TRACKING THE LONG-DISTANCE MIGRATION AND ABUNDANCE OF PHALAROPES (*PHALAROPUS SPP.)* AT SALINE LAKES ACROSS THE WESTERN HEMISPHERE

by

SYDNEY MORGAN MILLER

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Thesis examining committee:

Matt Reudink (PhD), Thesis Supervisor and Professor, Biological Sciences, Thompson Rivers University
Ann McKellar (PhD), Thesis Co-Supervisor and Research Scientist, Environment and Climate Change Canada
Erfanul Hoque (PhD), Committee Member and Assistant Professor, Community Health and Epidemiology, University of Saskatchewan
Diana Hamilton (PhD), External Examiner, and Professor, Department of Biology, Mount Allison University

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Thesis Supervisor: Professor Matthew Reudink

ABSTRACT

Migration and habitat selection are fundamental processes shaping the ecology of migratory shorebirds, yet the patterns, routes, and drivers underlying these behaviours remain poorly understood for many species. Tracking migration allows the identification of routes and staging sites birds use throughout their annual cycle, information essential for understanding population health and targeting conservation efforts. Similarly, identifying the habitat characteristics that support high bird abundance is vital for protecting key ecosystems during migration. Wilson's (*Phalaropus tricolor*) and Red-necked (*Phalaropus lobatus*) phalaropes are long-distance migratory shorebirds that rely on saline lakes as staging sites during southward migration, where dense invertebrate prey support fueling for migration; however, these ecosystems are increasingly threatened by water diversion and habitat degradation. Although the ecological importance of saline lakes is well recognized, key aspects of phalarope ecology within these systems remain poorly understood. The migratory routes and environmental drivers influencing Wilson's Phalarope migration have never been directly tracked, and the habitat features that determine the abundance and distribution of both Wilson's and Red-necked phalaropes are unclear. Addressing these knowledge gaps is essential for understanding how phalaropes behave throughout their annual cycle.

I first tracked the migration of Wilson's Phalaropes using radio and satellite telemetry tags deployed on birds at their breeding grounds in Saskatchewan, Canada, and staging grounds in California, USA. Tracking data from 45 individuals revealed that the Wilson's Phalaropes in this study that departed from the staging grounds migrated overland through North and Central America to South America, providing the first direct evidence of an overland route during southbound migration. Analysis of the migration timing of Wilson's Phalaropes departing from the breeding grounds showed variation in departure dates between years and that Wilson's Phalaropes were more like to depart when there were favourable tailwinds to support their flight. Lastly, migration tracks showed individuals travelling between saline lakes, highlighting the connections between these ecosystems.

Next, I examined habitat features influencing the abundance of Wilson's and Red-necked phalaropes across six saline lakes in western North America. When analysing phalarope abundance alongside habitat variables classified from satellite imagery, I found that water extent was a key predictor of phalarope abundance. Greater overall water extent supported higher abundance of total phalaropes and Red-necked Phalaropes. The two species differed in their associations with specific habitat types, with Wilson's Phalaropes showing a negative association with seasonal saline habitats, while Red-necked Phalaropes were positively associated with semipermanent salt ponds; these differences can likely be explained by each species' particular foraging strategies. Similarly, patterns of abundance across the migration season also differed between species, with Wilson's Phalaropes peaking earlier in summer and Red-necked Phalaropes later in early fall, likely due to differences in migration distance and breeding phenology.

Together, these findings provide a greater understanding of Wilson's Phalarope migration routes, and the habitat features that support phalaropes at saline lakes in North America. They underscore the ecological importance of maintaining hydrologically stable saline lake networks across the Americas, which are vital to sustaining phalarope populations, and other avian taxa, throughout their annual cycles.

Keywords: migration ecology, habitat selection, saline lakes, telemetry, Wilson's Phalarope, Red-necked Phalarope

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Additional research was carried out on the ancestral lands of the Kootzaduka’a and Nüümü (Northern Paiute) peoples (Mono Lake, California); the Cayuse, Umatilla, Walla Walla, and Modoc peoples (Lower Tule Lake and Lower Klamath, California-Oregon border); the Timpanogos, Newe Sogobia (Eastern Shoshone), Goshute, and Núu-agha-tʉvʉ-pʉ̱ (Ute) peoples (Great Salt Lake, Utah); the Nüümü Witü (Eastern Mono/Monache), Newe Sogobia (Western Shoshone), and Nüümü (Northern Paiute) peoples (Owens Lake, California); the Yahooskin and Nüümü (Northern Paiute), as well as the Cayuse, Umatilla, and Walla Walla peoples (Lake Abert, Oregon); and the Tamien Nation, Ramaytush, Muwekma, Ohlone, and Confederated Villages of Lisjan peoples (South San Francisco Bay, California). As an uninvited guest on these lands, I hold myself accountable to listen deeply to the land, its stories, and its original peoples.

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CHAPTER 1: INTRODUCTION

Migratory birds are declining worldwide due to challenges faced during all phases of their annual cycle (Kirby *et al.* 2008, Rosenberg *et al*. 2019, Wilcove and Wikelski 2008). As such, studying migratory birds throughout the annual cycle and making links between breeding and non-breeding sites is critical for providing insight into the status of populations, highlighting areas where the populations are struggling or thriving (Newton 2024, Wilcove and Wikelski 2008). Focusing on the breeding grounds offers insight into breeding success and can identify critical breeding habitats. Similarly, studying staging and stationary non-breeding grounds can reveal the birds' status during migration and highlights the state of their habitat and food availability throughout their migration and the non-breeding period (Wilcove and Wikelski 2008). Moreover, there may be carryover effects between seasons, where an individual's success in one phase of their annual cycle is influenced by events occurring during a previous phase (Norris 2005, Reudink *et al*. 2009, Sherry and Holmes 1996). For example, if an individual experiences poor food availability and habitat quality during its stationary non-breeding phase, this can influence its reproductive success on the breeding grounds (Norris 2005, Reudink *et al*. 2009).

Habitat loss is a key threat that migratory birds are facing. Climate change, pollution and human activities are degrading or altering habitats that birds rely on throughout all stages of their lives (Galbraith *et al*. 2014, Robinson *et al.* 2009, Xu *et al*. 2019, Zhao *et al*. 2019). For example, loss of wetlands due to agricultural expansion or urbanization is reducing the availability of vital shorebird habitat and food sources across their annual cycle (Asselen *et al*. 2013). The loss of natural wetland habitat forces birds to seek alternative habitats such as flooded agricultural fields. In these agricultural fields birds can become exposed to chemical threats such as pesticides or physical threats from agricultural equipment, both of which can impact survival and reproduction (Malaj *et al*. 2020, Strum *et al*. 2010). Two shorebird species in particular that are being exposed to widespread habitat loss are the Wilson's Phalarope (*Phalaropus tricolour*) and Red-necked Phalarope (*Phalaropus lobatus)*, both saline lake specialists.

Wilson's Phalarope distribution and ecology

The Wilson's Phalarope is a long-distance migratory shorebird that breeds in wetlands in the North American prairies, staging at North American saline lakes and spending the stationary non-breeding period (i.e., boreal winter/austral summer) at saline lakes in the interior of South America (Figure 1.1, Canales-Gutiérrez *et al.* 2020, Jehl 1987, Lesterhuis and Clay 2010). Historically, the Wilson's Phalarope breeding range covered most of the wetlands throughout North America, but extensive loss of wetland habitat due to agriculture expansion during the early 20th century has decreased the breeding range to be primarily in the Western, interior, region of North America (Figure 1.1, Colwell and Jehl 2020, Lesterhuis & Clay 2010, Wetmore 1926).

Figure 1.1. Breeding, staging and non-breeding range of Wilson's Phalaropes (Data from BirdLife International 2025).

During southward migration, Wilson's Phalaropes will stop at a variety of habitats including flooded meadows, alkaline ponds, artificial saline ponds, coastal estuarine marshes, and sewage ponds; more notably, large flocks of up to hundreds of thousands will gather at saline lakes (Jehl 1988, Jehl & Miller 2020). During southward migration Wilson's Phalaropes are believed to take the intermountain west and central flyways through North America before taking a rapid, non-stop migration route over the Pacific Ocean from their staging grounds in North America to their stationary non-breeding grounds in South America (Jehl 1988, Colwell and Jehl 2020). Their migration range extends throughout the western United States and into Mexico and Central America (Figure 1.1, Colwell and Jehl 2020). During their time at these stopover sites during southward migration, Wilson's Phalaropes will moult their feathers and double their body mass to prepare for the rest of their southbound migration (Colwell and Jehl 2020). The large energetic cost of this rapid moult and increase in body weight is the reason that these birds are so heavily reliant on saline lakes with large abundances of food sources like brine flies (Conover and Bell 2020).

The stationary non-breeding period is spent at saline lakes in South America, extending from northern Peru to the southern tip of South America in Tierra del Fuego, and as far east as Uruguay (Figure 1.1, Colwell and Jehl 2020). The first birds arrive in early August and remain in South America up until March, before making their way up Central and South America on their northbound migration back to the breeding grounds (Castellino *et al*. 2024, Colwell and Jehl 2020).

Northward migration begins in early March when birds begin to leave the stationary non-breeding grounds (Reynolds *et al.* 1986) During Northward migration Wilson's Phalaropes will stop at a variety of natural and manmade wetlands while following an interior flyway through the Americas, still stopping at saline lakes, but in low numbers (Andrei *et al*. 2006, Lesterhuis and Clay 2010).

To date, knowledge of the migratory behaviour of Wilson’s Phalaropes is derived solely from observational studies, as their migration has not yet been directly tracked. This leaves a large gap in the basis of our knowledge on the migratory behaviour of Wilson's Phalaropes, including links between breeding, stopover, and stationary non-breeding areas, which can now be filled with the advancement of tracking technologies.

Population status of Wilson's Phalaropes

Wilson's Phalaropes are listed as a species of least concern on the IUCN Red List and secure in the Wild Species report for Canada; however, habitat loss across their migratory route threatens the species and has sparked the motivation to protect these birds and their habitats at a hemispheric level (BirdLife International 2024, Castellino *et al.* 2024, Environment and Climate Change Canada 2020). In the United States, a recent petition was put forth to list the species as Threatened under the Endangered Species Act based on the threat of ecosystem collapse at the saline lakes they depend on in the western United States (Center for Biological Diversity 2024). Population trends from the North American Breeding Bird Survey show an overall stable population trend for Wilson's Phalaropes from 1970-2021 (Smith AC *et al*. 2024); however, based on migration monitoring surveys primarily from the eastern part of their range, Smith PA *et al.* (2023) reported a 70 percent decline in Wilson's Phalarope populations from 1980-2019. The results of these studies may not fully capture the population status of the species since Wilson's Phalaropes, as the species often uses large waterbodies that are poorly represented in the roadside-based Breeding Bird Survey (Smith AC et al. 2024), and the survey sites that Smith PA *et al*. used are heavily skewed towards eastern North America, which does not encompass the core of the Wilson's Phalarope range (Smith PA *et al*. 2023, Smith AC *et al*. 2024).

Red-necked Phalarope distribution and ecology

Red-necked Phalaropes are long distance migratory shorebirds that breed near freshwater bodies such as lakes, marshes or small streams within tundra vegetation across most of the Holarctic region (Figure 1.2, COSEWIC 2014, Rubega *et al*. 2020). They spend their stationary non-breeding period in the open oceans throughout the tropics, notably off the coasts of North, Central and South America, and Western and Southeast Asia (COSEWIC 2014, Rubega *et al*. 2020).

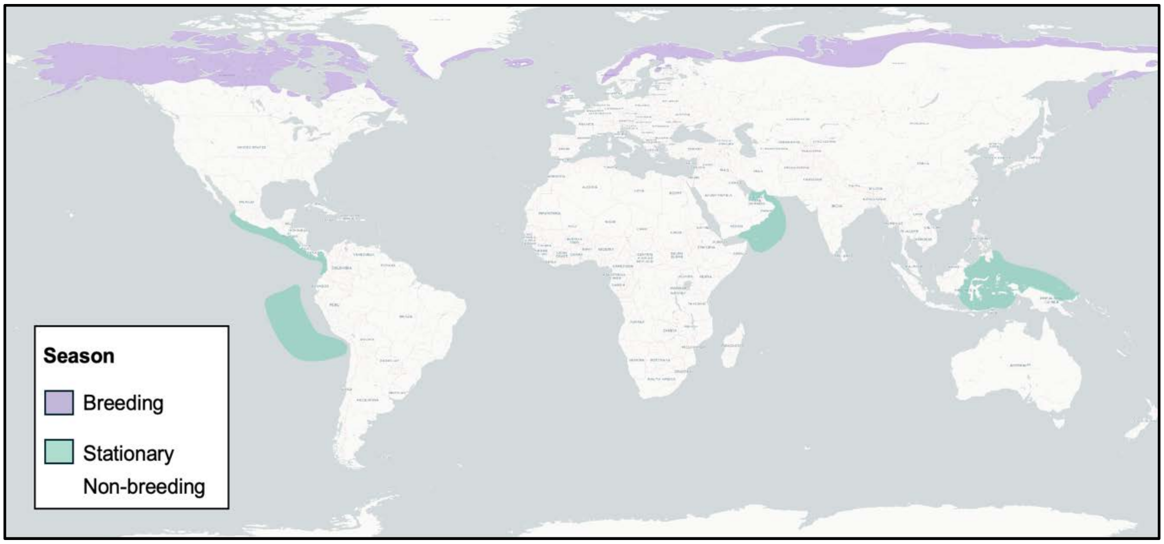

Figure 1.2. Breeding and stationary non-breeding range of Red-necked Phalaropes (Data from BirdLife International 2025).

During southward migration, Red-necked Phalaropes spend time both in the open ocean and inland near a variety of wetlands, including salt marshes, freshwater lakes, and irrigated rice fields, but most notably gather in large groups at saline lakes to stage (Golet *et al*. 2018, Jehl 1986, Rubega *et al*. 2020). Their migration range extends to a wide array of habitats that can support these birds with high amounts of food to fuel their migration, but there have been notable changes in their distribution during migration over the past several decades (Rubega *et al*. 2020). One example of this is that in the 1990's there was a complete disappearance of Red-necked Phalaropes from the western portion of the Bay of Fundy which historically hosted up to three million birds during fall migration (Duncan 1995, Rubega *et al*. 2020).

Most individuals spend the stationary non-breeding period in tropical waters of the open ocean (Figure 2.1, Rubega *et al*. 2020). In the Western Hemisphere, they can be found as far north as off the west coast of southern Mexico, and as far south as the western coast of Peru. In the Eastern Hemisphere, they spend the stationary non-breeding period in the Arabian Sea and off the coast of the Philippines, extending as far east as Papua New Guinea (Rubega *et al*. 2020). There have also been fewer than 100 birds regularly recorded spending the stationary non-breeding period in California on salt evaporation ponds (Garrett and Dunn 1981, Rubega *et al.* 2020).

During northward migration, most individuals take a coastal or offshore route (Jehl 1986, Rubega *et al*. 2020). In the western hemisphere it is also not unusual for groups to migrate overland especially through the great basin in the United States and the prairie provinces of Canada, with large aggregations stopping at saline lakes (COSWIC 2014, Jehl 1986, Rubega *et al*. 2020). During spring migration in the Eastern Hemisphere, Red-necked Phalaropes use different routes depending on where they breed. Birds from northern Europe and western Russia that spend the stationary nonbreeding period in the Arabian Sea move north through inland seas before reaching their breeding grounds, usually making only short stops along the way (van Bemmelen *et al*. 2016, 2019). In contrast, birds from farther east, such as in Siberia, that spend the stationary nonbreeding period around Southeast Asia return north mostly over the open ocean, with very few stopovers (Mu *et al*. 2018).

The migratory routes of Red-necked Phalaropes have been tracked via light-level geolocators in several studies; however, much of their migratory behavior remains unknown (van Bemmelen *et al*. 2016, 2019; Smith M *et al*. 2014, 2018; Mu *et al*. 2018).

Population status of Red-necked phalaropes

The conservation status of Red-necked Phalaropes is inconsistent across its annual cycle and among the countries it migrates to. In Canada, Red-necked Phalaropes are listed as a species of Special Concern under the Species at Risk Act, and there has been a negative population trend since 1970 according to the North American Breeding Bird Survey (COSEWIC 2014, Smith & Edwards 2020, Smith AC 2024). Contrasting this, Red-necked Phalaropes are as listed as apparently secure in Canada by Wild Species (Government of Canada 2020). The European and Global assessment by IUCN listed Red-necked Phalaropes as a species of least concern, but states that globally the species is decreasing (BirdLife International 2019, 2021). Overall, the inconsistency in the conservation status of these birds can be attributed to a lack of reliable data (BirdLife International 2021, Smith AC 2024). These birds are challenging to monitor due to their highly pelagic lifestyle and long migrations. However, substantial declines in the use by Red-necked Phalaropes from major stopover sites such as Deer Island in New Brunswick, along with widespread threats to their breeding and non-breeding habitats highlights the need to better monitor the population across its entire annual cycle (Duncan 1995, Nisbet and Veit 2015).

Phalarope habitat loss

Both Wilson’s and Red-necked Phalaropes face habitat loss due to water diversion, agriculture, and industrial expansion (Frank and Conover 2021). An example of this can be seen at Mono Lake, California, which has long been recognised as an important area for phalaropes and other migratory birds. Historically, Mono Lake has supported up to 80,000 Wilson's Phalaropes and 65,000 Red-necked Phalaropes during southward migration (Jehl 1988). Starting in 1941, the City of Los Angeles began diverting water to its aqueduct system and by 1981 the surface elevation of Mono Lake had dropped by 13.7 meters, drastically reducing available saline lake habitat (Wiens *et al*. 1993). Similarly, at Great Salt Lake, Utah, 1.7 km^3 of freshwater is diverted annually from the streams that feed the lake, dropping the water level by 3.6 meters and reducing the availability of habitat that supports up to 500,000 staging Wilson’s Phalaropes and 250,000 staging Red-necked Phalaropes each year (Frank and Conover 2021).

All around the world, water levels in saline lakes are dropping, decreasing available habitat for phalaropes and increasing water salinity (Wiens *et al*. 1993). If salinity becomes too high, the prey species of phalaropes, primarily brine flies (*Ephydridae*), chironomids (*Chironomidae*), and Daphnia *(Daphniidae*), cannot survive, leading to a reduction in food resources (Frank and Conover 2021). At Great Salt Lake, the construction of a rail causeway restricted the flow of water within the lake and led to the gradual increase in the salinity of Gunnison Bay (Frank and Conover 2021, White *et al*. 2015). Gunnison Bay makes up just under 40% of the total area of Great Salt Lake and historically could host up to 197,000 phalaropes at a time (Figure 1.4, Frank and Conover 2021). The gradual increase in salinity has led the bay to reach the point where it can no longer support aquatic invertebrates, removing any food sources from that portion of the lake and resulting phalaropes no longer being present in Gunnison Bay (Frank and Conover 2021, White *et al*. 2015).

Figure 1.3. Map of Great Salt Lake showing the Union Pacific Causeway separating Gunnison Bay from the rest of the lake (Data from Utah Geological Service 2023).

Understanding how birds interact with their habitats, and which habitat factors are associated with bird abundance, is an important step in conserving healthy bird habitats (McKinney *et al.* 2011). Bird habitat associations are typically described in relation to land cover types such as wetlands, mudflats, grasslands, agricultural fields and urban areas, and can be assessed by measuring bird presence, abundance, or behavior across different habitat types (Debela *et al*. 2021, Li *et al*. 2024). Field surveys, remote sensing, and spatial modeling are often used to link bird presence with habitat features such as land cover type, water quality, vegetation, or prey availability (Hunt *et al.* 2020, Kerr and Ostrovsky 2003, Rhodes *et al.* 2015). Information gained from these links is critical to understanding the specific habitat features that support healthy bird populations (Hunt *et al.* 2020, McKinney *et al.* 2011, Rösch *et al*. 2023). For Wilson's and Red-necked Phalaropes there are major gaps in knowledge regarding their habitat associations within saline lakes. In particular, it is unknown how variation in water and land cover within saline lake habitats influences phalarope abundance. Addressing these knowledge gaps is essential for understanding how saline lake habitats can be conserved to ensure they continue to support phalarope populations.

With all this in consideration, there is an urgent need for research on the migratory behaviour and habitat use of Wilson's and Red-necked Phalaropes to understand their population status and requirements at saline lakes across the annual cycle.

Tracking technologies

Tracking birds through space and time can provide valuable insight into various aspects of their migratory behaviour. For example, tracking can offer important information about the timing of a birds' migration, which can be influenced by factors such as individual condition or nesting success, changes in weather patterns, and habitat quality (Newton 2007, Wilcove and Wikelski 2008). Additionally, tracking allows us to gain insights into flight paths and habitats that birds use throughout their annual cycle (Newton 2024).

Avian tracking has advanced over the last 40 years through the introduction of new ways to track species and the miniaturization of existing technologies. Automated radio telemetry has become more widely used in the last few years to track the migration of small birds due to improvements in the technology that has made the radio tags smaller and lighter, making them safer to apply to a wider range of birds (Fiedler 2009, Kenward 1987, Newton 2024). Researchers are also not required to recapture birds to obtain tracking information while using radio tags, unlike geolocators or GPS loggers. Radio tags emit radio signals that are detected by receiving antenna. The power of using radio telemetry to track small birds has recently been improved by the development of the Motus network, which is an established network of radio receiving towers across the world, mainly concentrated in the western hemisphere (Figure 1.3; Newton 2024). The Motus network utilizes uniquely coded avian nano-tags that allow researchers to distinguish between individually tagged birds, with all the tags emitting signals on the same radio frequency (Taylor *et al.* 2017). This contrasts traditional radio telemetry technology, which would involve researchers cycling between different radio frequencies to detect individuals, and typically tracking birds with a receiver by hand or with a small, local array of stationary receivers (Taylor *et al*. 2017). With Motus, receiving stations across countries detect radio pulses when individuals fly by the towers within approximately 10 - 20 km, allowing researchers to see the general path the birds are taking (Taylor *et al.* 2017). The major drawback with Motus comes with the gaps that are often present in the network of receiving stations (especially in Central and South America), given that knowing where the birds have gone is reliant on them flying near a tower (Fiedler 2009, Newton 2024).

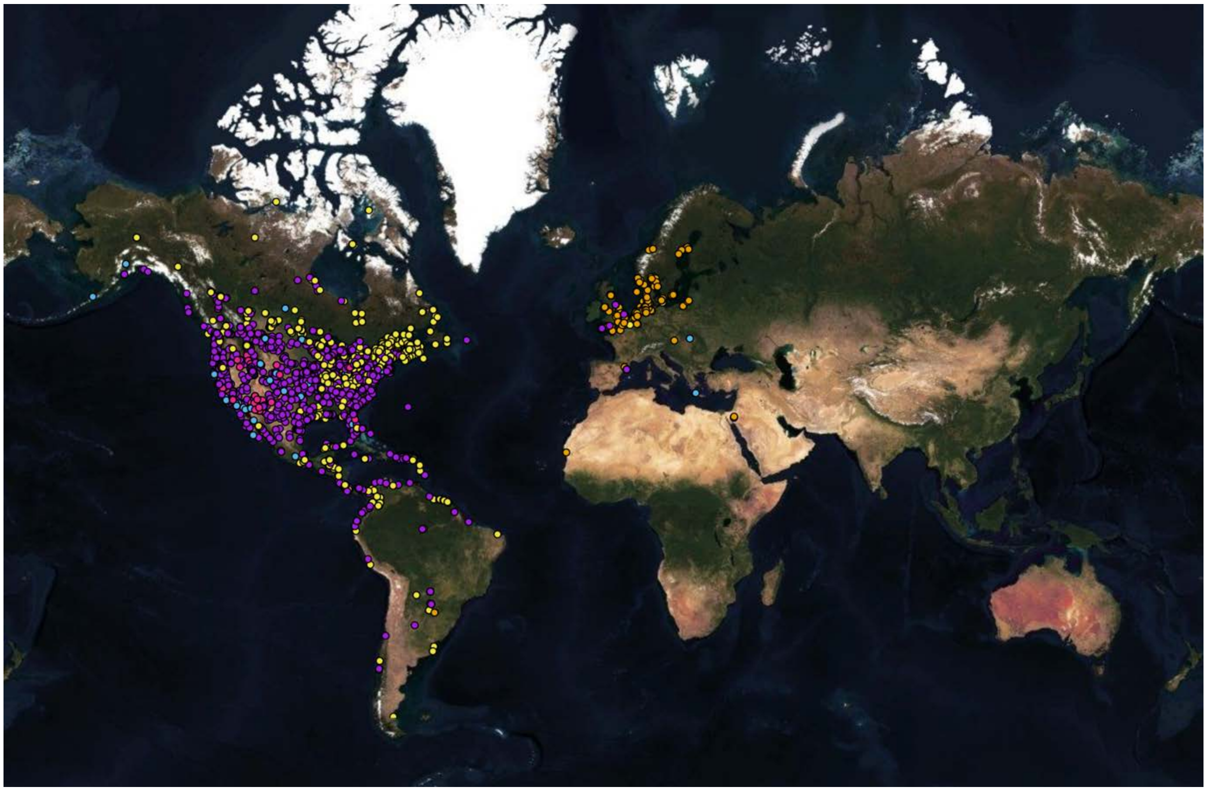

Figure 1.4. Worldwide distribution of Motus radio receiving towers, as of September 2025 (Birds Canada 2024).

Other types of tracking devices are also undergoing technological advances and further miniaturization, allowing them to be applied to smaller animals (Fiedler 2009, Newton 2024). Satellite tags send and receive signals via orbiting satellites, which can result in detailed migratory routes, and have the advantage of not requiring recapture of the birds, unlike geolocators and GPS loggers. However, there are still constraints on the use of this technology because the tracking devices are still often too heavy to apply to smaller birds (Fiedler 2009, Newton 2024). Additionally, satellite tags are significantly more expensive than simpler devices such as light level geolocators and radio tags, often liming the sample size of tagged birds in a given project (Newton 2024).

Thesis objectives

The objective of this thesis is first to track the migration of Wilson's Phalaropes departing from their breeding and staging grounds. By tracking the movement and staging locations of individuals throughout their migration I can assess their migratory timing, identify important habitats, and determine connections between important locations for Wilson's Phalaropes across their annual cycle. Secondly, I aim to understand how habitat and land use characteristics influence the abundance of Wilson's Phalaropes and Red-necked Phalaropes at six major staging sites in North America: Great Salt Lake (Utah, USA), Mono Lake (California, USA), Lake Abert (Oregon, USA), Owens Lake (California, USA), the south San Francisco Bay (California, USA), and Chaplin Lake (Saskatchewan, Canada).

This thesis contains two research chapters and a conclusion chapter. The first research chapter focuses tracking the migration of Wilson's Phalaropes. The second research chapter investigates how habitat and land use characteristics influence the abundance of Wilson's and Red-necked Phalaropes at 6 saline lakes in North America. The conclusion chapter of this thesis focuses on management recommendations and suggests directions for future studies.

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CHAPTER 2: TRACKING THE SOUTHBOUND MIGRATION OF WILSON'S PHALAROPES FROM THEIR BREEDING AND STAGING GROUNDS

ABSTRACT

Migration is a critical stage of the annual cycle of many bird species, yet the migratory routes and drivers of migration timing remain poorly understood for many species. This chapter presents the first migration tracking study of Wilson’s Phalaropes (*Phalaropus tricolor*), with the goal of describing the species’ migration routes and identifying factors influencing the timing of departure from the breeding grounds. Using radio and satellite tracking technologies deployed from breeding grounds in Saskatchewan, Canada, and staging grounds in California, USA, I tracked the migration of 45 individuals in 2023 and 2024. Detections from individuals departing the staging grounds showed individuals traveled through North and Central America on their southbound migration, revealing the first direct evidence of an overland migration route between North America and South America, contrary to previous assumptions of an exclusively over ocean migration route. Tracking results also showed individuals traveling between saline lakes, highlighting the connections between these ecosystems. Analysis of departure data from the breeding grounds showed that wind direction played a significant role in shaping the timing of migratory departure, with birds more likely to depart under favorable tailwind conditions. Additionally, I found significant interannual variation in departure timing between the two years of this study, showing that there is some degree of flexibility in Wilson’s Phalarope departure timing from the breeding grounds. These findings bridge a key gap in the knowledge of Wilson’s Phalarope migration ecology, providing information on migration routes, timing, and use of staging sites. This study also highlights the importance of protecting saline lake networks, which serve as links in the migration of individuals throughout the Western Hemisphere and are becoming increasingly vulnerable to human disturbance.

INTRODUCTION

Migratory birds typically make long-distance journeys twice a year, moving between breeding and stationary non-breeding grounds to take advantage of seasonal availability of food resources while reducing predation risk and competition (Alerstam *et al.* 2003).

Migration is closely tied with life history events such as reproduction and growth, making proper timing of migration vital (Cornelius *et al.* 2013, Jacobs and Wingfield 2000, Newton 2007). The timing of migration can be impacted by events occurring throughout the annual cycle, ultimately having major fitness consequences (Marra *et al.* 1998). For example, birds occupying lower quality habitat on the stationary non-breeding grounds often depart the stationary non-breeding grounds earlier, arrive later to the breeding grounds, and subsequently obtain lower-quality breeding territories and have reduced reproductive success compared to birds that arrive earlier (Marra *et al.* 1998, Norris *et al.* 2005, Reudink *et al.* 2009). Similarly, late departure from the breeding grounds can result in late arrival to the stationary non-breeding grounds and the inability to acquire high-quality habitat (Akresh *et al.* 2021).

Timing of migratory departure is influenced by both internal and external factors. Internal factors include age, sex, and overall body condition, which encompasses factors such as muscle mass, structural size, and fat stores (Deppe *et al.* 2015, Duijns *et al.* 2017, Jenni and Jenni-Eiermann 1998). A bird's physical condition can dictate its ability to undertake long flights, as individuals require a substantial amount of fuel to support their migratory journey. In preparation for migration, birds often improve their body condition by increasing energy reserves to support sustained flight (Duijns *et al.* 2017, Newton 2007). External factors influencing migration timing include environmental factors such as weather conditions (e.g., wind, temperature, and precipitation; Deppe *et al.* 2015, Duijns *et al.* 2017, Marra *et al.* 2005). Birds typically time their departure with favourable weather, such as a good tail wind, to support their flight and reduce energetic cost (Åkesson and Hedenström 2007, Butler *et al.* 1997, Deppe *et al.* 2015, Dossman *et al.* 2016, Howell *et al.* 2020).

Though seasonal interactions and migration timing can have important impacts on individual fitness, we often lack information on migration routes and connectivity between breeding and non-breeding populations. Information on migratory pathways is critical for identifying where populations face threats and resource limitations during their annual cycle, therefore providing insight into population health and guiding conservation priorities (Iwamura *et al.* 2013, Stutchbury *et al.* 2009). Migratory birds rely on multiple habitats throughout their annual journeys, often spanning multiple countries, making it essential to understand how habitat conditions experienced throughout migration and during stationary periods ultimately affect individual condition and survival (Stutchbury *et al.* 2009). For example, shorebird populations that use tidal mudflats in the Yellow Sea region of East Asia as stopover sites have declined by up to eight percent per year after substantial loss of the mudflat habitat (Studds *et al*. 2017). As such, protecting high-quality non-breeding sites along the migration route can play a significant role in ensuring the long-term persistence of breeding populations.

Wilson's Phalaropes (*Phalaropus tricolor*) are a species with limited information available on their migratory routes, timing, and connectivity. Wilson's Phalaropes are long-distance migratory shorebirds that breed within the western interior of Canada and the United States and spend their stationary non-breeding period at saline lakes in South America, extending from northern Peru to the southern tip of Tierra del Fuego, and as far east as Uruguay (Colwell and Jehl 2020). It has been proposed that Wilson's Phalaropes departing from their breeding and staging grounds travel overland through the western United States before undertaking a direct non-stop flight off the United States coast to South America (Jehl 1988). This theory is supported by evidence of Wilson's Phalaropes loading fuel for a long journey at their staging grounds in the United States, the apparent absence of individuals in Central and northern South America during Northen hemisphere fall, and the short duration of time between when the last individuals are seen at the staging grounds and the first individuals arrive at the stationary non-breeding grounds (Figure 2.1; Jehl 1988). Throughout their southbound migration, Wilson's Phalaropes are reliant on saline lakes to fuel their journey, such as Chaplin Lake in Saskatchewan, Canada, and Great Salt Lake in Utah, USA (Jehl 1988). Water diversion and draining, mining practices, and climate change are degrading the health of saline lakes and jeopardizing critical migratory habitat for Wilson's Phalaropes (Williams 2002, Wurtsbaugh *et al.* 2017).

Figure 2.1. Presumed great circle distance migration route of the Wilson's Phalarope on its southbound migration after departing North American staging sites.

In terms of population status, the Breeding Bird Survey (BBS) has shown little change in the abundance of Wilson's Phalaropes within Canada since 1970, and the IUCN Red List lists Wilson's Phalaropes as a species of least concern (BirdLife International 2024, Smith AC *et al*. 2024). On the other hand, Smith PA *et al.* (2023) analysed migration counts of shorebirds primarily within Eastern Canada and the United States from 1980 to 2019 and found that Wilson's Phalarope populations have decreased by 70 percent. The above surveys are not ideal for monitoring Wilson's Phalaropes, given that the BBS is primarily designed for acoustic detection of landbirds, and migration counts are concentrated in eastern North America outside the species' main migratory route, leaving their conservation status uncertain and potentially putting their future at risk (Lesterhuis & Clay 2010, Smith AC *et al.* 2024). Nonetheless, the loss of saline lake habitat throughout the western hemisphere, along with the potential decline in Wilson's Phalaropes numbers and lack of proficient survey coverage, has sparked motivation to protect Wilson's Phalaropes and their saline lake habitats, including a recent legal petition filed with United States Fish and Wildlife Service to have Wilson's Phalaropes protected under the Endangered Species Act (Centre for Biological Diversity 2024).

In this chapter, I use a combination of radio and satellite telemetry to track the southbound migration of Wilson's Phalaropes departing from their breeding grounds in Saskatchewan and their staging grounds in California. Although the locations of non-breeding sites are known, the patterns of migratory connectivity and the flyways used by the species remain poorly understood and their migration has yet to be directly tracked. My goals were to describe the migration routes used by Wilson's Phalaropes and investigate the factors influencing the timing of departure from the breeding grounds. I expected birds to travel from their breeding grounds in Saskatchewan to known staging sites of importance in the United States (e.g., Great Salt Lake, Utah, and Mono Lake, California; Frank and Conover 2019), and to subsequently use an oceanic route to South America, as proposed by Jehl (1988). I predicted that birds in better condition would depart the breeding grounds earlier and that birds would depart more often on days with southerly winds (Deppe *et al.* 2015, Dossman *et al.* 2016, Howell *et al*. 2019).

METHODS

Tracking technologies

I tracked the migration of 45 Wilson's Phalaropes using two types of tracking technologies: VHF radio tags and satellite transmitting tags (Table 2.1). First, I fitted 31 Wilson's Phalaropes with Lotek Nanotags (NTQB2-3-2) and nine with Cellular Tracking Technologies Lifetags (CTT Lifetags) over the spring and summer of 2023 and 2024. The Lotek Nanotags used in this study function by emitting four uniquely coded radio pulses every 10 seconds at a frequency of 166.380 MHz, while CTT Lifetags emit a coded pulse every two seconds at 434 MHz and 433 MHz. Both types of radio tags create a distinctive identification code that can be detected by radio receiving stations. We used the Motus Wildlife Tracking System, which is a collaborative research network of automated radio receiving stations distributed worldwide that are designed to track the movements of small animals carrying compatible radio tags, to collect our movement data. Receiving stations that are part of the Motus network are designed to detect one or both types of radio tags when they are within approximately 15 km of a station, depending on habitat and topography (Taylor *et al.* 2017).

Second, I fitted five Wilson's Phalaropes with Lotek Sunbird Argos tags in the summer of 2023. The tags transmit a signal every 90 seconds, which is detected whenever orbiting satellites that are part of the Argos network are passing over. Satellite telemetry allows continuous monitoring, and relative to radio telemetry via the Motus network, provides daily detections and more precise (~150 m up to >1 km) detections of each tagged bird's location (Exo *et al.* 2019).

Table 2.1. Deployment of tags to track the migration of Wilson's Phalaropes in 2023 and 2024, including type of tag, sample size, deployment location, and whether the location was a breeding or staging site.

Tag type	Technology	Sample size	Deployment location	Life history stage
Lotek Nanotags	Radio	31	Saskatchewan, Canada	Breeding
Cellular Tracking Technologies Life Tags	Radio	9	Tule Lake, California, USA Mono Lake, California, USA Lower Klamath National Wildlife Refuge, California, USA	Staging
Lotek Sunbird Argos transmitters	Satellite	5	Tule Lake, California, USA	Staging

The Lotek Nanotags used in this project had an expected lifespan of approximately 6 months, or until the tag detaches from the bird. CTT Lifetags and the Lotek Sunbird tags were fitted with a solar panel to power the tag and were expected to transmit for the lifetime of the bird, or until the tag detaches from the bird.

Capture, banding, and deployment of tracking devices

I captured adult Wilson's Phalaropes on the breeding grounds near the communities of St-Denis (52.158928, -106.097552) and Allan Hills (51.660620, -106.074533) and the village of Chaplin (50.458272, -106.654664) in Saskatchewan, Canada. Collaborators also captured adults during their southbound migration at the Lower Klamath National Wildlife Refuge (41.979376, -121.735985) and Tule Lake National Wildlife Refuge (41.899218, -121.525174) at Tule Lake, California, USA, and at Mono Lake (37.997542, -119.007995), California, USA. At breeding sites, I located nests using behavioural cues or rope dragging and captured adult males on the nest during incubation using manual or remote-controlled bow nets, as well as mist nets placed over top of the nest. I recorded the mass, maximum flat wing length, tarsus, tail and bill length, and fat score of each captured bird (Meissner 2009). I fitted each bird with a CWS metal band and a unique combination of three coloured bands on their upper legs. Individuals then either received a Lotek Nanotag glued directly to their back, between the scapulae, with a five-minute curing marine epoxy (Howell *et al*. 2020) or a Lotek Nanotag attached via a leg-loop harness constructed of stretch magic (Rapploe and Tipton 1991). Weight of all attachments was 0.68 grams and less than 3% of an individual’s body mass.

At staging sites, my collaborators at Oikonos Ecosystem Knowledge, University of Connecticut, and US Geological Service captured Wilson's Phalaropes at night via spotlighting on an airboat. Birds captured at staging sites were weighed and had a metal band applied to their left upper leg. Individuals either received a CTT Lifetag, weighing 0.45g (less than 2% of an individual’s body mass) with a leg loop harness made from stretch magic or a Lotek Sunbird Argos transmitter, weighing 2g (less than 3% of an individual’s body mass) with a leg loop harness made of floating fly-fishing line (Rappole and Tipton 1991).

Data filtering and preparation

I performed all data manipulation in R v4.4.3 (R Core Team 2024). I followed the methods outlined in the “In-depth detections filtering” section of the “Motus R book for data analysis” for data downloading, filtering and preparation for Lotek Nanotags and CTT Lifetags (Birds Canada 2024). A group of detections of a single tag detected by one antenna on a Motus receiving station is known as a run, and the shorter the run the more likely it is to represent a false positive detection (Birds Canada 2024). My filtering method removed run lengths of two or less for the Lotek Nanotags and run lengths of one or less for the CTT Lifetags (Birds Canada 2024), which was chosen due to my relatively small sample size, which made it more appropriate to examine detections on an individual basis rather than applying more strict filters commonly used in studies with larger sample sizes. This method allowed me to assess whether each detection was biologically feasible for each individual: specifically, detections needed to occur within the known migratory route and stopover sites, during expected seasonal time windows, and with realistic flight speeds (< 80 km/h). This ensured that detections did not result from tower noise or signals mimicking birds with similar burst intervals (Jehl 1988, Colwell and Jehl 2020).

I used the “move” package and followed the “ExMove” workflow in R to prepare data for Lotek Sunbird tags (Kranstauber *et al*. 2025, Langley *et al*. 2024). I filtered the data using the hybrid filter of the Douglas-Argos Filter (Douglas *et al*. 2012, McKellar *et al*. 2025). This filter removes detections with an estimated error radius that is unknown or greater than 1500 m (Douglas *et al*. 2012).

I used QGIS 3.38.2-Grenoble to visualize the movement trajectories of each individual. For birds fitted with radio tags, I mapped the coordinates of each Motus station where the bird was detected and used the ‘Points to Path’ function to connect the stations, creating an inferred migration route (QGIS Development Team 2025). For birds fitted with satellite tags, I added each detection coordinate to the map and used the ‘Points to Path’ function to connect the coordinates (QGIS Development Team 2025).

Migratory timing

Departure time, arrival time, and duration of stay

For radio-tagged birds, I was able to assess departure date for birds that were tagged in areas with an active Motus receiving station at the time of the study. This included Chaplin Lake and Allan Hills in Saskatchewan. I classified departure from the tagging site as the last day the individual was detected by a receiving station located at the tagging site or within 10 km of its tagging site (Imlay *et al.* 2021). For birds tagged with satellite transmitters, I classified departure from the tagging site as the last day the individual was detected within 10 km of its tagging site (Imlay *et al.* 2021)

For radio-tagged birds, I classified arrival at staging sites as the first date of detection of individuals by one or more Motus stations within a 10 km radius for two or more days (Bianchini *et al*. 2020, Farmer and Parent 1997, Gomez *et al*. 2017). I calculated duration of stay at staging sites as the number of days individuals were detected by stations within the 10 km radius, inside their staging range, which extends throughout the western united states as far north as Minnesota and south through Central America as far as Honduras (Bianchini 2020). For satellite-tagged birds, I used the same criteria: arrival at a staging site was defined as the first date an individual remained within a 10 km radius for two or more days, and duration of stay was calculated as the number of days the bird remained within that area (Bianchini et al. 2020; Farmer and Parent 1997; Gomez et al. 2017).

Migration speed

For radio-tagged birds, I determined the distance traveled by using the "siteTrans" function with the "Motus R book for data analysis", which calculates the distance between the Motus receiving stations where birds were detected (Birds Canada 2024). I then divided the distance traveled by the time between detections to determine travel speed, measured as kilometers traveled per day (Bianchini and Morrissey 2018, Bianchini *et al.* 2020). This calculation of travel speed is not a direct indication of flight speed since it does not take into consideration any time the birds may have stopped without being detected by Motus receiving stations; instead, this represents a minimum migration rate (Bianchini and Morrissey 2018, Bianchini *et al.* 2020).

For birds tracked with satellite tags, I used the "Move" package in R (Hill et al. 2019) to calculate travel speed. For each bird, I divided the straight-line distance between consecutive detections by the time between those detections to obtain movement rates in kilometers per day. I then averaged these rates across all detection intervals during the duration of the tracking period to estimate each individual's overall daily migration speed.

Weather data

For birds tagged in Saskatchewan at Chaplin and Allan Hills, I collected local weather data for the hour prior to the departure of each bird (Howell *et al.* 2020). I collected weather data from Environment Canada weather stations for wind direction (tens of degrees), and wind speed (km/h; http://climate.weather.gc.ca/). I used data from the three nearest weather stations (all within 76 km of the tagging location) and averaged the data from those three sites for each departure hour (Howell *et al.* 2020). For Chaplin this included: Lucky

Lake (50.950000, -107.150000), Moose Jaw (50.331681, -105.537508) and Swift Current (50.291944, -107.690556). For Allan Hills this included: Watrous (51.666667, -105.400000), Elbow (51.166667, -106.550000) and Saskatoon Airport (52.170833, -106.700000). Additionally, the daily measurements of mean temperature (°C) were collected for each tagging site from May through to the end of July in order to examine yearly variation in temperature in the months prior to departure (http://climate.weather.gc.ca/).

Statistical Analysis

To examine the factors that could explain variation in departure date from the breeding grounds, I used a linear model with log-transformed departure date as the response variable and body condition and year, and their interaction, or mass and year, and their interaction, as predictor variables. I ran two separate models that were identical in structure but differed in which measure of fuel load was included. In one model, I included body condition along with year and their interaction as predictor variables. In the other model, I included mass along with year and their interaction as predictor variables. The reason I analyzed both body condition and mass is that the best indication of fuel load is highly debated with some arguing mass alone is a sufficient indication of fuel load, and others arguing that mass along with body size is a better indicator of fuel load because it accounts for the structural composition of the bird (Labocha and Hayes 2012). I calculated body condition using a two-step linear regression. First, I calculated the Scaled Mass Index (SMI) following Peig and Green (2009). I assessed alternate methods for estimating body condition, but the SMI provided the best performing and most biologically interpretable measure for this dataset. The SMI uses a standardized major axis regression of body mass on a structural body measurement (in this case, maximum flat wing length) to estimate the scaling exponent (b_{SMA}). This exponent is then applied to adjust each individual's mass to the population mean wing length, producing a size-corrected measure of body condition. In the equation, M_i represents the observed body mass of individual i, L_i is that individual's maximum flat wing length, L_0 is the mean wing length of all individuals in the study population, and b_{SMA} is the slope of the standardized major axis regression of mass on wing length.

$$\mathrm{SMI_i} = \mathrm{M_i}\left[\frac{L_0}{L_i}\right]^{b_{SMA}}$$

Then, to account for any changes in body condition as the season progressed, as well as yearly difference, I extracted the residuals from a linear model with SMI as the response variable and capture date and year as predictor variables (Duijns *et al.* 2017, Peig and Green 2009). In all regression equations, β_0 represents the intercept, β_1, β_2 and β_3 are regression coefficients estimating the effects of the predictor variables, and ε is the residual error term.

$$\mathrm{SMI} \sim \beta_0 + \beta_1(\text{Tag deployment date}) + \beta_2(\text{Year}) + \varepsilon$$

Next, I log-transformed both the departure date and the SMI-derived body condition values to improve normality. I then fit a linear model with log-transformed departure date as the response variable and log-transformed body condition (SMI residuals) and year, as well as their interaction, as predictor variables.

$$\log(\text{Departure Date}) \sim \beta_0 + \beta_1(\log(\text{SMI residual})) + \beta_2(\text{Year}) + \beta_3(\log(\text{SMI residual}) \times \text{Year}) + \varepsilon.$$

Lastly, I fit a linear model with log-transformed departure date as the response variable and mass and year, as well as their interaction, as predictor variables.

$$\log(\text{Departure Date}) \sim \beta_0 + \beta_1(\text{Mass}) + \beta_2(\text{Year}) + \beta_3(\text{Mass} \times \text{Year}) + \varepsilon$$

I performed all analyses in R v4.4.3 using the “lm” function and assessed model assumptions using residual vs fitted and Quantile-Quantile plots. In all models, the regression error term (ε) was assumed to be independent, normally distributed with mean zero, and to have constant variance. Statistical significance in all models was assessed using a threshold of $p \leq 0.05$.

To assess whether wind direction was associated with departure decisions, I first determined if wind direction at the date and time of departure was uniformly distributed and if not, identified which directions were most common at the date and time of departure. I performed this analysis with departure dates from 2023 and 2024 combined and with the data from the two years separated. Unlike linear data, wind direction is circular, meaning 0° and 360° represent the same point, so standard linear models are not appropriate (Fitak and Johnsen 2017, Landler *et al.* 2019). Instead, I performed a Hermans and Rasson test for uniform distribution using the "CircMLE" package in R (Fitak and Johnsen 2017, Landler *et al.* 2019). The null hypothesis of this test is that wind directions at departure are uniformly distributed around the compass (i.e. no preferred wind direction), whereas the alternative hypothesis is that departures are clustered in one or more directions, indicating a non-random orientation relative to wind. I then calculated the circular mean wind direction and the standard deviation using the "Circular" package. Finally, to visualize the distribution of wind directions and speeds during departures, I created wind roses using "ggplot" (Agostinelli and Lund 2024, Wickham 2016).

RESULTS

Migratory routes

From the 31 Lotek Nanotags deployed, I received detections from 21 individuals. Of those 21, the Motus network detected eight individuals outside of Saskatchewan during southbound migration into the United States and Mexico (Figure 2.2). Individuals fitted with Lotek Nanotags were detected over an average of 20 days (Mdn = 14, Standard devation = 17, n = 21), with the shortest detection period being one day and the longest detection period being 62 days for an individual that traveled to the state of Chihuahua in Mexico. The deployment of nine CTT Lifetags resulted in eight individuals with detections outside of their tagging location during southbound migration (Figure 2.2). This included five individuals that traveled to Southern California or Mexico and two others that were detected arriving in South America, with one on the coast of Ecuador and one at Laguna Mar Chiquita, in Cordoba Argentina. The Motus network detected one individual over 320 days on both its southbound migration, as far south as Costa Rica, then also on its northbound migration where it traveled back to the United States and into Oregon (Figure 2.3). The Motus network detected CTT Lifetags, on average, over 116 days (Mdn = 46.50, SD = 167, n = 8), with the shortest detection period being one day and the longest detection period being 430 days for the bird that traveled to Argentina.

For satellite-tagged birds, the Argos system detected four out of the five tags deployed in California for at least one day. Three of the birds were detected on their southbound migration as far as Baja California and Central Mexico (Figure 2.2). The Argos system detected one individual traveling over the ocean after departing California, then turning around and travelling back toward the coast of Baja California. Satellite-tagged birds were detected on average over a period of 26 days (Mdn = 12, SD = 36, n = 4), with the shortest detection period being one day and the longest detection period being 79 days for an individual that traveled to central Mexico.

Figure 2.2. Migratory paths of Wilson's Phalaropes departing from Saskatchewan and California. Lotek Nanotags tracks are in green (n= 21), Cellular Tracking Technology LifeTags are in orange (n=8) and Lotek Sunbird Argos tags are in Blue (n=4).

Figure 2.3. Migration path of a Wilson's Phalarope tagged with a Cellular Tracking Technology LifeTag at Tule Lake in California, USA. Southbound migration is marked with a solid line; northbound migration is marked with a dashed line.

Migratory timing

I was able to determine the departure date for 21 individual Wilson's Phalaropes which either departed from a tagging area with an active Motus receiving station or were fitted with a satellite tag. The mean departure date for 18 birds departing from Saskatchewan was June 29th (SD = 12 days) and the mean departure time was 12:01 am (SD = 2 hours and 27 minutes). The mean departure date for the three birds departing from Tule Lake in California was August 29th (SD = 8 days) and the mean departure time was 3:45 am (SD = 38 minutes). I identified five individuals at staging sites within North America and calculated their length of stay. Chaplin lake was used as a staging site for two birds tagged in St. Denis, Saskatchewan, with the two birds arriving on July 7th and 31st, and staging for a minimum of 32 and 23 days, respectively. Three birds tagged in California staged at sites in California and Mexico. The first staged at Bicycle Lake Army Airfield near Barstow California, arriving on September 17th and staging for 2.5 days. The second staged at the Salton Sea in

California, arriving on September 29th and staging for 29 days. The final bird staged at Laguna Atotonilco in Jalisco, Mexico, arriving on October 16th, staging for a minimum of 19 days. Motus receiving stations detected one bird that was tagged in California on its stationary non-breeding range at Laguna Mar Chiquita, in Cordoba Argentina on September 18th, where it remained for 39 days.

Birds tagged in Saskatchewan with radio tags exhibited relatively lower average travel speeds, with the birds that were also detected outside of Saskatchewan traveling on average faster than the birds that were only detected by stations within Saskatchewan (Table 2.2). Birds tagged in California showed higher average travel speeds overall, with calculated speeds of satellite-tagged individuals being higher than those of radio-tagged birds. For birds tagged with radio tags in Saskatchewan, who also departed Saskatchewan the mean travel speeds tended to be higher than all tagged individuals (Table 2.2). I see the same patterns when looking at the radio and satellite tagged birds in California separately, with both tag types having the mean travel speeds of individuals that departed the state, higher than all tagged individuals.

Table 2.2. Travel speeds of Wilsons Phalaropes tagged with radio and satellite tags on the breeding grounds in Saskatchewan and the staging grounds in California.

Tagging Location	Tag Type	Group	n	Mean (km/day)	SD	Median	IQR
Saskatchewan	Lotek Nanotags	All birds	21	32.55	32.57	28.47	1.22 – 44.47
		Departed birds	8	59.39	29.30	56.14	34.27 – 83.59
California	CTT Lifetags	All birds	8	79.45	59.70	55.29	36.89 – 109.32
		Departed birds	7	84.72	62.44	68.04	35.40 – 124.03
	Lotek Sunbird Argos Transmitters	All birds	4	131.27	130.64	114.40	35.50 – 210.17
		Departed birds	3	173.10	122.88	183.38	114.40 – 236.95

Departure date

Due to the small sample size of departure dates from the staging grounds (n=3) the following analyses were only performed on birds tagged in Saskatchewan on the breeding grounds. Additionally, all birds included in the analysis are after hatch year males, so age and sex were not included as variables in the models.

Regression models

We used residuals from a linear model with SMI as the response variable and tag deployment date and year as predictor variables as a size- and season-corrected index of body condition (Table 2.3).

Table 2.3. Model coefficients and their significance of the linear model examining SMI as a function of tag deployment date and year.

Predictor variable	**β**	**SE**	**t**	**p**
Tag Deployment Date	0.094	0.190	0.50	0.627
Year	0.901	3.018	0.30	0.769

When analysing departure date as a function of body condition, year, and their interaction, individuals departed later in 2024 then in 2023 (Figure 2.4). The interaction between body condition and year and body condition alone did not have a significant association with departure date (Table 2.4).

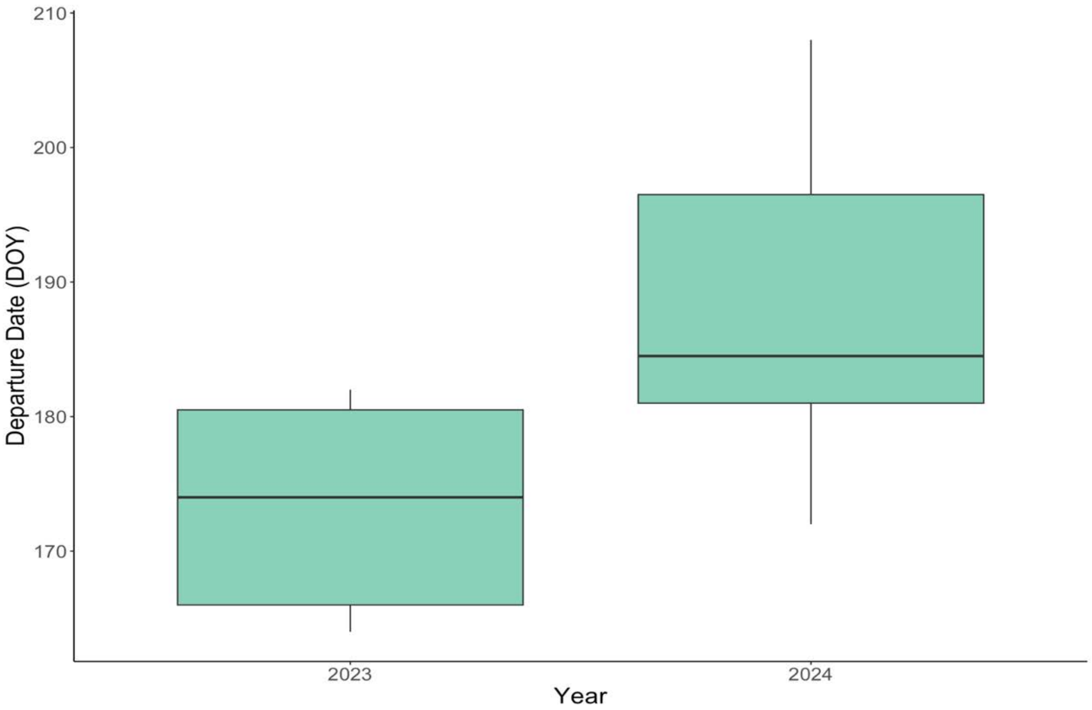

Figure 2.4. Departure dates for Wilson's Phalaropes tagged in Saskatchewan in 2023 and 2024.

Table 2.4. Linear model coefficients and their significance for Wilson’s Phalarope departure dates in relation to body condition, year and their interaction. * represents a significant effect.

Predictor variable	**β**	**SE**	**t**	**p**
Body condition	0.084	0.151	0.555	0.588
Year	0.082	0.026	3.188	0.007 *
Body condition × Year	-0.392	0.218	-1.793	0.095

When analysing departure date as a function of body mass, year, and their interaction, there was a nearly significant difference in departure date between years ($\beta = 0.538$, $p = 0.051$), with individuals tending to depart later in 2024 than in 2023 (Table 2.5). The interaction between mass and year, and mass alone did not have an association with departure date (Table 2.5).

Table 2.5. Linear model coefficients and their significance for Wilson's Phalarope departure dates in relation to body mass, year and their interaction.

Predictor variable	**β**	**SE**	**t**	**p**
Mass	0.001	0.004	0.362	0.723
Year	0.538	0.252	2.136	0.051
Mass × Year	-0.009	0.005	-1.898	0.079

Wind direction

The results from the Hermans-Rasson test for uniformity showed that the wind direction for the 18 birds departing Saskatchewan in 2023 and 2024 did not have a uniform distribution (T= 10.51, p = 0.0048). The circular mean wind direction on the day and time that the birds departed from Saskatchewan was 197.30 degrees (SD = 1.11), or in the south-southwest direction (Figure 2.5). The mean wind speed on the day and time that the birds departed from Saskatchewan was 15.17 km/h (SD = 5.7).

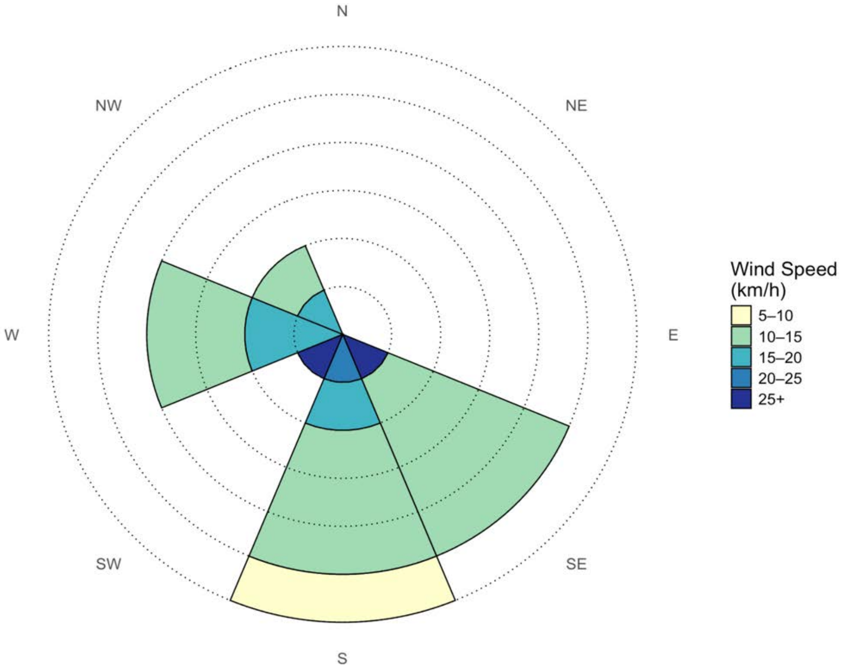

Figure 2.5. Wind direction and speed at the date and time of departure for Wilson's Phalaropes departing from Saskatchewan in 2023 and 2024 combined (n = 18).

When examining the years separately, wind during departure was not uniformly distributed in 2023 (T=11.93, p = 0.0007), and the circular mean wind direction was 187.2 degrees (SD = 0.90), or in the southward direction (Figure 2.6). In 2023 the mean wind speed on the day and time that the birds departed from Saskatchewan was 15.57 km/h (SD = 6.62). In contrast, for the Hermans and Rasson test of wind direction during departure in 2024, we failed to reject the null hypothesis, indicating no evidence that wind direction deviated from a uniform distribution (T=4.67, p =0.19), and the circular mean wind direction was 217.55 degrees (SD = 1.32), or in the southwest direction (Figure 2.6). In 2024 the mean wind speed on the day and time that the birds departed from Saskatchewan was 14.66 km/h (SD = 2.83).

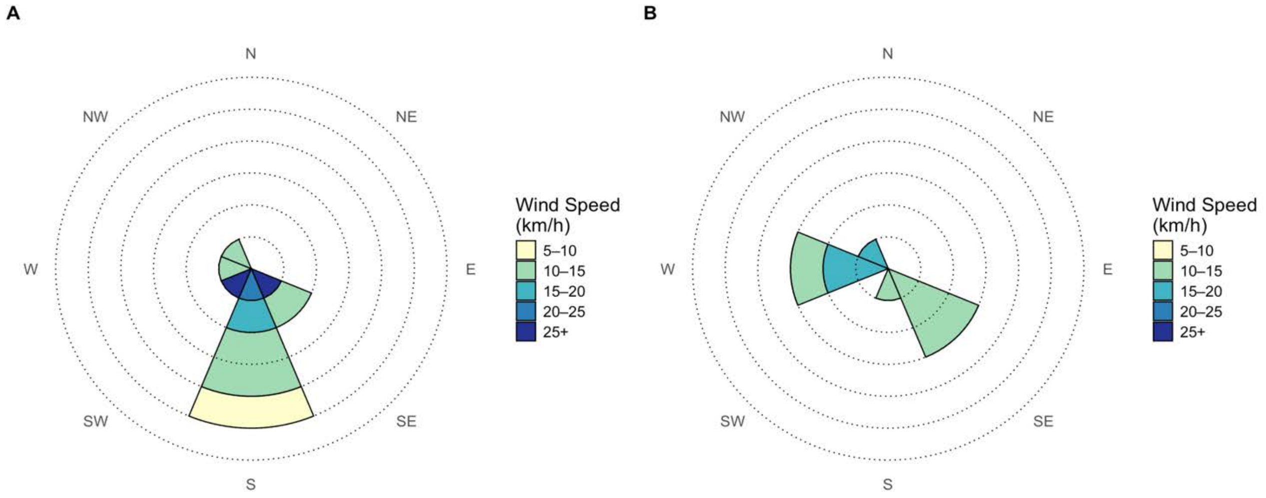

Figure 2.6. Wind direction and speed at the date of departure for Wilson's Phalaropes tagged in Saskatchewan in (A) 2023 (n = 10) and (B) 2024 (n = 8).

DISCUSSION

This is the first study to demonstrate that Wilson's Phalaropes do not strictly follow an over-the-ocean migration route as was previously believed (Jehl 1988, Colwell and Jehl 2020). Instead, 11 of the 14 birds tagged on the staging grounds in California used an overland route, travelling over North and Central America before arriving on their stationary non-breeding grounds in South America. For birds tagged on the breeding grounds in Saskatchewan, departure dates varied between years, and most individuals selected days with favorable wind conditions to initiate migration. Finally, this study highlights how differences in tracking technologies influence the type of migration information obtained, showing the importance of carefully considering methodologies when assessing migratory behaviour.

By tracking the migration of birds that stage in Northern California, I showed that Wilson's Phalaropes from this area traveled via the central and pacific flyways on their southern migration and utilized a primarily overland route towards Central and South America. Notably, the individual tracked for a full annual cycle stopped at multiple wetlands in the southern United States, Mexico, and Central America (Figure 2.3). Although I have a relatively small sample size of birds traveling south (n=10), the finding of an over-land migration is supported by sightings of Wilson's Phalaropes on eBird throughout Southern Mexico and Central America during their southbound migration period (Cornell Lab of Ornithology 2025).

Previous work has highlighted important staging sites for Wilson's Phalarope populations (Jehl 1985, 1999), but I was able to show examples of how individual birds connect major inland saline lakes in North America. Specifically, two birds that were breeding at Chaplin Lake, Saskatchewan, were recorded taking a seemingly direct flight to the Great Salt Lake in Utah. These birds represent a link between two significant saline ecosystems separated by over 1,000 kilometers. Furthermore, additional unpublished tracking data from 2025 revealed similar migration routes in another eight individuals departing from Chaplin Lake and traveling to Great Salt Lake. These migratory connections suggest that these saline lakes may form part of a broader ecological network supporting the migration of individual Wilson's Phalaropes. This highlights the importance of conserving multiple saline lake systems, as changes in one location may have effects across an interconnected network of saline lakes. Similar network dynamics have been documented in other migratory systems, where the loss or degradation of individual habitats, such as wetlands used by cranes or shorebirds along major flyways, can reduce network connectivity, limit stopover options, increase travel distances or energetic costs, and thereby influence migration efficiency and population dynamics (Donnelly 2021, Skagen and Knope 1993).

Departure dates from the breeding grounds differed between the two tagging years, with birds that were tagged in 2023 departing on average 12.6 days earlier than the birds tagged in 2024, based on a model that included body condition as a function of departure date, year, and their interaction. The difference in departure dates over the two years may reflect yearly environmental variation, as 2023 had on average warmer temperatures (17.2, SD = 3.7 C) at the tagging sites in the three months prior to departure relative to 2024 (15.0, SD = 5.1 C). Indeed, cold springs can delay egg-laying, which for species like phalaropes where males are solely responsible for incubation and nest defense, could in turn delay male nesting dates and subsequent departure. This pattern has also been seen in Red-necked Phalaropes (*Phalaropus lobatus*) which delayed egg-laying by approximately five days in years with lower temperatures during the pre-laying and laying windows (Kwon *et al.* 2017). Alternatively, greater breeding success in a given year could influence departure dates, with higher breeding success resulting in later departure (Mitchell *et al*. 2012). While I did not quantify nest success in this study, it is possible that nest success was greater in 2024 than in 2023, resulting in later departure dates. Overall, the differences in departure date between the two years suggests that these birds can be flexible with their departure timing. Similarly, other shorebirds show plasticity in their departure, such as Semipalmated Sandpipers (*Calidris pusilla*) that adjust departure timing and strategies when leaving the staging grounds based on local environmental cues like weather conditions (Neima *et al.* 2022).

Neither both body condition nor mass was associated with departure date for Wilson's Phalaropes. I speculate that this finding was due to the fact that Wilson's Phalaropes perform most of their fuel loading on the staging grounds, rather than on the breeding grounds prior to the start of migration (Jehl 1988). Because they fuel primarily on the staging grounds, Wilson's Phalaropes likely only need to accumulate enough energy stores on the breeding grounds to support the shorter journeys to their staging grounds. In addition, timing of capture was during the incubation period, and so males may not yet have begun to fuel for the first leg of their migration at that time. Further studies would benefit from larger sample sizes while incorporating factors such as nest initiation date, nest success, and body mass/condition just prior to departure to identify what individual factors influences departure dates.

In contrast, I did find an effect of weather on Wilson’s Phalarope departure decisions. When looking at the weather conditions during 2023 and 2024 on the date and time of departure, Wilson’s Phalaropes were more likely to depart when the wind was blowing in a southward direction. This is consistent with the Optimal Bird Migration Theory and other studies that show that birds utilize tailwinds to reduce the energetic cost of migration (Alerstam and Lindström 1990, Bathrick *et al*. 2024, Butler *et al*. 1997). This pattern is also seen in other shorebird species including Red Knots (*Calidris canutus*) and Sanderling, which preferentially initiate migration on days with favorable winds (Howell et al. 2020, Gobbens *et al*. 2024). In 2023, birds predominantly departed with southward winds, providing strong tailwind support for their flights. In contrast, 2024 showed greater variability in wind direction on departure days. The difference between the two years could result from internal factors, such as physiological condition or fat stores, or external factors not included in our study, ultimately influencing departure decisions. It is possible that when ideal wind conditions are absent, birds may still initiate migration due to pressures to maintain timing and avoid delays or secure optimal foraging habitats at subsequent staging sites. Similar behavior has been observed in other migratory shorebirds, including the Common Sandpiper (*Actitis hypoleucos*) that can depart under suboptimal wind conditions when delaying would incur other ecological costs (Mondain-Monval *et al*. 2023). Therefore, I speculate that when birds depart without favorable tailwinds, additional internal or external drivers are likely influencing their decision, with the benefits of departure outweighing the energetic costs of adverse winds. For example, if a bird has not yet encountered a day with ideal wind support, it may ultimately choose to depart to avoid delaying its migration, ensuring timely arrival at high quality staging or breeding habitats, which could be critical for survival and reproductive success. The later departure timing observed in 2024 consistent with the possibility that individuals could not delay departure further, suggesting that individuals may have reached a point beyond which further delay was no longer advantageous.

Mean travel speeds varied across tagging locations and tracking technologies, with birds equipped with satellite transmitters generally appearing to have faster movements than those tracked with radio-based Motus tags. For example, California birds tracked with Lotek Sunbird Argos transmitters that departed from California moved at an average of 173.10 km/day, while those with CTT LifeTags averaged 84.72 km/day. In contrast, birds that departed from Saskatchewan, fitted with Lotek Nanotags, exhibited slower movements, averaging 59.39 km/day. Although satellite tags recorded faster average migration speeds than Motus tags, these differences are most likely methodological, arising from differences in data resolution and detection frequency, rather than behavioral. For example, long-distance flights between receiver stations may go undetected by Motus systems, creating the appearance of slower movement (Hebblewhite and Haydon 2010). Despite variation among individuals and tag types, the observed migration rates fall within the typical range reported for long-distance shorebirds. For instance, Semipalmated Sandpipers (*Calidris pusilla*) migrating along the Gulf Coast have been recorded traveling at approximately 201 km/day during migration (Brown *et al.* 2017).

The absence of migration routes over the ocean in our dataset does not necessarily mean that no Wilson's Phalaropes take a direct, over ocean migration route, but instead could indicate that there are multiple migratory strategies taking place within the species. The tracking results showed one occurrence of an individual traveling over the ocean, then turning around and traveling back toward land. During the time that the bird was migrating through Baja California, Hurricane Hillary hit off the coast, likely disrupting its normal migration path. While this observation shows insight into behaviour during inclement weather, the study is limited by the absence of other tracked individuals migrating over the ocean. Therefore, future studies that include additional birds from more populations with satellite tags will shed light on the frequency of oceanic migration. While using satellite telemetry alone offers the highest resolution tracking data, limitations arise due to the increased cost and weight of the tags (Hebblewhite and Haydon 2010). This limits both the number of devices that can be purchased and the types of birds that can be tagged. In this case, only the heavier females, which are more challenging to capture on the breeding grounds, were capable of supporting satellite tags. For these reasons, my study also incorporated radio telemetry. Radio tags are both less expensive and lighter, which allowed me to have a larger sample size and the ability to smaller males, which are easier to capture on the breeding grounds as they are the sole incubators.

Lotek Sunbird satellite tags provided longer tracking durations than glue-on Lotek Nanotags powered by internal batteries, but shorter durations than solar-powered CTT LifeTags. Five Lotek Nanotags that were attached with harnesses also yielded extended detections, underscoring the influence of attachment method on tag retention. The relatively short tracking periods of glue-on Lotek Nanotags (mean = 12 days, SD = 11 days) likely reflect both limited battery capacity and less secure attachment, whereas the longer detection periods of harness-attached Lotek Nanotags (mean = 43 days , SD = 13 days) and CTT LifeTags (mean = 116 days, SD = 164 days) and Sunbird satellite tags (mean = 26 days, SD = 36 days) are probably due to sustained power supply and more stable attachment. As discussed above, calculated travel speeds also varied by tag type due to the frequency and accuracy with which detections were recorded. For example, long-distance flights between receiver stations may go undetected by Motus systems, creating the appearance of slower movement. Overall, these comparisons highlight important trade-offs between tag weight, cost, and performance, emphasizing that tag type and attachment method can substantially affect both data quantity and apparent migration metrics. Future work should prioritize standardized attachment techniques and complementary use of multiple tag types to balance data resolution, tracking duration, and sample size.

Overall, this study provides new information on the migratory strategies of Wilson’s Phalaropes, demonstrating novel insights into their migration routes and variation in departure behaviours. My findings show that Wilson’s Phalaropes employ also travel overland during southbound migration, and that environmental factors such as wind influence the timing of their departure from breeding grounds. These insights are critical for identifying key staging and non-breeding habitats, assessing potential threats along migratory corridors, and informing conservation strategies for the species. Additionally, they can help highlight potential carry-over effects within populations. Continued tracking across diverse populations and tag types will enhance our ability to predict how Wilson’s Phalaropes respond to environmental change and to guide the effective management of critical habitats throughout their annual cycle.

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CHAPTER 3: EXAMINING TRENDS IN PHALAROPE ABUNDANCE IN RELATION TO HABITAT AT WESTERN NORTH AMERICAN SALINE LAKE STAGING SITES

ABSTRACT

Saline lakes across western North America provide some of the most important staging habitats for migratory shorebirds, yet many of these lakes are shrinking and becoming increasingly saline due to anthropogenically driven water loss. Among the species that are highly dependent on these habitats are Wilson's (*Phalaropus tricolor*) and Red-necked (*Phalaropus lobatus*) phalaropes, which gather at saline lakes in large numbers to refuel during southward migration. In this study, I investigated the habitat features that drive phalarope abundance at six North American saline lakes. To assess how habitat features influence phalarope abundance, I analyzed annual survey data (2019-2024), paired with monthly habitat classification of satellite imagery at each lake. I modeled abundance of Wilson's Phalaropes, Red-necked Phalaropes, and total phalaropes using generalized additive models, and examined two predictor variable structures (principal component analysis of all habitat features vs. models with specific habitat features) and two spatial scales (surveyed area vs. greater lake area). Across species and scales, phalarope abundance was associated with water extent, with greater water extent supporting higher numbers of phalaropes. Associations with specific habitat features varied between species and across spatial scale models. At the surveyed area scale seasonal saline water was positively associated with total phalarope abundance but negatively associated with Wilson's Phalarope abundance, while Red-necked Phalarope abundance was positively associated with semipermanent salt ponds at the greater lake scale. Within years, temporal patterns of abundance also differed between species, with Wilson's Phalarope abundance peaking earlier in summer and Red-necked Phalarope abundance peaking later in early fall. Overall, my results show that phalarope habitat use is shaped by a combination of broad lake conditions and fine scale habitat features, and that seasonal timing is important to interpreting species specific habitat requirements. Maintaining sufficient water levels to preserve stable saline foraging habitat will be essential for supporting migratory phalaropes within North America and throughout the broader saline lake network.

INTRODUCTION

Understanding the habitat requirements of bird species is critical for their effective conservation and management. Birds are highly responsive to environmental change, and their presence, abundance, and distribution often reflect the quality of different habitats (Anderle *et al.* 2024, Furness and Greenwood 1993, Gaston *et al.* 2003). As natural landscapes are increasingly altered by agriculture, urbanization, and forestry, the composition and structure of bird habitats can change in ways that directly influence bird populations (Gaston *et al*. 2003). Examining how changes in habitat characteristics alter the patterns of bird abundance and distribution can provide critical insight to help recover and conserve species (Gumede *et al.* 2022, Lima *et al.* 2025). Furthermore, identifying the specific habitat features most strongly associated with diversity and abundance is essential for designing effective conservation strategies, mitigating biodiversity loss, and informing land-use policies that balance the integrity of ecosystems with human development (Ausprey *et al*. 2023, Wu *et al.* 2022).

Saline lakes are distinctive wetland ecosystems that support unique species and are sensitive to environmental change (Hammer 1986). Characterised as terminal basins without outlet streams, these lakes accumulate salts and minerals over time, creating alkaline waters with high salinity (Hammer 1986). Despite their seemingly inhospitable chemical composition, saline lakes support diverse life forms adapted to hypersaline conditions, including invertebrates such as brine shrimp (*Artemia*) and brine flies (*Ephydridae*), as well as large numbers of waterbirds (Andrei et al. 2008, Frank and Conover 2021a, Hammer 1986). Key habitat features within saline lakes, such as shallow-water areas and shoreline vegetation, provide critical foraging resources and roosting opportunities for a variety of species of shorebirds (Andrei et al. 2008). Unfortunately, saline lakes are increasingly threatened by anthropogenic stressors, including water diversion for agriculture and urban use, pollution, and mineral extraction, all of which can reduce water levels, alter salinity, and degrade habitat quality for wildlife (Saini and Pandey 2023). For example, at Lake Abert in Oregon, USA, water diversion has elevated the salinity of the lake, leading to declines in invertebrate populations and, consequently, reduced abundance of waterbirds including Eared Grebes (*Podiceps nigricollis*), Northern Shovelers (*Spatula clypeata*), American Avocets (*Recurvirostra americana*), gulls (*Laurs spp*.), Calidrid shorebirds (*Calidris spp*.), and phalaropes (*Phalaropus spp*.; Senner et al. 2018). Similarly, at Great Salt Lake in Utah, USA, there has been a complete disappearance of phalaropes in the Gunnison Bay portion of the lake due to the construction of the Union Pacific Railway that began in 1959, which restricted waterflow to the bay, lowering water levels and increasing the salinity to the point where it could no longer support phalaropes' invertebrate food sources (Frank and Conover 2021a, White *et al*. 2015).

Wilson's (*Phalaropus tricolor*) and Red-necked (*Phalaropus lobatus*) phalaropes are two iconic saline lake species, both of which congregate in groups of hundreds to tens of thousands at saline lakes during different phases of their migratory journeys (Colwell and Jehl 2020, Rubega et al. 2020). Wilson's Phalaropes can be found at saline lakes during all major life history events, including breeding, staging, and the stationary non-breeding period (Colwell and Jehl 2020). While Red-necked Phalaropes breed in the Arctic tundra and spend the non-breeding period on the ocean, they use saline lakes as staging areas during migration (Rubega *et al.* 2020). Given their reliance on saline lake habitats, phalaropes are particularly vulnerable to anthropogenic stressors that threaten the hydrology and productivity of these systems (Center for Biological Diversity 2024). Understanding which habitat features most strongly influence phalarope abundance is therefore critical for ensuring effective conservation (Center for Biological Diversity 2024).

In this study, I combined annual phalarope migration survey data (2019 - 2024) with classification of monthly habitat characteristics at six North American saline lakes to investigate how habitat features influence the abundance of Wilson's and Red-necked phalaropes. I predicted that phalarope abundance would be higher at lakes with a greater proportion of seasonal and semi-permanent saline water habitats, which likely provide stable foraging opportunities during staging events (Frank and Conover 2021a). In contrast, sites dominated by temporary wetlands may support fewer phalaropes due to reduced food availability (Palacios *et al.* 2022). By linking phalarope abundance to temporally variable habitat characteristics, I aim to identify the habitat features most strongly associated with phalarope use of saline lakes during migration, providing insights to guide effective conservation of these species and the ecosystems they depend on.

METHODS

Study sites

Surveys of phalarope abundance at six staging sites began in 2019 as part of a coordinated effort to monitor the abundance of both Wilson's and Red-necked phalaropes at major staging sites throughout North America. Surveys occurred during southbound migration from July to September, 2019 to 2024, at the following sites: Chaplin Lake, Saskatchewan, Canada (50.428959, -106.688718), Lake Abert, Oregon, USA (42.632961, -120.217163), Great Salt Lake, Utah, USA (41.117859, -112.471915), Mono Lake, California, USA (37.999165, -118.997352), the south San Francisco Bay, California, USA (37.457452, -122.029850), and Owens Lake, California, USA (36.444741, -117.962197; Figure 3.1). Survey sites were selected based on having reoccurring and historically large congregations of phalaropes, as well as being in close proximity to local organizations that were able to conduct the surveys (Carle *et al*. 2023).

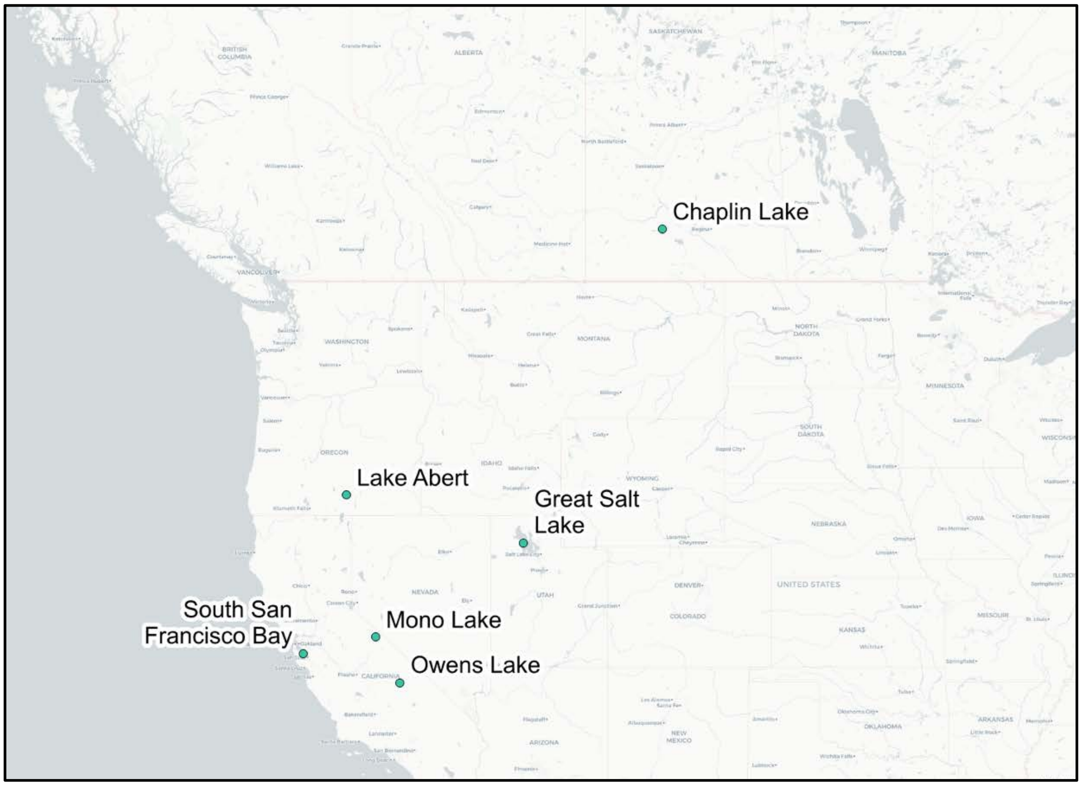


Figure 3.1. Locations of saline lake study sites where phalarope surveys occurred during southbound migration, 2019 - 2024.

Survey methods

Surveys at each site were conducted a minimum of three times per year (Table 3.1) between July and September and were performed within one-week survey windows that were selected to minimize potential double counting of birds that could be moving between sites. Survey methods (i.e., aerial, ground or boat) varied based on the capacity of the surveyors and the characteristics of each lake. Each survey involved counting the number of phalaropes seen at various points at the lake over one or two days. Although survey methods and efforts varied among sites and years, this study is not directly comparing abundance across survey sites or years but instead aims to evaluate overall trends of habitat associations with phalarope abundance.

Table 3.1. Number of annual phalarope surveys conducted at six North American lakes from 2019 to 2024.

Year	Site	N	Total
2019	Chaplin Lake (Saskatchewan, CA)	8	30
	Lake Abert (Oregon, USA)	9	
	Great Salt Lake (Utah, USA)	4	
	Mono Lake (California, USA)	6	
	Owens Lake (California, USA)	3	
2020	Chaplin Lake (Saskatchewan, CA)	4	35
	Lake Abert (Oregon, USA)	5	
	Great Salt Lake (Utah, USA)	5	
	Mono Lake (California, USA)	8	
	South San Francisco Bay (California, USA)	7	
	Owens Lake (California, USA)	6	
2021	Chaplin Lake (Saskatchewan, CA)	3	33
	Lake Abert (Oregon, USA)	4	
	Great Salt Lake (Utah, USA)	5	
	Mono Lake (California, USA)	8	
	South San Francisco Bay (California, USA)	8	
	Owens Lake (California, USA)	5	
2022	Chaplin Lake (Saskatchewan, CA)	3	39
	Lake Abert (Oregon, USA)	6	
	Great Salt Lake (Utah, USA)	5	
	Mono Lake (California, USA)	12	
	South San Francisco Bay (California, USA)	7	
	Owens Lake (California, USA)	6	
2023	Chaplin Lake (Saskatchewan, CA)	6	45
	Lake Abert (Oregon, USA)	11	
	Great Salt Lake (Utah, USA)	4	
	Mono Lake (California, USA)	11	
	South San Francisco Bay (California, USA)	7	
	Owens Lake (California, USA)	6	
2024	Chaplin Lake (Saskatchewan, CA)	14	61
	Lake Abert (Oregon, USA)	10	
	Great Salt Lake (Utah, USA)	6	
	Mono Lake (California, USA)	12	
	South San Francisco Bay (California, USA)	13	
	Owens Lake (California, USA)	6	

Wilson’s and Red-necked phalaropes were identified based on diagnostic plumage characteristics, structural features (Figure 3.2), and behavioral traits, such as the distinctive spinning behavior exhibited during foraging (Colwell and Jehl 2020, Rubega *et al*. 2020). Observations were categorized as Wilson's Phalaropes, Red-necked Phalaropes or unidentified phalaropes (individuals recognised through behaviour or structure as a phalarope but could not be distinguished between Wilson’s and Red-necked phalaropes).

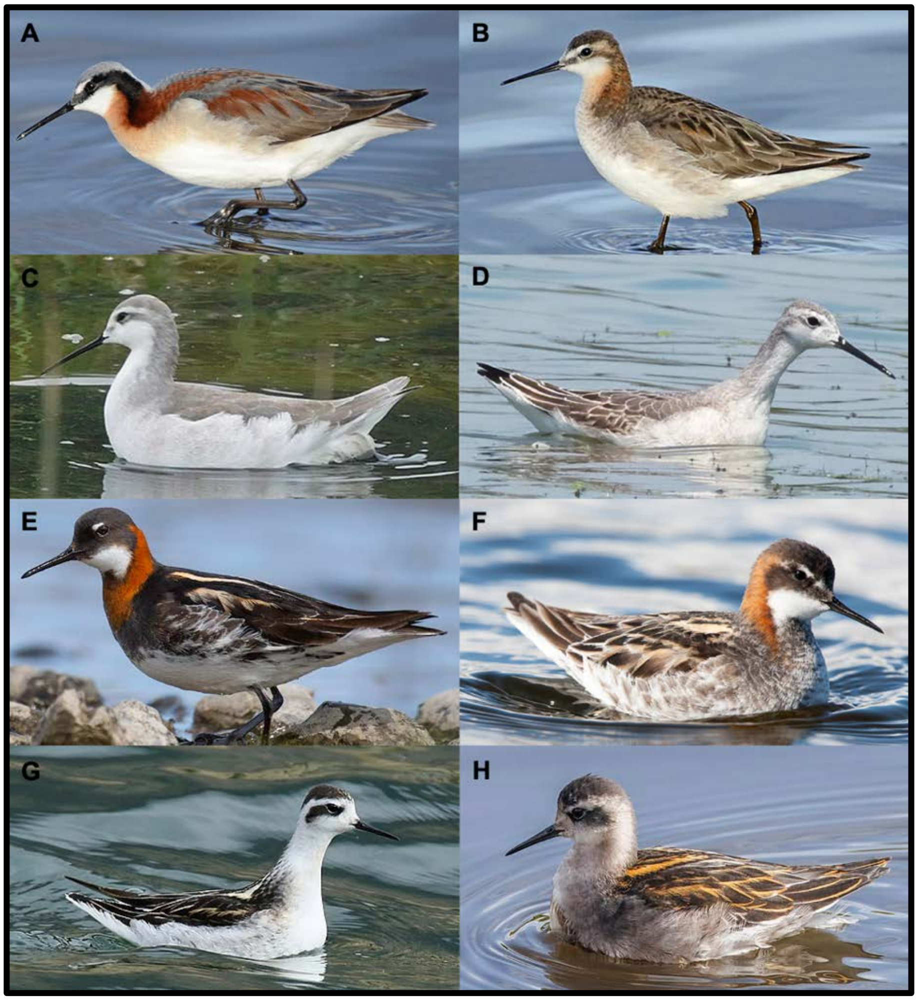


Figure 3.2. Identification of Wilson's and Red-necked phalaropes. A–D Wilson’s Phalarope: female, male, non-breeding, and juvenile. E–H Red-necked Phalarope: female, male, non-breeding, and juvenile. Photos credit Alan Vernon (A, B), Andreas Trepte (C), Nagesh Jayashankar (D), József Szabó (E), Juan Emilio (F), John Haslam (G), and Jóhann Óli Hilmarsson (H; Creative Commons licences).

At Chaplin Lake, surveys took place at eighteen point-count stations surrounding the lake, where surveyors drove along roads surrounding and within the lake, using binoculars and spotting scopes to identify and count birds. All phalaropes were counted within a pre-determined radius (either 200 or 500 meters) specific to each point-count station (Howell *et al*. 2020). In 2020 - 2022, surveys conducted at Chaplin Lake also included all phalaropes seen while traveling between point count stations, including the entire road/dyke system at Chaplin Lake. Surveys at Lake Abert (Oregon, USA) were shore-based, where surveyors stopped at fifteen locations along the lake, using binoculars and scopes to identify and count all phalaropes that could be seen from each location. These surveys encompassed approximately half of the lake. At Great Salt Lake (Utah, USA), surveys consisted of aerial observations from a fixed wing aircraft flown 25 to 60 meters above the surface of the water, with two observers counting the number of phalaropes and recording their location. The surveys were conducted approximately 800 meters from the shoreline. Coverage varied among each survey but typically covered the shoreline extent of Ogden Bay, Farmington Bay, Gilbert Bay, Carrington Bay, Bear River Bay, and a southern portion of Gunnison Bay. Surveys at Mono Lake (California, USA) were both shore and boat-based and included stops at up to 67 locations within and around the lake. Surveyors used binoculars and scopes to identify and count all phalaropes within a 400-meter radius of the boat or a standardized count area at each shore location. At South San Francisco Bay (California, USA), surveys were shore-based with surveyors driving along roads surrounding the bay. Surveys were conducted across 31 sites, including former salt production ponds, water treatment ponds, and diked wetlands. Surveyors used binoculars and scopes to identify and count all phalaropes within the pond or wetland, covering an estimated 12% of available habitat. Surveys at Owens Lake (California, USA) were also shore-based, with surveyors driving along roads surrounding the lake, using binoculars and scopes to identify and count all phalaropes within 16 dust control ponds. Owens Lake dust control ponds are shallow, managed wetlands created to reduce airborne dust emissions from the dry lakebed.

Satellite imagery and habitat classification

At each lake, I generated two types of polygons for classification of habitat characteristics, allowing me to compare the abundance of phalaropes at both a fine scale of the surveyed area and a broader scale that encompassed more of the lake. The first method was based on applying a 500-meter buffer to the surveyed area (hereafter 'surveyed area polygon'; Figure 3.3). I adjusted this method based on the survey approach: for lakes using point counts, I applied a 500-meter buffer around the area covered by each survey stop (Figure 3.3 A); for lakes where entire ponds/wetlands were surveyed, I applied a 500-meter buffer around the whole surveyed pond/wetland (Figure 3.3 B). This method allowed me to analyze the habitat within the approximate area where surveyed birds were located. The buffer distance was selected to encompass adjacent habitat types that can also contribute to bird abundance (Albanese and Davis 2015)

The second method involved applying a minimum bounding polygon around the above buffered areas within each lake (hereafter 'greater lake area polygon'; Figure 3.3). This method allowed me to include more of the lake area in the analysis, under the assumption that phalaropes were likely also using portions of the lake that we were unable to survey. Survey polygons were created in QGIS 3.38.2.

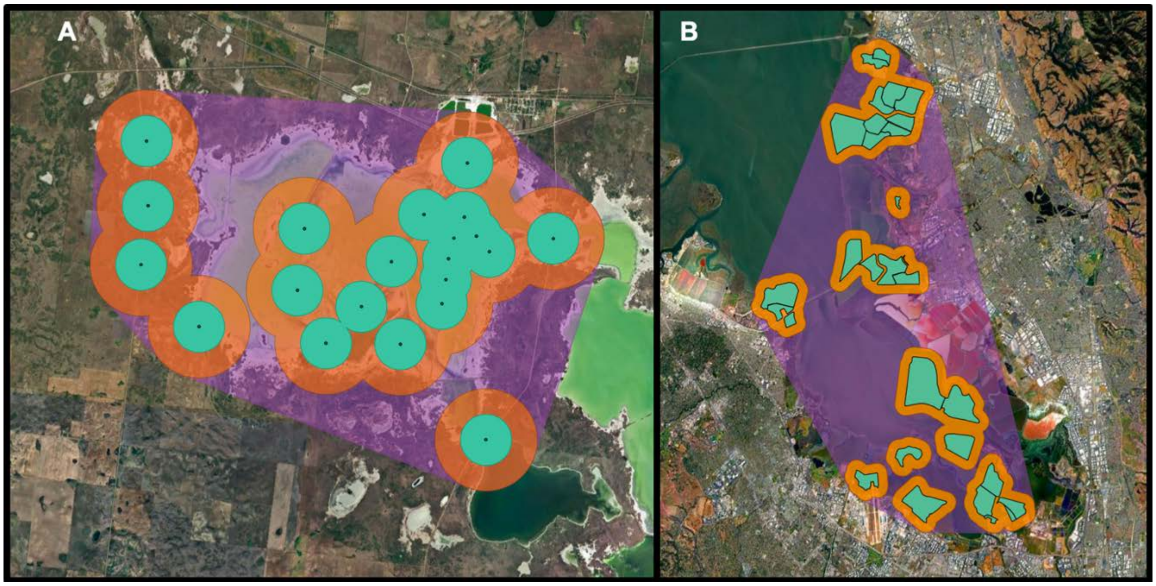


Figure 3.3. Sample of surveyed area polygons for annual phalarope surveys conducted at Chaplin Lake (A) and San Francisco Bay (B). At Chaplin Lake, teal dots represent the center of point count stations, teal circles indicate the surveyed area and orange circles include a 500-m buffer ('surveyed area polygon'), and the purple polygon outlines the minimum bounding polygon of the greater lake area ('greater lake area polygon'). At San Francisco Bay (B), teal represents surveyed ponds/wetlands, orange shows a 500-m buffer surrounding each block, and the purple polygon outlines the minimum bounding polygon.

The Wetland Evaluation Tool was used to classify phalarope habitat. The Wetland Evaluation Tool is a Google Earth Engine supported app that uses Landsat 5 Thematic Mapper and Landsat 8 Operational Land Imager satellite imagery to detect water type and the duration of time that water is present (Donnelly *et al.* 2022, Intermountain West Joint Venture 2022). Habitat was classified monthly into temporary (inundated with water less than two months), seasonal (inundated with water for more than two months and less than six months), and semi-permanent (inundated with water for more than six months) wetland areas for each site. Furthermore, each wetland area was categorized as salt pond, fresh water, or saline water, thus resulting in nine habitat classifications (e.g., temporary salt pond, seasonal fresh water, semi-permanent saline water, etc.).

Habitat analysis

I used a generalized additive model for location, scale and shape (GAMLSS) to evaluate the relationship between habitat characteristics on the abundance of Wilson's and Red-necked phalaropes (Rigby and Stasinopoulos 2005). GAMLSS is a flexible regression framework that models not only the mean but also the variability and shape of a response distribution (Rigby and Stasinopoulos 2005). Initial data exploration showed that phalarope count data were left-skewed and zero-inflated, making GAMLSS an appropriate choice because it can accommodate non-normal and zero-inflated count data. This approach is also suitable for repeated count observations collected over multiple dates and years. I fit models for the total number of phalaropes (combining Wilson's, Red-necked, and unidentified phalaropes) as well as for Wilson's and Red-necked phalaropes separately, excluding unidentified phalaropes.

First, to examine relationships between general habitat characteristics and phalarope abundance, I summarized all nine habitat characteristics in a Principal Component Analysis (PCA) for both surveyed area polygons and greater lake area polygons. This allowed me to analyse all measured habitat variables, even those that are highly correlated. All habitat variables were centered and scaled before the PCA, and principal components were retained until they explained at least 80% of the total variance. PCA loadings plots were examined to identify the habitat characteristics that contributed most strongly to each significant principal component.

GAMLSS models included with general habitat characteristics represented by principal components included the first and second principal components from the respective surveyed area or greater lake area PCA, and a smoothing term for Julian date using a cubic spline to account for any nonlinear seasonal trends in phalarope abundance. Survey month was included as a categorical fixed effect, and site and year were included as random effects to account for expected spatial and temporal differences in abundance counts. The model was fitted using the negative binomial type I distribution in the gamlss package (Rigby and Stasinopoulos 2005) in R v4.4.3 (R Core Team 2024).

$$\text{Phalarope Abundance} \sim \beta_0 + f_1(\text{Julian day}) + \beta_1(PC1) + \beta_2(\text{PC2}) + \beta_3(\text{Survey month}) + u_{\text{Site}} + u_{\text{Year}}$$

In these models, β_0 is the intercept and $\beta_1, \beta_2, \beta_3$ and $\beta_4$are fixed effect regression coefficients describing the effects of the corresponding predictors on log-transformed expected abundance. The term f_1(Julian day)represents a cubic spline smoothing function capturing nonlinear seasonal trends. The random effects u_{Site} and u_{Year} re random intercepts for site and year, assumed to be independent draws from a normal distribution with mean zero and constant variance.

Second, to examine the relationship between specific habitat features and phalarope abundance, I selected three habitat features that were not correlated ($r < 0.7$) and that I predicted would most strongly influence phalarope abundance: seasonal saline water, temporary fresh water, and semipermanent salt ponds. Pairwise Pearson correlations among the predictors were: $r = 0.54$ between seasonal saline water and temporary fresh water, $r = 0.57$ between seasonal saline water and semipermanent salt ponds, and $r = 0.36$ between temporary fresh water and semipermanent salt ponds. Then, as above, I created GAMLSSs with the above as fixed effects, a smoothing term for Julian date, survey month as a fixed effect, and site and year as random effects.

$$\text{Phalarope Abundance} \sim \beta_0 + f_1(\text{Julian day}) + \beta_1(seasonal\ saline\ water) + \\ \beta_2(\text{temporary fresh water}) + \beta_3(\text{Semipermanent salt pond}) + \beta_4(\text{Survey month}) + u_{\text{Site}} + u_{\text{Year}}$$

Partial effects from the GAMLSS models were visualized using partial effects plots, which show the modelled effect of each predictor on the log-scale abundance while holding all other variables constant. Smoothing terms (e.g., Julian day) are displayed as the fitted spline functions with 95% confidence intervals. All partial effects plots were produced in R v4.4.3 using gamlss and base graphics (R Core Team 2024, Rigby & Stasinopoulos 2005).

For all models I assessed model fit and assumptions using residual vs fitted plots, and Quantile-Quantile plots. The Akaike Information Criterion (AIC) was used to compare model performance between models fit with principal components vs. specific habitat variables. Pseudo R^2 values were calculated by comparing the log-likelihood of each fitted model to the log-likelihood of a corresponding null model, to indicate how much of the variation in abundance was explained by the predictors in the model (Smith *et al.* 2019). Statistical significance in all models was assessed using a threshold of $p \leq 0.05$.

RESULTS

Phalarope abundance

Across the six surveyed lakes over six years, there was a total of 243 surveys conducted with a total of 6,391,758 individual birds recorded (Figure 3.4). Of these, 2,038,595 (31.89 %) were Wilson's Phalaropes, 1,339,417 (20.96 %) were Red-necked Phalaropes and 3,013,746 (47.15 %) were unknown phalarope species (described herein as unidentified phalaropes). Overall, Great Salt Lake had the highest abundance of phalaropes (4,890,554), and Chaplin Lake had the lowest abundance (55,833).

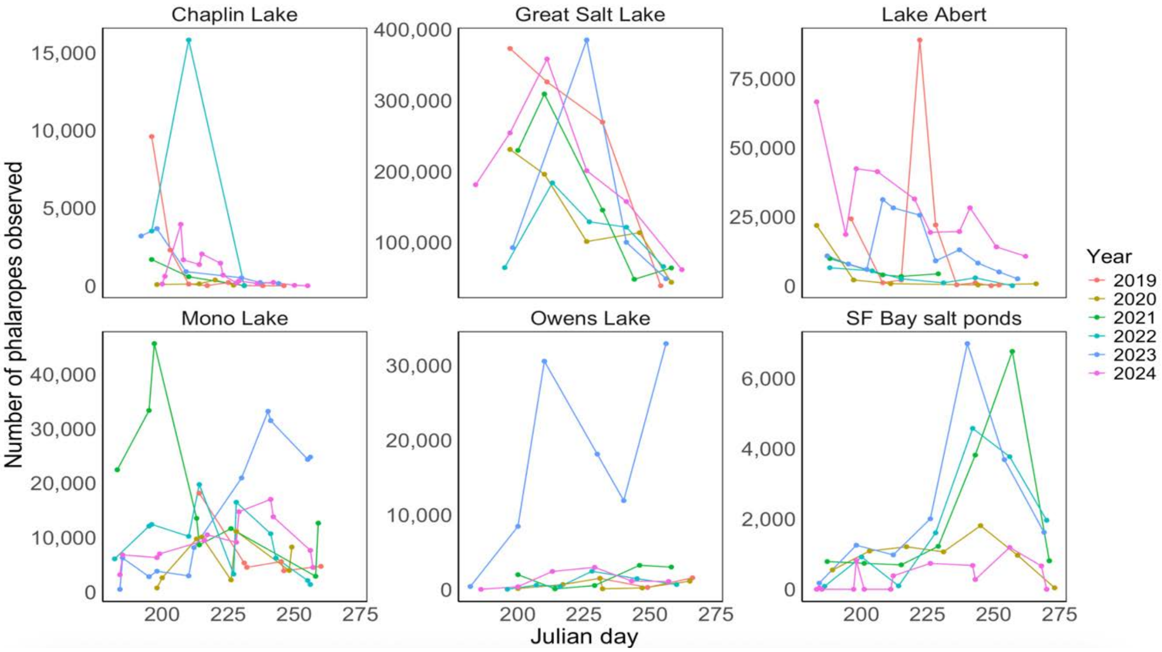
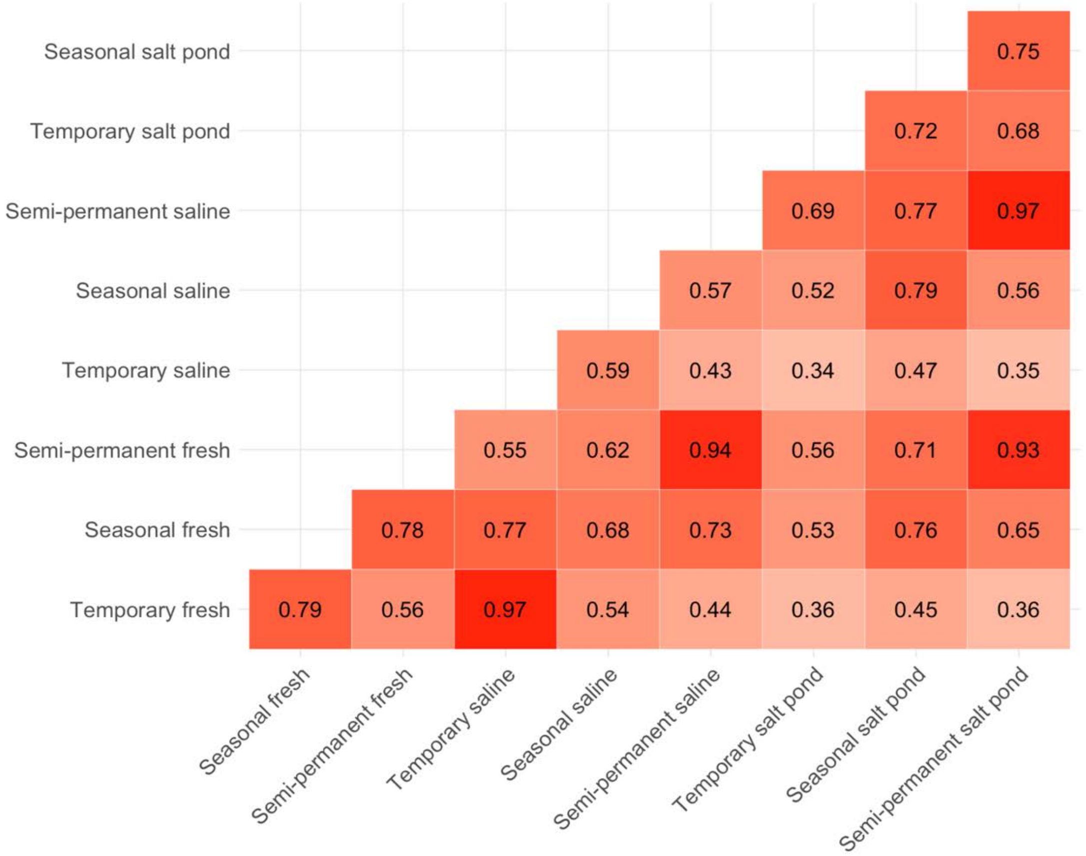


Figure 3.4. Total number of Wilson's, Red-necked, and unidentified phalaropes recorded during 243 surveys at six North American saline lakes from 2019 to 2024.

Principal component analysis

Strong correlations among habitat variables indicated substantial multicollinearity (Figure 3.5). All habitat types were positively correlated, with especially strong correlations among hydroperiod classes within each water type (e.g., r = 0.94 between seasonal and semi-permanent freshwater, and r = 0.97 between seasonal and semi-permanent salt ponds), indicating that sites with high water availability tended to have high values across multiple habitat classes.



	Seasonal fresh	Semi-permanent fresh	Temporary saline	Seasonal saline	Semi-permanent saline	Temporary salt pond	Seasonal salt pond	Semi-permanent salt pond
Seasonal salt pond								0.75
Temporary salt pond							0.72	0.68
Semi-permanent saline						0.69	0.77	0.97
Seasonal saline					0.57	0.52	0.79	0.56
Temporary saline				0.59	0.43	0.34	0.47	0.35
Semi-permanent fresh			0.55	0.62	0.94	0.56	0.71	0.93
Seasonal fresh		0.78	0.77	0.68	0.73	0.53	0.76	0.65
Temporary fresh	0.79	0.56	0.97	0.54	0.44	0.36	0.45	0.36

Figure 3.5. Pearson correlation matrix for North American saline lake habitat variables.

The surveyed area polygon PC1 explained 63.9% of the variation in the data and represented the overall amount of water at surveyed areas (Table 3.2). All habitat types (freshwater, saline, and salt ponds; temporary, seasonal, and semi-permanent) were strongly and negatively loaded along this axis, indicating that negative PC1 values reflected habitats with more water (Figure 3.6). The surveyed area polygon PC2 explained 15.8% of the variation in the data and loaded on hydroperiod and water type (Table 3.2). Positive PC2 values were associated with more temporary (water present for <2 months) fresh and saline water habitats. Negative PC2 values corresponded to sites with more semi-permanent (water present for >6 month) saline water and salt ponds.

Table 3.2. Principal component scores and relative weightings of variables from a PCA on habitat variables of six North American saline lakes within the surveyed area polygons.

Variable	**PC1**	**PC2**
Seasonal saline water	-0.34	0.06
Semipermanent saline water	-0.37	-0.32
Temporary saline water	-0.32	0.53
Seasonal fresh water	-0.39	0.12
Semipermanent fresh water	-0.38	-0.18
Temporary fresh water	-0.31	0.53
Seasonal salt ponds	-0.34	-0.04
Semipermanent salt ponds	-0.31	-0.48
Temporary salt ponds	-0.22	-0.21
Percentage of total variation explained by each component	63.9%	15.8%

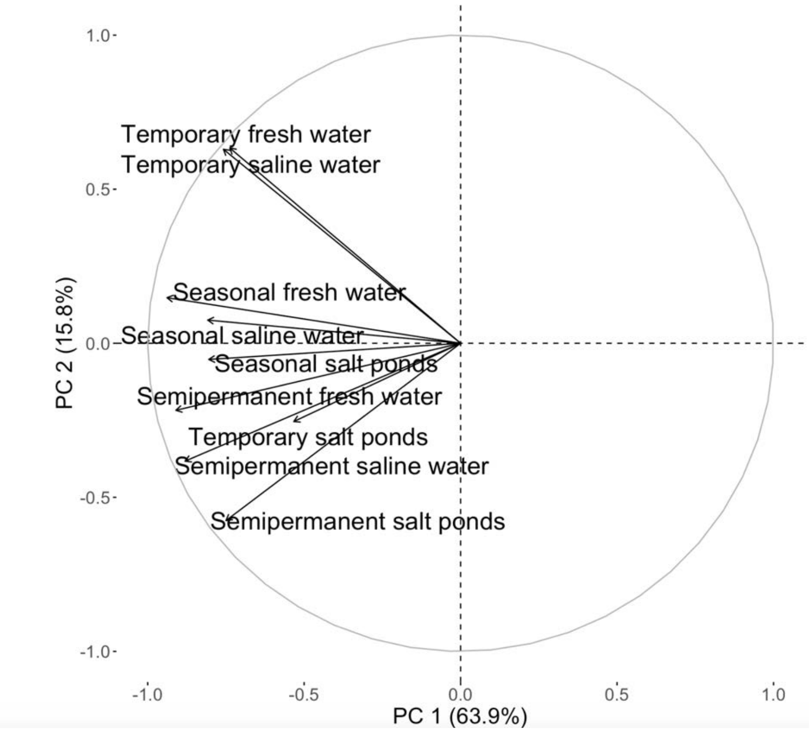


Figure 3.6. Principal component loadings from a PCA on habitat variables of six North American saline lakes within the surveyed area polygons.

PCA results for the greater lake area polygons were very similar to those from the surveyed area polygons. PC1 explained 68.2% of the variation in the data and represented the amount of water at surveyed areas; habitat characteristics were similarly and negatively loaded along the axis (Table 3.3, Figure 3.7). The greater lake area polygon PC2 explained 15.8% of the variation in the data and, as above, distinguished between habitat types based on hydroperiod and water type (Table 3.3).

Table 3.3. Principal component scores and relative weightings of variables from a PCA on the habitat variables of six North American saline lakes within the greater lake area polygons.

Variable	PC1	PC2
Seasonal saline water	-0.32	0.08
Semipermanent saline water	-0.36	-0.29
Temporary saline water	-0.29	0.56
Seasonal fresh water	-0.36	0.20
Semipermanent fresh water	-0.37	-0.15
Temporary fresh water	-0.29	0.55
Seasonal salt ponds	-0.35	-0.16
Semipermanent salt ponds	-0.35	-0.37
Temporary salt ponds	-0.29	-0.27
Percentage of total variation explained by each component	68.2%	15.8%

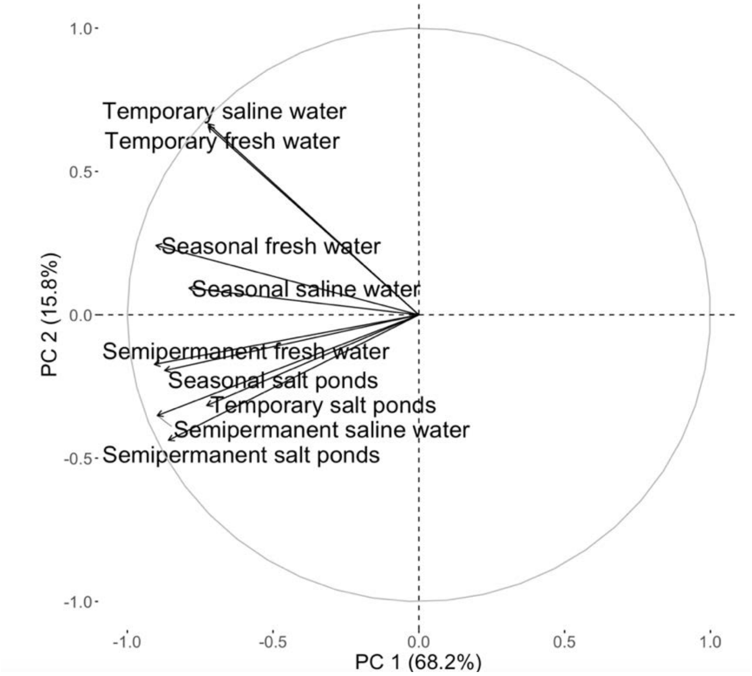


Figure 3.7. Principal component loadings from a PCA on habitat variables of six North American saline lakes within the greater lake area polygons.

Predicting total phalarope abundance with habitat PCs

When total phalarope abundance was modeled as a function of habitat PC1 and PC2, Julian date, and month as fixed effects, PC1 was the only significant predictor for both surveyed area and greater lake area polygons. Higher PC1 values, indicating less water coverage, were associated with lower total phalarope abundance (surveyed area: $\beta = -0.08$, $p = 0.02$; greater lake area: $\beta = -0.11$, $p < 0.001$; Figure 3.8). All other predictors were not significant (Table 3.4).

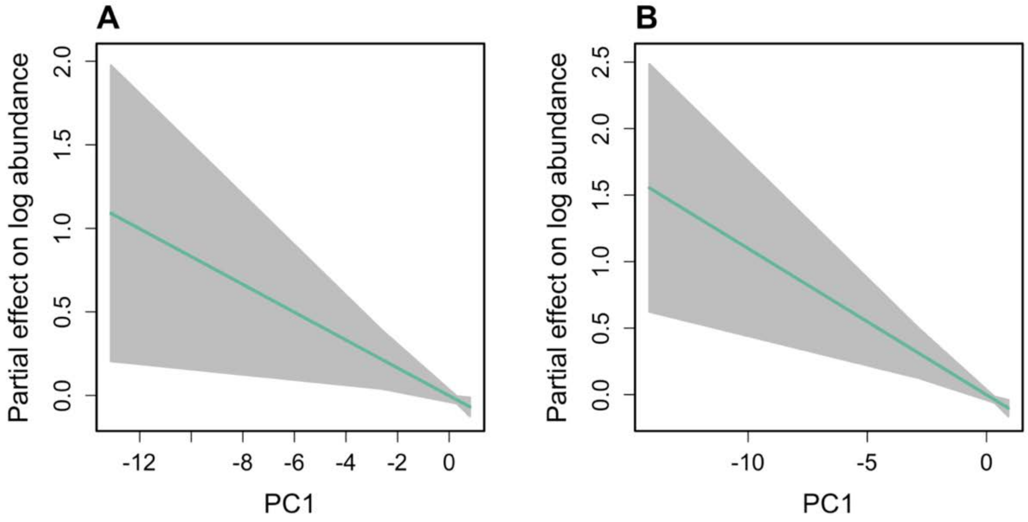


Figure 3.8. Partial effects of habitat PC1 on total phalarope abundance in (A) surveyed-area polygons and (B) greater lake area polygons. The y-axis shows the estimated effect of PC1 on log-transformed abundance, holding all other predictors constant (PC2, Julian date, survey month, and random variation among sites and years). Shaded area shows 95% confidence intervals.

Table 3.4. GAMLSS model coefficients and their significance for total phalarope abundance in relation to habitat principal components, Julian date, and survey month for surveyed area and the greater lake area polygons. * represents a significant effect.

Polygon	**Predictor variable**	**β**	**SE**	**t**	**p**
Surveyed area	Habitat PC1	-0.08	0.03	-2.45	0.02*
	Habitat PC2	-0.04	0.07	-0.64	0.52
	Julian date	0.01	0.01	1.03	0.31
	Survey month (August)	-0.59	0.34	-1.71	0.09
	Survey month (September)	-1.01	0.59	-1.71	0.09
Greater lake area	Habitat PC1	-0.11	0.03	-3.39	<0.001*
	Habitat PC2	-0.08	0.07	-1.12	0.27
	Julian date	0.01	0.01	0.94	0.35
	Survey month (August)	-0.53	0.34	-1.55	0.12
	Survey month (September)	-0.93	0.59	-1.58	0.12

Predicting total phalarope abundance with specific habitat variables

Next, I modeled total phalarope abundance as a function of three habitat variables (seasonal saline water, temporary fresh water, semipermanent salt ponds), Julian date, and month as fixed effects. For the surveyed area polygons, seasonal saline water was a positive predictor of abundance, ($\beta = 7.27\times10^{-5}$, $p < 0.001$), showing total phalarope abundance increased with higher amounts of seasonal saline water (Figure 3.9). None of the other predictors were significant. For the greater lake area polygons, no predictors were significant (Table 3.5).

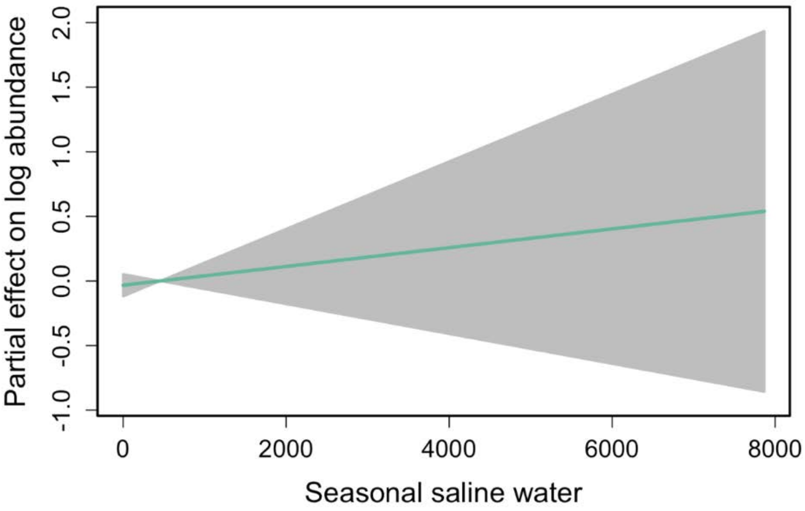


Figure 3.9. Partial effects of seasonal saline water on total phalarope abundance for the surveyed area polygons. The y-axis represents the estimated effect of seasonal saline water on log-transformed abundance after controlling for all other predictors. Shaded areas show 95% confidence intervals.

Table 3.5. GAMLSS model coefficients and their significance for total phalarope abundance in relation to specific habitat variables, Julian date, and survey month for surveyed area and greater lake area polygons. * represents a significant effect.

Polygon	**Predictor variable**	**β**	**SE**	**T**	**p**
Surveyed area	Seasonal saline water	7.27×10^{-5}	2.29×10^{-6}	31.69	$<2\times10^{-16}$ *
	Temporary fresh water	1.32×10^{-4}	9.25×10^{-5}	1.43	0.16
	Semipermanent salt ponds	2.78×10^{-4}	1.55×10^{-4}	1.80	0.07
	Julian date	9.35×10^{-3}	9.32×10^{-3}	1.00	0.32
	Survey month (August)	-0.56	0.36	-1.56	0.12
	Survey month (September)	-0.97	0.59	-1.64	0.10
Greater lake area	Seasonal saline water	1.01×10^{-4}	9.01×10^{-5}	1.13	0.26
	Temporary fresh water	2.00×10^{-5}	2.30×10^{-4}	0.09	0.93
	Semipermanent salt ponds	5.12×10^{-5}	3.73×10^{-5}	1.37	0.17
	Julian date	9.50×10^{-3}	9.12×10^{-3}	1.04	0.30
	Survey month (August)	-0.54	0.34	-1.58	0.12
	Survey month (September)	-0.93	0.58	-1.61	0.11

Predicting Wilson's Phalarope abundance with habitat PCs

When modeling Wilson's Phalarope abundance as a function of habitat PC1 and PC2, Julian date, and month as fixed effects, for both surveyed area polygons and greater lake area polygons smoothed Julian date had a significant effect (surveyed area: $\beta = -0.08$, $p < 0.001$; greater lake area: $\beta = -0.08$, $p < 0.001$), indicating there was a non-linear relationship between survey date and Wilson's Phalarope abundance. Abundance tended to be higher until about mid-July, then showed a decline (Figure 3.10). None of the other predictors were significant (Table 3.6).

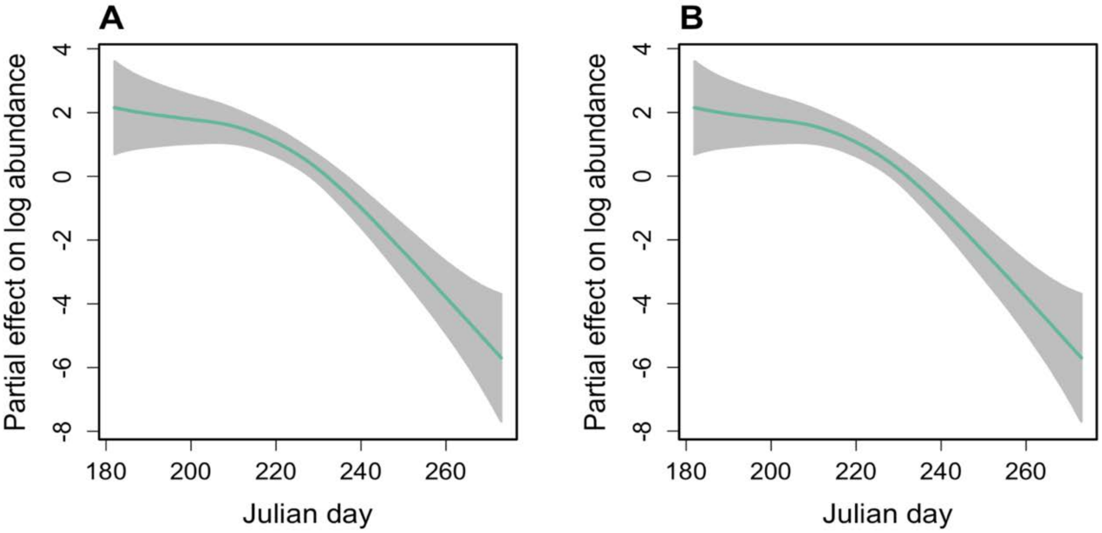


Figure 3.10. Partial effect plots for the smoothing Julian day term predicting Wilson’s Phalarope abundance in (A) surveyed-area polygons and (B) whole-lake polygons. The y-axis represents the estimated effect of Julian day on log-transformed abundance of Wilson's Phalarope abundance, holding other predictors constant. Shaded areas show 95% confidence intervals.

Table 3.6. GAMLSS model coefficients and their significance for Wilson’s Phalarope abundance in relation to habitat principal components, Julian date, and survey month for surveyed area and greater lake area polygons. * represents a significant effect.

Polygon	Predictor variable	β	SE	t	p
Surveyed area	Julian date	-0.08	0.01	-5.67	4.29×10^{-8}*
	Habitat PC1	0.05	0.05	0.97	0.33
	Habitat PC2	0.10	0.10	0.99	0.32
	Survey month (August)	-0.98	0.53	-1.84	0.07
	Survey month (September)	-0.98	0.90	-1.09	0.28
Greater lake area	Julian date	-0.08	0.01	-5.64	4.95×10^{-8}*
	Habitat PC1	0.03	0.05	0.56	0.58
	Habitat PC2	0.07	0.10	0.72	0.47
	Survey month (August)	-0.97	0.53	-1.83	0.07
	Survey month (September)	-0.98	0.90	-1.09	0.28

Predicting Wilson's Phalarope abundance with specific habitat variables

Next, I modelled Wilson’s Phalarope abundance as a function of three habitat variables (seasonal saline water, temporary fresh water, semipermanent salt ponds), Julian date, and month as fixed effects. For surveyed area polygons, smoothed Julian date (β = -

0.082, $p < 0.001$) and seasonal saline water ($\beta = -5.53\times10^{-5}$, $p < 0.001$) had significant effects on abundance (Figure 3.11). For greater lake area polygons, only smoothed Julian date was significant ($\beta = -0.0812$, $p = 7.77\times10^{-9}$), while all other predictors were not significant (Table 3.7). In both models, Wilson's Phalarope abundance varied non-linearly with survey date, tending to be higher until about mid-July then decreasing (Figure 3.11 A, B). In the surveyed area polygon model, Wilson's Phalarope abundance decreased as the amount of seasonal saline water increased (Figure 3.11 C).

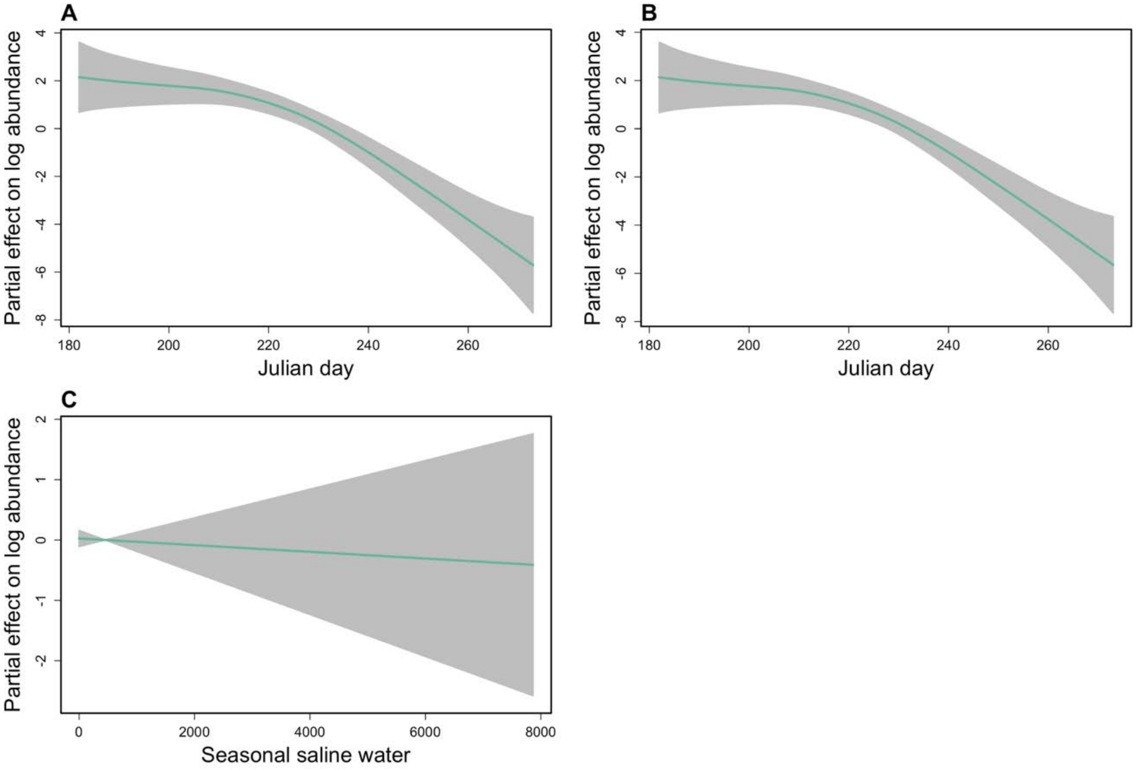


Figure 3.11. Partial effect plots showing the relationship between (A-B) smoothed Julian day and Wilson's Phalarope abundance in surveyed area (A) and greater lake area (B) polygons, and (C) seasonal saline water extent and Wilson's Phalarope abundance in surveyed area polygons. The y-axes represent the estimated effect of each significant predictor variable on log-transformed abundance of Wilson's Phalarope abundance, holding other predictors constant. Shaded areas indicate 95% confidence intervals.

Table 3.7. GAMLSS model coefficients and their significance for Wilson's Phalarope abundance in relation to specific habitat variables, Julian date, and survey month for surveyed area and greater lake area polygons. * represents a significant effect.

Polygon	Predictor variable	β	SE	t	p
Surveyed area	Julian date	-0.0823	0.0145	-5.67	4.42×10^{-8}*
	Seasonal saline water	-5.53×10^{-5}	2.51×10^{-6}	-22.01	$<2\times10^{-16}$*
	Temporary fresh water	2.17×10^{-4}	1.14×10^{-4}	1.90	0.06
	Semipermanent salt ponds	-1.54×10^{-4}	2.06×10^{-4}	-0.75	0.46
	Survey month (August)	-0.987	0.556	-1.78	0.08
	Survey month (September)	-0.987	0.920	-1.07	0.28
Greater lake area	Julian date	-0.0812	0.0135	-6.00	7.77×10^{-9}*
	Seasonal saline water	6.74×10^{-5}	1.24×10^{-4}	0.54	0.59
	Temporary fresh water	8.68×10^{-5}	2.72×10^{-4}	0.32	0.75
	Semipermanent salt ponds	-7.86×10^{-5}	5.59×10^{-5}	-1.41	0.16
	Survey month (August)	-0.922	0.505	-1.83	0.07
	Survey month (September)	-0.967	0.842	-1.15	0.25

Predicting Red-necked Phalarope abundance with habitat PCs

I modeled Red-necked Phalarope abundance as a function of habitat PC1 and PC2, Julian date, and month as fixed effects. For surveyed area polygons, smoothed Julian date had a significant effect on abundance ($\beta = 0.06$, $p < 0.001$; Figure 3.12) while other predictors were not significant. For greater lake area polygons, both smoothed Julian date ($\beta = 0.06$, $p = 0.0001$) and PC1 ($\beta = -0.13$, $p = 0.02$) were significant (Figure 3.12 A, C); all other predictors were not significant (Table 3.8). In both models Red-necked Phalarope abundance varied non-linearly with survey date, appearing to show a steady increase from July to September, with a slight dip in abundance in mid-August (Figure 3.12 A, B). In the greater lake area polygon model, Red-necked Phalarope abundance decreased with higher PC1 values, which indicate less water present (Figure 3.12 C).

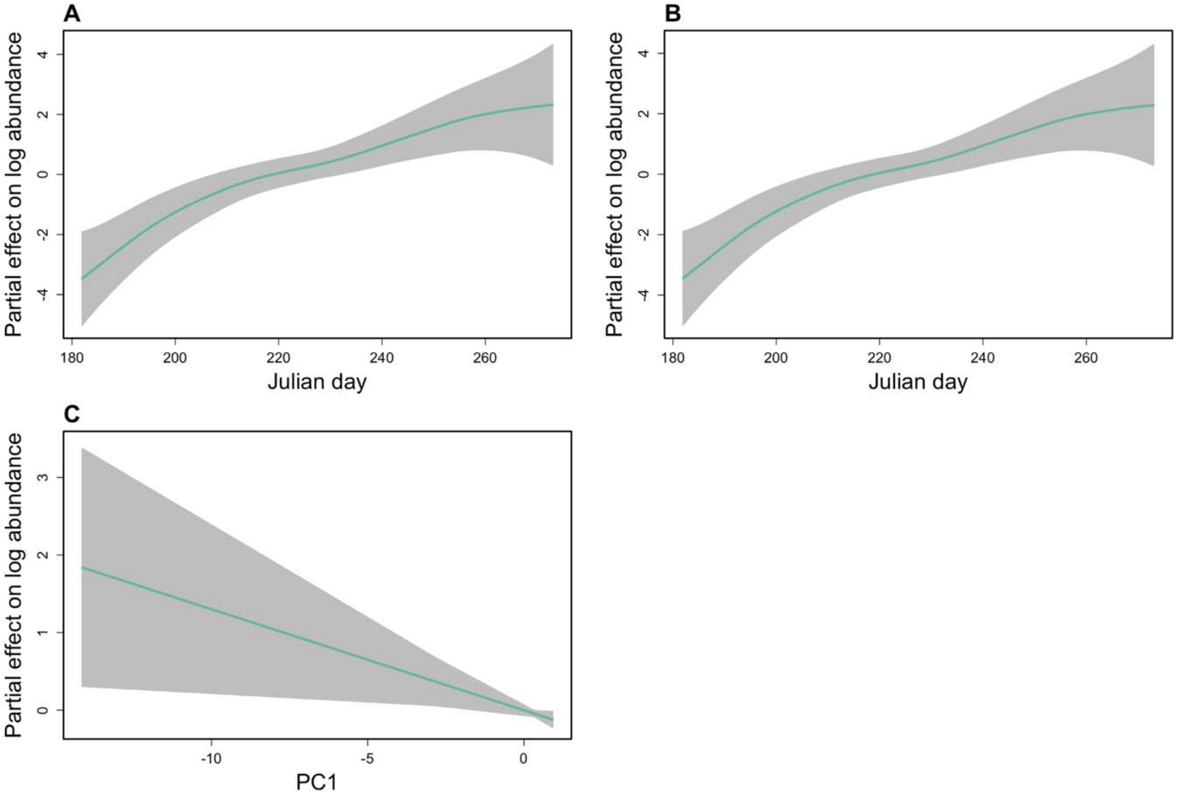


Figure 3.12. Partial effect plots showing the relationship between (A, B) smoothed Julian day and Red-necked Phalarope abundance in surveyed area (A) and greater lake area (B) polygons, and (C) PC1 and Red-necked Phalarope abundance in greater lake area polygons. The y-axes represent the estimated effect of each significant predictor variable on log-transformed abundance of Red-necked Phalarope abundance, holding other predictors constant. Shaded areas indicate 95% confidence intervals.

Table 3.8. GAMLSS model coefficients and their significance for Red-necked Phalarope abundance in relation to habitat principal components, Julian date, and survey month for surveyed area and greater lake area polygons. * represents a significant effect.

Polygon	**Predictor variable**	**β**	**SE**	**t**	**p**
Surveyed area	Julian date	0.06	0.02	3.97	9.66×10^{-5}*
	Habitat PC1	-0.09	0.06	-1.50	0.14
	Habitat PC2	-0.04	0.10	-0.34	0.74
	Survey month (August)	-0.13	0.55	-0.24	0.81
	Survey month (September)	-1.41	0.96	-1.47	0.14
Greater lake area	Julian date	0.06	0.02	3.93	0.0001*
	Habitat PC1	-0.13	0.06	-2.30	0.02*
	Habitat PC2	-0.07	0.11	-0.61	0.54
	Survey month (August)	-0.06	0.55	-1.10	0.92
	Survey month (September)	-1.32	0.96	-1.38	0.17

Predicting Red-necked Phalarope abundance with specific habitat variables

Lastly, I modeled Red-necked Phalarope abundance as a function of three habitat variables (seasonal saline water, temporary fresh water, and semipermanent salt ponds), Julian day, and survey month as fixed effects. For surveyed area polygons, the smoothed Julian day term was a significant predictor of abundance ($\beta = 0.0592$, $p = 9.74\times10^{-10}$), indicating a gradual, non-linear, increase in abundance across the survey period (Figure 3.13 A). Survey month was also significant, and although raw counts were relatively high in September, once the seasonal trend in abundance (contributed by the smoothed Julian date) was accounted for, abundance in September was significantly lower than expected relative to July ($\beta = -1.25$, $p = 0.02$). This suggests surveys in September occurred after the seasonal peak in abundance. In the greater lake area polygon model, both the smoothed Julian day term ($\beta = 0.0606$, $p = 3.33\times10^{-5}$) and the area of semipermanent salt ponds ($\beta = 1.49\times10^{-4}$, $p = 0.03$) were significant predictors, with Red-necked Phalarope abundance increasing with greater area of semipermanent salt ponds (Figure 3.13 B, C). All other predictors were not significant (Table 3.9).

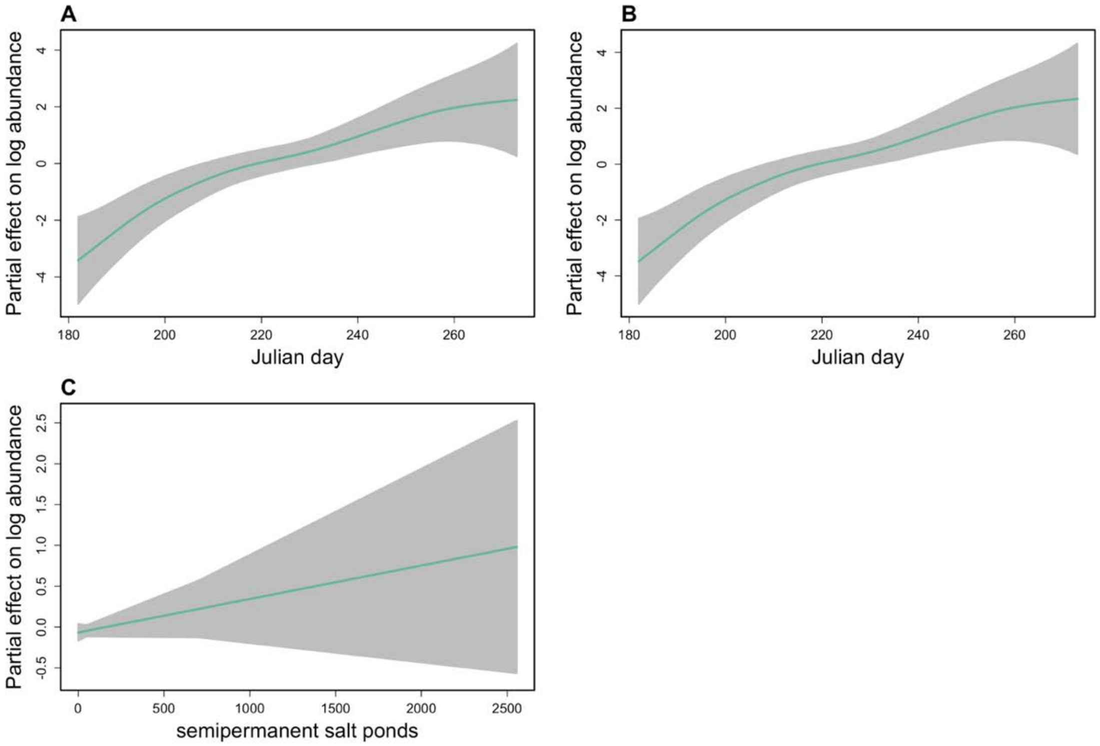


Figure 3.13. Partial effect plots showing the relationship between (A, B) smoothed Julian day and Red-necked Phalarope abundance in surveyed area (A) and greater lake area (B) polygons, and (C) semipermanent salt ponds and Red-necked Phalarope abundance in greater lake area polygons. The y-axes represent the estimated effect of each significant predictor variable on log-transformed abundance of Red-necked Phalarope abundance, holding other predictors constant. Shaded areas indicate 95% confidence intervals.

Table 3.9. GAMLSS model coefficients and their significance for Red-necked Phalarope abundance in relation to specific habitat variables, Julian date, and survey month for surveyed area and greater lake area polygons. * represents a significant effect.

Polygon	**Predictor variable**	**β**	**SE**	**t**	**p**
Surveyed area	Julian date	5.92×10^{-2}	9.26×10^{-3}	6.39	9.74×10^{-10}*
	Seasonal saline water	1.47×10^{-4}	1.58×10^{-4}	0.93	0.35
	Temporary fresh water	1.36×10^{-4}	4.13×10^{-4}	0.33	0.74
	Semipermanent salt ponds	4.10×10^{-4}	3.46×10^{-4}	1.18	0.24
	Survey month (August)	-2.32×10^{-2}	0.13	-0.18	0.86
	Survey month (September)	-1.25	0.52	-2.43	0.02*
Greater lake area	Julian date	6.06×10^{-2}	1.43×10^{-2}	4.24	3.33×10^{-5}*
	Seasonal saline water	1.07×10^{-3}	1.02×10^{-3}	1.05	0.30
	Temporary fresh water	-1.98×10^{-4}	2.25×10^{-4}	-0.88	0.38
	Semipermanent salt ponds	1.49×10^{-4}	6.76×10^{-5}	2.20	0.03*
	Survey month (August)	-0.175	0.499	-0.35	0.73
	Survey month (September)	-1.38	0.883	-1.56	0.12

Model diagnostics

For all models, examination of residual vs. fitted plots and Quantile-Quantile plots indicated no issues with model fit. For all three response variable groups, models using principal component predictors and models using individual habitat variables performed similarly. Differences in AIC between predictor sets were very small (≤ 2.5), indicating no meaningful improvement in model fit when using one predictor set over the other (Table 3.10). Pseudo-R^2 values were similar across predictor sets and spatial scales, suggesting that both sets of predictors explained a similar proportion of variation in abundance (Table 3.10).

Table 3.10. AIC and pseudo-R^2 values for GAMLSS models of phalarope abundance, comparing predictor variable sets (principal components vs. specific habitat variables) and spatial scale (surveyed area vs. greater lake area).

Response	Polygon	Predictor Set	AIC	R^2 (pseudo)
Total phalaropes	Surveyed area	PCs	4744.50	0.0545
		Habitat variables	4746.38	0.0545
	Greater lake area	PCs	4743.90	0.0546
		Habitat variables	4745.57	0.0547
Wilson's Phalaropes	Surveyed area	PCs	3253.73	0.0635
		Habitat variables	3256.16	0.0634
	Greater lake area	PCs	3254.31	0.0633
		Habitat variables	3255.64	0.0636
Red-necked Phalaropes	Surveyed area	PCs	3377.66	0.0438
		Habitat variables	3379.09	0.0438
	Greater lake area	PCs	3377.32	0.0439
		Habitat variables	3378.31	0.0442

DISCUSSION

For both Wilson’s and Red-necked phalaropes surveyed during southward migration through Western North America, a greater amount of water at saline lakes, which provides habitat that supports prey species, was associated with higher numbers of phalaropes. There were also notable differences in abundance patterns between species, with abundance associated with different habitat features at different spatial scales, as well as peaks in abundance differing between Wilson’s and Red-necked phalaropes, possibly due to differences in their life histories. Overall, the results from this study capture the broad lake characteristics and specific habitat features that drive patterns of abundance for phalaropes and can inform general and species-specific management strategies to support these species at saline lake staging sites.

At both spatial scales for total phalaropes, and in the surveyed area model for Red-necked Phalaropes, abundance was significantly and negatively associated with PC1 scores, where higher PC1 values correspond to lower water coverage. This indicates that phalarope abundance was higher in areas with more open water. This finding aligns with established patterns in phalarope migration behaviour, where habitat availability and foraging opportunities decline as water levels drop (Senner *et al.* 2018). One example of this pattern has been observed at Lake Abert in Oregon, which experienced periods of extremely low water and almost complete drying in 2014, which was largely caused by water diversion for agricultural practices and drought conditions (Larson *et al.* 2016). The dried lake basin resulted in a nearly complete absence of phalaropes from the lake, and no substantial use by phalaropes until water returned and prey communities recovered in 2016 (Larson *et al.* 2016; Senner *et al.* 2018). Similarly, at Gunnison Bay in Great Salt Lake, Utah, the construction of a rail causeway that cut off most of the freshwater inflow to the bay has resulted in salinities too high to support prey species, resulting in phalaropes no longer using this area (Frank and Conover 2021a, White *et al*. 2015). These examples show that habitat that supports prey availability depends on sufficient lake water levels, highlighting that conservation and water management actions that maintain higher lake levels are essential. On the other hand, too much water can also be a problem for shorebirds. When lake depths increase beyond the shallow margins preferred by wading species, the extent of exposed mudflats and nearshore foraging areas is reduced or eliminated. At the same time, if freshwater inflows dilute water salinity enough, the invertebrate communities can collapse, reducing prey availability even when water is abundant (Wurtsbaugh 1992). Additionally, even though higher water levels can benefit phalaropes, other species that utilize saline lakes may have different responses. For example, a study examining how water levels influence bird presence at Bear River Bay in Great Salt Lake showed that higher water levels were associated with higher abundance of some species, but a lower abundance in others (Tavernia *et al.* 2021). These cases demonstrate that while maintaining sufficient water is essential, hydrological management must also consider the thresholds beyond which habitats become unsuitable for shorebird and other bird foraging and habitat use.

Mono Lake in California illustrates the link between socioeconomic and environmental challenges of maintaining adequate water levels in saline lakes. Diversions of freshwater inflow by the City of Los Angeles began in 1941 and subsequently lowered Mono Lake by approximately 45 vertical feet and increased the salinity (National Research Council 1987). In 1994, the California State Water Resources Control Board Decision 1631 mandated that water diversions be reduced and set a target lake elevation of 6,392 ft (1,948 m) to restore and protect ecological function (SWRCB 1994). However, over thirty years later, the lake has still not reached the mandated level, demonstrating how long-term lake recovery is difficult to achieve under continued water demand and increasing climate pressures (Mono Lake Committee 2024). Strengthening saline lake protections and enforcing current protections for minimum lake levels would help sustain saline lake habitat for both Wilson's and Red-necked phalaropes during migration. However, managers must also take into account species-specific differences in the benefits of various water management regimes when aiming to support overall biodiversity for the many species that utilize saline lake ecosystems (Senner *et al.* 2018).

When looking at the role of specific habitat features on phalarope abundance, I found differences between species and spatial scales. In models that included just the surveyed area at the lakes, total phalarope abundance increased with greater extent of seasonal saline water, whereas Wilson's Phalaropes showed a slight negative association with seasonal saline water. Seasonal water habitats are typically shallower portions of the lake that hold water for only part of the year (2–6 months, Donnelly *et al.* 2019). These areas may offer good foraging habitats when flooded, but their temporary nature and fluctuating water levels may make them less reliable as stopover habitat (Donnelly *et al.* 2019, 2022). The positive association for total phalaropes may reflect short term use of seasonal saline waters from both species and unknown phalarope when conditions are favorable, while the negative association for Wilson's Phalaropes suggests that Wilson's Phalaropes may prefer more stable saline habitats with more consistent water depth and prey availability (Castellino *et al.* 2024, Frank and Conover 2019, Jehl 1988). A study comparing the foraging behaviors of Wilson's and Red-necked Phalaropes at Great Salt Lake found that Wilson's Phalaropes used a spinning foraging method more frequently, where individuals rotate on the water surface to generate an upwelling vortex that brings prey toward the surface (Frank and Conover 2021b). This spinning behavior is particularly advantageous in deeper water, where prey may be otherwise inaccessible. The greater reliance on spinning in Wilson's Phalaropes relative to Red-necked Phalaropes could contribute to a higher abundance in more stable saline wetlands with deeper and more reliable water levels (Frank and Conover 2021b). When considered alongside the PCA results indicating the importance of overall water extent, these findings suggest that management actions that maintain or restore more permanent saline water bodies, rather than ephemeral or seasonally variable ones, are likely to support more reliable foraging conditions for migrating phalaropes (Senner *et al.* 2018).

Additionally, Red-necked Phalarope abundance was positively associated with semipermanent salt ponds, which are inundated with water for more than six months and are typically a result of salt production practices or dust control efforts for lakes that have dried. These human-made structures are likely supporting Red-necked Phalarope abundance by providing them with stable foraging habitats, since the water levels are typically managed and do not often change (Van Schmidt *et al.* 2025). This is the case at Chaplin Lake, Saskatchewan, where there is an active sodium sulfate mine that manages water levels and salinity of various management sub-basins in order to maintain commercial salt production (Saskatchewan Mining and Minerals n.d.), while at the same time providing apparently suitable habitat conditions and prey availability for multiple shorebird species (Howell *et al.* 2019). Together, species-specific habitat features that drive abundance highlight the importance of considering both habitat structure and seasonal context in understanding phalarope use of saline lakes and that, when appropriately managed, some human-modified saline systems can play a beneficial role in supporting phalaropes and other biodiversity.

The differences found in seasonal patterns of abundance between Wilson’s and Red-necked phalaropes likely reflect differences in their life histories. Wilson’s Phalaropes tended to reach peak abundance earlier in the season (mid-July), whereas Red-necked Phalaropes peaked later (early September). These contrasting seasonal patterns are consistent with differences in migration and breeding strategies. Wilson’s Phalaropes nest farther south on average and have shorter overall migration distances to reach interior North American staging sites. Nest initiation in Wilson's Phalaropes can begin as early as the beginning of May and females depart breeding grounds soon after laying (Colwell and Jehl 2020). As a result, Wilson’s Phalaropes are typically one of the earlier fall migrants (Colwell and Jehl 2020). While Red-necked Phalaropes have similar patterns with females departing shortly after egg laying, nest initiation typically does not begin until late May. Additionally Red-necked Phalaropes typically breed farther north and have a longer journey to interior North American staging sites (Rubega *et al.* 2020). Because total phalarope abundance combines both species, these opposing seasonal patterns likely offset one another, resulting in no clear temporal trend in the total phalarope abundance models. Combined with the differences in specific habitat features driving abundance, these results highlight that although both species rely on saline lakes as critical stopover habitat, they are doing so under different conditions and at different times. Thus, effective habitat management must account for species specific needs and ensure that suitable habitat is available throughout both species' migration windows, not only at a single peak period.

Comparing surveyed area and greater lake area polygon models provided complementary insights into habitat use at different spatial scales. The surveyed area models reflect conditions in the specific locations where birds were observed, capturing habitat features that phalaropes were likely actively selecting during surveys. In contrast, greater lake area models incorporate more of the available habitat within the lake basin, offering a broader representation of ecosystem scale conditions. This distinction is important because greater lake area models can detect overall habitat conditions, but they may also include areas that are not used by birds due to habitat factors like unsuitable water depth, salinity, or prey availability (Senner *et al.* 2018). Meanwhile, surveyed area models may better reflect fine scale habitat selection but could underestimate the influence of the broader makeup of the lake on abundance. Similarly, the use of principal components versus individual habitat variables provided two ways of representing habitat structure. Principal components offered a simplified view of major environmental gradients such as overall water extent or hydroperiod, allowing multiple highly correlated habitat variables to be combined. Models with individual habitat variables supplemented the principal component models by allowing the identification of specific habitat features associated with phalarope abundance. Both predictor variable approaches produced similar model performance results, indicating that they were detecting the same key pattern that phalarope abundance at staging sites during southward migration was largely driven by water availability and the stability of saline habitats. Together, these model comparisons indicate that phalarope abundance is influenced across both spatial scales, and that the broad hydrologic conditions of the lake and fine scale habitat features contribute to shaping abundance patterns.

Overall, the findings of this study show a clear picture of the management needs for saline lakes to continue to support phalaropes during fall migration. Maintaining sufficient water levels at saline lakes, with water inundation for six months or more, will contribute to a stable prey abundance and reliable staging location for both species. Additionally, the continued practise of maintaining salt production ponds and dust control areas, with careful monitoring, could help support Red-necked Phalarope abundance by providing stable foraging areas, while also supporting activities that are positive to economic growth. Ultimately these results contribute to a growing body of knowledge that the patterns driving avian use of saline lakes are complex and stem from different spatial scales and species-specific traits and need to be balanced with human activities in a way that will still support biodiversity.

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CHAPTER 4: CONCLUSION

Overview of thesis

The goal of my thesis was to gain a deeper understanding of the migration behaviour of Wilson's Phalaropes and to identify the habitat features driving patterns of abundance for both Wilson's and Red-necked Phalaropes at key saline lake staging sites in western North America. With the widespread loss and alteration of saline lake habitats worldwide, understanding migratory paths and habitat use throughout migration and how these species respond to habitat changes is essential for ensuring their long-term survival. Chapter 2 focused on tracking the migration of Wilson's Phalaropes from their breeding and staging grounds. Chapter 3 examined how different lake features (e.g. temporary vs seasonal vs semipermanent; fresh vs saline water) influenced the abundance of Wilson's and Red-necked phalaropes at six saline lakes across North America.

Results from Chapter 2 provided the first detailed tracks of the southbound migration of Wilson's Phalaropes, revealing an alternative migration strategy. Previously, it was believed that Wilson's Phalaropes made a direct, non-stop flight over the Pacific Ocean during southbound migration after leaving North American staging sites. However, I found that some individuals tagged at staging sites in California instead took an overland migration route, stopping at wetlands and streams throughout Mexico and Central America before reaching South America. These findings highlight the need to extend conservation efforts across Mexico and Central America to protect habitats used by overland migrants during southbound migration. I also found that departure dates from breeding grounds in Saskatchewan differed between years, but body condition and mass did not influence departure timing. This suggests that variation in departure timing is likely driven by factors not included in my analysis such as breeding success or local habitat conditions, and that fueling likely occurs primarily at staging sites rather than on the breeding grounds. Additionally, I found that Wilson’s Phalaropes most often initiated migration when supported by southbound winds, as predicted by Optimal Bird Migration Theory (Alerstam and Lindström 1990).

Results from Chapter 3 showed that for total phalaropes (i.e., Wilson’s, Red-necked, and unclassified phalaropes) at both the specific surveyed area and the whole-lake scale, and for Red-necked Phalaropes at the whole-lake scale, abundance was higher where there was greater water extent, indicating that overall water availability plays a major role in habitat suitability. Additionally, associations with specific habitat types varied between the two species. In surveyed area models, seasonal saline water was positively associated with total phalarope abundance, but Wilson’s Phalaropes showed a negative association with this habitat type, demonstrating species level differences in how temporary saline habitats are used. Red-necked Phalaropes were positively associated with semipermanent salt ponds in whole lake models, indicating that more stable saline habitats supported greater abundance. Seasonal timing also differed between species. Wilson’s Phalaropes exhibited peak abundance earlier in the season in approximately mid-July, whereas Red-necked Phalaropes peaked later, in early September. These contrasting temporal patterns resulted in no strong seasonal trend in abundance in relation to Julian date when the two species were combined into the total phalarope response variable. Overall, the results demonstrate that water extent, stability of saline habitat types, and migration timing all contribute to variation in phalarope abundance, with species responding differently to habitat conditions across the survey period.

Significance to the field of ornithology

The findings of my research fill gaps in our understanding on the migratory behaviour and patterns of abundance of phalaropes in the Western Hemisphere. A key strength of this research lies in the multifaceted approach, integrating tracking data with habitat assessments to provide a more comprehensive perspective on the conservation needs of Wilson's Phalaropes. This study contributes to the field of ornithology by illustrating how more detailed movement data can reveal unexpected behavioral flexibility in migratory birds. The discovery of an alternate migration route in Wilson’s Phalaropes highlights the importance of questioning long standing assumptions and provides an example of how species may follow more diverse strategies than previously believed. These findings also reinforce the value of full annual cycle research and demonstrate how saline lakes across the hemisphere are connected by migratory birds. As migratory species face increasing pressures from climate change and habitat loss, studies like this help in guiding effective conservation at meaningful spatial and temporal scales (Galbraith *et al*. 2014, Robinson *et al.* 2009, Xu *et al*. 2019, Zhao *et al*. 2019).

This study also contributes to a growing body of research emphasizing the importance of saline lakes as critical staging habitats for long-distance migrant shorebirds. While it is well established that phalaropes depend on hypersaline systems during migration, relatively few studies have quantified how habitat conditions at different spatial scales influence abundance across the staging season. The strength of Chapter 3 stems from the broad collaboration that enabled six years of count data to be collected across six different lakes. This large dataset provides valuable insights into the drivers of bird abundance at saline lake habitats across regions and years. By evaluating habitat use for both Wilson's and Red-necked phalaropes and examining species-specific differences in timing and habitat associations, this study highlights the importance of considering seasonal dynamics, water extent, and habitat stability when assessing migratory staging suitability. Additionally looking at phalarope abundance at the species level revealed that even closely related birds using the same lake basin may rely on different habitat features at different times, highlighting the importance of species-specific research and conservation efforts.

Limitations and directions for future study

Because this was the first study to apply tracking devices to Wilson's Phalaropes on breeding and staging grounds, there were challenges in learning to trap and tag birds safely and effectively, resulting in a small sample size and few female birds included in the study; however, given the novelty of this work, the study provides a strong starting point for future research. With the knowledge gained on trapping techniques and tracking methods for Wilson's Phalaropes, future studies could expand on this research by continuing to investigate their migratory connectivity and expand tagging efforts to female and juvenile birds to examine sex or age differences in migration routes and timing. In my field efforts, I found that harness attached tags were more effective and reliable than tags that were glued on, and I had more success capturing incubating males with bow net traps rather than mist nets. Additionally, the migration tracking from this study can be supplemented by stable isotope analysis of the feathers collected from individuals in this study, which were grown on the stationary non-breeding grounds. Stable isotope analysis works by measuring the ratios of naturally occurring isotopes, such as hydrogen, carbon, or nitrogen, in bird feathers, which reflect the environmental conditions where the feathers were grown (Hobson *et al.* 2001).

Isotope ratios vary geographically due to climate, vegetation, or water sources, and they can be used to infer where a bird was located during molt, helping to identify links between breeding and stationary non-breeding grounds, and providing information on diet and habitat use during the non-breeding period (Hobson *et al.* 2001). Importantly, this analysis can be done with a single sampling event of an individual bird and could potentially involve a much larger sample of birds relative to more expensive and less reliable tracking devices.

In Chapter 3, survey effectiveness was partly limited by difficulties in coordinating data collection across multiple sites, leading to variability in survey coverage, effort, and methods. Surveying from long distances and the small size of phalaropes also made species identification difficult, resulting in a substantial proportion of unclassified phalaropes in the total counts. These limitations may have influenced my results by introducing uncertainty into abundance estimates and reducing the precision of species-specific models. In particular, difficulty identifying Wilson's and Red-necked Phalaropes resulted in high unclassified phalarope counts and may have masked some differences in habitat associations when species were analyzed together and individually.

Future studies could be strengthened by incorporating direct measures of habitat quality, including water chemistry sampling and measuring of prey availability. Specifically, salinity is known to influence brine shrimp and alkali fly populations, the primary food resources for migrating phalaropes (Senner *et al.* 2018, Wurtsbaugh *et al.* 2017). By pairing phalarope counts with measurements of salinity or prey availability at specific survey locations, future research could more explicitly test the links between how habitat conditions influence prey production, and ultimately phalarope habitat selection within lakes. This type of integrated monitoring would provide stronger evidence for the ecological drivers of phalarope abundance and distribution and could improve the ability of managers to anticipate and respond to environmental change.

Management implications

This research supports ongoing efforts to use phalaropes as indicator species for the conservation of saline lake ecosystems (Castellino *et al.* 2024, Center for Biological Diversity 2024). More broadly, it shows the value of these ecosystems and the need for management strategies that address both species-specific needs and broader ecological functions (Edwards and Null 2019, Saccò et al. 2021, Tavernia *et al*. 2021). Prioritizing habitat protection and restoration is essential to maintaining the health and resilience of saline lakes (Edwards and Null 2019). Specifically, sustaining freshwater inflows and preventing further lake desiccation will help maintain salinity ranges that support brine shrimp and alkali fly production, which are the primary prey of migrating phalaropes and other migratory bird species. Protecting and restoring saline water foraging areas, whether natural wetlands or managed salt pond systems, will also improve habitat quality during southward migration. Collaborative, basin-scale water management involving conservation organizations, local communities, and state agencies will be critical to achieving these goals.

Wilson's and Red-necked phalaropes' reliance on saline lakes during migration makes them effective indicator species for monitoring ecosystem health (Centre for Biological Diversity 2024). For example, large flocks of Wilson's Phalaropes are observed at Great Salt Lake during peak migration, where their presence is supported by high invertebrate productivity (Frank and Conover 2023). Conversely, phalaropes are largely absent during drought years at Lake Abert in Oregon, indicating a strong response to habitat suitability (Larson *et al*. 2014, Senner *et al,* 2018). Because phalaropes respond quickly to habitat changes, tracking their abundance and habitat preferences can provide early warning signs of broader ecosystem threats (Larson *et al*. 2014, Senner *et al,* 2018). This makes them important to conservation and management strategies aimed at preserving saline lake ecosystems, which are increasingly vulnerable to water diversion, climate change, and pollution (Wurtsbaugh *et al.* 2017). Integrating phalarope monitoring into lake management plans ensures not only the protection of these species, but also the resilience of the ecosystems they depend on (Castellino et al. 2024, Center for Biological Diversity 2024, Senner *et al,* 2018). Lake management plans can then, in turn, provide protections for invertebrate communities that are saline lake specialists, as well as a variety of bird species like American Avocets (*Recurvirostra americana*) and gulls (*Larus spp*.; Herbst 2006, Larson *et al*. 2016, Senner *et al,* 2018).

Beyond the benefits of supporting biodiversity, the conservation of saline lake habitats also provides significant human and economic benefits through the ecosystem services these lakes supply (Edwards and Null 2019). A well-managed saline lake with sustained water levels can function at salinity levels that support both ecological diversity and economically valuable activities such as mineral extraction (Wurtsbaugh *et al.* 2017). Sustaining water levels at saline lakes also acts as a dust control measure by reducing airborne particulates that are created when the lakebed is exposed and thereby mitigating respiratory health risks for nearby communities (Johnston *et al*. 2019, Wurtsbaugh *et al.* 2017). Saline lakes also drive ecotourism in many of their surrounding communities, drawing in birdwatchers, photographers, and kayakers (Saccò *et al*, 2021).

In addition to ecological and economic value, saline lakes hold deep cultural significance for many Indigenous communities. One example is Mono Lake, traditionally known as Kootzabaa'a, located within the ancestral lands of the Kootzaduka'a people (Tribes of the Mono Basin 2021). Since time immemorial, Kootzabaa'a has provided food, medicine, and spiritual value to the Kootzaduka'a people (Tribes of the Mono Basin 2021). Notably, the name Kootzaduka'a translates to "Brine Fly Pupae Eaters," highlighting the cultural importance of brine flies to the community, which were used as both a food source and a trading resource (Tribes of the Mono Basin 2021).With all this in consideration, preserving saline lake ecosystems not only supports ecological integrity and species diversity, but also contributes to economic resilience and the continuation of Indigenous cultural traditions.

Altogether, this thesis provides new insight into the migration ecology and habitat use of Wilson's and Red-necked phalaropes across the saline lake network of western North America. By combining individual-level tracking with multi-year habitat and abundance data, I show that Wilson's Phalaropes can follow alternate southbound migration strategies and that both species respond strongly to increased water extent and the stability of saline habitats during staging. These findings demonstrate that phalarope abundance is shaped by both broad lake conditions and finer-scale habitat characteristics, and that species differ in their seasonal timing and habitat associations. As saline lakes continue to be affected by water loss these results emphasize the importance of maintaining sufficient lake water levels and protecting stable foraging areas to support large migratory staging aggregations. Ultimately, this work contributes to a growing effort to understand and conserve the saline lake systems that are critically important to phalaropes and many other migratory species.

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