showed a core area of use on the southern end of Haida Gwaii island during the month of September, corresponding with the period when birds are presumed to be undergoing their prebasic molt. Individuals moved northeast to Dixon Entrance and Hecate Strait in British Columbia, and Revillagigedo Island in Southeast Alaska during the months of November and January, representing the core winter residency locations where tagged birds remained relatively stationary. By March, most of the tagged birds dispersed from British Columbia and southeast Alaska as they conducted their southern migration back to SEFI.

4. DISCUSSION

Geolocator tagging from this study reveals for the first time the non-breeding movements of pigeon guillemots, filling a previous gap in our understanding of the winter habitat use of the SEFI population and providing conclusive evidence of a direct migration north in the fall to the waters of British Columbia and southeast Alaska. Estimates of movements and wet/dry data reveal that guillemots likely make long flights during the day on the fall and spring migrations and spend nearly all of the nocturnal hours roosting at the colony during the breeding season. It is assumed guillemots avoid shore-based predators during molt and are rarely seen on land during the fall and winter in British Columbia (A. J. Gaston pers. comm.), so most of the nocturnal dry periods between approximately September through February likely represent leg tucking while resting on the water. Nocturnal roosting behavior has been reported for Mandt’s black guillemot *Cephus grylle*

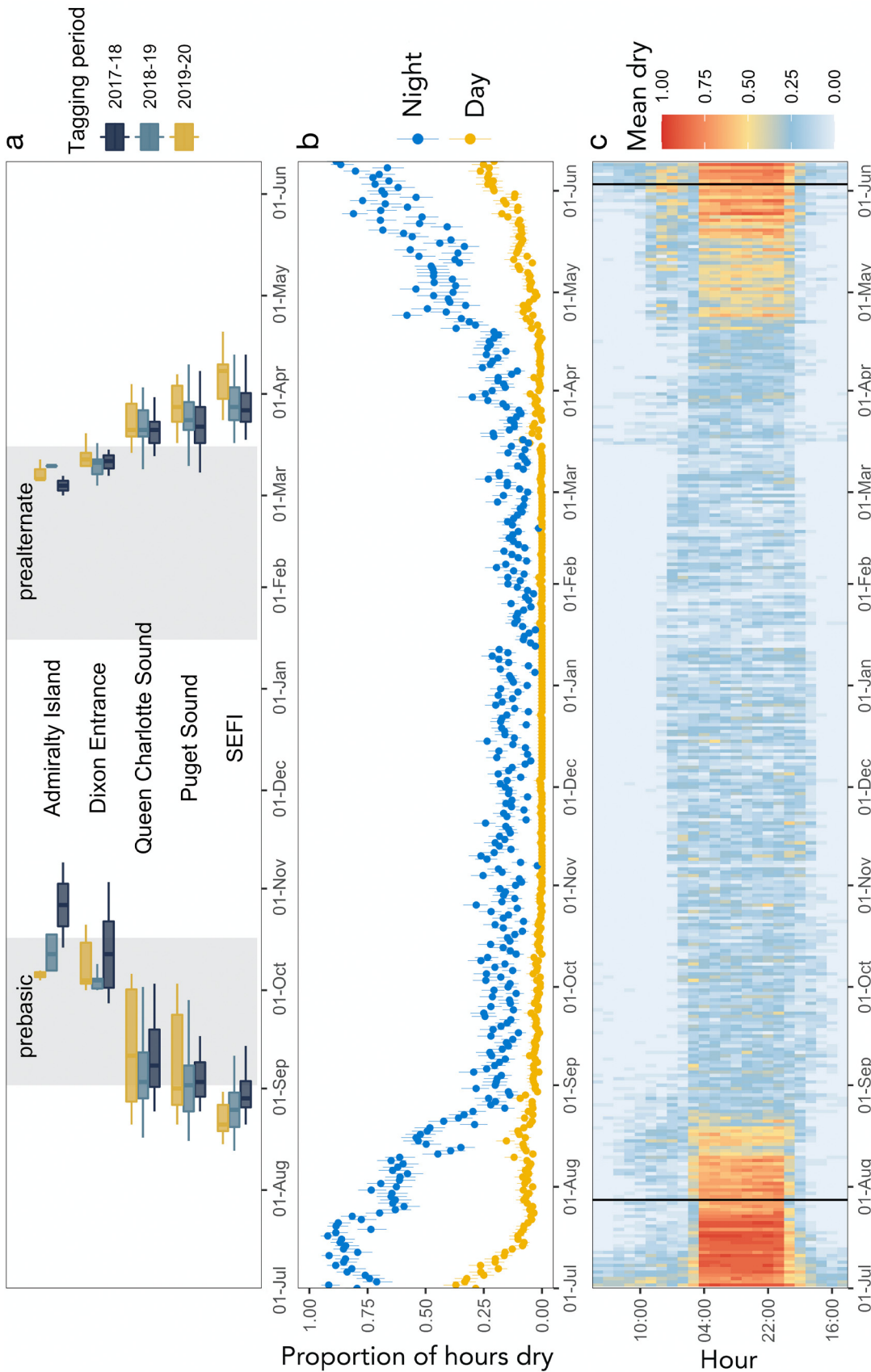


Fig. 2. (a) Estimated arrival and departure dates (0.5 quantile) clustered at each benchmark latitude (center labels; SEFI: Southeast Farallon Island) for tagged pigeon guillemots across all years. Boxes span the interquartile range (Q1 and Q3) of arrival and departure dates, with vertical line showing the median, and horizontal whiskers showing the minimum and maximum values. Shaded grey regions depict presumed molting periods based on the literature (Ewins & Kirk 1988, Pyle 2009). (b) Average proportion of time spent completely out of the water (presumed on land, in constant flight, or leg tucked) in the 2017–18 tagging period during the day (local sunrise to sunset) and night (local sunset to sunrise). Error bars show 95% confidence intervals. Local sunrise and sunset times were derived from the daily estimated location (latitude and longitude) of each individual. For example, 0.5 for day means the sample of birds spent, on average, 50% of the local daylight hours on land or in flight. (c) Average hourly time where tag was completely dry (no interaction with water) during the 2017–18 tagging period. For example, 0.5 means that 50% of sampled birds did not interact with water during a specific 1 h period

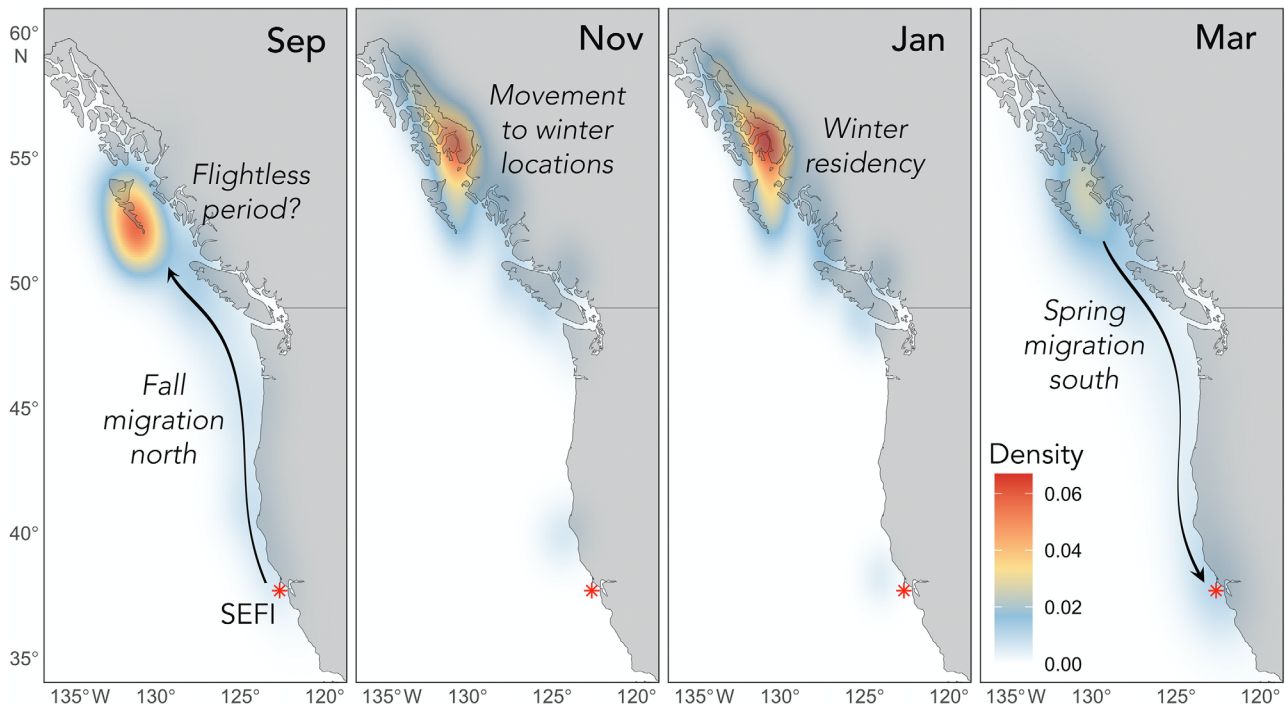


Fig. 3. Monthly kernel density plots with pooled individuals and years, showing the progression of the migration, possible pre-basic molting habitat, and overwintering residency habitat. Color scale shows the density of points for each pixel (number of estimated used locations per 0.1×0.1 degrees). Red star is the location of the breeding colony at Southeast Farallon Island (SEFI). Basemap created using the R package 'rnatuarearth' version 0.1.0 (South 2017)

mandtii on sea ice in the Arctic (Divoky et al. 2016), so it is possible that pigeon guillemots may also occasionally roost out of water on rocks and shorelines during the non-breeding period. Timing of migration from this study aligns with counts from Grays Harbor, Washington, conducted from 1971 to 1999 (Wahl & Tweit 2000), which documented peak numbers in August (northern migration) and May (southern migration) and agrees with the observations of a large pulse of pigeon guillemots off southern Vancouver Island in the fall and early winter (D. Bertram pers. comm.).

There are several possible explanations for what drives pigeon guillemots to depart central California from late fall to early spring, including escaping strong winter storms that produce rough seas during the prebasic molt when birds are less mobile, and reduced access to prey near the breeding colony or improved prey availability in northern locations in the fall and winter. Predictable severe weather phenomena over the eastern North Pacific are exemplified by 'atmospheric river' events, i.e. narrow bands of water vapor ahead of cold fronts capable of producing significant rainfall and extreme winds when they reach land (Ralph et al. 2005, Dettinger et al. 2012). The onset of these major storms predictably

occurs off central and northern California in September, aligning with the timing of departure of guillemots from SEFI. Atmospheric rivers are less present at higher latitudes where guillemots spend the winter months in November (Gershunov et al. 2017). Compounding the potential impacts of severe winter storms may be diminished access to preferred prey off central California. Pigeon guillemots favor age-1 sculpin, rockfish, and flatfish when provisioning their chicks at SEFI (Ainley & Boekelheide 1990, Johns et al. 2020a), and these species that likely represent important prey for adults may either exceed manageable sizes or settle into depths beyond the diving capacity of guillemots as the fish mature during the winter months. In contrast, the protected inlets and straits of British Columbia and southeast Alaska likely provide safe sheltered locations for birds to undergo molt while still allowing access to an abundant supply of demersal fish such as gunnells and pricklebacks (Stichaeidae) (Vermeer et al. 1993), along with invertebrates which are an important component of the winter diet in birds sampled from Alaska (Kransnow & Sanger 1982). Dogfish Bank on the northern side of Hecate Strait is an extensive shallow shelf (<50 m) that may represent important foraging habitat for pigeon guillemots during the

vulnerable molting period and winter months, as this region would provide access to benthic prey far away from shore-based predators (A. J. Gaston pers. comm.). A tendency for guillemots to break up their fall migration north in late September and early October with a temporary stationary period in Hecate Strait provides strong evidence that this location is indeed used for their prebasic molt.

We did not have sufficient data to address the question of whether pigeon guillemots cue in on environmental signals to initiate migration, but consistent departure and arrival dates from SEFI across individuals and over the 4 years of this study suggest that pigeon guillemots at this colony follow an obligate or 'hard-wired' approach to migration (Newton 2012). This endogenous approach to migration timing is a common feature in songbirds, where timing of departure from and arrival to breeding localities remains fixed despite changes in timing of key environmental conditions related to resource availability (Both et al. 2006, Stanley et al. 2012, Åkesson et al. 2017). The predictability of the onset of winter storms off the central California coast and perhaps the necessity to arrive at more protected waters prior to the prebasic molt likely explains in large part the obligate migratory behavior of this population. Predictability in an enhanced supply of prey resources in British Columbia and southeast Alaska relative to the California coast may also explain the regularity in the timing of their fall migration north; however, confirmation of this would require sampling the foraging habitat occupied by this population in the winter months.

Long-term reproductive monitoring of pigeon guillemots on SEFI provides the opportunity to discuss possible carryover effects from non-breeding conditions. Recoveries of tagged individuals in 2020 were comparatively lower than in the previous 2 years of this study (Table 1), which could be interpreted as a reduction in the return rate of breeding individuals following an increase in adult mortality during the winter of 2019. Sea surface temperature observations showed anomalously warm waters in the Northeast Pacific beginning in the summer of 2019 (Amaya et al. 2020), similar to the marine heatwave observed in 2014–2015 that negatively impacted the survival and breeding success of some seabird communities (Bond et al. 2015, Jones et al. 2018, Piatt et al. 2020). Mean annual productivity for pigeon guillemots on SEFI in 2019 (0.21 chicks fledged per pair) was 73% lower than the long-term average from 1971 to 2020 (0.78), likely explained by a near absence of juvenile rockfish in the chick-rear-

ing diet (Johns et al. 2020a). Juvenile rockfish are an important prey for this population and colonies in Puget Sound (Johns et al. 2020a, Buckner et al. 2022); thus, in the absence of this prey, birds may have already been in poor physical condition at the start of their migration north, resulting in a reduced probability of surviving the winter months. A lack of adequate prey may also explain the significant decrease in hatching success for tagged birds observed in 2019, as birds that were already in poor condition would have a higher likelihood of abandoning the nest in response to disturbance from handling. However, we did not observe a decrease in peak raft counts around the island in the spring of 2020 (Johns et al. 2020a), contradicting the theory that high adult mortality in the winter resulted in lower return rates of tagged individuals. Instead, the lower return rates in 2020 may simply be explained by fewer years post deployment to relocate and recapture tagged birds, for example if individuals skipped breeding or moved to a different breeding site.

If the SEFI colony is representative of the migratory behavior of pigeon guillemots, British Columbia and southeast Alaska likely provide a winter refuge for birds from other colonies in California and Oregon that undertake a northern migration post breeding. Yet, it remains unclear to what extent this annual migration of pigeon guillemots represents movements from other colonies throughout their expansive range. A comparative study on the morphology of pigeon guillemots range-wide found a decreasing trend in wing length from California to British Columbia, and an increasing trend from British Columbia to the Alaska Peninsula and islands in the Bering Sea and Siberia (Storer 1950). Given the results from our tagging study, wing length measurements may indicate that individuals from colonies in the northern and southern extremes undertake longer migrations and may also congregate in the inland waters throughout the Gulf of Alaska and British Columbia in the winter, as opposed to birds that breed locally in these areas. We should note that this trend in wing length may simply represent latitudinal differences in body size, and information on wing shape would provide a stronger basis for speculation on the migratory tendency of sub populations of pigeon guillemots. Given there was little evidence for any effects of tagging on the breeding performance of pigeon guillemots, we encourage researchers working with other colonies of this species to consider tagging opportunities to answer range-wide movement questions. If in fact much of the worldwide population of pigeon guillemots congregates in

a small geographic range during the winter months, increased effort and attention should be paid to the types of prey and potential human- or climate-related threats that could impact this ubiquitous North Pacific seabird.

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