Research Article

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Using Geolocator Data to Address Changes in Migration Patterns for Black Turnstone

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Abstract: Black Turnstone is an obligate Pacific coast shorebird that is included as a "Species of High Concern" in both the U.S. and Alaska Shorebird Conservation Plans. Specific migration routes for this species are not well understood, which makes its recent disappearance at a major spring stopover site, northern Montague Island in Prince William Sound, Alaska, difficult to interpret. We tracked 23 Black Turnstones between breeding and wintering areas and examined migration timing, duration, and routes used. We identified two high-use regions during migration: 1) Cook Inlet/Shelikof Strait, Alaska, and 2) the Haida Gwaii Archipelago in British Columbia/Alexander Archipelago in southeastern Alaska. This second region was also an important wintering area. We found that northbound migration was longer than southbound (the reverse of what is often observed in shorebirds) and that staging behavior was primarily seen during northbound migration. No birds were tracked to northern Montague Island, and only a few individuals stopped anywhere in Prince William Sound. Alterations in patterns of spring herring spawn in Prince William Sound may be affecting the routes and stopovers used by Black Turnstones, and birds may be wintering farther north in recent decades due to warmer winter conditions. Additionally, the increasing availability and popularity of citizen science efforts like eBird has created a mechanism for disseminating observations from less accessible parts of the Black Turnstone range, a fact which may confound our understanding of whether migration routes for this species have changed over the last 30 years.

Keywords: Short-distance migrant, Rocky coast shorebird, Alaska, Pacific Northwest, Warming winters

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1 Introduction

Conservation efforts for non-game species like migratory shorebirds are often prioritized based on population size, trend, range, and existing threats across a species' annual cycle [1]. Such prioritization schemes for many shorebirds that nest in the Arctic or sub-Arctic are hampered by a lack of information from the breeding grounds due to their remoteness, as much of the Arctic and sub-Arctic are roadless and difficult to access in the summer. This places additional importance on data gathered from the nonbreeding range and requires an understanding of migratory routes, timing, and connectivity to interpret the significance of occupancy or abundance trends at important stopover or wintering sites.

Black Turnstone (*Arenaria melanocephala*) is a medium-sized shorebird associated exclusively with Pacific coast shorelines. Both the U.S. and Alaska Shorebird Conservation Plans list Black Turnstone as a "Species of High Concern" due to a relatively small population size and significant threats at breeding and non-breeding areas [1, 2] and it also appears on the US Fish and Wildlife Service's recently released "Birds of Conservation Concern 2021" list [3]. An estimated 85% of the global Black Turnstone population nests on the central Yukon-Kuskokwim Delta in Alaska in low-lying salt grass meadows and sparsely vegetated habitats within 2 km of the coast [4]. During migration and winter, the species is primarily found in rocky intertidal habitats and coastal beaches from Kodiak, Alaska, to Mexico [5]. Because Black Turnstone is dependent on coastal habitats throughout the year, this species is vulnerable to habitat loss or degradation resulting from coastal pollution, infrastructure development, and climate change effects (such as more frequent and intense coastal storms) across its range [1]. On the breeding grounds, sea-level rise and more frequent and intense storms are resulting in seasonal flooding, saltwater intrusion, and changes in erosion and sedimentation rates in the low elevation habitats preferred for nesting [6, 7, 8].

Black Turnstone has been the subject of few breeding season studies because the population is relatively small (~100,000 birds) [4, 9] and sparsely distributed in remote, roadless western Alaska. The species is also difficult to study during the winter, when individuals aggregate in small, widely dispersed groups on rocky coastlines or coastal structures (e.g., docks, jetties), unlike many shorebird species which congregate in large numbers on coastal mudflats where they can be enumerated, captured, banded, and resighted *en masse*. In particular, little is known regarding individual Black Turnstone migration routes and connectivity, and only a few major stopover sites have been identified on their migration route to and from western Alaska. These include northern Montague Island in Alaska's Prince William Sound (PWS) [10, 11], which was designated an Important Bird Area for the species in 2006 by the National Audubon Society and BirdLife International. Surveys conducted at Montague Island during spring 2010 showed that numbers of turnstones stopping over on northbound migration had declined substantially in the 13 years since previous surveys were conducted, from a single-day high of 11,300 individuals in 1997 to <4000 over 19 survey days of the same area [12]. Given that observations and gut contents from turnstones at Montague Island indicated Black Turnstone relies heavily on herring spawn to fuel migration north from PWS in the spring [10, 11] this reduction in the number of individuals using northern Montague Island could be a result of a shift in migration distribution in response to the Pacific herring (*Clupea pallasii*) population in PWS declining in the years since the Exxon Valdez Oil Spill [13, 14]. Alternatively, Black Turnstones may be another Alaskan species that is shifting its wintering distribution northward due to climate change, similar to Pacific flyway Black Brant (*Branta bernicla nigricans*) [15] and Emperor Geese (*Anser canagicus*) [16], and therefore changing its use of historical stopover sites.

Given the already small population size of this species and the changes observed in numbers of individuals using their primary spring stopover area in PWS, there is a need to reassess the conservation status of Black Turnstone. However, we lack important information on migration routes of individuals through time and space, which precludes an understanding of whether observed changes in the species' use of their primary spring stopover site indicate a decline in the breeding population size, or merely a shift in choice of migration routes or stopover sites. To address this data gap, we studied Black Turnstone migration in Alaska and Washington State from 2011 to 2015 using light-level geolocators, which allowed us to estimate geographic locations from patterns of ambient light and therefore infer approximate daily positions and seasonal movement patterns of individual birds [17]. During processing of geolocator data, latitude is derived from day length and longitude from the time of solar noon, while error in these calculations is derived from ambiguity and variability in the light data caused by weather, habitat, and bird behavior [17]. We chose to use geolocators because the satellite tag technology available at the outset of this study was too heavy for use on Black Turnstones. We used the information provided by the geolocator data to enhance our understanding of Black Turnstone migratory routes, timing, and connectivity, and to answer the question: If geolocator-tagged Black Turnstones are not stopping at Montague Island, are they using other stopover sites in PWS, and if so, what proportion of individuals use these sites? This information can be used to update and improve future conservation planning efforts for this iconic Alaskan shorebird.

2 Methods

2.1 Study Sites

Our primary study site for geolocator deployment was near the mouth of the Tutakoke River on the Yukon-Kuskokwim Delta, western Alaska (61.25°N, 165.62°W), located in the center of the main breeding range for Black Turnstones [4]. We also deployed geolocators at a breeding site at Cape Krusenstern, northwest Alaska (67.12°N, 163.46°W), and at Oak Harbor in Puget Sound, Washington, (48.28°N, 122.64°W), a wintering and stopover site (Fig. 1).

The Tutakoke site is located on a flat plain of coastal tundra bisected by the Tutakoke River, which flows into the Bering Sea at the western edge of the study area. Black Turnstone habitat generally occurs in bands parallel to the coast, with densities declining along a gradient of increasing elevation and decreasing moisture and salinity [4]. Along the more tidally influenced northern and western edge of the study area closest to the Bering Sea, sedge meadows form "fingers" of habitat on eroding barren mudflats along the coast and the river delta. These protrusions of vegetated land surrounded by mudflats are favored by nesting turnstones. Other individuals nest in lower densities along the edge of rivers and slightly inland from the coast in higher meadows, dominated by graminoid and dwarf shrub vegetation and dotted by thaw lakes [5].

The Cape Krusenstern site is located on the edge of Cape Krusenstern Lagoon, a shallow 48 km^2 coastal barrier lagoon adjacent to the Chukchi Sea. The study area includes a suite of diverse wetland habitats interspersed with small lagoons and hundreds of brackish lakes [18, 19]. Turnstone habitat in this region lacks the distinct zonation patterns of the central Yukon-Kuskokwim Delta [5]; individuals nest in coastal graminoid meadows on the mainland or on small islands formed by thaw lakes around the main lagoon.

The Oak Harbor site is a man-made marina on the northeast side of Whidbey Island in northern Puget Sound. Turnstones use this site primarily as a high-tide roost during the non-breeding season (August to April). A small wintering population of 200-300 birds swells to approximately 1000 birds during spring migration in March and April (A. Taylor, *pers. obs.*). Birds roost on concrete docks, boat decks, and log pilings while waiting for the ebbing tide to expose foraging areas dispersed around the Oak Harbor/Penn Cove vicinity.

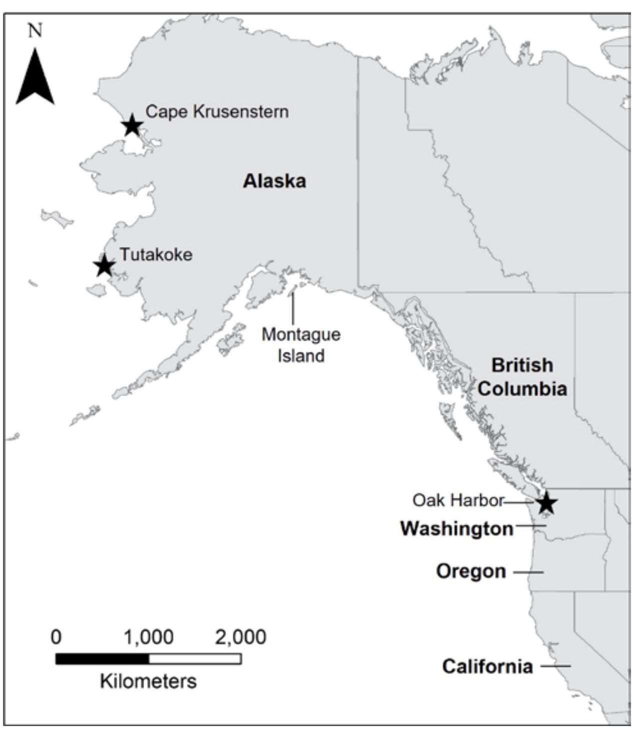

Figure 1. Location of geolocator deployment sites where breeding (Tutakoke and Cape Krusenstern) and wintering (Oak Harbor) Black Turnstones were captured in 2011-2013. Also shown is Montague Island, a historic northbound stopover site.

2.2 Field Methods

We deployed a total of 55 geolocators on Black Turnstones over two field seasons. We used bownet traps to capture breeding turnstones on nests at Tutakoke and Cape Krusenstern, and a combination of noose mats and a compressed air-powered net launcher (Super Talon model, Net-Gun, Inc.) to capture roosting birds at Oak Harbor. We deployed model MK12-S geolocators in 2011 and MK5780 geolocators in 2013; both models weighed approximately 1.5g and were manufactured by Lotek Wireless/Biotrack Ltd, Wareham, UK. Geolocators were attached using a leg-loop harness [20] made of stretchy, flexible beading cord (StretchMagic™, Pepperell Braiding Company, MA). We also color-banded each individual, performed standard biometric measurements, and collected whole blood on filter paper for sexing. Black Turnstones cannot be sexed in the hand [5], therefore the blood was sent to an outside laboratory for genetic analysis to determine sex (Antech Diagnostics, Fountain Valley, CA).

We revisited our field sites multiple times during 2012 (Oak Harbor) and 2014 and 2015 (Tutakoke and Cape Krusenstern) to recover geolocators from returning birds. Recapture of birds with geolocators was accomplished using the same methods as described for initial capture. All capture procedures and protocols were approved by one or more Institutional Animal Care and Use Committees (Prince William Sound Science Center (2011-2013); University of Alaska Anchorage Protocol Nos. 461500 and 463550 (2013-2015).

2.3 Geolocator Analysis

Recovered geolocators were downloaded and the data initially processed using the BASTrak software suite provided by the British Antarctic Survey [21]. The locations were determined primarily by longitude averaging and intersection with the coastline. In places of north/south coastal orientation, the latitude cluster was examined to find the least shaded fixes using methods reported in [22]. We calibrated the geolocator output using post-deployment fixes collected prior to the individual's departure from the capture site (Yukon Delta's Tutakoke breeding grounds, Cape Krusenstern breeding grounds, or Oak Harbor wintering area). We used a fixed light threshold value (16) and a minimum night length of one hour to delineate day to night transitions and to filter out false locations caused by shading. We ignored fixes collected within ± 15 days of the fall and spring equinoxes when latitude cannot be reliably estimated [17].

We mapped the output from each geolocator in Google Earth after analysis with BASTrak software and eliminated obvious longitudinal outliers. For Black Turnstones, these outliers were mostly fixes indicating the birds were occupying inland, terrestrial sites or sites in eastern or central Canada, opposite the expected direction of migration. To determine stopover sites during northbound and southbound migration, we evaluated each track one fix at a time to identify periods when a bird was traveling vs. stationary. We used the recorded maximum light levels to determine up to two locations per day. We then defined a stopover site as a location for which three or more consecutive fixes were recorded (total length 36+ hours) and a staging area as a location where a bird was recorded for > seven days. We plotted direct connections between stopover sites, but actual travel routes may have deviated from direct-line paths.

Because geolocators are sensitive to the effects of shading due to factors including weather conditions, BASTrak output displayed substantial noise at each stopover location, resulting in a cluster of fixes. We assessed weather conditions during each flight and at each stopover location using archived weather and atmospheric pressure data from the National Oceanic and Atmospheric Administration (www.wpc.ncep.noaa.gov/dailywxmap/index.html) and WeatherSpark (www.weatherspark.com). We then assessed the most likely effect of shading based on weather patterns to look for the least displaced latitude of the fix cluster (the most northerly point between March and September and most southerly point between September and March [22]. We also used Google Earth to refine stopover locations using the orientation of the coastline and our knowledge of habitat use and requirements (for example, Black Turnstones are almost always found close to rocky intertidal habitat or on man-made structures such as docks or jetties [5].

2.4 Surveys at Northern Montague Island

We investigated the presence of Black Turnstones in Prince William Sound using boat surveys during the peak of spring migration in 2015. We specifically surveyed areas previously known to have high densities of roosting and foraging birds in the vicinity of northern Montague Island from 30 April-6 May 2015. We also recorded any turnstones observed during a test survey on 27-28 April 2015. For all boat surveys, observers surveyed rocky intertidal habitat favored by turnstones from the deck of an 11.9-m boat that remained within 20 m of the shoreline during surveys. Flock sizes were estimated and GPS coordinates recorded for each observation.

3 Results

We recovered 18 geolocators from Black Turnstones that had been outfitted with geolocators during 2013 at the Tutakoke site, and two geolocators from birds tagged in 2013 at the Cape Krusenstern site, all upon their return to breeding territories in 2014. One of the Tutakoke units did not record any usable data so was excluded from further analysis. We recovered an additional geolocator during a short trip to the Tutakoke site in 2015; this unit provided two full years of migration and wintering data for a single individual. In 2012 at Oak Harbor, we recovered three geolocators from individuals tagged in spring 2011. In total, our data represent migration patterns of 15 males and 8 females (n=23; see Table 1 for breakdown by site and sex). Geolocators recovered from the Cape Krusenstern and Oak Harbor birds and all but four of the Tutakoke birds provided a full year of data, including northbound and southbound migration dates and durations, as well as stopover, wintering, and breeding grounds locations. Four Tutakoke units (three males and one female) failed or were damaged prior to spring migration and thus did not provide information on northbound migration back to Tutakoke.

Individuals whose geolocators were recovered in a subsequent year did not differ in mass (Table 2) or body condition (A. Taylor, *pers. obs.*) at capture compared to all individuals captured at breeding or wintering sites. Birds captured at wintering sites were slightly lighter than birds captured at breeding sites, but this difference was not significant (Table 2). We only sexed individuals whose geolocators were recovered in a subsequent year; within this group, females were significantly heavier at initial capture than males (t-test pooled across all sites: $t=6.75$, $df=22$, $p<0.001$; Table 2). However, when pooled across sexes, the initial mass of individuals whose geolocators were later recovered was not different than that of all individuals captured (121.2 ± 9.5 g).

3.1 Migration Routes and Stopovers

Routes were similar for northbound (Fig. 2) and southbound (Fig. 3) migration, with turnstones following the Outer Coast and Inside Passage coastlines of Alaska and British Columbia in both spring and fall seasons. The error

Table 1. Number of geolocators deployed and recovered at two breeding sites and a wintering site, and the number of individuals tracked on northbound (NB) and southbound (SB) migration by sex. Most individuals were tracked on both northbound and southbound migration, thus the number of each sex tracked on each migration sums to more than the number of geolocators recovered at each site.

		Males		Females	
Capture Location	**Recovered**	**NB**	**SB**	**NB**	**SB**
Alaska Breeding					
Tutakoke	19*	8	11	6**	7**
Cape Krusenstern	2	2	2	-	-
Washington Wintering					
Oak Harbor	3	2	2	1	1
Total	24*	12	15	7	8

*data from one geolocator were not usable so data presented are for 23 individuals across all sites

**includes two southbound migrations for a single Tutakoke female

Table 2. Mass of Black Turnstones fitted with geolocators (pooled across capture sites) compared to mass of all individuals captured at breeding and wintering sites during fieldwork in 2011-2014 to deploy and recover geolocators.

Group (n)	Weight (g)
Geolocator-tagged individuals	
Males (16)	116.2 ± 7.0
Females (8)	131.3 ± 3.9
All captured individuals	
Tutakoke 2013-2014 (109)	122.1 ± 8.3
Cape Krusenstern 2012-2013 (22)	120.9 ± 10.2
Oak Harbor 2011-2013 (42)	118.5 ± 8.5

around each point location was on average ~51 km longitude (range= 1–320 km) and ~153 km latitude (range= 7–800 km).

We identified two high-use regions during migration: 1) western Cook Inlet/Shelikof Strait, Alaska, and 2) the Alexander Archipelago in coastal southeastern Alaska plus the Haida Gwaii Archipelago in British Columbia, and their associated mainland coastlines. Both areas were frequented by turnstones consistently during spring and fall migration (Fig. 4). In the Alexander and Haida Gwaii Archipelagos region alone, Black Turnstones made 17 of 31 (55%) northbound and 8 of 20 (40%) southbound migratory stops. Of 51 migration stopover locations in total, only 5 (9.8%) occurred in interior locations away from the coastline: 3 during northbound and 2 during southbound migration. These interior stopover sites all occurred in Alaska, west of the Aleutian Range, with 3 of the 5 stopovers occurring around the Lake Iliamna and Lake Clark area. No birds were recorded stopping at or around the historically important northern Montague Island stopover site, although one turnstone stopped at the southern tip of Montague Island. Note that for all maps, locations indicated by colored symbols are approximate and subject to error estimates as described above.

3.2 Migration Timing and Duration

Black Turnstones departed the western Alaska breeding grounds in mid-July (range: July 1-24) and moved rapidly to wintering areas along the North Pacific coast, arriving in late July or early August (mean arrival date = 21 July ± 5.3 days; range: 9 July - 2 August). Southbound migration lasted an average of 5.4 days (range = 0.6–15 d) for all 23 tracked turnstones. In spring, the average departure date from the wintering grounds was 1 May ± 5.6 days (range: 19 April – 9 May; n=19). All birds arrived back to the breeding grounds by mid-May (mean arrival date = 12 May ± 3.1 days; range: 5 May – 20 May; n=20). Northbound migration lasted 10.8 days on average (range = 0.6 – 23 days; n=19), approximately double that of southbound migration. We found no significant sex-specific differences in duration of either northbound or southbound migration (NB: $t=0.90$, $df=10$, $p=0.39$; SB: $t=-0.72$, $df=17$, $p=0.48$).

While migrating, turnstones made relatively short "hopping" flights along the coast, stopping between flights for 3.9 days on average (range = 1.5–15 days). Turnstones were more likely to stopover on northbound migration than on southbound migration, and the number of stopovers made by females vs. males were similar in each

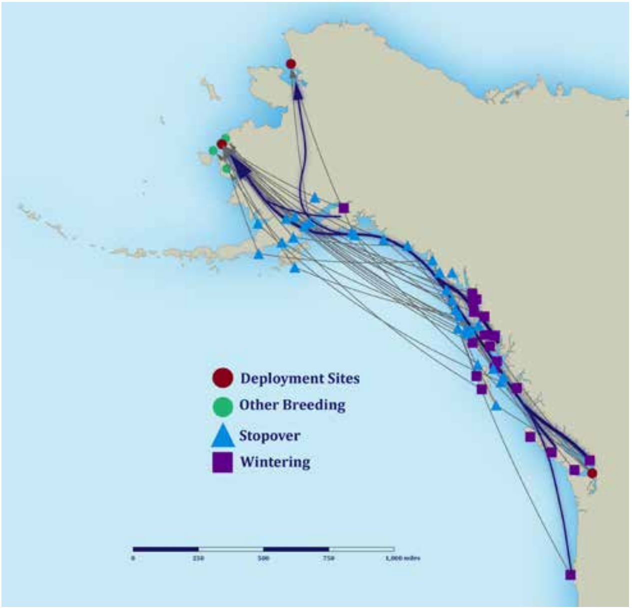

Figure 2. Northbound migration routes of Black Turnstones tracked with light-level geolocators between 2011 and 2015. A stopover was defined as a site where an individual stopped for at least 36 hours. Thin gray lines represent great-circle routes between stops whereas dark blue lines represent theorized “average” migration routes for northbound Black Turnstones based on individual stopover locations and coastal topography. The number of tagged turnstones likely taking each leg of the theorized route is indicated by the thickness of the dark blue line.

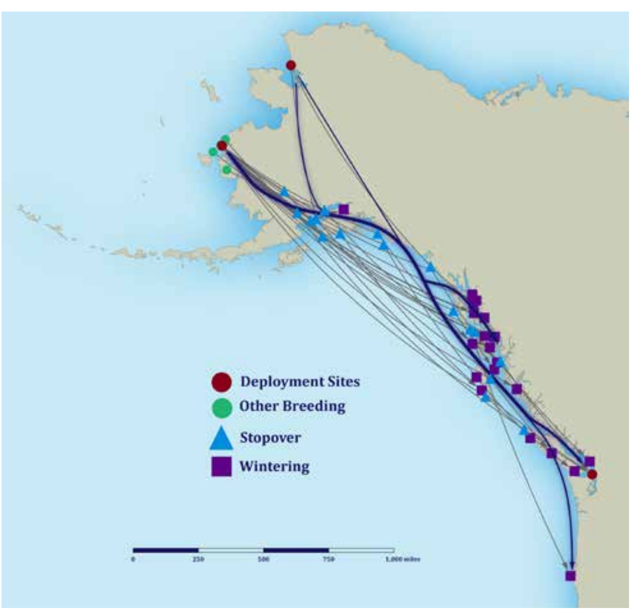

Figure 3. Southbound migration routes of Black Turnstones tracked with light-level geolocators between 2011 and 2015. A stopover was defined as a site where an individual stopped for at least 36 hours. Thin gray lines represent great-circle routes between stops whereas dark blue lines represent theorized “average” migration routes for southbound Black Turnstones based on individual stopover locations and coastal topography. The number of tagged turnstones likely taking each leg of the theorized route is indicated by the thickness of the dark blue line.

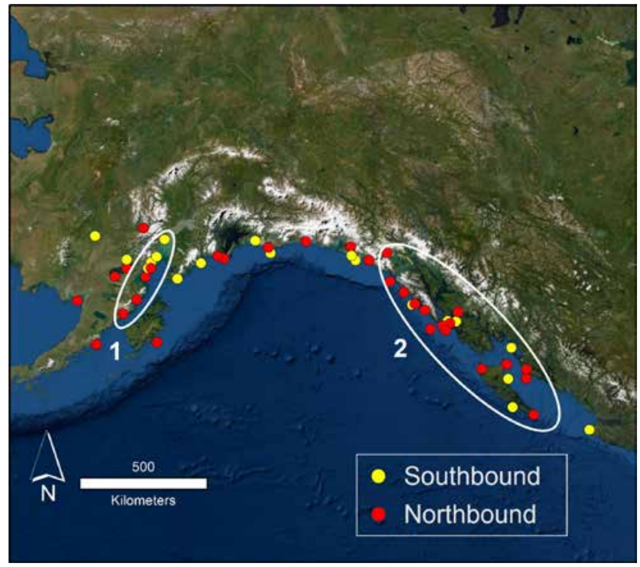

Figure 4. Comparison of stopover locations for Black Turnstones fitted with light-level geolocators, 2011-2015. High-use areas during migration are circled in white: 1 = western Cook Inlet/Shelikof Strait, 2 = the Alexander Archipelago in coastal southeastern Alaska, the Haida Gwaii Archipelago in British Columbia, and their associated mainland coastlines. A stopover was defined as a site where an individual stopped for at least 36 hours.

direction (northbound: 7 females made 15 stops and 9 males made 16 stops; southbound: 8 females made 8 stops and 9 males made 12 stops). However, a larger proportion of females than males stopped during both northbound and southbound migration: 7 of 8 (88%) females stopped over during northbound and 8 of 8 (100%) stopped over going southbound (including the single female for which we have two years of data), whereas only 9 of 15 (60%) males stopped on either north or southbound migration. Four individuals moved to wintering areas within 36 hours of their departure from the breeding grounds without stopping at an intermediate location; all of these individuals wintered in Alaska. These included the female tagged at Tutakoke whose geolocator was recovered in 2015 and therefore provided two years of migration data: she moved to her wintering area within 24 hours of departing Tutakoke in 2013 but took three days to complete southbound migration in 2014. In 2015, she migrated back to the breeding grounds without stopping, as did one other turnstone, a male which had also migrated south in less than 36 hours.

Black Turnstones stopped for >7 days (defined as staging) eight times during our study. Staging events were evenly split between females and males, but seven of eight were on northbound migration. Females tended to stage for longer than males (10 ± 3.6 days vs. 8.5 ±1.7 days; n=4 for both sexes) but the difference was not significant. Staging areas were located primarily on islands in southeastern Alaska's Alexander Archipelago (Prince of Wales and Baranof Islands) and on the Haida Gwaii Archipelago in British Columbia.

3.3 Wintering Locations and Migratory Connectivity

Wintering locations of Black Turnstones in our study spanned 18 degrees of latitude (43–61°N) from the southern Oregon coast to southcentral Alaska's Kenai Peninsula (Fig. 2 and 3). The average distance between breeding and wintering locations across all tagged individuals was 835 ± 504 km.

Of the 20 birds tagged at Alaskan breeding areas, the majority (70%, n=14) wintered on or between British Columbia's Haida Gwaii Archipelago and southeastern Alaska's Alexander Archipelago (corresponding to our high-use area 2, Fig. 4). Wintering areas in this region tended to be located farther inland than migration stopovers, corresponding to greater use of Inside Passage than Outer Coast locations (Figs. 2 and 3). Another five birds wintered in the Pacific Northwest: three on the outer coast of Vancouver Island, one in the northern Puget Sound/San Juan Islands area of Washington State, and one on the southern coast of Oregon. The female tagged at Tutakoke whose geolocator provided 2 full years of location data wintered on the Kenai Peninsula, Alaska, in both years. There was no significant difference ($t=-0.41$, $df=9$, $p=0.69$) in the mean wintering latitude for females vs. males tagged at Alaskan breeding areas: the mean wintering latitude for both sexes was the north end of the Haida Gwaii Archipelago.

While the birds tagged at Tutakoke wintered throughout the range, the two turnstones tagged on the breeding grounds at Cape Krusenstern wintered on the Haida Gwaii Archipelago in British Columbia and on Admiralty Island, Alaska (high-use area 2). The breeding locations of the three wintering turnstones captured at Oak Harbor, Washington, were on the central coast of the Yukon Kuskokwim Delta, where the Tutakoke breeding site is located. One Oak Harbor individual spent the summer at the Tutakoke study site, while the individual that nested furthest from Tutakoke was estimated to be 145 km away.

3.4 Turnstone Abundance in Prince William Sound

During the boat survey conducted between 30 April and 6 May 2015, 765 Black Turnstones were observed during 535.6 km of survey effort in and around northern Montague Island. In addition, turnstone habitat in Prince William Sound was scouted by boat on 27 and 28 April 2015 to test survey methodology; on these days 107 Black Turnstones were observed during 140.2 km of survey effort. Despite a total of 8.4 km-days of Pacific Herring spawn being observed along the shores of northern Montague Island during aerial flights by the Alaska Department of Fish and Game on 27 April and 4 May 2015 [23], the boat survey crew did not observe an increase in the number of Black Turnstones using these areas either during or directly after the spawn events.

4 Discussion

4.1 Migratory and Wintering Patterns and Migratory Connectivity

Our geolocator data identified the Alexander Archipelago in southeastern Alaska and the Haida Gwaii Archipelago in British Columbia, along with their associated mainland coastlines, as an important region for Black Turnstones. Seventy percent of the birds we tagged at Alaskan breeding areas overwintered in this area, and almost half of all stopovers during migration occurred here. Both the Alexander and Haida Gwaii Archipelagos are characterized by long, inaccessible rocky shorelines with minimal human infrastructure or activity. As a result, historic observations of turnstones are available from only a few locations in this region. In the Alexander Archipelago, Black Turnstones were recorded as common during winter in the early 1900's at Prince of Wales and Wrangel Islands [24, 25], while at the Haida Gwaii Archipelago, 2000-3000 turnstones were estimated to be migrating through the area between 30 April and 11 May 1935 [26]. In more recent decades, eBird sightings [27], Christmas Bird Count data [28], and observations made during the British Columbia Coastal Waterbird Survey [29] documented flocks of Black Turnstones during the nonbreeding season (late August through mid-April). At Haida Gwaii, winter flocks often number between 100-300 birds [27, 29]. Near major communities on the inner coast of the Alexander Archipelago, wintering flocks numbering between 100-400 are regularly recorded, although as many as 1400 and 2000 birds have been recorded during October at Juneau and Petersburg, respectively. In both archipelagos, flocks numbering >500 have been commonly observed during spring and fall migration in both the protected waters of the Inside Passage and at more wave-splashed Outer Coast locations

[27]. These observations underscore our geolocator results that Black Turnstones migrate and winter along the outer as well as the inner coast of both archipelagos and the mainland coastline.

Our study also highlights for the first time the importance of western Cook Inlet/Shelikof Strait as both a northbound and southbound migration stopover area. Movements by geolocator-tagged birds revealed that Black Turnstones did not follow the outer coastline between the breeding grounds and this stopover area. Instead, turnstones flew directly over interior habitats, including the Aleutian Range, when en route to and from the Tutakoke and Cape Krusenstern breeding grounds. None of our geolocator-tagged birds stopped along the western coastline of the Alaska Peninsula, although eBird sightings and other historic accounts have regularly recorded southbound flocks of turnstones stopping along the eastern coastline of Bristol Bay from Ugashik (Pilot Station) to Naknek [27, 30]. We suggest that for turnstones traversing the 600-700 km distance to or from the breeding grounds, the Cook Inlet/Shelikof Strait coastline, the eastern coastline of Bristol Bay, and the large lakes on the west side of the Aleutian Range represent the first suitable stopover (for southbound migrants departing the breeding grounds) or the last suitable stopover (for northbound migrants heading to the breeding grounds) before they must traverse an area that lacks their preferred high-energy rocky or sandy shoreline habitat [5].

Interestingly, none of our geolocator-tagged turnstones wintered south of coastal Oregon despite their documented winter range extending south into Mexico [5] and previous band resighting data specifically linking the Tutakoke breeding site with a wintering site at Laguna Beach, CA [31]. An examination of data segmented by 10-year intervals in the eBird database [27] suggests that Black Turnstones are wintering farther north each decade; for example, 1980-1990 shows few individuals wintering north of Vancouver Island whereas 2011-2021 shows individuals wintering all the way into Southeast Alaska (~750 km farther north). eBird and Christmas Bird Count records indicate that flocks >200 birds have rarely been recorded over the past several decades in California, while large flocks regularly occurred during the winter in Washington, British Columbia, and southeast Alaska during the same time period [27, 28]. Pyle and DeSante [32] reported a significant decline in turnstone numbers on Southeast Farallon Island, CA, during the nonbreeding season between 1974 and 1993, although Christmas Bird Count trends were variable along the adjacent mainland coast. It is possible that California may now represent the southern edge of the Black Turnstone nonbreeding range rather than the mid-point. However, the increasing popularity and utility of citizen science programs like eBird and the Christmas Bird Count [33] may obscure true trends in the distribution and abundance of Black Turnstones in the winter in the Pacific Northwest (where the human population is also increasing rapidly), because more people are now making and recording observations in places where few people were recording data in earlier decades. This phenomenon has not been studied scientifically, therefore we cannot estimate the magnitude of its possible effect on our understanding of turnstone migration patterns.

If turnstones are indeed more likely to be found wintering in the northern half of their nonbreeding range, this pattern may be reflective of shorter and warmer winters in the Pacific Northwest. Widespread seasonal warming trends were reported from the early twentieth century through 2012 for the U.S. Pacific Northwest (Washington, Oregon, Idaho, and western Montana and Wyoming) that included a longer frost-free season by approximately two weeks since 1920, and increasing temperatures for the coldest night each winter [34]. Winter (Dec-Jan-Feb) temperatures in the Alaska Panhandle, Northeast Gulf of Alaska, and Cook Inlet regions (comprising the coastal areas of southeastern Alaska to our designated high-use area of Cook Inlet/Shelikof Strait) exhibited an average increase of 2.1 to 3.3°C over the period 1949-2012 [35]. Specifically, for Cook Inlet, Alaska, where one of the geolocator birds wintered in two consecutive winters, climate model projections predict future temperatures increasing as much as 4°C during the winter months, resulting in less snowfall and more rainfall [36]. Taken together, this evidence suggests that Black Turnstones may be able to winter farther north today than in previous decades, and that this trend may continue in and around areas such as southeastern Alaska, Cook Inlet, and Kodiak Island.

The phenomenon of shortening migration distance is thought to be a climate-driven response in numerous other avian species: European Greylag Geese, another short-distance migrant, have significantly decreased their migration distance over the last 60 years, and the average migration distance of this population was shorter in milder winters [37]. The benefits of a shorter migration distance may include reduced mortality during migration, and birds arriving earlier or in better body condition to breeding territories [38, 39]. Earlier arrival to breeding grounds may allow individuals to choose more suitable habitats, which can lead to a consequent increase in breeding success (e.g. [40, 41]). Black Turnstones have the advantage of being relatively short-distance, short-hop migrants, and most of their Pacific Coast migration route provides suitable wintering habitat. For this species, shortening their migration distance in response to climate change could be an easily realized strategy that has the potential to increase overall fitness.

Our estimates of error in the location data, used to assess migration routes and stopover sites described above, were based on post-deployment calibration procedures, which comprise relocations of individuals prior to departure from a known capture site and after arrival back at that capture site the following year [22]. In addition to weather conditions, error in location estimates can be caused by shading of the geolocator due to steep terrain, habitat characteristics (e.g., thick or tall vegetation), individual behavior (e.g., the bird facing away from the sun), or the presence of feathers over the sensor [22]. Shading was determined to cause error in location estimates for many of the geolocators deployed in our study in 2013. In contrast, there was almost no shading error detected in analysis of data from the geolocators deployed in 2011.

An additional source of error related to understanding stopover sites and duration of their use was related to our definition of a stopover site (three consecutive fixes spanning ~36 hours). It is possible that some individuals stopped for <36 hours and therefore these stopover locations were not recognized as such during data analysis.

4.2 Migration Timing and Duration

Although the time spent on either migration was relatively short, Black Turnstones took twice as long to migrate north than south, which is unusual for shorebirds (see congener Ruddy Turnstone, [42]). It is unclear whether this difference in migration timing is typical of Black Turnstone migration in general, because there is a dearth of information on the timing of individual turnstones' migration with which to compare our results. A single male Black Turnstone banded at the Tutakoke breeding area in spring 1978 was observed multiple times each winter at Laguna Beach, CA, during the non-breeding seasons of 1978-1982 [31]. Because the end points of this individual's migration were known, investigators were able to record approximate dates of departure and arrival at each site. In some years but not all, this individual's southbound migration appeared to be faster than its northbound (similar to what we found), although not knowing the exact dates of departure and arrival prevented a precise calculation of migration duration in any one year.

If warming conditions along the Pacific coast migration route have enabled Black Turnstones to shorten their migration length, one result could be increasingly shorter migration durations in the fall but not in the spring. After arriving on the breeding grounds, Arctic-nesting shorebirds rely on local food resources and must time their arrival to coincide with the availability of snow-free habitat [43]. Therefore, turnstones may be constrained in terms of earlier arrival to the breeding grounds, and thus in the speed of northbound migration, by snow and inclement weather at their western Alaska breeding areas in early May. Long-term monitoring of migration at several field sites on the central Yukon-Kuskokwim Delta (close to our Tutakoke breeding site) indicated that shorebird arrival was highly correlated with the timing of the break-up of ice on the Kashunuk River, which varied by year but did not advance significantly during the years of the study (1977-2008) [44].

In contrast to northbound migration, southbound migration is often more flexible, as it is less constrained by weather conditions and food resources as birds fly south. Additionally, many shorebird species time their southbound migration to stay ahead of the migration of avian predators [45, 46]. Four species of waders of varying overall migration lengths generally took longer to migrate in fall but flew faster speeds; the difference in migration duration stemmed from a tendency to take longer stopovers going south [47]. Stopover lengths for Black Turnstones in our study were slightly but non-significantly longer going northbound, and birds were more likely to stopover and to stage (stopover > seven days) on northbound migration, possibly because it is advantageous to move more slowly in the spring while waiting to receive cues regarding conditions on the breeding grounds. Black Turnstones have a relatively short migration length overall: the distance from Haida Gwaii to Tutakoke is approximately 2200 km, which is substantially shorter than the ~5000 km species considered "short-distance" migrants in [47]. Faster migration speeds in the fall, fewer compelling reasons to stopover, and a relatively short distance to migrate (that may be getting shorter with climate change) lead us to predict that southbound migration duration for Black Turnstones may continue to decrease in the future.

However, the pattern we observed (of shorter migration duration in fall than in spring) may have a more localized cause, given that the majority of our estimates of southbound migration duration were derived from geolocators deployed at the Tutakoke site in 2013. The breeding season of 2013 was unusual on the central Yukon-Kuskokwim Delta: it was a cold, late spring with snow cover remaining until early June and the breakup of river ice occurring 18 days later than the 1985-2012 average for the region [48]. Many bird species at Tutakoke initiated nests later than average, including Black Turnstones. Then on

29 June 2013, there was a significant flood event on the Bering Sea coast in the vicinity of the Tutakoke site [48], which corresponded to the average predicted hatch date of the turnstones captured at Tutakoke during our geolocator deployment effort. Many turnstones would have lost nests or flightless chicks during this event. The late spring (causing a delayed breeding season) combined with largescale nest failure prior to chicks fledging could have hastened southbound migration departure, and therefore increased the duration of fall migration, for turnstones captured at Tutakoke in 2013.

4.3 Importance of Prince William Sound as Migration Stopover

The observation that initiated this study was a significant reduction in the number of Black Turnstones recorded at northern Montague Island (an Important Bird Area for the species) during the spring of 2010 compared to previous observations in the late 1990s [12]. During our 2011-2015 geolocator study, <10% of Black Turnstone stopovers (5 of 51) were recorded in the vicinity of Prince William Sound, and no birds stopped over at northern Montague Island. This, in addition to the diversity of stopover sites we did observe, suggests that northern Montague Island is not an obligate stopover and birds are using alternative stopover sites on northbound migration.

We additionally suggest that turnstones are flexible and opportunistic in their choice of stopover sites and are not reliant on herring spawn to continue their northbound migration. Herring spawn each year from mid-March through early May from Puget Sound, WA/Vancouver Island, BC to the northern end of Alexander Archipelago in southeastern Alaska [49, 50]. Despite the presence and abundance of herring spawn during the same months that Black Turnstones are migrating north through these areas, reports of turnstones foraging on spawn are lacking except from northern Montague Island in Prince William Sound. Additionally, while previous diet studies at Montague Island in the early 1990s found that herring spawn formed an important component of the diet of migrating turnstones, individuals also exhibited a varied diet that included mussels and barnacles, and no spawn was found in the gut contents of 31% of the turnstones collected [11].

Similar to other areas along the Pacific Northwest, herring spawn in Prince William Sound has historically been an ephemeral resource characterized by dramatic fluctuations in timing and quantity [51]. In particular, the herring population in Prince William Sound expanded and peaked around 1988 and declined significantly thereafter, for a variety of reasons likely including the Exxon Valdez oil spill, infectious disease, poor nutrition, and overexploitation by the fishing industry [51]. As a result, during the 1980s and most of the 1990s the average spawn deposition around the Montague Island area was ~66 km-days per year and may have been a significant and predictable resource for northbound turnstones. After 1999, however, spawning around Montague Island steadily declined, culminating in the years 2016-2018 when no spawning activity was recorded [51]. These changes in herring spawn availability and distribution may have led to reduced reliance of Black Turnstones on herring spawn in Prince William Sound to fuel northbound migration after the late 1990s, and the observed decline in turnstone use of northern Montague Island each spring. Turnstone reliance on herring spawn at northern Montague Island during northbound migration may have a temporary pattern exhibited by an opportunistic species to take advantage of an ephemeral resource, rather than herring spawn being the primary driver of turnstone distribution during migration, and Montague Island being a critical stopover for the population. We also acknowledge that we do not know whether we sampled a portion of the Black Turnstone breeding population that would have stopped over at northern Montague Island in the past, or if there is some portion of the population that never used this area as a stopover site. To our knowledge, there has been no research done on population structuring in this species that would help illuminate this distinction.

4.4 Conservation Implications and Future Directions

Our examination of Black Turnstone migration routes and duration has provided insight into broad patterns of migratory routing, duration, and connectivity for this charismatic rocky coast shorebird. In particular, geolocator-derived location estimates confirmed a changed reliance on the Prince William Sound/northern Montague Island area during spring migration, and documented significant use of the western Cook Inlet area and the Alexander and Haida Gwaii Archipelagoes by both migrating and wintering birds, including that some individuals may be using the latter area for staging on northbound migration. Matching our geolocator data with citizen science efforts such as eBird, Christmas Bird Count, and the British Columbia Coastal Waterbird Survey makes obvious the need for focused surveys for Black Turnstones during the non-breeding period in more remote parts of our documented high-use areas, as these areas have not historically been visited frequently in the winter and casual observations are rare. Focused surveys could help determine whether there are specific locations within these high-use areas that should be recognized as important for migrating or wintering turnstones. Surveys in these areas could also provide further insight into which habitat characteristics drive stopover and staging decisions by turnstones. Such surveys done in conjunction with the use of smaller GPS tags that have been recently developed for migration tracking could reduce the error associated with our assessment of migration routes and stopovers, and further assist with understanding important use areas for turnstones during the non-breeding season.

Additional information is also needed to understand the population-level significance of our findings regarding changing patterns of stopover and wintering site abundance. For example, it is unclear from our study where turnstones wintering in the southern half of the non-breeding range (south of Oregon) are nesting. And while current population estimates do not indicate a significant change in the breeding population size for Black Turnstones (95,000 individuals in 1992 [4] vs. 135,859 individuals currently [95% LCL = 87,603, 95% UCL = 184,115; J. Lyons et al., *unpubl data*.]), the central coast of the Yukon-Kuskokwim Delta is experiencing a loss of the low-lying sedge meadows favored as nesting habitat by Black Turnstones [6]. Additionally, storm surges that inundate vast swaths of nesting habitat during the breeding season, and deliver large quantities of sediment (potentially leading to elimination of low-lying sedge meadow habitats), may increase in frequency as climate change alters weather patterns and protective sea ice formation along the Bering Sea coast [7]. An updated understanding of the density of Black Turnstones nesting in the most at-risk coastal habitats (a two-kilometer band of habitat immediately adjacent to the coast on the Central Yukon-Kuskokwim Delta, [4]) would help interpret changing migration and wintering patterns and inform future breeding season population estimates.

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