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Low Migratory Connectivity and Use of Multiple Non-Breeding Sites in American Golden-Plovers Breeding Across the Nearctic Tundra

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ABSTRACT

Aim: Many populations of migratory birds are currently declining. Understanding space use throughout the entire annual cycle, as well as migratory connectivity (i.e., geographic linkage of individuals and populations across different stages of the annual cycle), can improve our ability to identify factors driving population declines and influencing extinction risk. The main objectives of our study were to (i) document the space use and phenology of migration during the non-breeding period and (ii) quantify the degree of migratory connectivity across the range of the American Golden-Plover (*Pluvialis dominica*) breeding across the North American Arctic.

Location: American Golden-Plovers that breed across their entire breeding range (northern North America) and migrate up to their main wintering site located in South America.

Methods: We used archival light-level geolocators to track the migration. We quantified migratory connectivity based on the non-breeding range spread of all individuals and the breeding population spread. We used Mantel tests to evaluate whether the relative spatial configuration of the sampled breeding area was preserved on the non-breeding ground.

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Results: We identified 13 and 7 stopover sites used during the fall (post-breeding, southbound) and spring (pre-breeding, northbound) migrations, respectively, and one main site used during the wintering period. We highlight stopover sites that were previously unknown and show the transatlantic and transpacific routes used by plovers during migration. We found that individuals breeding in proximity tended to be closer to each other during brief and highly limited portions of the non-breeding period. Broadly, individuals from different breeding populations were well mixed during the wintering period and throughout most of the spring and fall migrations.

Main Conclusions: Overall, the migratory connectivity of American Golden-Plovers is relatively low for most of the non-breeding period, suggesting that breeding populations separated by large distances should be similarly affected by disturbances and changes encountered at some migratory stopovers and in the wintering area.

1 | Introduction

Many migratory animals are currently suffering global declines (Smith et al. 2020, 2023; Wilcove and Wikelski 2008). Determining the main drivers of those trends is complex, especially when a species range is large and in the absence of adequate knowledge of the scale (population or species) at which the main stressors are operating (Cresswell 2014; Knight et al. 2021). In migratory animals, the relative impact of events occurring in one area of a species distribution range depends on the level of population mixing at that given place and time (Esler 2000). A good knowledge of individual movements among populations during different seasons of the annual cycle is thus critical for predicting the response of migratory species to environmental changes. Understanding patterns of migratory connectivity, which typically describe how breeding and non-breeding sites are connected via the trajectories of individual migrants (Bauer et al. 2015; Boulet and Norris 2006; Webster et al. 2002), is of paramount importance to develop and implement adequate conservation strategies.

Migratory connectivity (Bauer et al. 2015; Boulet and Norris 2006; Webster et al. 2002) is typically described along a continuum from low to high (Finch et al. 2017; Webster et al. 2002). Under low migratory connectivity, individual migrants from a particular breeding population spread widely over a shared area during the non-breeding period, mixing with individuals from different breeding populations. Conversely, strong connectivity reflects the use of discrete, population-specific non-breeding areas by individuals from discrete breeding areas (Webster et al. 2002). Although migratory connectivity can apply to all periods of the annual cycle (Boulet and Norris 2006), most studies contrast the breeding and wintering locations of individuals (e.g., Ambrosini et al. 2009; Finch et al. 2015; Trierweiler et al. 2014; van Wijk et al. 2018). Yet, determining the level of mixing during migration and at staging sites is equally, if not more important, because mortality can peak during migration (Newton 2025). Moreover, time should be considered when quantifying migratory connectivity as it can have strong conservation implications. Indeed, birds from several populations can asynchronously use the same area, and hence may never be together at the same time (Bauer et al. 2015; Briedis et al. 2016; Knight et al. 2021; Lagassé et al. 2022). In such a case, focusing solely on space could yield results about the migratory connectivity that would not hold when considering both space and time (Bauer et al. 2015). Finally, the spatial distribution of the studied breeding populations should be as wide as possible and aim to represent the whole breeding range of a given species to generate solid conclusions on the level of migratory connectivity (Cohen et al. 2018; Knight et al. 2021; Vickers et al. 2021).

The main objectives of our study were to (i) determine non-breeding site use of American Golden-Plovers breeding across the North American Arctic (*Pluvialis dominica*) and (ii) quantify the range-wide degree of migratory connectivity using archival light-level geolocators while accounting for temporal variation in space use. American Golden-Plovers (hereafter referred to as plovers, Figure 1A) are transequatorial migrants with a wide breeding longitudinal distribution across the North American Arctic, from Western Alaska to Eastern Nunavut (Clay et al. 2009; Johnson et al. 2020) (over 3,300,000 km^2). These plovers follow an elliptical migration pattern, flying over the Atlantic during their southbound migration to reach their wintering grounds in southern South America, and then returning to their northern breeding area by flying along a mid-continental route (Antas 1983; Dinesen et al. 2019; Johnson 2003; Lamarre et al. 2021). A better understanding of migratory connectivity is highly relevant for the conservation of American Golden-Plovers. The species is declining (Clay et al. 2009; Smith et al. 2023) and exposed to various threats during the non-breeding period, including exposure to agrochemicals, loss of habitat, climate change and hunting (Clay et al. 2009; Johnson et al. 2020; Stodola et al. 2014).

2 | Methods

2.1 | Capturing and Marking Plovers

Incubating adult American Golden-Plovers were captured at eight study sites distributed across the entire breeding range of the species (Figure 1B). The studied breeding populations were separated by an average of 1864 km and as much as 3800 km (distance between Nome and Bylot Island, Figure 1B). Plover nests were located by searching appropriate habitats and individuals were trapped with a 60 cm dome bow-net placed over their nest. Individuals were fitted with metal and plastic bands, along with a light-level geolocator (archival data logger) attached to a leg flag, all placed on the tibiotarsus (Figure 1A, Table S2). Geolocator models deployed included British Antarctic Survey MK10b (weight ~1.1 g) and Migrate Technology Ltd Intigeo geolocators W65A9RK (weight ~0.9 g), and they represented < 0.8% of the minimum body mass of plovers (average mass: 142.4 g, range 126–162 g, $n = 25$). Geolocators are archival devices that estimate latitude and longitude by recording light levels (Lisovski et al. 2012) and must be retrieved to collect data. Geographic variation in the timing of sunrise and sunset is used to estimate the geographic location of individuals (Lisovski et al. 2012). Night and day length are approximately equal across latitudes

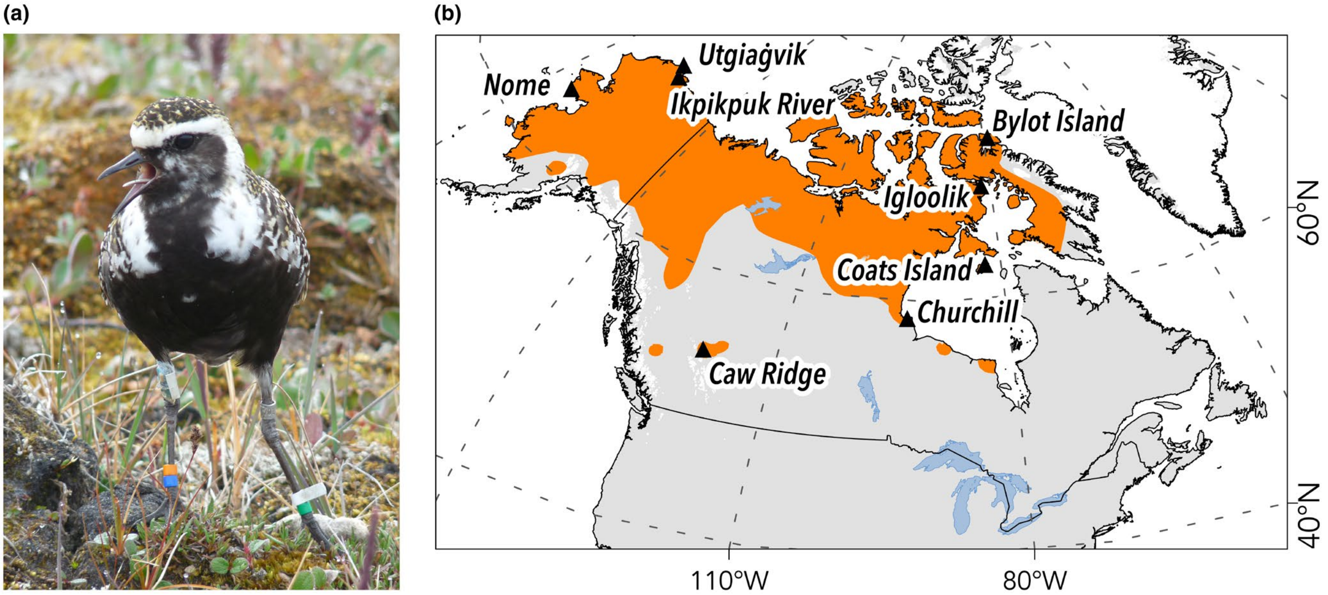

FIGURE 1 | (A) Picture of a marked adult American Golden-Plover. Photo credit Josée-Anne Otis. (B) Map of the American Golden-Plover breeding range (orange; based on Johnson et al. 2020) showing the locations of study sites (triangles) distributed across the breeding range.

during the spring and autumn equinoxes, which increases the degree of uncertainty in estimates of latitude at that time, but not in longitude.

A total of 262 geolocators were deployed from 2009 to 2015, and 45 of them (~17%) were retrieved by recapturing plovers 1–4 years after their initial capture (Table S1). The distance between nest locations of marked individuals monitored for more than 1 year was 319 m on average (range 54–1119 m; $n = 22$). No effects of the geolocator on annual survival were detected (Weiser et al. 2016) and the relatively low recovery rate of geolocators likely reflects the difficulty of re-sighting and recapturing marked plovers on their breeding grounds (i.e., the breeding site fidelity has to be high; the individual must initiate breeding and be re-observed in the field; its nest must be located and the individual recaptured prior to nest depredation or hatching). The effort deployed in the field to recapture plovers was also variable between breeding populations. Although 45 geolocators were retrieved (Table S2), nine of them only showed partial migration tracks due to equipment failure, which left 36 loggers with tracks covering most of the non-breeding period. Of these tracks, 33 came from different individuals and were used in the analyses, unless otherwise indicated.

2.2 | Processing Geolocator Data

Plovers that were recaptured had their geolocator leg flag removed and light data was downloaded using the Communicate program in BAStrack for BAS geolocator (Fox 2010) or Intiproc for Intigeo geolocators (Fox 2018). Data were processed through GeoLight 2.0 (Lisovski et al. 2015) to convert light-level data to location estimates. Following Finch et al. (2015), we used a light threshold of 3 for BAS devices and of 2 for Intigeos, as light data output is different between models of geolocators. We converted light data into two daily locations (morning and evening values in latitude and longitude) for each bird from geolocator deployment to recovery, except when devices malfunctioned during the non-breeding period. For Arctic-breeding birds exposed to full daylight when at high latitude, the dataset was restricted to dates when nights were detected. To reduce light noise during night-time, the lightFilter function in GeoLight 2.0 was used (Lisovski et al. 2015). Most loggers were calibrated using the rooftop method ($n = 27$, 64%) to provide a start angle for the Hill-Eckstrom calibration (mean = 6.63° range [−7.33, −2.73], $n = 27$). Residency periods were identified with the ChangeLight function in GeoLight 2.0 (quantile = 0.9) with a specified minimum residency length of 2 days. For movement periods or if no optimal sun elevation angle could be obtained by either rooftop or Hill-Ekstrom calibration, we used the angle provided by the rooftop calibration, and if unavailable, the civil twilight (i.e., 6°; Lisovski et al. 2015; $n = 9$). We filtered the estimated locations obtained with a loess filter ($k = 2$) to remove outliers.

Following Hobson and Kardynal (2015), the migration track of each plover was smoothed with a state-space Kalman filter and the most probable path was obtained with kftrack (Sibert and Nielsen 2002) in R. Kalman filtering provides the most probable track from location data and reduces observer bias when dealing with raw location estimates obtained with geolocators (Gow 2016; Hobson and Kardynal 2015). As the estimated flight speeds of American Golden-Plovers vary widely (see Johnson et al. 2020), we used a relatively high flight speed estimate (104.6 km/h; Johnson and Morton 1976), corresponding to a maximum of 2510 km/day, to set the diffusion component of the model. Kftrack uses an asymmetric error structure peaking on the winter side of the equinoxes, which is typical for geolocator data. Location precision was calculated from calibration data and yielded a mean error of 163 ± 75 km ($n = 20$), comparable to prior studies (Lisovski et al. 2012 and references therein).

As outlined by Knight et al. (2018), the use of geolocators for determining how migratory birds are spatially connected between breeding and non-breeding periods has some important limitations. The uncertainty in location estimates obtained using geolocators can be up to 300 km, particularly around the equinox. Hence, this method is not adequate for detecting small-scale spatial segregation between individuals from different breeding populations. Moreover, our conclusions apply only to individuals who successfully returned to their breeding site and initiated nesting in more than 1 year. We cannot exclude that those not recaptured on their breeding site may have used different migratory strategies.

2.3 | Non-Breeding Site Use

We combined geolocator data obtained from all individuals to characterise non-breeding site use. We first defined the location of 'non-breeding sites' by inspecting each individual track and by identifying clusters of locations where movements had lost directionality and became erratic for at least five consecutive days. Hence, the minimum stopover duration at a given non-breeding site could be 5 days. The contour of a cluster associated with a given individual was first defined using the minimum convex polygon (MCP 95%) (Ghetta et al. 2022). Clusters obtained for different individuals were merged into a single cluster when the contour lines overlapped with the contour of an adjacent cluster. All locations assigned to the same cluster were subsequently used to define the boundary of each non-breeding site using Kernel density estimates (75%; R library ks—function kde; Duong 2018). As American Golden-Plovers are terrestrial birds, non-breeding sites were clipped to remove any areas over oceans. The southernmost site used the longest by an individual was designated as its wintering site, while stopovers were designated according to the direction of the migratory path (fall stopovers for southward movement; spring stopovers for northward movement). Departure date was the date of the first location out of a given site when birds initiated unidirectional movement away from the site, and arrival date was the date of the first location within the site when movement was reduced, lost directionality and became erratic.

2.4 | Quantitative Measure of Migratory Connectivity

We investigated the temporal change in migratory connectivity during the non-breeding period using the Mantel test (Ambrosini et al. 2009; Cohen et al. 2018; Knight et al. 2021; Vickers et al. 2021). We characterised the migratory connectivity relative to the breeding locations of individuals by estimating the correlation between two distance matrices (Goslee and Urban 2007). The Mantel correlation coefficient (r_M) can range from −1 to 1, with 0 indicating random mixing of individuals when comparing their breeding spatial distribution with their spatial distribution during the non-breeding period, 1 indicating that individuals retain their relative spatial positions across seasons (Ambrosini et al. 2009). A positive r_M value does not inherently imply that individuals from a breeding population are in close spatial proximity to one another during the non-breeding period. Rather, it indicates that the relative spatial configuration on the sampled breeding area is maintained at non-breeding sites.

During the non-breeding period, daily distance matrices (measuring distances between all individuals on a given day) were generated and a new r_M value was calculated for each date, alongside a confidence interval that was computed using a bootstrap approach (Goslee and Urban 2007). The r_M thus represents the degree of spatial organisation of individuals at a specific date relative to their breeding distribution. As geolocators can provide up to two locations per day, we used the centroid of those locations to calculate the great circle distance between two individuals positioned at a given date.

Statistical significance of the Mantel correlation coefficient was determined by random permutations. We randomly permutated the position of individuals at the breeding grounds 9999 times; for each permutation, a distance matrix was calculated and its correlation coefficient with the actual distance matrix of individuals at a given date of the non-breeding period was calculated. The significance of the observed Mantel coefficient was assessed by comparing its rank among the coefficients generated through the randomisation procedure (Ambrosini et al. 2009). When significant connectivity was detected ($r_M > 0$), we investigated the process that generated it by assessing the number of potential clusters in case of migratory structuring (using the 'pamk' function in the R package fpc; Hennig and Hennig 2025; see Ambrosini et al. 2009; Ramos et al. 2015). The number of clusters was identified as the number that maximised the overall average silhouette width (oasw), a measure of the goodness of fit of the overall classification of points in a given number of clusters (Rousseeuw 1987).

To quantify the strength of migratory connectivity and to facilitate the interpretation of temporal variation in r_M, we extracted, for each distance matrix calculated for different dates, the average distance observed between all individuals. This provided a proxy of the non-breeding range spread of individuals at a given date (Finch et al. 2017) and an indication of the variation through time in the scale of the spatial structure (Cresswell and Patchett 2024). We also calculated for each date the mean distance among individuals originating from the same breeding area to examine the temporal variation in breeding population spread across the non-breeding period (Finch et al. 2017). For this purpose, we used breeding areas represented by > 2 individuals. The Ikpikpuk River and Utqiaġvik study sites were grouped into a single Alaskan breeding population as they are separated by only 111 km. Finally, we measured the distances between locations obtained at the same date but during two different years for the same individuals to assess individual consistency in space use and timing (Bauer et al. 2015).

Individual locations could not be estimated every day during the non-breeding period because of extended daylight periods at high latitudes or imprecise estimations of latitude around the equinox. Hence, we could not compare the distance among individuals on those dates. We first ran the analyses using all individuals ($n = 33$), which included birds tracked during most of the non-breeding period but located less regularly (total of 115 days, spread from October 7 to May 3; Nome: $n = 2$, Utqiaġvik: $n = 1$, Ikpikpuk River: $n = 1$, Caw Ridge: $n = 1$, Churchill: $n = 4$, Coats Island: $n = 1$, Igloolik: $n = 6$, Bylot Island: $n = 17$). We also repeated our analyses (variation of r_M and of mean distance between individuals through time) using a subset of 20 individuals that were regularly located on the same dates over most of the non-breeding period (total of 149 days, spread from August 27 to May 14). All studied breeding locations were represented (Nome: $n = 1$, Utqiaġvik: $n = 1$, Ikpikpuk River: $n = 1$, Caw Ridge: $n = 1$, Churchill: $n = 3$, Coats Island: $n = 1$, Igloolik: $n = 3$, Bylot Island: $n = 9$). Results were similar in these two analyses (see Section 3) and thus the description in the main text is based on those obtained with the sample of 33 individuals. Because geolocators were deployed over different years, the 33 individuals were not tracked over the same annual cycle. Therefore, we also ran our analyses separately for each annual cycle and compared the results with those obtained using pooled years. All distances provided in the results are great-circle distances and all analyses were performed using R version 3.5.3 (R Core Team 2019).

3 | Results

3.1 | Non-Breeding Site Use

We identified a total of 13 and 7 stopover sites used by plovers during the fall (post-breeding, southbound) and spring (pre-breeding, northbound) migrations, respectively, and one wintering site (Table 1, Figure 2). Those 21 non-breeding sites were used for periods ranging from 6 to 169 days (Table 1, Figures 2 and 3). Among the stopover sites identified, 40% were used by more than one individual (Table 1, Figure 2, Table S2).

During the first leg of the fall migration, birds from distant breeding populations (e.g., Ikpikpuk River and Bylot Island) used the same stopover site located in the eastern Canadian Arctic (Foxe peninsula, in Nunavut; Table 1, Figure 3). Between late August and mid-October, 70% of the birds (23 out of 33 individuals) flew over eastern Canada and New England and undertook a transoceanic route to reach South America. Birds breeding at Churchill and Caw Ridge used slightly different paths and flew mostly overland. After the transatlantic flight, central Brazil was used as a stopover site by birds originating from most breeding populations (6 out of 8; Table 1, Figure 2). All birds wintered in La Plata River Basin, a large area (447,615 km^2) encompassing southern Brazil, Uruguay and northeastern Argentina (Figure 2), from late September to mid-March (Table 1, Figure 2).

Most plovers initiated spring migration in late February. Plovers originating from six out of eight breeding populations stopped in the upper Amazon basin (Peru, Western Brazil) before resuming migration (Table 1, Figure 3). In spring, 48% of the individuals flew through the western part of South America and over Central America, while the rest flew over the Pacific Ocean to reach North America. Then, 97% of tracked individuals continued their northbound journey along the Mississippi basin. The West North Central states stopover site, mainly located in South Dakota, Nebraska and Kansas in the USA (Figure 2), was the last stopover site shared by individuals originating from all breeding populations in spring (Table 1, Figure 2).

3.2 | Migratory Connectivity

Non-breeding range spread of all individuals and population spread (average distance observed between individuals originating from the same breeding population) were highest during the early fall migration, decreased sharply afterward and were lowest during the wintering period when all birds were in the La Plata River Basin, in early December (Figure 4A). Moreover, non-breeding range spread of all individuals and population spread for specific breeding populations were similar during the wintering period (Figure 4A). Interestingly, the non-breeding range spread increased during the early spring migration but decreased sharply in late April/early May, when all plovers were located in the Mississippi Basin (Figure 4A).

Significant positive r_M values, indicating that the relative spatial configuration present on the sampled breeding area was maintained on the non-breeding ground, were observed for only 5 out of 115 days (4%) for which all tracked individuals ($n = 33$) were located (Figure 4B). During fall migration (October 7 to November 8), a positive r_M was present for 2 out of 23 days (9%) even though individuals were spread over a relatively large area, 1008 km on average (95% CI: [823 km, 1192 km]). During the few weeks following the arrival of birds on their wintering area (from November 9 to December 21), 2 out of 30 days (7%) were characterised by positive r_M values, and individuals were spread over 464 km on average (95% CI: [436 km, 492 km]). During the rest of the winter and the early spring migration (from December 22 to April 15), individuals from different breeding locations were well mixed, as no positive r_M values were detected over 49 days. During that period, individuals were spread over 815 km on average (95% CI: [673 km, 956 km]). During the spring migration (April 16 to May 3), r_M values gradually increased over time but were significantly positive only for the last day with data from all individuals (out of 13 days). During that period, individuals were spread over 526 km on average (95% CI: [470 km, 581 km]). Analyses based only on birds tracked over the same annual cycle (see Appendix S1, Figure S1) or restricted to individuals most frequently located (Figure S2), hence with lower sample sizes, generated similar overall patterns and indicated that plovers from different breeding locations were well mixed during most of the non-breeding period.

In all cases ($n = 5$) where significant positive r_M values were observed, plovers could be grouped into two distinct clusters (overall average silhouette width value, oasw, varying from 0.70 to 0.74; Figures S4 and S5). This indicates that, for at least a few days, groups of individuals had a relative spatial configuration on the non-breeding ground similar to their breeding location. One cluster included plovers from all four breeding populations located in the western part of the breeding range

TABLE 1 | Timing and intensity of use of non-breeding sites by adult American Golden-Plovers ($n = 33$) originating from eight breeding populations spread across the entire species breeding range (see Figure 2 for location of sites). For each site, median arrival and departure dates [range: month/day when more than one individual], median duration, number of individuals detected along with percentage of all individuals and number of breeding areas from which individuals originated are shown.

Non-breeding site name	Median arrival date [range]	Median departure date [range]	Median duration [range]	Total number of individuals (percentage)	Number of breeding populations
1. Southern British Columbia, Canada	07/12	07/27	16	1 (3%)	1
2. Kivalliq-A, Nunavut, Canada	08/10	08/25	16	1 (3%)	1
3. Kivalliq-B, Nunavut, Canada	08/09	08/19	11	1 (3%)	1
4. Kivalliq-C, Nunavut, Canada	08/11	08/20	10	1 (3%)	1
5. North Hudson Bay, Nunavut, Canada	08/17 [08/12–08/23]	08/26 [08/21–09/01]	10 [10–10]	2 (6%)	1
6. Foxe Peninsula, Nunavut, Canada	08/13 [08/03–08/20]	08/23 [08/14–08/31]	11 [7–18]	18 (55%)	3
7. Hudson Bay Lowlands, Ontario, Canada	07/09 [06/29–08/07]	08/22 [08/18–08/25]	45 [12–57]	5 (15%)	2
8. North Dakota, USA	08/01	08/06	6	1 (3%)	1
9. South-Central USA	09/27	10/09	13	1 (3%)	1
10. Northeast USA	09/03	09/10	8	1 (3%)	1
11. Northeast South America	09/15	10/03	19	1 (3%)	1
12. Central Brazil	09/20 [08/31–10/05]	10/07 [09/09–10/14]	14 [6–29]	11 (33%)	6
13. Northern Brazil-A	09/28 [09/06–10/21]	10/10 [09/17–11/01]	12 [12–12]	2 (6%)	2
14. Northern Brazil-B	09/19	10/07	19	1 (3%)	1
15. La Plata River Basin	10/10 [09/23–11/10]	02/19 [01/20–03/15]	135 [102–169]	33 (100%)	8
16. Upper Amazonian Basin	02/15 [02/04–03/09]	03/10 [02/25–04/11]	20 [7–39]	18 (55%)	6
17. Northwest South America	03/03	03/10	8	1 (3%)	1
18. South Mexico	03/02	04/04	34	1 (3%)	1
19. Lower Mississippi Basin, USA	04/08 [03/26–05/04]	05/09 [04/18–05/16]	33 [8–46]	32 (97%)	8
20. Southeastern USA	04/22	05/07	16	1 (3%)	1
21. West North Central states, USA	05/13 [04/16–05/20]	05/24 [05/03–05/28]	11 [6–22]	26 (79%)	8

(Nome, Utqiaġvik, Ikpikpuk River and Caw Ridge), whereas the second cluster consisted exclusively of birds from breeding populations located in the eastern part of the breeding range (Churchill, Coats Island, Igloolik and Bylot Island). While the western cluster showed non-significant connectivity ($n = 5$, $r_M = -0.25$, $p = 0.58$), the eastern cluster was structured as two significant sub-clusters ($n = 28$, $r_M = 0.19$, $p = 0.03$; oasw = 0.76): one sub-cluster only included individuals breeding in Churchill and Coats Island, whereas the second sub-cluster consisted exclusively of birds from Bylot Island and Igloolik.

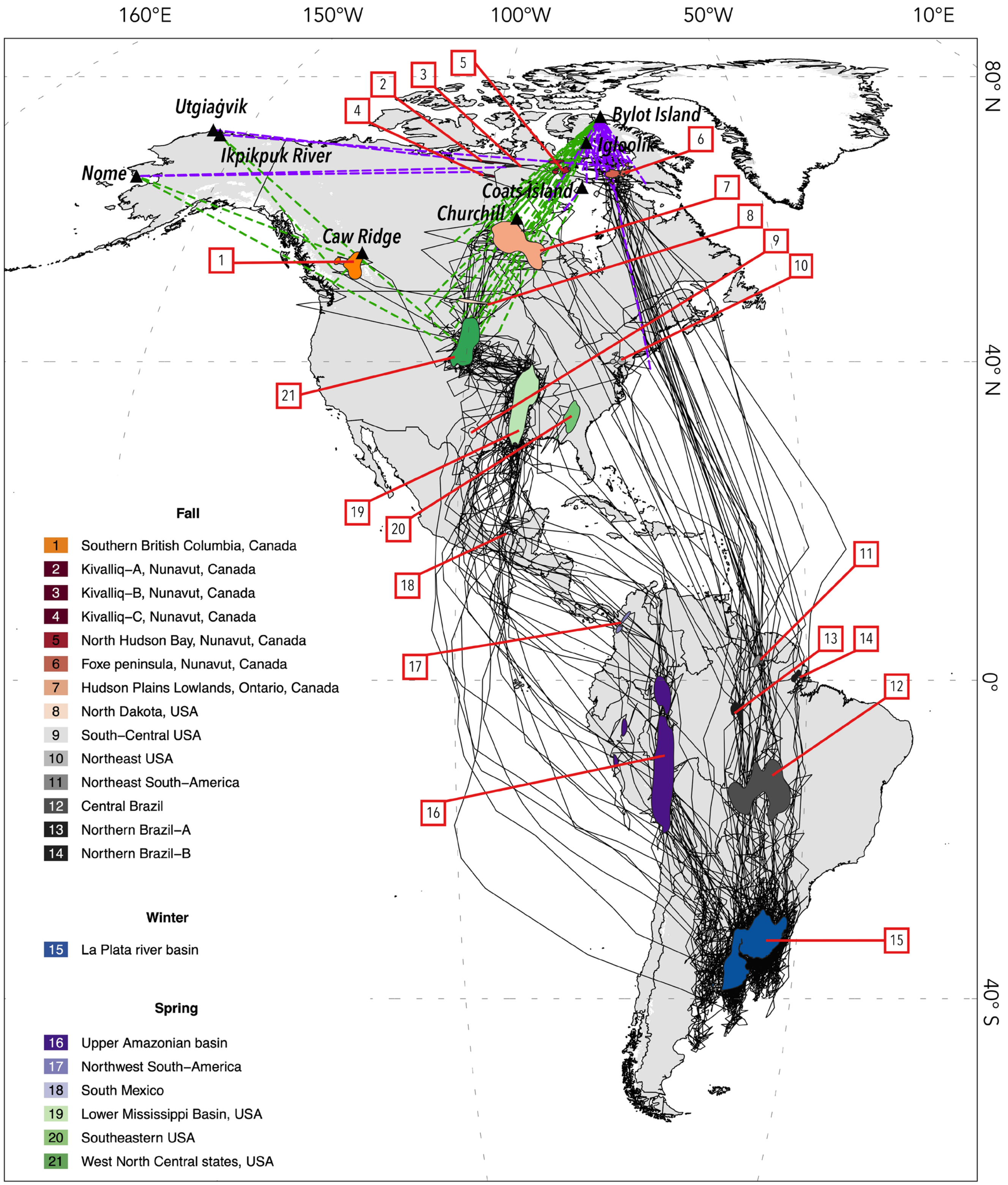

FIGURE 2 | Individual paths and kernel density estimate (75%) of non-breeding sites used by adult American Golden-Plovers tracked with geolocators throughout the annual cycle. Only individuals with near complete tracks ($n = 33$) were used for the analysis. Kernels were post processed with a land mask to retain only terrestrial areas. Individuals were marked at eight breeding areas (black triangles) spread over the entire breeding range. Straight dashed lines were used to connect the breeding site and the first or the last location obtained during the fall (purple) or spring (green) migration.

Three birds were successfully tracked over two annual cycles. Distances between locations obtained from the same individual on the same date in different years, suggested a relatively high individual consistency in space use and timing, during winter (from late October to early February) but less so during spring and fall migration (Figure 3, Figure S3).

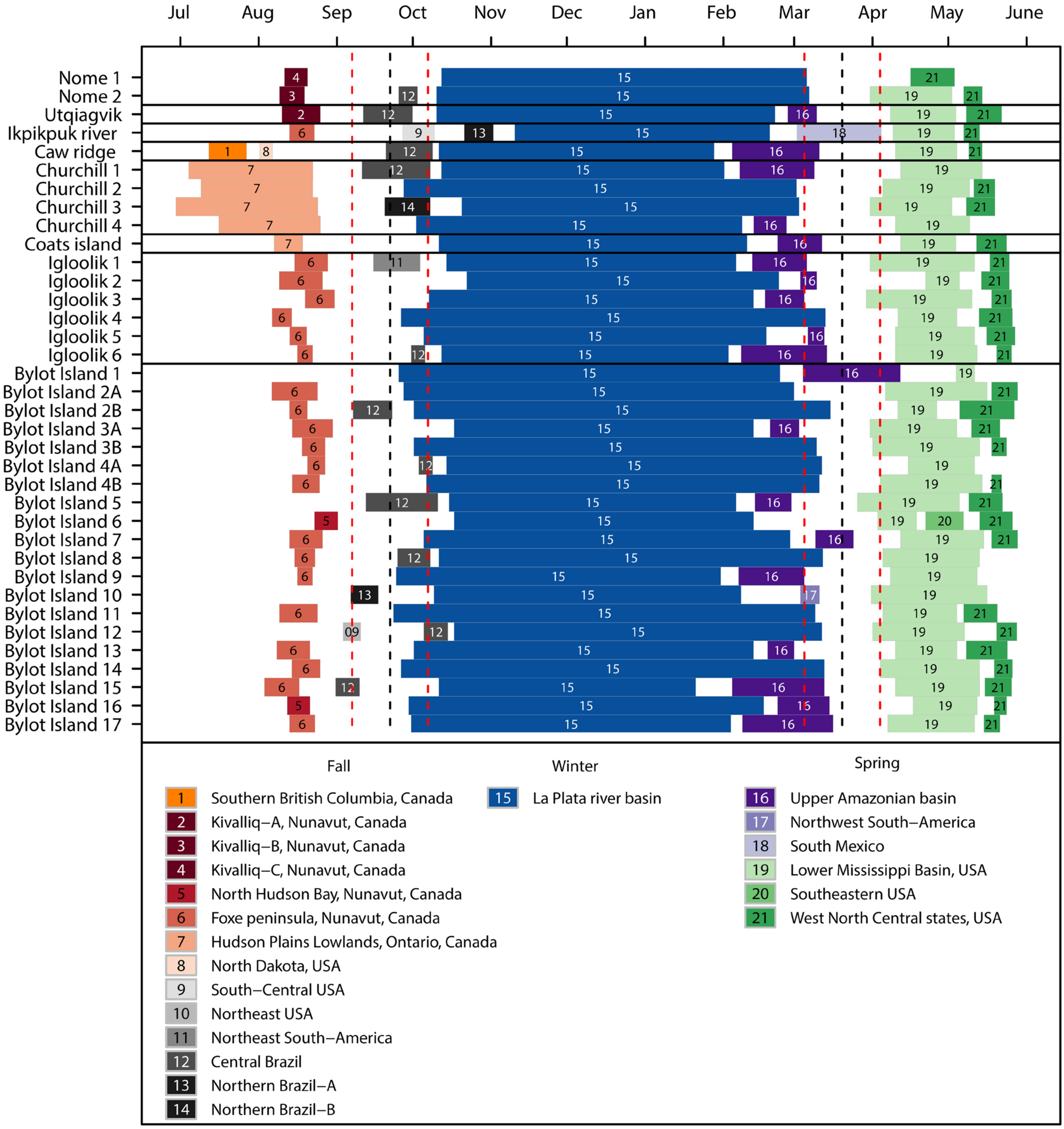

FIGURE 3 | Timing of use of non-breeding sites throughout the annual cycle by 33 adult American Golden-Plovers marked with geolocators in eight breeding populations (indicated on the *y*-axis with suffix indicating individual plover number at given site; alphabetic suffix [A, B] is for the same individual tracked in different years). Red vertical dashed lines indicate the periods with less reliable locations (i.e., obtained 15 days before and after the equinoxes indicated by the black vertical dashed lines). Each tick mark is the first day of the month.

4 | Discussion

Unlike most studies that track only one or a few populations of species with broad breeding ranges (e.g., Finch et al. 2015; Trierweiler et al. 2014; van Wijk et al. 2018), our study provides detailed information on non-breeding site use and migratory routes of individuals from across the entire breeding range of American Golden-Plovers. Our unique database also provides the first range-wide quantification of migratory connectivity and temporal variation in breeding population spread for this species. This critical information is poorly known in most migratory animals (Vickers et al. 2021) and generally not available for arctic-breeding shorebirds because such studies are logistically difficult and prohibitively expensive to conduct on their breeding grounds. The low number of marked individuals at certain breeding populations may have limited our ability to detect the persistence of the spatial configuration observed on the breeding ground. Nonetheless, we clearly show that individuals

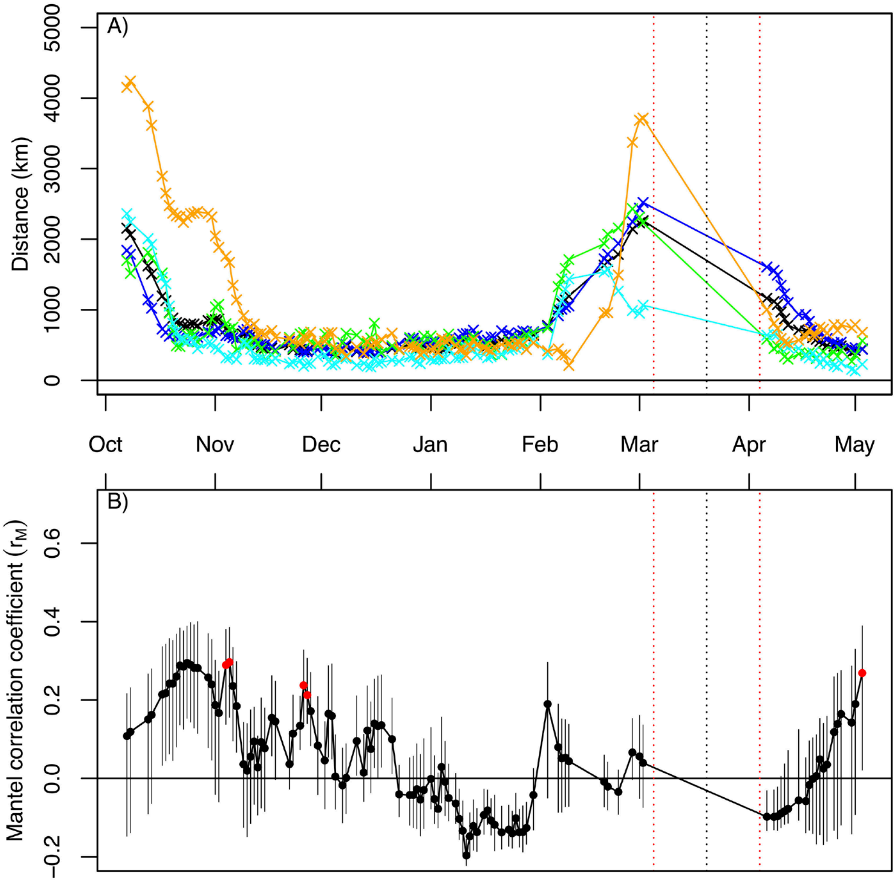

FIGURE 4 | Spatial structure of migrating and wintering adult American Golden-Plovers ($n = 33$ individuals) through time. (A) Non-breeding range spread of all individuals (variation in mean distances between individuals through time in black) and population spread for specific breeding population (dark blue: Bylot Island, light blue: Igloolik, green: Churchill, Orange: Alaskan populations); (B) Temporal variation in the Mantel coefficient ($r_M \pm 95\%$ confidence interval). Dates with significant positive r_M values are in red (permutation test, $p < 0.05$). Red vertical dashed lines indicate the periods with less reliable locations (i.e., obtained 15 days before and after the spring equinox, indicated by the black vertical dashed lines). Each tick mark is the first day of the month.

originating from widely separated breeding populations were well mixed during most of the non-breeding period, which corresponds to a low migratory connectivity.

4.1 | Migratory Routes and Non-Breeding Sites

As indicated in a previous study relying on band recoveries (Byrkjedal and Thompson 1998), our results confirm the elliptical migratory pattern of American Golden-Plovers. As expected, most plovers tracked in our study used a transoceanic route over the North Atlantic during the fall migration, although some locations obtained with geolocators during this period were less accurate due to the equinox. During the return migration, plovers used different routes to reach North America as birds were equally split between an overland route and an offshore route located over the Pacific Ocean. The offshore Pacific route had not been previously documented (Byrkjedal and Thompson 1998; Johnson et al. 2020). Plovers travelling on that path may be using the strong winds from the South Pacific subtropical high and the equatorward low-level jet stream to their advantage (Cherchi et al. 2018). A similar migration pattern over the Pacific Ocean has been documented for Buff-breasted Sandpiper (L. Tibbitts and R. Lanctot, unpublished data), which shares habitats and wintering sites with the American Golden-Plover and some spring stopover sites (Johnson et al. 2020; McCarty et al. 2020).

Some stopover sites identified in our study were either unknown or poorly known prior to our study, including sites used by American Golden-Plovers during the first leg of the fall migration, like the Foxe Peninsula situated in the eastern Canadian Arctic. This area may represent an important stopover as it is the last one used prior to the long flight over the North Atlantic to reach South America. Additionally, the central Brazil stopover site was only identified recently (Linscott et al. 2024) and a large proportion of our tracked individuals used this site prior to reaching their wintering site in the La Plata River Basin, which was previously documented by Byrkjedal and Thompson (1998). Sites used prior to or after long-distance flights, and during the final leg of the pre-breeding migration, are likely particularly important and should be the focus of special attention and further study (e.g., Foxe Basin in the Canadian Arctic, Upper Amazon Basin in South America, and the West North Central states site in the USA; Figure 2).

As expected, plovers moved via the Mississippi Basin during the spring migration once they reached North America and, interestingly, all veered westward before stopping at the West North Central states stopover site (mainly in South Dakota, Nebraska, Kansas). It is noteworthy that we did not find any stopover site in northeastern Indiana and adjacent Illinois, areas where large spring aggregations of plovers have been documented (Johnson et al. 2020). This suggests that some stopover sites used by American Golden-Plovers may not have been detected with our methodological approach and dataset. Our tracked individuals may have skipped some stopover sites or may have used them for < 5 days (the temporal threshold duration used to identify non-breeding sites, see methods). Finally, it is important to note that our study is based on migratory tracks of adult plovers that survived at least one full annual cycle and initiated reproduction in at least two breeding seasons (the latter being necessary to recapture birds at nests). Therefore, some risky migratory paths or low-quality non-breeding sites used by adults who subsequently died or failed to breed, as well as non-breeding sites used by juveniles, may not have been detected in our study. As survival is likely low in the first year of life, a better knowledge of age-specific migration route and space use is critically important to identify the drivers of population dynamics (Cheng et al. 2019). Moreover, differences in migration parameters can also occur between sexes (Maness and Anderson 2013). We did not include sex as a variable in our analysis due to potential uncertainties in accurately identifying gender. However, migration patterns are not known to differ between sexes in the study species (Byrkjedal and Thompson 1998; Johnson et al. 2020).

4.2 | Migratory Connectivity

Our study is among the first to investigate whether the spatial configuration observed on the breeding area was preserved during the other phases of the annual life cycle using Mantel correlation coefficient calculated at a fine temporal resolution throughout a species annual cycle (Knight et al. 2021; Korpach et al. 2022). While Mantel correlations offer standardised, interpretable, and comparable estimates across species, they should be used and interpreted with caution when assessing migratory connectivity (Cresswell and Patchett 2024). Positive correlation coefficients do not necessarily indicate that individuals are in close spatial proximity at that time. For example, we found significant positive values even when individuals from the same breeding area were more than 1000 km apart. However, by examining the temporal variation in correlation coefficients—while maintaining a consistent spatial sampling pattern of initial locations—we were able to assess whether the spatial configuration observed on the breeding grounds was preserved during the non-breeding period. This approach was appropriate to demonstrate how the spatial arrangement of breeding populations became less distinct over time, shifting from a more segregated to a more mixed structure across different stages of the annual cycle. The results show that clustering among individuals nesting close to one another contributes to migratory connectivity but that plovers nesting far apart became progressively more mixed with one another during fall migration and early winter. Although individuals remained well mixed throughout most of the winter and early spring migration, a non-random spatial structure re-emerged near the end of spring migration, which could partly result from differences in migration timing between breeding populations during the final leg of spring migration (see Lamarre et al. 2021).

Using archival light-level geolocators to determine migratory connectivity has some limitations (Knight et al. 2018), especially due to the uncertainty in location estimates (see Section 2). Higher resolution tracking datasets, based on larger sample sizes for certain breeding populations, would allow a more accurate assessment of migratory connectivity, as well as non-breeding site use and locations in American Golden-Plovers. Tracking a larger number of birds at several breeding areas would likely have improved our ability to detect the persistence of the spatial configuration observed on the breeding grounds during the non-breeding period. Nonetheless, we are confident that our main conclusion (i.e., breeding populations increasingly mix as they move from the breeding to non-breeding period) is robust considering that our breeding populations were spread over the entire breeding range of the species (Cohen et al. 2018; Vickers et al. 2021).

Documenting year-round space use and migratory connectivity can provide important information for identifying key drivers of demographic trends of migrants and the extinction risk of populations or species (Marra et al. 2015). In an era with many rapidly declining migratory bird populations (Runge et al. 2015; Smith et al. 2023; Wilcove and Wikelski 2008), studies like ours are urgently needed to make knowledge-based, species-specific conservation decisions that could reverse these trends. Our results indicate that stressors occurring during the non-breeding period and especially during the winter could affect all breeding populations of American Golden-Plovers more or less equally, as widely separated breeding populations seem to be well mixed for most of this period. Also, as all individuals can sometimes occupy the same space at the same time of the annual cycle (e.g., the Mississippi Basin in spring), the species can be at high risk in the face of rapid and strong environmental changes occurring at those sites (Briedis and Bauer 2018). On the other hand, plovers appear generally spread over a relatively large area (i.e., typically between 450 and 1000 km according to our data) at any given time of the non-breeding period. Such relatively high population spread during the non-breeding period could reduce the potential impact of spatially restricted environmental stressors on the species and should not disproportionately affect specific breeding populations (Cresswell 2014).

Our study offers critical insights into the non-breeding sites used by a long-distance migratory species and, importantly, the timing of their use by individuals from populations across the full breeding range of the species. This spatiotemporal integration across the annual cycle provides valuable measures of migratory connectivity and spread, which can inform conservation priorities on the non-breeding grounds. With global changes strongly impacting migratory populations, such integration is urgently needed to guide conservation strategies, stop biodiversity loss, and protect ecosystems.

Author Contributions

J.-F.L. and J.B. led data collection and curation, developed the methodology and study conceptualisation, conducted the formal analyses, prepared the visualisations, and drafted the original manuscript. J.-F.L., G.G., J.B., and R.B.L. contributed substantially to data interpretation and manuscript writing, with additional input from all authors. G.G.,

R.B.L., O.P.L., E.T.R., O.W.J., J.L., R.M., M.R., E.N., P.A.S., S.B., N.L., M.-A.G., and J.B. contributed to funding acquisition. All authors contributed to data collection and were involved in reviewing and revising the final manuscript.

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Ethics Statement

All methods including capture, banding and tagging were approved by Committees for Animal Care relevant to a particular study site. Also, federal (Parks Canada, Environment and Climate Change Canada, US Fish and Wildlife Service, US and Canadian Bird Banding Offices) and state and provincial permits were obtained for attaching tags and recapturing birds to remove tags.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The datasets (logger data, animal tracks and metadata) for this study can be found on Dryad https://doi.org/10.5061/dryad.280gb5n0v.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** ddi70126-sup-0001-AppendixS1.docx.