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Shorebirds and the Dispersal of Bipolar Plant Species to South America

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Abstract: Among the most distantly separated plant species are those that are found on the polar regions of the northern and southern hemispheres, the so-called bipolar species. Two routes of introduction have been proposed—long-distance dispersal (LDD) and mountain hopping (MH). Shorebirds have been implicated in the distribution of the bipolar species by several authors, but the most likely participants and the most probable routes of introduction have been little investigated. The Global Biodiversity Information Facility database was accessed to determine the geographic range of those angiosperm species that have been reported to have bipolar distributions. A bipolar plant species was considered most likely to have been dispersed by LDD if it has a distinct disjunct distribution between North and South America, and through MH if it is found in intermediate latitudes. The Atlas of Bird Migrations and the Cornell Birds of the World database were searched to discover which birds make long-distance migrations from Arctic North America to the tip of South America, and their mode of travel. Twenty-three plant species have been identified as bipolar. LDD appears to have been more important than MH in their dispersal, as seventeen (75%) have disjunct distributions and six (25%) are found in intermediate latitudes. The most likely players in the LDD dispersal of the bipolar plant species are the Eskimo Curlew, Hudsonian Godwit, Red Knot, Ruddy Turnstone and Whimbrel. Of these five long flyers, the Hudsonian Godwit may have delivered the most seeds as its breeding and migration ranges overlap with the most bipolar species, 12 in all.

Keywords: long-distance dispersal (LDD); mountain hopping (MH); bipolar plant species; amphitropical plant distributions; migratory patterns of birds

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1. Introduction

Among the most distantly distributed species are those that are found on the polar regions of the northern and southern hemispheres, the so-called bipolar species. Moore and Chater originally defined bipolar as only those species that have populations distributed at latitudes >55° N and >52° S [1]. Using this criterion, 23 species have been identified by multiple authors as bipolar—all in the southernmost tip of South America in the Fuego-Patagonian Cordilleras [2,3].

The most popular hypotheses explaining how plant species traveled between the poles are "long-distance dispersal" (LDD) and "mountain hopping" (MH) [3–6]. In the LDD hypothesis, it is predicted that seeds were directly dispersed to suitable habitats on the other side of the equator. Species dispersed in this way would have disjunct distributions between North and South America. The mountain hopping hypothesis predicts that there was a corridor of temperate microhabitats running along the mountains of the two continents on which a species could have "hopped" in stages before it arrived at its current polar location. Such species would be found dispersed at intermittent latitudes between the hemispheres.

Raven [4] speculated that "Either these bipolar disjuncts were dispersed from one polar region to the other in a single jump (LDD) or they migrated along the fairly continuous

mountain chain afforded by the Rocky Mountains and the Andes (MH)", and that "at least some of the identical or paired species of arctic and Antarctic regions may have attained their present ranges via a series of way-stations along the mountains".

LDD has been hypothesized to occur through several mechanisms [5,7]: zoochory (dispersal by animals), anemochory (dispersal by wind) and hydrochory (water dispersal). The great distance between the bipolar distributed plants makes dispersal of seeds by wind or water unlikely. Zoochory can happen through epizoochory (propagules attach to the animals) or endozoochory (animal ingests propagules at one site and defecates them at another). There is growing evidence that endozoochory may be more important overall than epizoochory in LDD, particularly in birds that actively preen any foreign material off their bodies to reduce drag [8–11]; however, most shorebirds are carnivorous and eat a range of insects, mollusks, crustaceans, worms, larvae and similar prey, and do not consume plant material. The possible exceptions are the Whimbrels, Godwits and Curlews, who do eat berries when available.

To successfully introduce seeds between the polar regions via LDD, a bird would have to make the trip in a relatively short period of time with minimal stopovers if they are to retain seeds on or within their bodies when they arrive. This may seem highly unlikely, but with tens of thousands of birds traveling annually to the southern South, "some transport of seeds seems probable" [4].

Shorebirds in the order Charadriiformes have been most commonly implicated in the LDD of bipolar species [3,5,12,13]. Shorebirds travel from their breeding grounds south to the Antarctic South America by three major pathways [14]: (1) the Pacific Americas, generally following the western coastline along the Pacific Northwest, California, Mexico, Central America and NE South America; (2) the Mississippi Americas through the Central US and over the Gulf to South America; and (3) the Atlantic Americas, hugging the Atlantic Coast before passing over the Atlantic to South America.

The shorebird species follow three general travel schemes, although there is considerable overlap between them, even within species. These are hink (hop), strap (skip) and sprong (jump) [14,15], with most making multiple stopovers for refueling, ranging in length from a few days to weeks [16]. Hop migrants make a number of relatively short flights (<1000 km) between stopovers until they reach their final destination. Skip migrants make a series of intermediately long flights (<2000 km) between stopovers, while Jump migrants make at least one very long flight of 3–6000 km to their final destination, with a limited number of stopovers before that flight. Presumably, the Jump migrants would be most likely to carry seeds between the Arctic and Antarctic regions as they would have the fewest number of stopovers and the quickest arrivals.

While shorebirds have been commonly implicated in the LDD of bipolar species, no study has tried to measure the relative importance of LDD vs. MH or determine the most likely participants in LDD. Herein, we use publicly available databases and a deductive framework to approach these questions. We compare shorebird flight paths and habitats with the geographic ranges and habitats of the bipolar plant species to determine the extent of their overlap. This information is then used to deduce the likelihood that shorebirds introduced the bipolar species to Antarctica via LDD and hypothesize which species were most likely to have been the dispersers.

2. Materials and Methods

To discover which birds make long-distance migrations from North America to the tip of South America and identify their flight paths, we first searched the Atlas of Bird Migrations [17] and the Cornell Birds of the World (https://birdsoftheworld.org/bow/home, accessed on 19 November 2021)). The Birds of Chile [18] was then consulted to confirm that these birds were in Southern Chile and Tierra del Fuego and these observations were bolstered by an older report in Bulluck [19] and more recent eBird reports (https://ebird.org/map/ (accessed on 21 December 2021)). To determine the habitats of the shorebirds in their breeding grounds and migration stopover sites, the Cornell Birds of

the World (https://birdsoftheworld.org/bow/home (accessed on 12 December 2021)) and Audubon Guide to North American Birds (https://www.audubon.org/field-guide/bird (accessed on 12 December 2021)) were consulted.

To establish the geographical distribution of each of the bipolar plant species, we searched the herbarium specimen records of the Global Biodiversity Information Facility (https://www.gbif.org/ (accessed on 20 January 2022) [20]. We looked at the overall distribution patterns of each of the species and compared them to the migration patterns of the various shorebird species recorded on eBird. A bipolar plant species was considered more likely to have been distributed by MH if there were records of preserved specimens from intermediate latitudes in Mexico, Central America and South America, and they were considered more likely to have arrived via LDD if there were no records from intermediate latitudes.

To determine the habitats of the bipolar species, the passport data of GBIF were examined where available from the collection/observation sites. A number of plant taxonomies were also consulted, including Arctic Flora of Canada and Alaska (myspecies.info), Plants of the World Online/Kew Science, Flora of the Canadian Arctic Archipelago (nature.ca), Flora of Chile at efloras.org and Flora of North America at efloras.org.

3. Results

Of the 23 bipolar species that have been identified, 17 have clear disjunct distributions between North America and the tip of South America, and six are found at intermediate latitudinal locations (Table 1). All the bipolar plant species have circumpolar distributions across North America and Eurasia (Table 1; Figure 1), except *Avenella flexuosa,* which is mostly restricted to eastern North America and Europe. Five of the bipolar species also dip to attach to feathers but were small down along the Pacific Coast as far south as Central California (*Armeria maritima*, *Calamagrostis stricta*, *Empetrum nigrum*, *Phleum alpinum* and *Plantago maritima*). In eastern North America, most of the bipolar species' ranges extend well down through the US seaboard states, with some ranging as far south as Georgia.

Table 1. Geographical ranges of the bipolar plant species. Source—Herbarium specimen records of the Global Biodiversity Information Facility (https://www.gbif.org/ (accessed on 20 January 2022); GBIF, 2020).

			Geographic Range		
Species	**Dispersal Structures [1]?**	**Coastal?**	**W. North American**	**E. North American**	**Intermediate Latitudes**
Alopecurus magellanicus Lam	Yes	No	AK, CA (rare), Rocky Mt. states	New York	Ecuador and Peru
Anemone multifida Poir	Yes	No	AK, PNW, CA, Rocky Mt. states	New York	
Armeria maritima (Mill.) Willd.	No	Yes	AK, PNW, CA, Rocky Mt. states	New Brunswick	
Avenella flexuosa (L.) Drejer	Yes	No	Not in AK, W and C. Canada but in Siberia	Alabama	Mexico
Calamagrostis stricta (Timm) Koeler	Yes	Limited	AK, PNW, CA, Rocky Mt. states, C. USA	New York	
Carex arctogena L.	No	No	Limited—AK, BC, CA, Rocky Mt. states	Maine	
Carex canescens L.	Yes	No	AK, PNW, CA, Rocky Mt. states	Georgia	
Carex macloviana D'Urv.	Yes	Yes	AK, PNW, CA, Rocky Mt states	New York	

Table 1. *Cont.*

			Geographic Range		
Species	**Dispersal Structures [1]?**	**Coastal?**	**W. North American**	**E. North American**	**Intermediate Latitudes**
Carex magellanica L	Yes	No	AK, PNW, CA, Rocky Mt. states	New York	
Carex maritima Gunnerus	Yes	Yes	AK, CA (rare), Rocky Mt. states	Maine	
Carex microglochin Wahlenb	Yes	No	AK, BC, Rocky Mt. states	New York	Ecuador and Argentina (7)
Catabrosa aquatica (L.) P. Beauv	Yes	Yes	AK, CA, Rocky Mt. states, C. USA	Maine	
Deschampsia caespitosa (L.) P. Beauv	Yes	Yes	AK, PNW, CA, Rocky Mt. states	New York	
Empetrum nigrum L.	Yes	Limited	AK, PNW, CA, N. Rocky Mt. states	New York	
Gentiana prostrata Wahlenb	No	No	AK, BC, Rocky Mt. states	New York—local	Costa Rica, Columbia, Peru and Ecuador
Hippuris vulgaris L.	No	Limited	AK, PNW, CA, Rocky Mt. states, C. USA	New York	
Koenigia islandica L.	No	No	AK, BC, Rocky Mt. states	New Brunswick	
Phleum alpinum L.	Yes	Limited	AK, PNW, CA, Rocky Mt. states	New York	Guatemala and Mexico
Plantago maritima L.	No	Yes	AK, PNW, CA	New York	
Polygonum maritimum L.	No	No	Not in NA, sub-arctic Europe		
Triglochin palustris L.	No	Yes	AK, BC, Rocky Mt. states	New York	
Trisetum spicatum (L.) Richt.	Yes	No	AK, PNW, CA, Rocky Mt. states	New York	Mexico, Ecuador, Peru, Columbia and Guatemala
Vahlodea atropurpurea (Wahlenb.) Fr.	Yes	No	AK, PNW, CA, Rocky Mt. states	Maine	

[1] Have appendages that could attach to feathers.

Among the bipolar species, 65% have small seeds with dispersal structures that could have attached to feathers (Table 1). The seeds of the other eight species do not have these structures but are small enough to become lodged between toes of muddy feet or entangled between feathers.

Eleven extant bird species now migrate annually from Arctic Alaska and Canada to Southern Chile and Tierra del Fuego, and one that probably went extinct in the 1980s, the Eskimo Curlew (Table 2). Within this group, all three migratory patterns (*Hop*, *Skip* and *Jump*) are represented, along with all the North American flyways (Atlantic, Mississippi and Pacific). Among the *Jump* migrants, those most likely to be involved in LDD are the Eskimo Curlew, Hudsonian Godwit, Red Knot, Ruddy Turnstone and Whimbrel.

Of the bipolar plant species, only one, *Carex arctogena*, does not have significant overlap with the nesting and/or stopover habitats of at least one of the *Jump* migrants (Table 3). The second rarest bipolar species found in shorebird flight paths is *Avenella flexuousa*, which is only located in the former migration route of the Eskimo Curlew. All other bipolar species are found in the nesting and feeding habitat of two or more shorebird species. Ten of the bipolar species are found in the breeding habitat of the Ruddy Turnstone in open tundra, and six on rocky or stony shores along its coastal migratory range. Eight of the bipolar plant species are distributed in the tundra of Western Arctic Canada and Alaska, where the Eskimo Curlew nested, and four in grasslands and prairies, where it fed during migration. Three of the bipolar plant species reside in the Red Knot's breeding grounds

in the Canadian Arctic and six in the coastal, marine habitats of its stopovers. Twenty of the bipolar species are found in the subarctic and alpine tundra and taiga of Alaska and Northern Canada, where Whimbrels nest, and two in the coastal habitats, where it feeds during migration. Twenty of the bipolar plant species reside in the wet meadows and bogs, where Hudsonian Godwits breed in the Arctic, and seventeen along their migration route.

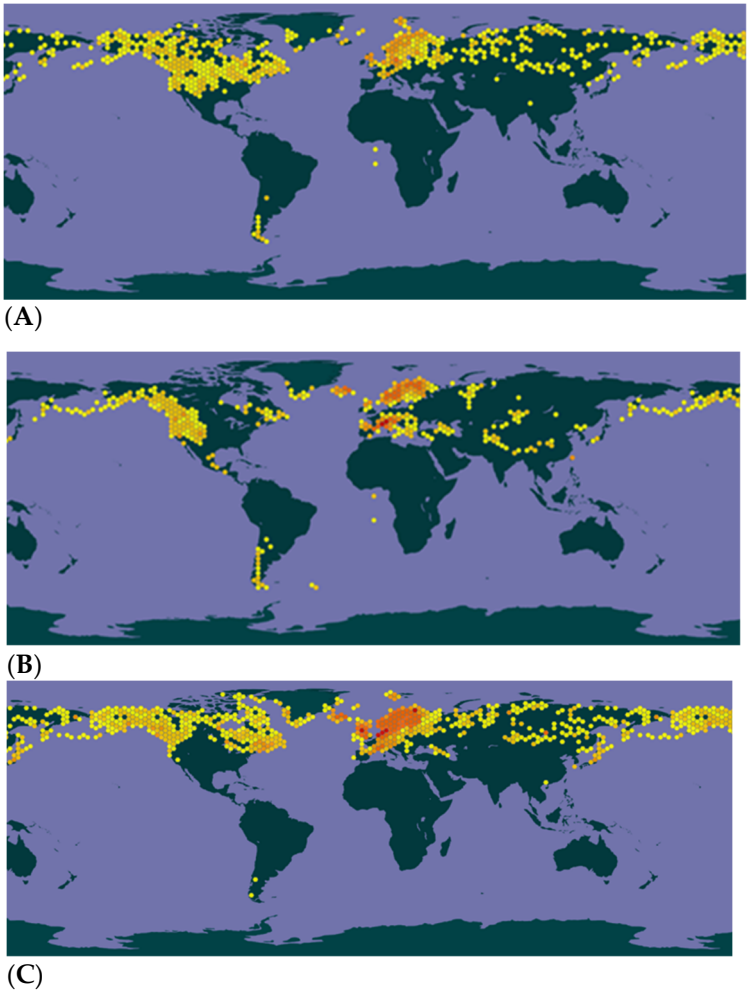

Figure 1. Representatives of the three distribution patterns of bipolar distributed plants in North America: (**A**) Circumpolar including Central US (*Calamagrostis stricta*), (**B**) Circumpolar minus Central US (*Empetrum nigrum*), and (**C**) Circumpolar minus Pacific Coast, Rocky Mountains and Eastern Maritime provinces (*Phleum alpinum*). (Source—GBIF, 2021).

Table 2. Flyways and migration patterns of the bipolar shorebird migrants. Sources—Atlas of Bird Migrations (Elphick, 2011), the Cornell Birds of the World (https://birdsoftheworld.org/bow/home, accessed on 21 December 2021) and The Birds of Chile (Jaramillo, 2013).

		Arctic	Antarctic	Migration	Flyway		
Common Name	**Species**	**Breeding**	**Wintering**	**Pattern**	**Atlantic**	**Mississippi**	**Pacific**
Baird's Sandpiper	*Calidris bairdii*	Arctic Canada	Coastal Chile and Tierra del Fuego	Hop		X	
Black-bellied Plover	*Pluvialis squatarola*	Alaska and Arctic Canada	Coastal Chile	Skip	X		X
Eskimo Curlew [1]	*Numenius borealis*	Alaska and Arctic Canada	Coastal Chile and Tierra del Fuego	Jump	X		
Greater Yellowlegs	*Tringa melanoleuca*	Alaska	Coastal Chile	Hop		X	

Table 2. *Cont.*

		Arctic	Antarctic	Migration	Flyway		
Common Name	**Species**	**Breeding**	**Wintering**	**Pattern**	**Atlantic**	**Mississippi**	**Pacific**
Hudsonian Godwit	*Limosa haemastica*	Alaska and Arctic Canada	Coastal Chile and Tierra del Fuego	Jump	X		
Lesser Yellowlegs	*Tringa flavipes*	Alaska	Coastal Chile	Hop		X	
Red Knot	*Calidris canutus*	Alaska and Artic Canada; Siberia	Coastal Chile and Tierra del Fuego	Jump	X		
Ruddy Turnstone	*Arenaria interpres*	Alaska and Arctic Canada	Coastal Chile and Tierra del Fuego	Jump	X		X
Sanderling	*Calidris alba*	Alaska and Arctic Canada	Coastal Chile and Tierra del Fuego	Skip	X		
Surfbird	*Calidris virgata*	Alaska	Coastal Chile and Tierra del Fuego	Hop			X
Whimbrel [2]	*Numenius phaeopus*	Alaska and Arctic Canada	Coastal Chile and Tierra del Fuego	Jump			X
White-rumpted Sandpiper	*Calidris fuscicollis*	Alaska and Arctic Canada	Coastal Chile and Tierra del Fuego	Skip	X	X	

[1] Now extinct; [2] Two subspecies, but only one migrates to southern South America.

Table 3. Geographical range of the bipolar plant species and their overlap with the breeding ranges and staging areas of five shorebird species.

			Present in Breeding/Stopover Sites			
Species	**Habitat in NA**	**Eskimo Curlew**	**Hudsonian Godwit**	**Ruddy Turnstone**	**Red Knot**	**Whimbrel**
Alopecurus magellanicus	Open wetlands	Y [1]/N	Y/Y	Y/N	Y/N	Y/N
Anemone multifida	Open wetlands and grasslands	L/Y	Y/Y	L/N	N/N	Y/N
Armeria maritima	Salt marshes and pastures	Y/N	Y/Y	Y/Y	Y/Y	Y/Y
Avenella flexuosa	Grasslands and dry woodlands	N/Y	N/N	N/N	NN	N/N
Calamagrostis stricta	Open wetlands	Y/N	Y/Y	Y/N	L/N	Y/L
Carex arctogena	Talus and rocky slopes	L/N	L/L	L/N	L/N	L/N
Carex canescens	Open wetlands	L/N	Y/Y	L/N	L/N	Y/N
Carex lachenalii	Open wetlands	Y/N	Y/Y	Y/N	N/N	Y/N
Carex macloviana	Open wetlands	L/N	Y/Y	N/Y	N/Y	Y/N
Carex magellanica	Open wetlands	N/N	Y/Y	N/N	N/N	Y/N
Carex maritima	Beaches, dunes and wetlands	Y/N	Y/L	Y/Y	Y/Y	Y/N
Carex microglochin	Open wetlands	N/N	Y/Y	Y/N	N/N	Y/N
Catabrosa aquatica	Wetlands and wet sandy beaches	N/N	L/Y	N/Y	N/Y	L/N
Deschampsia caespitosa	Grasslands	N/Y	Y/N	L/N	N/N	Y/N
Empetrum nigrum	Open wetlands	Y/N	Y/Y	L/N	L/N	Y/L
Gentiana prostrata	Open wetlands	Y/N	Y/Y	Y/N	N/N	Y/N
Hippuris vulgaris	Shallow water	Y/N	Y/Y	Y/N	L/N	Y/L

Table 3. *Cont.*

			Present in Breeding/Stopover Sites			
Species	**Habitat in NA**	**Eskimo Curlew**	**Hudsonian Godwit**	**Ruddy Turnstone**	**Red Knot**	**Whimbrel**
Koenigia islandica	Open wetlands	Y/N	Y/Y	Y/N	N/N	Y/N
Phleum alpinum	Open wetlands	N/N	Y/Y	N/N	N/N	Y/L
Plantago maritima	Sea shores and meadows	N/Y	Y/L	N/Y	N/Y	Y/Y
Triglochin palustris	Open wetlands	L/N	Y/Y	L/Y	N/Y	Y/N
Trisetum spicatum	Open dry to moist sites	L/N	Y/L	Y/N	N/N	Y/N
Vahlodea atropurpurea	Open wetlands	N/N	Y/Y	N/N	N/N	Y/N

[1] Y = yes (common), L = limited, N = no (not present).

4. Discussion

Of the 23 bipolar species that have been identified, six are found in intermediate latitudinal locations and 17 have a clear disjunct distribution between North and South America. This indicates that the majority of the bipolar plant species were dispersed by LDD. Of course, the lack of representation on the GBIF database does not necessarily mean that the species was not there—local populations could have gone extinct or it has not yet been collected. However, Central and South America have among the best taxonomic coverage in the GBIF database outside of North America and Europe [21]. The GBIF has become a widely used resource for tracking worldwide plant and animal distributions, and its use has skyrocketed in recent years, with 744 peer-reviewed articles citing GBIF data in 2019 alone [21].

The bird species most likely to have introduced Arctic plant species to the Antarctic sub-regions via LDD would be those that: (1) regularly forage in habitats with the dispersed plant species, and (2) are Jump migrants that fly in long continuous flights with a minimum number of stopovers. These criteria are met by five shorebird species—Eskimo Curlew, Hudsonian Godwit, Red Knot, Ruddy Turnstone and Whimbrel. Precise data on the length of the Eskimo Curlews flights do not exist, but all four of the extant species have been recorded to fly continuously for over 7500 km during migration (Ruddy Turnstones [22,23]; Whimbrel [24–26]; Red Knot [27]; Hudsonian Godwit [28]).

These four long-flying shorebirds are known to be numerous in southern South America. There are more than 30,000 Whimbrels and 20,000 Hudsonian Godwits on Chiloe Island alone, and across the rest of Southern Chile and Tierra del Fuego, there are likely many thousands more [29–32]. There are also over 25,000 Ruddy Turnstones in Patagonia and Terra del Fuego, and Red Knots number between 5000 and 10,000 in Chile [33]. Census data and flight distances were not recorded for the Eskimo Curlew, but it is thought that they were particularly numerous in Tierra del Fuego and likely flew long distances, similar to their close relatives [34,35]. The Hudsonian Godwits, Whimbrels, Red Knots and Ruddy Turnstones are among the most common shorebirds in Chile.

Of the marathoning shorebirds, Hudsonian Godwits had by far the most habitat overlaps with bipolar species and therefore must have been a major player in the dispersal of the bipolar plants through LDD. They share breeding and stopover habitats with 16 of the 23 bipolar species, and breeding habitats with all the rest except just two—*C. arctogena* and *A. flexuosa*. Hudsonian Godwits fly over vast areas of continent and ocean, stopping in open wetlands such as lakes, large rainwater pools, flooded agricultural areas (including rice farms), sewage ponds, freshwater impoundments and wet pastures. They also use saltmarshes, brackish swamps, estuaries and lagoons [32].

The Eskimo curlew may have been the second most important messenger, as its migration range once overlapped with the range of eleven bipolar species. Of the shorebirds, Eskimo curlews are the only ones that favor grasslands during migration, where three of the bipolar species potentially reside (*A. multifida*, *D. caespitosa* and *P. maritima).* Since

Whimbrels, Ruddy Turnstones and Red Knots are restricted to coastal beaches, they could only have been responsible for introducing the five coastal species, *A. maritima*, *C. stricta*, *E. nigrum*, *P. alpinum* and *P. maritima.*

It is not known with certainty that one of the shorebird species now extant introduced the bipolar plant species to the Antarctic. However, most scientists believe that the modern shorebird species arose during the glacial periods of the Pleistocene [36–38] and because of their long-distance migratory behavior and polygamous breeding structures have undergone only limited amounts of population divergence [39,40]. The last ice age ended only 12,500 years ago, certainly within the lifespan of most modern species.

While the longest-flying shorebirds were most likely to have contributed to the LDD of the bipolar plants, none of them could have traveled the whole route from the boreal regions of the Arctic to the Antarctic in one hop. The very longest continuous bird flights are in the range of 10,000 km, while the distance between the shorebird nesting sites and Antarctic South America is in excess of 15,000 km. This means that the bipolar species were likely to have first been dispersed across North America and then were carried the rest of the way by a *Jump* migrant.

The dispersal across North America could have been associated with the movement of any number of bird or animal species that come into contact with boreal, alpine plants. These could have been the Jump migrants before their big leap, any other *Hop* and *Skip* migrating shorebirds or any other bird species that disperses across mountain chains, such as the Grey-Crowned Rosy Finches (*Leucostichte tephrocotis)*

The six bipolar plant species that were found in intermediate latitudes could also have been carried via MH by a tandem of species. These could have included neotropical migrants that do not nest as far north as the Arctic or migrate as far south as Patagonia, as well as local South American migrants that do not travel to North America at all. Among the *Hop* and *Skip* shorebirds, the Lesser and Greater Yellowlegs are known to utilize alpine habitats, as well as the Baird's Sandpiper and White-Rumpted Sandpiper [18]. They also migrate through the mountains of Central America, Mexico and South America.

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