Migratory connectivity and spatio-temporal aspects of Pacific Barrow's goldeneye (*Bucephala islandica*) migration

by

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B.S., University of Alaska Anchorage, 2015

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science

in the
Department of Biological Sciences
Faculty of Science

SIMON FRASER UNIVERSITY
Spring 2021

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Abstract

Effective management of animals requires understanding movement throughout the annual cycle. We used satellite transmitters to track 229 adult Pacific Barrow's goldeneye (*Bucephala islandica*) captured across their full geographic range. We assessed the strength of migratory connectivity and determined latitudinal and sex effects on annual cycle phenology. Male and female goldeneye demonstrated strong migratory connectivity across wintering, breeding, and moulting stages. Males departed breeding grounds before females, spending less time on breeding grounds and more time on moulting grounds. Individuals at northern latitudes spent more time on wintering grounds than individuals at southern latitudes. These results indicate that, within a species, the timing of transitions throughout the annual cycle can vary with both sex and latitude. The spatio-temporal settings in which individuals occur, and the regional associations across annual cycle stages, inform the appropriate scale of management units and the effects of habitat perturbations at different places and times.

Keywords: Barrow's goldeneye; *Bucephala islandica;* migratory connectivity; annual cycle; latitude; satellite telemetry

Acknowledgements

I am indebted to several people deserving of acknowledgement for their hard work and contributions to this research. First and foremost, I would like to thank David Green, for his patience and unwavering support. Completing this dissertation required many steep learning curves, and David's quirky doodles, positivity and guidance made all the difference. I am forever grateful to my co-supervisors, Dan Esler and Sean Boyd, for their sea duck expertise, and edits of the millions of versions of this manuscript. Both were kind enough to allow me to tag along for once-in-a-lifetime field projects, just for fun. I thank my committee member, Ron Ydenberg, for his challenging questions and feedback on study bias and interpretation.

Data management and analysis would not have been possible without the patience and guidance from Bruno Grande. Bruno made the challenges of R feasible and even enjoyable. I additionally would like to thank Megan Willie for providing consultation on satellite data processing and filtering. I would be remiss if I did not mention the incredible support from the Environment and Climate Change Canada and Simon Fraser University Fellowships. This project would not have been possible without their financial support. I am also grateful for the hard work of many volunteers and researchers who planned and executed all the prior field work necessary for this project.

If I have learned one thing in grad school, at the end of the day, it is all about relationships. I would like to thank my fellow graduate students in the Centre for Wildlife Ecology for their support and companionship. I especially thank the Super Grads-Lena Ware, Jo Enns, Camilla Enns, Gwyn Case, Laura Kroesen, Rachel Munger-for the long lunches, bike rides, and positivity parties. They have taught me the truest meaning of friendship and have helped me through graduate school's toughest obstacles.

Finally, I thank my family for their unending support and for bestowing me with grit. You're the best fan club. You've all provided the perfect safety net, just at the right times. I especially like to thank Audrey Taylor, who inspired me to pursue this career entirely. Finally, a deeply felt gratitude for my partner, Charlie Boisselle. With you, I've accomplished so much more than just a thesis during these past years.

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Chapter 1.

General Introduction

1.1. Background

Migratory animals carry out different stages of the annual cycle in geographically distinct regions. Events or conditions during one stage can influence individuals in a subsequent stage (Harrison et al. 2010; Marra et al. 2015), making it difficult to determine which phase of the annual cycle has the greatest impact on population dynamics (Newton 2008). Nevertheless, events during the wintering season are known to affect productivity and population dynamics on the breeding grounds, which in turn can influence population dynamics in the subsequent wintering season (Sedinger and Alisauskas 2014). Understanding the full annual cycle movements of long-distance migrants is essential for delineating populations, assessing connectivity, evaluating carry over effects between life stages, and informing species management strategies. Only 17% of studies on migratory taxa incorporate the full annual cycle, with a high proportion focused only on the breeding grounds (Marra et al. 2015). This disproportionate attention to breeding grounds (61% of studies) most likely results from the assumption that productivity is a strong driver of population trends. Full annual cycle studies have been hampered by difficulties associated with following individuals across vast distances often in inaccessible locations (Marra et al. 2015). Additionally, technological and financial constraints have limited studies to describing movements of individuals from a single breeding or wintering location (e.g. Bobek et al. 2008; Lemke et al. 2013), a small number of individuals from a few locations (e.g. English et al. 2007; Robert et al. 2002), or one sex or age-class (e.g. De La Cruz et al. 2009; Meattey et al. 2018; but see Fraser et al. 2012; Stanley et al. 2015; Knight et al. 2018; Kramer et al. 2018;).

Documenting the full annual cycle is vital for species of conservation concern that have complicated annual cycles. For several species of North American sea ducks, long-term population declines have increased conservation concern and highlighted the need for focused understanding of annual cycle dynamics (Zydelis et al. 2006; De La Cruz et al. 2014; Bowman et al. 2015). The causes of these declines remain uncertain in part because sea ducks range across the northern hemisphere during the breeding stage and often inhabit remote marine environments during the wintering stage. Furthermore, connectivity studies of waterfowl are complicated by the presence of a remigial moulting stage, which is not typically relevant in studies on other taxa (Meattey et al. 2019). During this post-breeding flightless stage, population structure and mixing may differ from the wintering or breeding stage. These moult migrations add additional complexity to connectivity which typically considers only breeding and wintering areas as key life stages. However, the moult stage is an additional period where individuals from discrete areas may mix or remain isolated. Assessing the strength of migratory connectivity among wintering, breeding, and moulting areas for North American sea duck populations is crucial for species management and conservation (Mallory et al. 2006; Robert et al. 2008; De La Cruz et al. 2009). Because migratory connectivity highlights clusters of individuals that spend life stages together, it provides a method to identify subpopulations. The Sea Duck Joint Venture (Sea Duck Joint Venture Management Board 2014), considers population delineation a high priority objective. However, a lack of detailed information remains about the population structure, annual cycle movements, and migration strategies of most sea duck species, including the Barrow’s goldeneye (*Bucephala islandica*).

The Pacific Barrow’s goldeneye is a medium-sized diving duck with a relatively long lifespan. The Pacific Northwest is estimated to support >90% of the global population of Barrow’s goldeneye, with 60% wintering on the British Columbian coast (Eadie et al. 2020; Figure 1.1). Barrow’s goldeneye winter primarily in coastal waters, harbors, and inlets and, sometimes, ice-free inland lakes and rivers. However, during the breeding season, individuals use invertebrate-rich freshwater and alkaline lakes surrounded by mature forests, where they nest in tree cavities. Goldeneye, like most sea ducks, are rendered flightless for just over a month in late summer to early fall when they undergo simultaneous remigial moult (Hogan et al. 2013). Barrow’s goldeneye may moult on their breeding grounds or at separate, distant locations (Eadie et al. 2020; Figure 1.2).

Barrow’s goldeneye are monitored and managed by the Canadian Wildlife Service (CWS) and the U.S. Fish and Wildlife Service (USFWS). In Western North America, the CWS *British Columbia’s Interior Breeding Waterfowl Survey* (2006-2019) and the USFWS *Alaska Breeding Waterfowl* Surveys (1964-2019) monitor breeding populations. The breeding surveys show significant declines in abundance within the

Pacific population. Causes of declines are unknown, but multiple threats exist to goldeneye throughout the annual cycle (Breault 2020). For example, on wintering grounds, sport harvest was low and sustainable. However, increasing interest in sea duck sport hunting might add pressure to regional populations at risk from overharvest due to their already high level of site-fidelity (Willie et al. 2019; Breault 2020). Additionally, goldeneye forage primarily on bivalves in winter, which are known to concentrate heavy metals and organochlorine pollutants (Willie et al. 2017). On breeding grounds, habitat threats include landscape-level hydrological changes associated with forest cover loss, predator redistribution, and changes in wetland water quality (Breault 2020). From 2006-2018, forest cover loss from logging, forest fires and insect tree kills affected 54% of the *Interior British Columbia's Breeding Waterfowl Survey* area, affecting hydrology, aquatic habitats, and availability of suitable cavity-producing trees (Breault 2020). Two important moulting sites in North America (Cardinal and Leddy Lakes, Alberta) are not currently protected. Habitat loss or degradation for the Pacific population during any part of the annual cycle has potential for large scale demographic consequences (Esler 2000; Hostetler et al. 2015; Willie et al. 2017), because the Pacific population constitutes a high proportion of the global abundance of Barrow's goldeneye.

The Oceans Protection Plan (OPP) is a federal initiative by Transport Canada to improve emergency response readiness. The Plan calls for Baseline information on the distribution of marine birds to support decision-making during a marine pollution incident. In British Columbia, a handful of focal marine bird species were selected for tracking based on the presence of specific attributes that could be measured across time or space and used to monitor environmental conditions. For example, Barrow's goldeneye and their primary prey, blue mussels (*Mytilus spp.*), are considered focal indicator species for marine planning. Specifically, goldeneye are used as indicators of oil exposure and provide a means for quantifying ecosystem recovery over time (Esler et al. 2011; Willie et al. 2017). Therefore, describing the full annual cycle of Barrow's goldeneye not only provides crucial knowledge for managing goldeneye, but also for predicting ecosystem-wide impacts of negative anthropogenic effects.

1.2. Thesis Structure

This first chapter provides rationale for this research, supporting information on the species, context for the specific research objectives.

In my second chapter, I investigate where and when Barrow's goldeneye occur. Specifically, I use satellite telemetry to investigate where and when Pacific Barrow's goldeneye occur at all stages of the annual cycle (wintering, breeding, and moulting). To investigate spatial movements, I examine differences in male and female migratory connectivity throughout the full annual cycle. To investigate temporal movements, I examine timing of transitions between each stage of the annual cycle and migratory behavior. Thus, it provides science-based insight on management actions to conserve migratory bird species with a large geographic range.

The concluding chapter summarizes the movement ecology throughout the full annual cycle, resource management implications, and future research directions. The results are contextualized for their potential to aid in the management of similar species and ecosystems at risk from anthropogenic disturbances.

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1.4. Figures

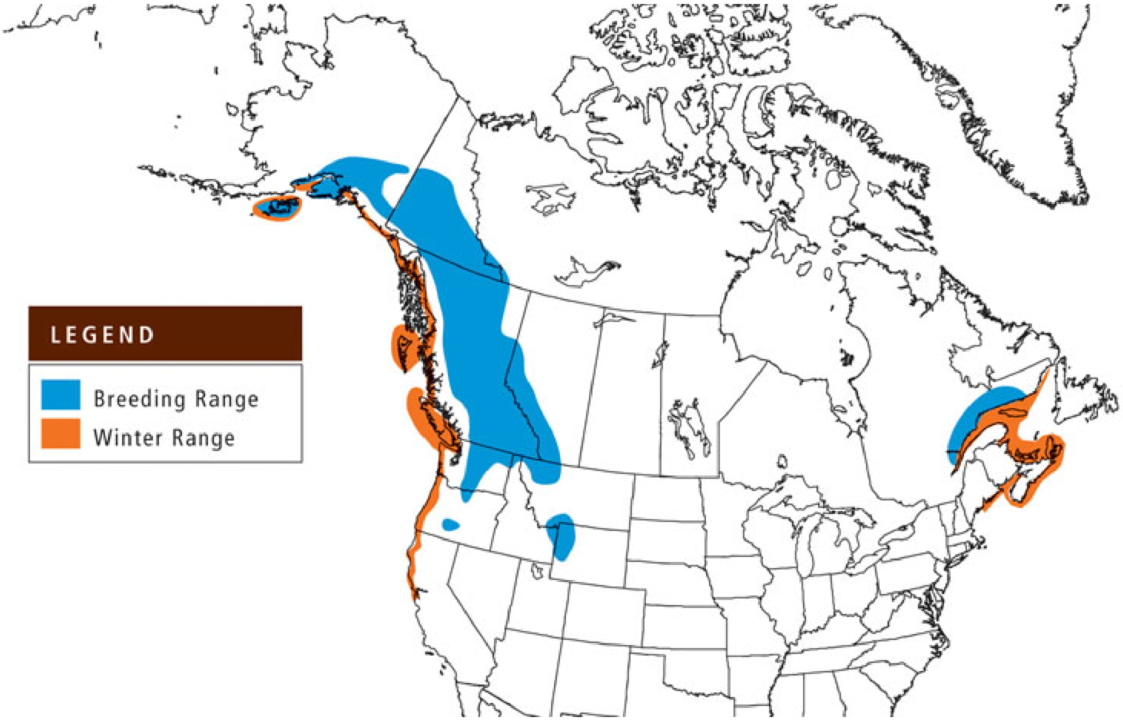

Figure 1.1 **North American Barrow's goldeneye range map. Map generated by the Sea Duck Joint Venture (2003).**

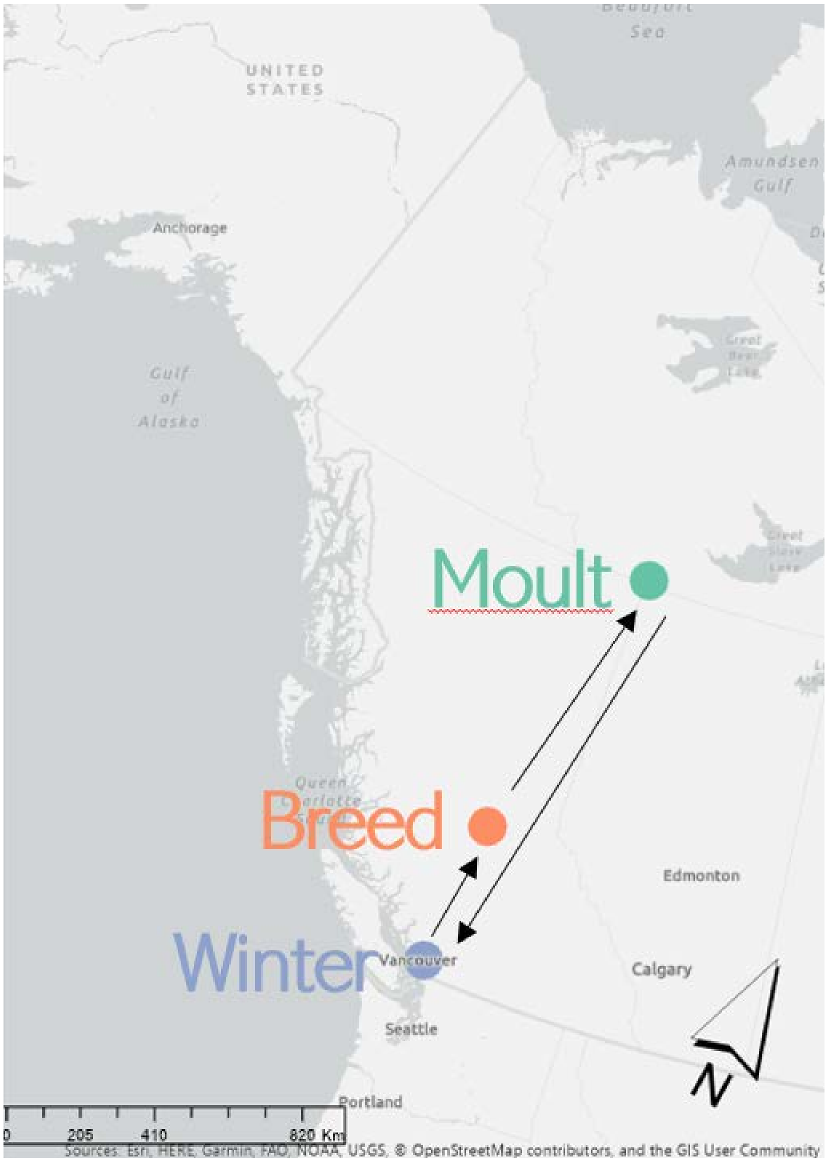

Figure 1.2 Expected annual cycle movments of adult male Pacific Barrow's goldeneye wintering in the Vancouver, BC area.

Chapter 2.

Migratory connectivity and annual cycle phenology

2.1. Introduction

Migratory animals carry out different stages of the annual cycle in geographically distinct locations that can be separated by thousands of kilometers. The geographic separation, and the very different conditions that may be encountered at each stage, complicate efforts to understand drivers of overall population change (Newton 2008; Harrison et al. 2011; Marra et al. 2015). Determining the importance of each stage for population dynamics is made even more difficult because events, conditions and processes during one stage of the annual cycle may influence individual performance in a subsequent period(Harrison et al. 2011; Marra et al. 2015). The majority of studies of migratory birds focus on breeding areas (Marra et al. 2015), and some researchers argue that factors on breeding grounds that influence productivity, juvenile survival and subsequent recruitment drive population dynamics (Sillett and Holmes 2005; Rushing et al. 2016). However, others suggest that migration, a stage when mortality rates can be extremely high (Scott Sillett and Holmes 2002; Loonstra et al. 2019), is the most important stage of the annual cycle (e.g. Lok et al. 2015; Robinson et al. 2020). Finally, conditions on wintering grounds, which can influence both adult and juvenile survival (Taylor and Stutchbury 2016) and affect timing of spring migration and subsequent breeding performance are also argued by some to be the most influential in driving population dynamics (Woodworth et al. 2017; Wilson et al. 2018). The relative effects of each season on population dynamics are likely life-history and species dependent. Importantly, these effects could also vary among demographically discrete subpopulations within a species; therefore, understanding the degree of demographic population structuring throughout the year allows greater detection and better interpretation of seasonal and carryover effects.

Timing of the stages of the annual cycle can vary widely among populations of the same species. Variation in timing can be influenced by sex, latitude or changing climate conditions, which in return can influence population dynamics (Dunn & Winkler 1999). In particular, the timing of breeding can influence individual reproductive success and can shape phenotypic differences in reproductive traits among populations (Verhulst and Nilsson 2008; Lany et al. 2015). In the northern hemisphere, within migratory species, individuals breeding farther north tend to breed later than southern counterparts. This can lead to northern breeding individuals experiencing shorter time periods for reproduction and tighter time constraints across the rest of the annual cycle (Gow et al. 2019; Winkler et al. 2014). Additionally, for many migratory bird species, males or pairs that arrive on breeding grounds earlier secure higher quality breeding territories (Myers 1981; Morbey and Ydenberg 2001). Many species are advancing their breeding initiation dates in response to warming temperatures and this can have both positive and negative reproductive consequences (Dunn et al. 2011; Bourret et al. 2015). For example, Moller et al. (2008) demonstrated that species unable to adapt their timing of migration become mismatched with their food sources, and thus experience population declines. However, whether and how differences in timing of stages among populations at different latitudes, and among sexes, carry over to influence subsequent timing events of the annual cycle is poorly understood (Conklin 2010; Briedis et al. 2016; Gow et al. 2019). Long-term datasets using tracking technology can establish annual cycle timing events that can be used as a baseline against which future climate scenarios can be compared.

Quantifying migratory connectivity and timing of annual cycle events can help reveal where and how limiting factors influence population trends (Webster and Marra 2005; Harrison et al. 2011; Bauer et al. 2016). The extent to which individuals from discrete breeding or nonbreeding areas remain in sympatry through the remainder of the annual cycle (strength of connectivity) and have similar demographic/vital rates can influence sub-population trends and have critical implications for conservation (Marra et al. 2006; Gilroy et al. 2016). For example, Kramer et al. (2018) demonstrated that Golden-winged Warblers (*Vermivora chrysoptera*) have high migratory connectivity and that population declines in the Appalachian Mountains are associated with habitat loss on their specific wintering grounds in South America. In contrast, Blue-winged Warblers (*Vermivora cyanoptera*) have low migratory connectivity and all populations, including the population in the Appalachian Mountains, are stable. Migratory connectivity dictates whether declines or increases in populations at one stage in one place affect the whole population or distinct subpopulations.

Advances in technology now allow animals to be tracked for extended periods of time providing high resolution data on movement of individuals throughout the year (Joo et al. 2020). This technology has facilitated discovery of unknown migration routes, identified critical stopover locations and wintering grounds, and provided insight on timing of transitions between stages of the annual cycle (Joo et al. 2020). For instance, Hooijmeijer et al. (2014) used both geolocators and satellite tags to reveal three distinct migration routes used by Black-tailed Godwits (*Limosa limosa*) and identified critical sites on each route. Lemke (2013) used geolocators to track migration of Great Reed Warblers (*Acrocephalus arundinaceus*) and found that birds used multiple spatially separated wintering sites in sub-Saharan Africa and showed differences in timing of both fall and spring migration. However, technological and financial constraints have limited many studies of migratory connectivity and movement during the annual cycle to describing movement of individuals from a single breeding or wintering location (e.g. Bobek et al. 2008; Lemke et al. 2013), a small number of individuals from a few locations (e.g. Robert et al. 2002; English et al. 2007), or the study of one sex or age-class (e.g. De La Cruz et al. 2009; Meattey et al. 2018; but see Fraser et al. 2012; Stanley et al. 2015; Knight et al. 2018; Kramer et al 2018).

Satellite transmitters (Platform Terminal Transmitters or PTTs) have been deployed to study aspects of the wintering ecology (Willie et al. 2019), moult (Hogan et al. 2011), and movement patterns of Barrow’s goldeneye (*Bucephala islandica*) in the Pacific Northwest since 2006 (Boyd and Esler 2012). PTTs were deployed in wintering locations ranging from southern British Columbia to south-central Alaska that encompass most of the winter distribution for the Pacific Coast population. PTTs also were deployed at a key moulting site in northwest Alberta, and a key breeding site in south-central British Columbia. This program has revealed previously unknown aspects of Barrow’s goldeneye spatial ecology (Hogan et al. 2011; Willie et al. 2019). The accumulation of data obtained over the course of this research provides a rare opportunity to examine large-scale patterns of migratory connectivity across the geographic range and annual cycle of a sea duck species. These data also allow for an assessment of sex and latitude effects on timing of transitions between stages of the annual cycle.

Here, we quantified the strength of migratory connectivity among three stages of the annual cycle (wintering, breeding and moulting) and used cluster analysis to illustrate whether observed connectivity depends on consistent aggregation of individuals in distinct regions linked by different migration routes (Ambrosini et al. 2009). In addition to describing migratory connectivity, we assess how sex and latitude influence timing of transitions between stages of the annual cycle and the migration behavior of Barrow's goldeneye. We expected that sex differences in parental care (female Barrow's goldeneye rear chicks alone on breeding ponds (Eadie et al. 2020)) would result in sex differences in timing of departure from breeding grounds. In contrast to many other birds, waterfowl often pair on wintering grounds (Savard 1985; Bluhm 1988) so we did not expect to find sex-differences in timing of departure from wintering grounds or arrival on breeding grounds. We also expected that latitudinal differences would lead to variation in timing of breeding and thus migration from the coast to inland breeding grounds in spring and to the coast in fall. Finally, we discuss implications of our results for population delineation and management of Barrow's goldeneye.

2.2. Methods

2.2.1. Study species and study design

Barrow's goldeneye are medium-sized sea ducks with a discontinuous world distribution (Pearce et al. 2014). The Pacific Northwest region of North America is estimated to support approximately 90% of the global population of about 200,000 birds, with 60% of the population breeding and wintering in British Columbia, Canada (Eadie et al. 2020). Barrow's goldeneye also occur in northeastern North America (ca. 4,500 birds) and Iceland (ca. 2,000 birds; Gardarsson 1978)

We collected movement data for Pacific Barrow's goldeneye from 2006-2017, based on 339 individuals implanted with PTTs (Table 1). We captured birds using a variety of capture methods (mist nets, drive traps and floating mist nets) at five wintering sites throughout their Pacific range (Kachemak Bay, Alaska; Prince William Sound, Alaska; Juneau, Alaska; Kitimat, British Columbia; and Indian Arm near Vancouver, British Columbia), one breeding site (Riske Creek, British Columbia), and one moulting location (Cardinal Lake, Alberta) (Table 1). We refer to birds from Kachemak Bay and Prince William Sound as being captured in south-central Alaska, and birds from Indian Arm as being captured in Vancouver. We recorded sex, age, and mass of each bird and assigned sex and age (hatch-year [HY] or after hatch-year [AHY]) based on plumage (Lewis et al. 2020), cloacal characteristics and bursal depth (Mather and Esler 1999).

Experienced wildlife veterinarians surgically implanted PTTs (26-38g Microwave Telemetry and Telonics transmitters) in the coelomic cavity of each goldeneye following standardized methods described in Mulcahy and Esler (1999). The PTTs were programmed to transmit locations for two to six hours every three to four days. PTT data (latitude, longitude, location error index, date (calendar day), time, temperature (°C), and battery voltage) were obtained from the Argos location and data collection system within 24 hours of a satellite receiving a transmission. The Argos system estimates locations by calculating the Doppler shift in transmission frequency received by the National Oceanic and Atmospheric Administration (NOAA) satellites as they move relative to a PTT. Locations are assigned an accuracy class; 3, 2, 1 and 0 are location classes with an estimated accuracy of <250 m, 250–500 m, 500-1500 m, and >1500 m, respectively; A and B are auxiliary locations where accuracy is not estimated; and Z is an invalid location (Argos 2015). Accuracy of each location is based on the transmitter-to-satellite geometry during a satellite pass, the number of transmissions received, and the stability of the transmission frequency (CLS America 2015).

2.2.2. Data management

We downloaded Barrow's goldeneye PTT data previously stored on the Movebank data repository (www.movebank.org) in the study "Migration Patterns of Pacific Sea Ducks". We used the Douglas Argos Filter (DAF) to remove redundant data and unlikely point locations (Douglas et al. 2012). We first employed the DAF hybrid filter, with MAXREDUN set to 15 km, and retained the highest accuracy location for each duty cycle. We subsequently applied additional filtering criteria manually by removing i) all data from birds that perished within 14 days of PTT implantation (Esler et al. 2000; Sexson et al. 2014) ii) locations after a bird had died (Willie et al. 2019), iii) locations > 2000 km from the previous location, which we considered the maximum plausible distance that could be travelled by a goldeneye within the inter-signal period, and iv) PTT locations that required a redundant movement of > 50 km (i.e., movements away from and back to the same location) when daily movements were < 50 km within a stationary period of the cycle (i.e., moulting). HY birds were marked in only two capture locations (see Table 1.1), and therefore, the same questions about movement among putative sub-populations couldn’t be asked at a continental scale, so analyses were restricted to AHY birds.

2.2.3. Defining stages of the annual cycle

Barrow’s goldeneye winter primarily in coastal waters, harbors, and inlets and, sometimes, inland lakes and rivers that don’t freeze over. Individuals may arrive at the coast and make directional daily movements of over 100 km along the coastline before arriving at their wintering site. We defined an individual’s date of arrival on their wintering grounds as the date they arrived at the coast and switched from making directional daily movements of > 100 km to non-directional daily movements of < 100 km. We defined an individual’s date of departure from their wintering ground as the day they left the coast and moved > 100 km inland. Following De La Cruz (2019) we calculated specific arrival and departure dates as the median date between the last and next signal; for instance, winter departure date from a wintering site is the median date between the last location at the wintering site and the first location in a new migration area. We estimated total length of stay within an area during each annual cycle stage as the difference between the departure date and the arrival date at each location, plus 1 day. This extra day is to account for the fact that a bird could have been present in the area both on the day of arrival and the day of departure (De La Cruz et al. 2009; Meattey et al. 2019).

During the breeding season, goldeneyes can be found on invertebrate-rich freshwater and alkaline lakes surrounded by mature forests, where tree cavities are used for nesting (Evans et al. 2002). Females incubate for ~ 30 days, brood young for 7-14 days and may defend young for an additional 28 days. Males, which do not incubate or provide parental care, typically remain on the breeding grounds for a short period after the female starts incubating (Palmer 1976). We defined arrival on breeding grounds as the date an individual arrived at an interior wetland in late spring or early summer (Boyd and Esler 2012). Individuals were considered to remain on breeding grounds if they made daily movements of ≤ 20 km during this period (Eadie et al. 2020).

Barrow’s goldeneye may moult on their breeding grounds or at separate, distant locations (Eadie et al. 2020). Like most sea ducks, goldeneye undergo simultaneous remigial moult in late summer to early fall, rendering the birds flightless for just over a month (Hogan et al. 2013). We defined date of departure from the breeding area as the date an individual left an interior wetland and travelled > 20 km without returning, and their date of arrival on the moulting grounds as the date they arrived at a location where they remained for > 30 days (with all movements over land estimated to be < 1 km, as individuals are flightless). If these criteria identified two potential moult sites, the site occupied during the most likely moult period was selected based on the following: arriving July-September and departing August-November (Eadie et al. 2020; Hogan et al. 2013). Post moult, we defined an individual's date of departure from their moulting site as the first day with directional movements of > 1 km towards the coast.

Adult sex ratios are heavily male biased (Rodway et al. 2015) so some males will be unpaired and may move directly from their wintering grounds to a moulting site. We expected to have non-breeding males in our sample based on the skewed sex ratio and thus, derived additional criteria to help identify those males. We assessed this possibility by identifying males that did not have a discrete breeding location followed by a discrete moulting location. Males were not assigned a breeding location if their putative "breeding" area was i) close to (< 200 km) a known moulting site used by several thousand individuals (Van de Wetering and Cooke 2000; Hogan et al. 2011), ii) outside of the assumed breeding range of the species (based on the SDJV 2003 map), iii) outside of the range of breeding areas indicated by female PTT data and iv) in habitat unsuitable for breeding (i.e., no large diameter trees suitable for a cavity-nesting sea duck).

Barrow's goldeneye may have migratory stopovers for 2 - 40 days at locations between wintering and breeding grounds, breeding grounds and moulting grounds, or moulting grounds and wintering grounds. We defined stopovers as periods when locations are clustered within a 20 km radius. A radius of 20 km per stopover was selected as some location classes retained were LC 0 which have accuracies of > 1,500 m. Clusters separated by > 20 km were considered separate stopover locations, as 20km as these seemed like usage of distinct habitat

For each individual we identified the geographic centre of their wintering, breeding and moulting locations by calculating the mean-centre centroids for each stage of the annual life cycle using ArcGIS Pro version 2.4.3 (Environmental Systems Research Institute (ESRI), Inc. Redlands, California, USA). We only used data collected over one annual cycle to calculate these centroids to avoid biasing the analysis toward individuals with PTT data spanning longer time periods. Where possible we used data from the second year an individual was tracked as the movement and behavior of birds immediately following capture and the surgical procedure may be affected (Barron et al. 2010; White et al. 2013; Lamb et al. 2020). We used the “argosfilter” package in R studio to measure the straight-line geodesic distances between consecutive centroids.

2.2.4. Statistical analyses

Migratory connectivity

We quantified the strength of migratory connectivity between wintering and breeding grounds, breeding grounds and moulting sites, and moulting sites and wintering grounds using Mantel tests that measure the correlation (r_m) between two matrices (Ambrosini et al. 2009). The matrices contained pairwise distances between the mean-centre centroids for all individuals in the study for each stage of the annual cycle. Because the distribution of Pacific Barrow’s goldeneye was not naturally spatially clustered, we chose to quantify migratory connectivity using Mantel correlations rather than the recent MC metric (Cohen et al. 2018). Mantel correlations (r_m) were estimated using the ade4 package in R (Dray and Dufour 2007) with significance determined by comparing the observed correlation coefficients with those from 9999 random permutations. To determine if wintering latitude and longitude were correlated with moulting and breeding locations, we calculated Pearson’s correlation coefficient for the latitude and longitude of each of the 3 stationary periods (wintering, breeding, moulting).

Migratory connectivity, when measured across the geographic range, may arise because individuals maintain the same position relative to one another during the wintering, breeding and/or moulting stages (“distribution pattern transfer”; see Besag and Diggle 1977) or because sub-populations or groups of individuals aggregate together in each stage of the annual cycle (Ambrosini et al. 2009, e.g., Cedar Waxwings; see Cohen et al. 2018). To assess the importance of these two processes we performed a cluster analysis using the mean-centre centroid locations for the different stages and assessed the extent to which individuals within a cluster remained together from one stage to the next. We performed the cluster analyses using the Hierarchical Density-Based Spatial Clustering of Applications with Noise function (HDBSCAN; Campello et al. 2015) of the Density-Based Clustering tool in ArcGIS Pro (ref). HDBSCAN is a data driven density-based clustering algorithm that allows clusters to vary in shape and density, assigning individuals to a cluster when centroids concentrate in a region while leaving individuals un-assigned (i.e., labelled as noise) if their centroids have no/few near neighbors. To avoid having a large number of small localized clusters we set the minimum number of individual centroids needed to identify a cluster at 5.

Timing and migratory behavior

We used a series of generalized linear models to examine sex and latitude effects on i) the timing of arrival and departure on the wintering grounds, breeding grounds and moulting sites, ii) the length of stay at each location, iii) the distance traveled during each migration (wintering-breeding, breeding-moulting, and moulting-wintering, iv) the probability that a migration included the use of a stopover site, v and vi) the number and length of stay at stopovers if they occurred, and vii) the total duration of each migration. Models for arrival, departure, length of stay, and distance travelled were fitted with gaussian distributions. Binomial distributions were fitted to migratory behavior variables, but poisson distributions were fitted for assessing if the individual stopped or did not stop on migration. We explored latitudinal effects using two alternative explanatory variables: the site of winter capture which restricted analyses to 132 individuals, or the latitude of the wintering grounds mean-centre centroid for each of all 197 individuals. We focused on wintering origins because waterfowl typically pair on the wintering grounds, and subsequently exhibit strong mate (Bluhm 1988; Savard & Eadie 1989) and wintering site fidelity (Willie et al. 2019), and most of our captures occurred on wintering sites. Thus, wintering latitude was generally representative of where that bird occurs within the broad span of the Pacific Range. The results of the two sets of models were consistent so we report only the results of the latter analysis using the larger dataset here. We provide a summary of the statistical analyses examining sex and winter capture site effects in the appendix. Means in the text are provided with standard deviations unless stated otherwise. All statistical analyses were performed using the statistical software R version 3.6.1 (R Core Team 2016).

2.3. Results

We deployed satellite transmitters on 339 Barrow’s goldeneye (AHY = 271; HY = 68; Table 2.1). We excluded data from 53 individuals because their transmitters provided invalid locations (n = 6) or the bird died or the tag failed within 14 days of implantation (n = 47). The filtered dataset therefore included data from 286 birds (AHY = 229, HY = 57), but we restricted our analysis to the larger, more geographically complete, sample of AHY birds that included 151 males and 78 females (Table 2.1). HY were additionally excluded from this study due to their different life cycle stages (no breeding stage, but additional hatch and prospecting stages), and the high mortality of individuals leading to few transmissions per individual. On average, the retained AHY birds were tracked for 346 days (range: 18-1171) and provided 82 locations (range: 4-307). The majority of locations were in the high accuracy location classes 3 or 2 (73%, n = 18,762). We calculated a centroid of activity for 197 birds on their wintering grounds, 179 birds on their breeding grounds, and 199 birds at moulting sites.

We identified 6 males that migrated from their wintering grounds directly to a moulting site. We identified an additional 5 males that moved to staging sites close to their moulting sites that were outside the known BAGO breeding range (SDJV 2003), where Barrow’s goldeneye breeding females (including satellite-tagged females) have never been observed, and where no large diameter trees exist for nesting cavities required by Barrow’s goldeneye. For these individuals, attributes associated with breeding areas were not calculated or analysed.

2.3.1. Migratory connectivity

We found that, at the scale of the Pacific population, both male and female Barrow’s goldeneye exhibited a high degree of migratory connectivity between each stage of the annual cycle (Table 2.1). However, females had stronger migratory connectivity than males, especially from breeding to moulting (Table 2.2). To further examine the spatial extent of connectivity, we conducted Mantel tests on wintering and breeding locations of birds from the most northern capture locations (south-central Alaska, n = 18) and the most southern capture location (Vancouver, n = 49). Migratory connectivity within these ‘sub-populations’ was low (south-central AK; r_m = 0.16, P = 0.05; Vancouver; r_m = 0.03, P = 0.38; Figure 2.1). These results demonstrate that migratory connectivity is scale dependent.

For both males and females, distinct spatial groupings were apparent (Figure 2.1, 2.2). The overlay of clusters and lines of movements highlight the fact that birds that spent one stage near each other, spent the subsequent stage near each other (Table 2.3), and this explained the strong correlation between pairwise distance matrices. The distinct clusters of wintering goldeneye captured the spatial structure of our five winter capture locations along the coast, one breeding capture site in south-central British Columbia, and one moulting capture site in northwest Alberta. Four moulting clusters coincided with breeding clusters, reflecting the fact that females who raise broods remained on their breeding ponds to moult (Figure 2.2 (5-6)). Both Figures 2.1 and Figure 2.2 show that birds that wintered in south-central Alaska and southern British Columbia are even more disjunct through the annual cycle than birds that wintered at coastal locations in between.

Birds tended to move in a northerly direction to breed, maintaining a similar longitude ($r_{\text{winter-breed longitude}} = 0.96$, $p < 0.001$). Birds that wintered at northern sites bred farther north, resulting in a correlation between an individual's wintering latitude and breeding latitude ($r_{\text{winter-breed latitude}} = 0.81$, $p < 0.001$). Birds that bred in south-central Alaska typically moved in a northeast direction to moult, whereas those that bred near Juneau traveled north, and all southern counterparts moved either north or northeast. Breeding longitude was a strong predictor of moulting longitude ($r_{\text{breed-moult longitude}} = 0.91$, $p < 0.001$). Similarly, breeding latitude was a predictor of moulting latitude ($r_{\text{breed-moult latitude}} = 0.65$, $p < 0.001$). Birds returned to coastal sites to winter, moving in a south-southwest direction. Specifically, birds returned to coasts from Alaskan moulting locations in a southwestern direction, and individuals that moulted in northern Yukon and northern Northwest Territories also traveled southwest. The longitude and latitude of moulting sites was a strong predictor of longitude and latitude of wintering sites ($r_{\text{moult-winter longitude}} = 0.91$, $p < 0.001$; $r_{\text{moult-winter latitude}} = 0.66$, $p < 0.001$).

2.3.2. Annual cycle phenology and migration strategies

Timing of life stages

We found latitudinal and sex differences in average timing of events in the annual cycle of adult Barrow's goldeneye (Table 2.4). Our models indicate that male and female goldeneyes that winter at northern latitudes along the south-central Alaskan coast (60ºN) arrived on their wintering grounds on average 26 ± 11 days earlier and departed on spring migration 20 ± 14 days later (Figure 2.3), and thus spent more time on their wintering grounds than birds that wintered at more southerly locations (50ºN) (Figure 2.4, Table 2.4). There were no sex differences in timing of arrival at, or departure from, wintering grounds (Table 2.4). Male and female goldeneye that bred at northern latitudes arrived on breeding areas on average 15 ± 12 days later and departed 20 ± 19 days later compared to birds that bred at southern latitudes (Figure 2.3). Although, both sexes arrived on the breeding grounds at approximately the same time, after accounting for latitude (Figure 2.3, Table 2.4), males departed breeding grounds for moulting sites on average 35 ± 18 days before females. Males, consequently, spent less time (40 days ± 18) on their breeding grounds than females (Figure 2.3, Table 2.4). Goldeneye that wintered at more northern latitudes arrived on their moulting grounds at the same time as their southern counterparts. However, birds at northern latitudes departed moulting areas on average 20 ± 19 days earlier (Figure 2.3), and therefore spent less time on their moulting grounds than birds that wintered at more southern latitudes (Figure 2.4, Table 2.4). On average, males arrived on the moulting grounds 30 ± 23 days before, and departed 10 ± 20 days after, females (Figure 2.3, Figure 2.4, Table 2.4). Integrating these analyses, there are important differences in the amount of time females and males spent in the three key stationary periods (wintering, breeding and moulting) and on migration between these annual stages.

Migratory behavior

We also found strong latitudinal and sex effects on migratory behavior of adult Barrow's goldeneye. Our models indicate that individuals that departed from wintering grounds at northern latitudes along the south-central Alaskan coast traveled on average 300 ± 99 km farther to reach their breeding grounds than birds that wintered at more southerly locations in southwest Canada. Most individuals (65%, n = 164) completed spring migration without stopping for more than 2 days. Individuals originating from wintering grounds at northern latitudes and subsequently departing from breeding grounds, traveled on average 500 ± 175 km farther than birds that wintered in southwest Canada. Approximately half of the individuals (n = 167) made at least one stop when traveling from breeding to moulting areas. Traveling to moulting areas, males were more likely to stop, and make multiple stops than females. On the return trip from moulting to wintering locations, birds that originated at wintering sites in northern latitudes travelled a shorter distance by 400 ± 186 km than those that wintered in southern latitudes. Males that travelled farther north when moving to their moulting sites, also had longer return trips (700 ± 171 km) than females. The fall migration included a stopover for most individuals (71%, n = 173). For all stages, there were no latitudinal effects for the probability of stopping, number of stops taken, length of stay at stopovers, nor the total duration of time in days spent on migration.

2.4. Discussion

To understand the factors that drive population trends and limit populations, there is a need to study migratory birds throughout the annual cycle and understand migratory connectivity at large geographic scales (Marra et al. 2015; Webster et al. 2002). Studies that incorporate the full annual cycle and geographic range are increasing (Fraser et al. 2012; Stanley et al. 2015; Knight et al. 2018) but remain rare. Our study shows that range-wide migratory connectivity of Barrow's goldeneye is high, and that wintering latitude and sex both affect when and where adults will be at different annual cycle stages. Latitudinal and sex differences in phenology will consequently alter how events and conditions across the annual cycle influence demographic rates like adult survival and breeding success and the trajectory of sub-populations of this, and potentially other, species.

Studies quantifying avian migratory connectivity using Mantel Tests (Ambrosini et al. 2009), or an MC Index (Cohen et al. 2018) can indicate high or low levels of mixing from wintering and breeding populations, depending on the natural history of the animal being considered. In a recent review, Finch et al. (2017) reported that 18 of 28 long-distance migrants exhibited weak, diffuse migratory connectivity. Knight et al. (2018) also noted that migratory connectivity tends to vary over the course of the annual cycle, and that stages with a high degree of fidelity are frequently followed by stages where there is a high degree of mixing. In contrast, Barrow's goldeneye exhibited high migratory connectivity throughout the entire cycle. Several authors have suggested that observed differences in migratory connectivity across species and studies may be a consequence of the scale at which studies are conducted; studies at larger spatial scales are more likely to capture the multiple migration routes associated with structured populations (Gilroy et al. 2016; Finch et al. 2017; Knight et al. 2018). Our results support this argument. Migratory connectivity measured over the majority of the species range was high, whereas it was low at smaller geographic scales. Studies that are often limited to a small portion of a species distribution (e.g. Johnson et al. 2010; Meattey et al. 2018) are therefore likely to underestimate the strength of connectivity that may exist at range-wide scales.

Information on migratory connectivity has been exceedingly sparse for sea ducks in North America, most of which winter in temperate coastal waters and breed in remote sub-Arctic and Arctic regions (Takekawa et al. 2011). Studies of connectivity in waterfowl species must also consider the post-breeding flightless remigial moult life stage as an additional critical life stage where population structure and mixing may differ from either breeding or wintering periods (Meattey et al. 2019). Population structure in waterfowl species is typically female mediated, as females from most species demonstrate strong natal and breeding site philopatry (Eadie and Savard 2015; Mallory et al. 2015), whereas males are more likely to disperse depending on their pair status (Anderson et al. 1992). Thus, most sea duck movement studies using PTTs have been conducted only on females, and migratory connectivity studies tend to focus only on wintering to breeding stages. Takekawa et al. (2011) using 53 female Pacific surf scoters (*Melanitta perspicillata*) found low, non-significant connectivity from wintering to breeding grounds. Similarly, Meattey et al. (2019) using 52 females, found low to moderate connectivity on Atlantic white-winged scoters (*Melanitta deglandi*) through the full-annual cycle. Using males and females, Oppel et al. (2008) found low connectivity in king eiders (*Somateria spectabilis*) from wintering to breeding grounds. In contrast, Pacific common eiders (*Somateria mollissima*), and spectacled eiders (*Somateria fischeri*) breeding in Alaska all were found to have high connectivity (Petersen et al. 1999; Petersen and Flint 2002). However, this is the only sea duck study on migratory connectivity that incorporates males and females, covers the full geographic span on the species, and includes captures at different annual cycle stages. This unique and large dataset allowed for a more detailed analysis of Pacific Barrow's goldeneye's migration ecology.

Migratory species with breeding and wintering ranges that span 25 degrees latitude would be expected to adjust the timing of stages of the annual cycle to latitudinal gradients in climatic conditions(e.g. Both et al. 2004; Gow et al. 2019). Latitudinal variation in timing of each stage may also carry over to later stages because the length of stay and timing of subsequent stages will depend on previous stages (van Wijk et al. 2017; Gow et al. 2019). We found that wintering latitude was linked to arrival and departure timing, length of stay, and distance to each stage, except moult arrival dates (Fig 2.4). On average, our PTT-tagged Barrow's goldeneye spent about 50% of the annual cycle on wintering grounds. Birds wintering in northern latitudes have an even longer wintering stage, spending about 60 days more on the coast than those wintering at southern latitudes. Latitudinal effects on timing of multiple stages of the annual cycle of Barrow's goldeneye are in part due to the high degree of migratory connectivity. Our study highlights the extent to which sub-populations are responsive to their local environment and the level of within-species variation in phenology of annual cycles.

Sex differences in timing of stages in the annual cycle of migratory birds may be driven by differences in benefits of early arrival on the breeding grounds (e.g. Myers 1981; Morbey and Ydenberg 2001), uniparental care (e.g. Whitefield and Tomkovich 1996), or differential migration of males and females (e.g. Cristol et al. 1999). Barrow's goldeneye are thought to pair on the wintering grounds (Savard 1985), leading to males and females arriving on the breeding grounds at the same time (Savard 1985). However, females incubate and care for young alone (Cramp and Simmons 1977), so we expected sex differences in phenology to arise after breeding. Consistent with this expectation, we found strong sex effects in timing of departure and length of stay of breeding, timing of arrival, departure and length of stay of moulting, probability of stopping, number of stops and distance travelled from breeding to moulting, and distance travelled from moulting to wintering. Females consequently spent 40 more days on their breeding grounds and 40 fewer days on their moulting grounds than males. Females that successfully raise a brood and moult on their breeding grounds are still on moulting grounds, and therefore spend the same amount of time away from wintering areas as females that migrate to moulting sites. Females were also less likely to travel long distances to more northerly moulting sites than males, perhaps due to constraints imposed by caring for young. Females that did not remain on breeding ponds but migrated early and moulted at areas at least 100 km to the north, were likely individuals that did not breed at all or were failed breeders. Females with broods are highly faithful and will remain with them through the summer and into fall, unless the brood is taken over by another hen early on or all the ducklings are predated (Eadie et al. 2020). Females and males, however, spent a similar amount of time on their wintering grounds, after accounting for effects of latitude.

Studies that fully describe migratory connectivity can aid in delineation of populations and effective management of migratory species (Webster et al. 2002; Meattey et al. 2018; Lamb et al. 2019). We show that Pacific adult Barrow's goldeneye populations are highly structured, with high migratory connectivity through all stages of the annual cycle. South-central Alaska and southern British Columbia had entirely distinct clusters, demonstrating a strong separation at that scale. Hunting recoveries of banded Barrow's goldeneye also showed strong separation between the Alaska and British Columbia subpopulations (Figure A1). The high level of migratory connectivity of adult Barrow's goldeneye combined with high breeding and wintering site fidelity would be expected to result in distinct genetic structures among subpopulations. However, a recent study found little to no genetic structure across the Pacific coast range (Brown et al. 2020). The authors suggested that lack of structure was likely a consequence of juvenile male dispersal. Subadult males of many species tend to disperse across wintering areas and rarely return to natal nesting grounds in contrast to juvenile females (e.g., Boyd et al. 2009; Pearce and Peterson 2009; Bentzen and Powell 2010). Boyd et al. (2009) showed that this true for Barrow's goldeneye, where juvenile males had higher dispersal probabilities, and the probability of dispersal likely increased once birds reached reproductive maturity to compete for breeding territories. Nevertheless, if subpopulations function as discrete units, as is the case with Barrow's goldeneye, they could be managed independently as trends within these units will depend primarily on the demography and productivity of adults.

2.5. References

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2.6. Tables

Table 2.1 Numbers of adult male and female Barrow's goldeneye that were marked with PTT tags and retained in analyses of movement throughout the annual cycle

Cohort			Number Marked		Number Retained	
Year	Capture Site	Annual Cycle Stage	Male	Female	Male	Female
2006	Riske Creek, BC	Breed	23	-	17	-
2007	Riske Creek, BC	Breed	15	-	15	-
	Vancouver, BC	Winter	10	10	5	7
2008	Riske Creek, BC	Breed	10	10	10	8
2009	South-central AK	Winter	19	8	6	4
	Riske Creek, BC	Breed	-	-	-	-
	Cardinal Lake, AB	Moult	20	-	14	-
2010	Cardinal Lake, AB	Moult	18	-	16	-
2011	Vancouver, BC	Winter	10	15	10	13
	Riske Creek, BC	Breed	-	2	-	1
2012	Juneau, AK	Winter	23	12	21	11
2013	South-central AK	Winter	5	11	4	8
2014	Kitimat, BC	Winter	19	12	15	11
2015	Vancouver, BC	Winter	8	11	8	10
Total	-	-	180	91	141	73

Note: An additional 68 HY birds were captured at Riske Creek in 2008, 2009, and 2011, Prince William Sound in 2009, and Vancouver in 2015.

Table 2.2 **Mantel test correlations (*r_m*) examining migratory connectivity between different stages of the annual cycle for male and female Barrow's goldeneye. Mantel correlation *r_m* values range from -1.0 to 1.0 where -1.0 indicates low connecitivity and 1.0 indicates high connectivity.**

Stage	Sex	r_m	95% CI	N	P
Winter-Breed	M	0.86	0.84, 0.9	86	< 0.001
Winter-Breed	F	0.90	0.89, 0.88	68	< 0.001
Breed-Moult	M	0.58	0.54, 0.62	101	< 0.001
Breed-Moult	F	0.90	0.88, 0.93	57	< 0.001
Moult-Winter	M	0.65	0.61, 0.68	113	< 0.001
Moult-Winter	F	0.79	0.75, 0.84	61	< 0.001

Table 2.3 **Number of clusters and noise points identified by cluster analysis for the winter, breeding, and moulting periods**

Stage	Sex	N	# Clusters	# Noise Points	Range of individuals per cluster
Winter	M	122	8	30	5 - 22
Winter	F	75	5	2	5 - 33
Breed	M	110	6	51	6 - 15
Breed	F	69	5	22	6 - 13
Moult	M	137	6	19	7 - 47
Moult	F	62	4	20	7 - 14

Table 2.4 **Latitude and sex effects on timing and migratory behavior variables**

		Latitude		Sex		Latitude* Sex		Full Model Stats		
Variable	Metric	$F_{[x1,x2]}$	P =	$F_{[x1,x2]}$	P =	$F_{[x1,x2]}$	P=	adjusted r2	$F_{[x1,x2]}$	P =
Winter	Arrive	$F_{[1, 159]}$ = 157.1	< 0.001	$F_{[1,159]}$ = 1.75	0.19	$F_{[1,159]}$ = 0.03	0.86	0.49	$F_{[3,159]}$ = 53.0	< 0.001
	Depart	$F_{[1,155]}$ = 62.1	< 0.001	$F_{[1,155]}$ = 0.08	0.78	$F_{[1,155]}$ = 0.17	0.68	0.27	$F_{[3,155]}$ = 20.8	< 0.001
	Length of Stay (days)	$F_{[1, 74]}$ = 81.1	< 0.001	$F_{[1, 74]}$ = 1.28	0.26	$F_{[1, 74]}$ = 0.87	0.03	0.51	$F_{[3, 74]}$ = 27.5	< 0.001
Breed	Arrive	$F_{[1, 141]}$ = 34.3	< 0.001	$F_{[1, 141]}$ = 0.20	0.90	$F_{[1,141]}$ = 0.32	0.57	0.17	$F_{[3, 141]}$ = 11.5	< 0.001
	Depart	$F_{[1, 130]}$ = 5.59	0.02	$F_{[1,130]}$ = 155.7	< 0.001	$F_{[1, 130]}$ =6.88	< 0.001	0.55	$F_{[3, 130]}$ = 56.0	< 0.001
	Length of Stay (days)	$F_{[1, 107]}$ = 0.41	0.52	$F_{[1, 107]}$ = 122.1	< 0.001	$F_{[1, 107]}$ = 5.98	0.02	0.53	$F_{[3, 107]}$ = 42.8	< 0.001
Moult	Arrive	$F_{[1,140]}$ = 1.99	0.16	$F_{[1,140]}$ = 97.6	< 0.001	$F_{[1,140]}$ = 1.64	0.20	0.41	$F_{[3,140]}$ = 33.7	< 0.001
	Depart	$F_{[1, 128]}$ = 21.7	< 0.001	$F_{[1, 128]}$ = 9.50	< 0.001	$F_{[1,128]}$ = 0.41	0.52	0.18	$F_{[3,128]}$ = 10.5	< 0.001
	Length of Stay (days)	$F_{[1, 116]}$ = 11.8	< 0.001	$F_{[1, 116]}$ = 16.4	< 0.001	$F_{[1, 116]}$ = 1.08	0.30	0.18	$F_{[3, 107]}$ = 9.75	< 0.001
Probability of stopping	Winter to Breed	$F_{[1, 149]}$ = 0.16	0.69	$F_{[1, 149]}$ = 0.91	0.34	$F_{[1, 149]}$ = 0.26	0.61	-0.01	$F_{[3, 149]}$ = 0.44	0.72
	Breed to Moult	$F_{[1, 149]}$ = 0.96	0.32	$F_{[1, 149]}$ = 5.49	0.02	$F_{[1, 149]}$ = 0.32	0.57	0.02	$F_{[3, 149]}$ = 2.26	0.08
	Moult to Winter	$F_{[1, 149]}$ = 0.18	0.67	$F_{[1, 149]}$ = 1.19	0.28	$F_{[1, 149]}$ = 3.17	0.07	0.01	$F_{[3, 149]}$ = 1.52	0.21
Number of stops on migration	Winter to Breed	$F_{[1, 149]}$ = 0.08	0.78	$F_{[1, 149]}$ = 1.04	0.30	$F_{[1, 149]}$ = 0.20	0.65	0.01	$F_{[3, 149]}$ = 0.45	0.72
	Breed to Moult	$F_{[1, 149]}$ = 0.07	0.79	$F_{[1, 149]}$ = 8.60	< 0.001	$F_{[1, 149]}$ = 0.59	0.44	0.04	$F_{[3, 149]}$ = 3.09	0.03
	Moult to Winter	$F_{[1, 149]}$ = 1.03	0.31	$F_{[1, 149]}$ = 0.83	0.36	$F_{[1, 149]}$ = 1.67	0.20	0.01	$F_{[3, 149]}$ = 1.18	0.32

		Latitude		Sex		Latitude*Sex		Full Model Stats		
Variable	Metric	$F_{[x1,x2]}$	P =	$F_{[x1,x2]}$	P =	$F_{[x1,x2]}$	P=	adjusted r2	$F_{[x1,x2]}$	P =
Stopover length of stay (days)	Winter to Breed	$F_{[1, 63]} = 0.80$	0.37	$F_{[1, 63]} = 0.08$	0.78	$F_{[1, 63]} = 0.01$	0.95	-0.03	$F_{[3, 63]} = 0.30$	0.83
	Breed to Moult	$F_{[1, 103]} = 2.47$	0.12	$F_{[1, 103]} = 0.38$	0.54	$F_{[1, 103]} = 0.78$	0.78	0.01	$F_{[3, 103]} = 0.97$	0.41
	Moult to Winter	$F_{[1, 151]} = 1.68$	0.20	$F_{[1, 151]} = 0.25$	0.62	$F_{[1, 151]} = 0.07$	0.79	-0.01	$F_{[3, 151]} = 0.67$	0.57
Distance travelled (km)	Winter to Breed	$F_{[1, 141]} = 14.7$	< 0.001	$F_{[1, 141]} = 0.01$	0.97	$F_{[1, 141]} = 0.64$	0.43	0.08	$F_{[3, 141]} = 5.14$	< 0.001
	Breed to Moult	$F_{[1, 121]} = 67.8$	< 0.001	$F_{[1, 121]} = 49.5$	< 0.001	$F_{[1, 121]} = 2.20$	0.14	0.48	$F_{[3, 121]} = 39.8$	< 0.001
	Moult to Winter	$F_{[1, 155]} = 8.84$	< 0.001	$F_{[1, 155]} = 79.4$	< 0.001	$F_{[1, 155]} = 4.74$	0.03	0.36	$F_{[3, 155]} = 31.0$	< 0.001
Total duration on migration (days)	Winter to Breed	$F_{[1, 92]} = 0.71$	0.79	$F_{[1, 92]} = 0.32$	0.57	$F_{[1, 92]} = 0.28$	0.60	0.03	$F_{[3, 92]} = 0.22$	0.88
	Breed to Moult	$F_{[1, 117]} = 0.01$	0.10	$F_{[1, 117]} = 0.01$	0.93	$F_{[1, 117]} = 1.30$	0.26	0.01	$F_{[3, 117]} = 0.42$	0.74
	Moult to Winter	$F_{[1, 147]} = 1.53$	0.22	$F_{[1, 147]} = 0.52$	0.47	$F_{[1, 147]} = 0.42$	0.52	0.01	$F_{[3, 147]} = 0.82$	0.48

2.7. Figures

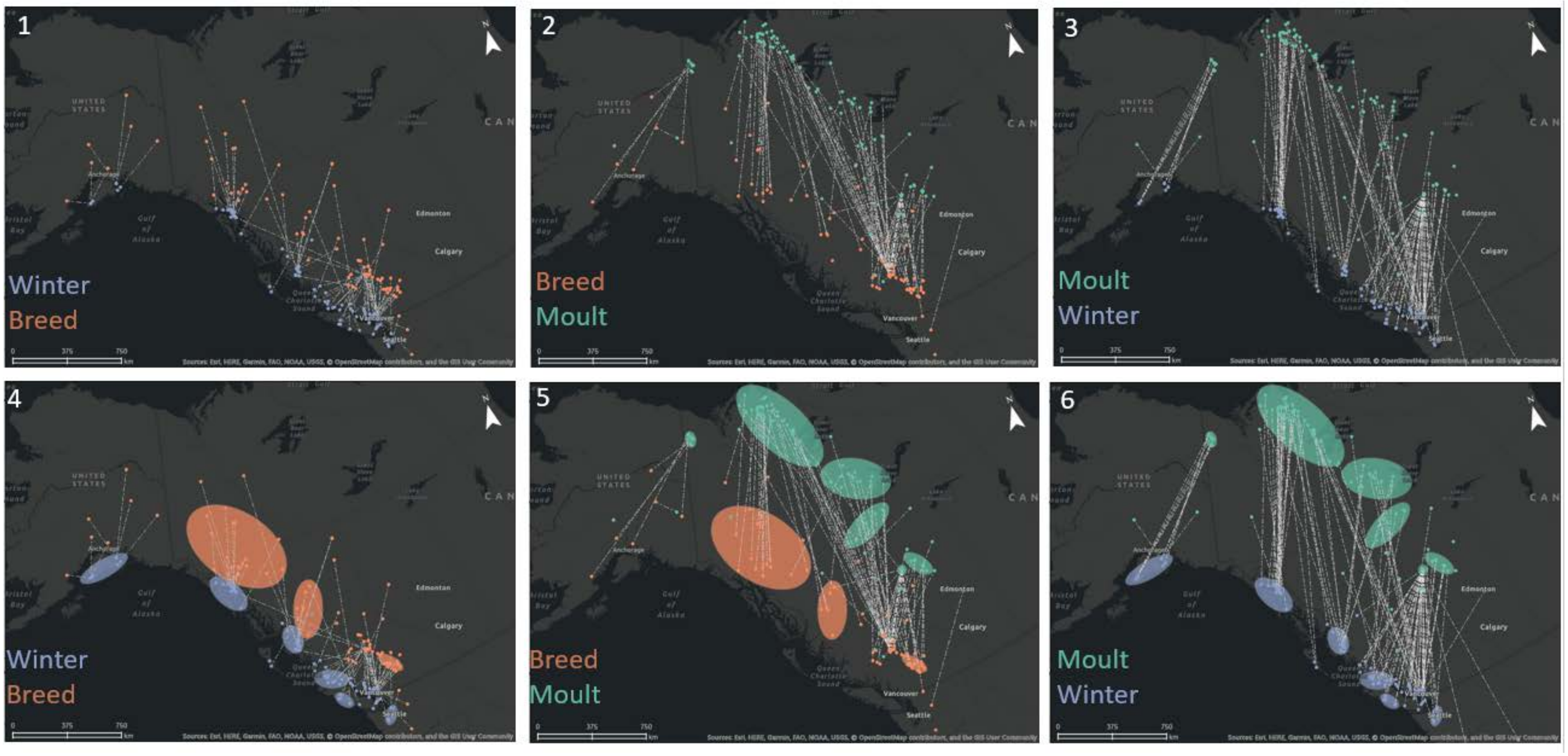

Figure 2.1 **Annual cycle connectivity of male adult Barrow's goldeneye that migrated between wintering, breeding, and moulting areas. Colored areas represent clusters of life-stage areas identified by the cluster analysis. Dashed lines link individual life stages but are not representative of actual migration routes.**

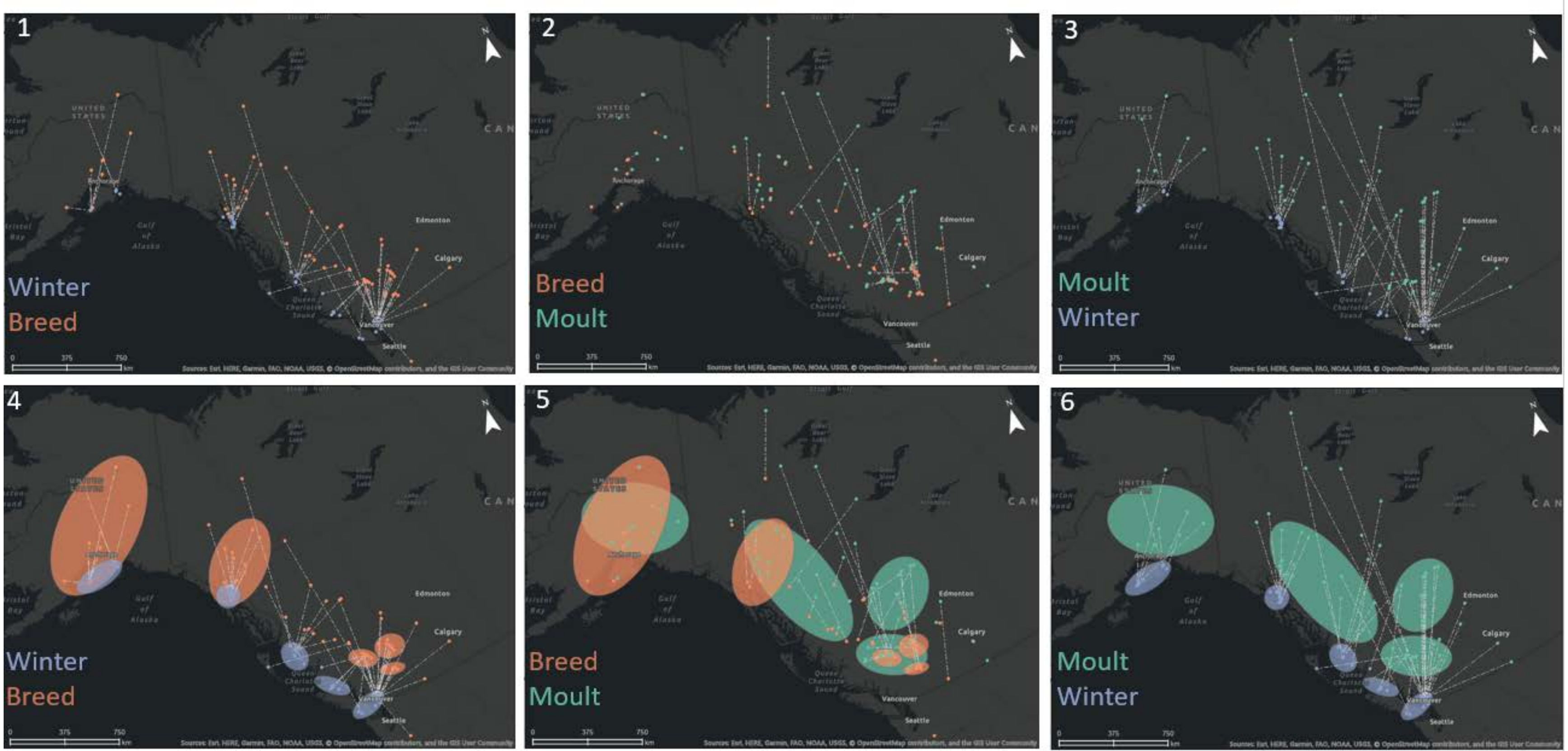

Figure 2.2 Annual cycle connectivity of female adult Barrow's goldeneye that migrated between wintering, breeding, and moulting areas. Colored areas represent clusters of life-stage areas identified by the cluster analysis. Dashed lines link individual life stages but are not representative of actual migration routes.

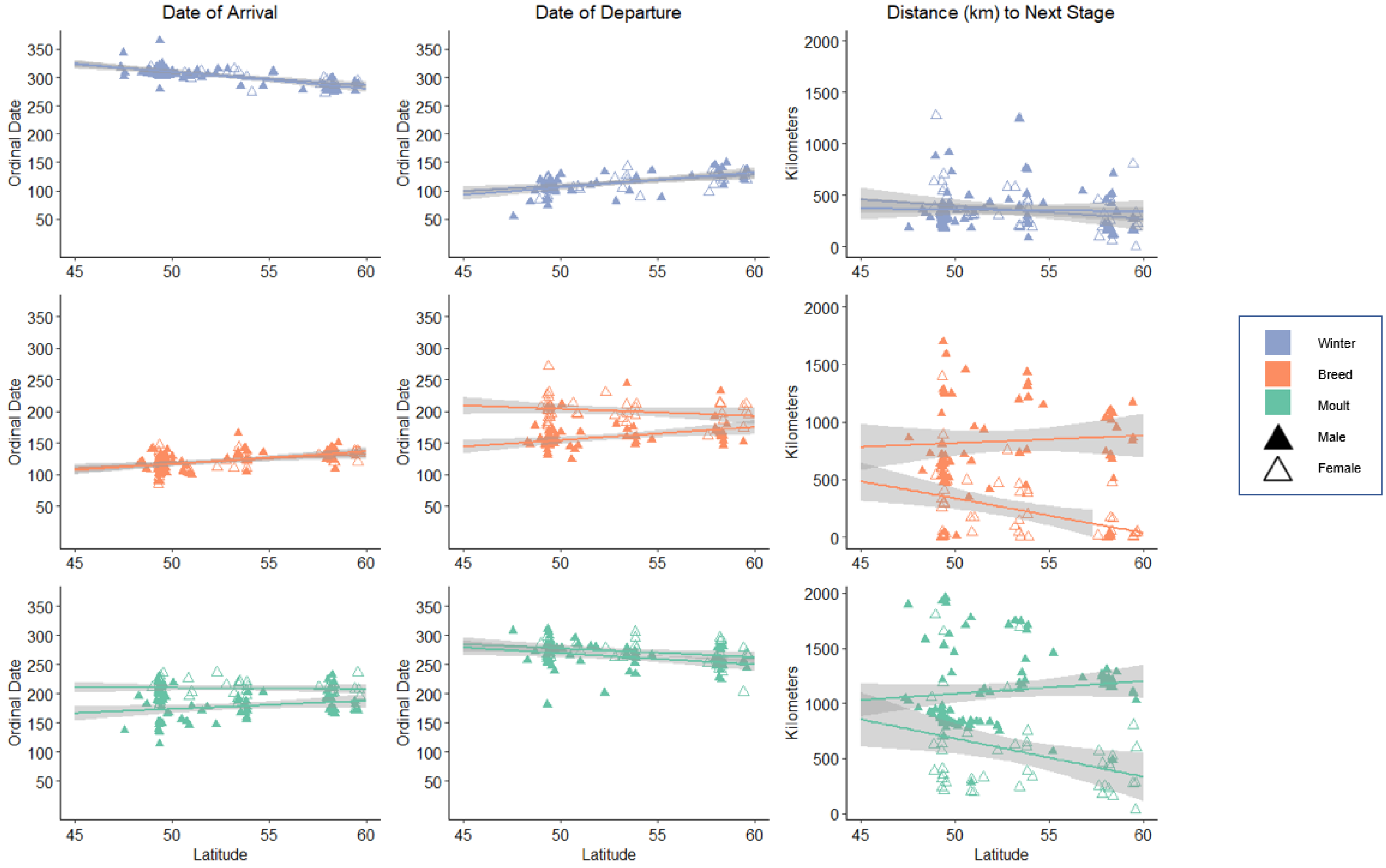

Figure 2.3 Wintering latitude and sex effects on the date of arrival, departure, and distance traveled to the subsequent stage for wintering (1,4,7), breeding (2,5,8), and moulting stages (3,6,9). Ordinal dates are the day of year, where ordinal day “1” =Jan 1, day “100”= Apr 10, day “200” = Jul 19, and day “365” = Dec 31.

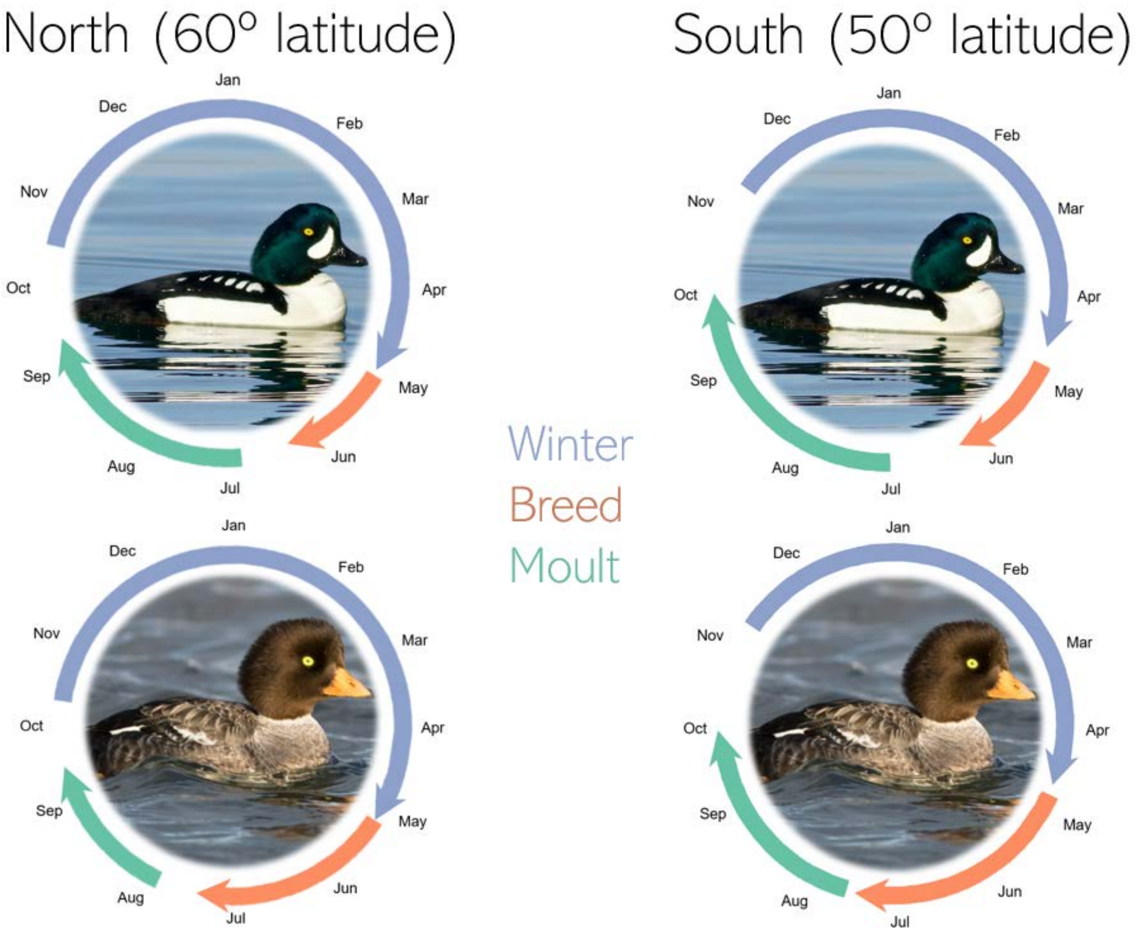

Figure 2.4 **Illustration of sex and latitude effects on arrival to, departure from, and length of stay Barrow's goldeneye on wintering, breeding, and moulting grounds. Northern latitudes include individuals wintering at latitudes of >55 degrees, and southern latitudes include individuals wintering at latitudes of <50 degrees. The white spaces between the arrows represent the duration of time spent on migration.**

Chapter 3.

General Conclusions

3.1. Overview

The geographic structure of a migratory network significantly influences population dynamics (Webster and Marra 2005; Knight et al. 2018). Linking spatially discrete parts of the annual cycle is needed to understand how population dynamics are shaped by events in different times of the year (Morales et al. 2010). Consequently, for migratory birds, describing migratory connectivity at large geographic scales is necessary to understand factors driving population trends (Marra et al. 2015; Webster et al. 2002). Studies that incorporate the full annual cycle and geographic range are increasing (Stanley et al. 2015; Knight et al. 2018) but remain rare. In this thesis, I investigated the migratory connectivity and spatio-temporal aspects of the Barrow’s goldeneye full annual cycle. First, I documented migratory connectivity of satellite-tagged adult Barrow’s goldeneye for both males and females across their full annual cycle (wintering, breeding, and moulting grounds). Second, I investigated temporal movements by examining the timing of transitions between each of these stages and the migratory behavior between each transition.

Migratory connectivity studies have increased as animal movement data becomes available at large spatial and temporal scales. However, even with a full annual cycle approach, migratory connectivity is still difficult to quantify accurately. For instance, recent reviews have suggested that connectivity metrics, such as the MC Index and the Mantel test, appear to be scale-dependent (Cohen et al. 2017; Knight et al. 2018). Additionally, migratory connectivity varies across stages of the annual cycle (Finch et al. 2017; Meattey et al. 2019) and has the potential to differ among age and sex classes (Cohen et al. 2017). Finally, uneven distribution of sampling increases the challenges of accurately quantifying migratory connectivity (Cohen et al. 2017; Ambrosini et al. 2009). Therefore, studies limited to a small portion of a species distribution (e.g. Meattey et al. 2018; Johnson et al. 2010) are likely to underestimate the strength of connectivity present at range-wide scales. Ultimately, studies at larger spatial scales are more likely to capture the multiple migration routes associated with structured populations (Gilroy et al. 2016; Finch et al. 2017; Knight et al. 2018).

With our long-term and robust dataset, our study was able to address some of the limitations of past migratory connectivity studies. The accumulation of 11 years of data provided a rare opportunity to examine large-scale patterns of movements across the core of the geographic range and annual cycle. Data were collected with one consistent methodology (satellite telemetry) from across the entire range, which increased confidence in our conclusion that migratory connectivity is scale dependent. For instance, migratory connectivity measured over the species full geographic range in the Pacific was high. In contrast, it was low at smaller geographic scales when tested within the most southern capture location and the most northern capture locations with rm scores of 0.03, and 0.16, respectively. Additionally, this study included the full annual cycle of a sea duck, including transition to the moulting stage, which had previously been missing from migratory connectivity studies (Johnson et al. 2010; Takekawa et al. 2011). This highlighted that migratory connectivity can differ between sexes, especially between the breeding to moulting stages.

The longest stage of the annual cycle for sea ducks is consistently the wintering period. Black scoters (*Melanitta americana*) (Loring et al. 2014), common eiders (*Somateria mollissima*) (Beuth et al. 2017), and white-winged scoters (*Melanitta deglandi*) (Meattey et al. 2019) wintering in southern New England, spent a mean of 147,135, and 189 days, respectively. Surf scoters (*Melanitta perspicillata*) wintering along the mid-Atlantic coast spent a mean of 133 days on the wintering grounds (Meattey et al. 2015), while king eiders (*Somateria spectabilis)* in Alaska spent a mean of 160 days wintering on the Bering Sea (Oppel et al. 2008). In this study, we found Pacific Barrow's goldeneye spent between 151 to 218 days on the wintering grounds depending on latitude. This highlights the extent of variation in the timing and length of stay during the wintering stage. This variation in phenology also emphasizes the importance of studying timing across the full geographic range of a species distribution. For instance, in our study there was significant variation in the length of time spent at wintering areas depending on latitude. Goldeneye wintering in northern latitudes had an even longer wintering stage, spending about 60 days more on the coast than those wintering at southern latitudes. Thus, latitudinal and sex differences in phenology can alter the timing of events and result in variation in exposure to different conditions across the annual cycle.

3.2. Recommendations for Future Studies

Overall, the results of this study demonstrate the importance of studying the full annual cycle of long-distance migrants to determine the scale of appropriate management units and the potential for carry-over effects among annual cycle stages. This study contributes significantly to our understanding of the migratory connectivity and spatio-temporal movements of Barrow's goldeneye, but several areas of research still warrant further investigation.

Male movement to northern moulting lakes – Following the breeding stage, waterfowl often migrate to specific moult sites far outside their core breeding range. Moult migration likely provides important benefits, including reduced human disturbance, access to larger and more drought-resistant wetlands, and abundant food and low predator densities relative to breeding areas (Madsen and Mortensen 1987; Hogan et al. 2012). Previous work has focused on understanding moulting and fall staging phenology (Hogan et al. 2011), survival and movements (Hogan et al. 2013), as well as physiological and behavioral strategies employed during remigial moult and fall staging (Hogan et al. 2012). In Chapter 2, I demonstrated that males use a diverse array of moulting sites (small inland lakes or wetlands with few or no trees), thousands of kilometers from their core breeding areas. Our tracking data revealed that male Pacific Barrow's goldeneye moved to moulting areas in the boreal forests of the Northwest Territories, whereas eBird range maps lacked this movement (Hogan et al. 2011; ebird, 2020). Previous publications (Hogan et al. 2011; Hogan et al. 2013), in conjunction with our results on the migratory connectivity, timing and duration of the moulting stage, have led to a more complete understanding of how Barrow's goldeneye use post-breeding habitats.

The remigial moult is a stage of high survival for male Barrow's goldeneye (Hogan et al. 2013). Given the relatively high levels of site fidelity to moulting areas observed in birds (Robert et al. 2002; Savard et al. 2013; Eadie et al. 2020) and high migratory connectivity, increased localized mortality during moult could significantly affect specific sub-populations. Future studies could analyse where males move to moult in relation to their breeding grounds. This could be paired with correlating the timing of departure from breeding grounds with distance traveled to moulting sites, and to subsequent wintering sites. Previous studies examining body mass and foraging studies of moulting adult males found that birds were not nutritionally constrained nor were they adaptively losing mass or restricting foraging to avoid predators (Hogan et al. 2012). This suggested that the few mortalities during remigial moult were likely not due to starvation or predation. However, as local eagle population densities and distributions change following the continued recovery of the bald eagle (*Halieaeetus leucocephalus*), there could be implications for the current male moult strategy. Additional research could overlay the spatio-temporal movements of eagles with those of goldeneye, as the timing of goldeneye movements may be related to eagle presence.

Juvenile dispersal linking sub-populations- Band recovery and our telemetry data for adult Barrow's goldeneye have highlighted strong linkages among stages of the annual cycle. However, a recent study found little to no genetic structure in Barrow's goldeneye populations sampled across the Pacific range (Brown et al. 2020). Brown et al (2020) suggested that the lack of structure was a consequence of juvenile male dispersal, because juvenile males tend to disperse across wintering areas and rarely return to natal nesting grounds, whereas juvenile females have higher natal fidelity (e.g., Boyd et al. 2009; Pearce and Peterson 2009; Bentzen and Powell 2010). However, data on natal and juvenile dispersal of Barrow's goldeneye is limited, with individuals in this study providing few transmissions per year (Boyd et al. 2009).

Further work could focus on the spatio-temporal movements of juveniles to evaluate if, and when, mixing occurs among sub-populations. Mixing could happen at two transitions in the annual cycle: i) from an individual's natal site to their first wintering site and ii) from an individuals first wintering site to their subsequent prospecting site, where they search for a potential future breeding location. Currently, there is a limited amount of unanalysed PTT telemetry data on the year-round movement of hatch-year birds captured on their natal sites and on wintering locations. Data on juvenile movements is available, but limited due to the small sample size, high mortality of juveniles after surgical implantation of PTTs, and short transmission periods. Additional focused telemetry data on juveniles could be conducted with less impact on mortality using newer, lighter tags. The movements of juveniles could be used to evaluate hypotheses of Brown et al. (2020) and determine whether juvenile dispersal was linking discrete sub-populations. Specifically, work on juvenile dispersal could assess the possibility that the mixing occurred either at the transition from natal site to wintering site or the transition from wintering site to subsequent prospecting site.

Winter habitat analysis- Barrow’s goldeneye spend a large part of their annual cycle on their wintering grounds; estimates from this study range from 151 to 218 days. Coastal development in British Columbia is increasing rapidly and there is predicted to be a 7-fold rise in marine oil tanker traffic (Govt. of Canada & National Energy Board 2016), significantly increasing the risk of an oil spill. Future research should focus on identifying fine-scale resource selection and habitat use patterns of Barrow’s goldeneye wintering along the coast of British Columbia. This could include developing resource selection functions to map the probability of habitat use by Barrow’s goldeneye and quantifying the degree of overlap between winter habitat use of Barrow’s goldeneye, water vessel traffic, and oil spill risks to inform marine planning.

3.3. Conservation and Management Implications

This thesis provided data relevant for conservation initiatives such as the Sea Duck Joint Venture (SDJV) and the Oceans Protection Plan (OPP). The mission of the SDJV is to promote conservation of all North American sea ducks by increasing knowledge and understanding of sea duck biology to improve management. Some of the SDJV’s priority information needs for Barrow’s goldeneye are population delineation and quantification of seasonal movements. Our research demonstrates that Barrow’s goldeneye have high migratory connectivity throughout the entire annual cycle when measured over the entire core range. The high migratory connectivity means that an oil spill that occurred on the wintering grounds could have significant negative effects on a discrete subpopulation during the breeding stage. This implies that anthropogenic impacts on the British Columbian coast will influence the breeding population in British Columbia and anthropogenic impacts on the Alaska coast will impact breeding populations in interior Alaska. However, we found low migratory connectivity at smaller regional scales, meaning that negative carry-over effects would be distributed over a broader suite of breeding areas within a region. This implies that although oil spills in Alaska are likely to influence the population dynamic of the Alaska subpopulation, the negative effect would be dispersed throughout the breeding population in Alaska. Consequently, continued long-term monitoring of Barrow’s goldeneye at a few wintering sites distributed across their wintering range would allow assessment of breeding population trends across the core of the Western North American breeding range.

The OPP is a Canadian federal initiative that in part aims to improve emergency response readiness and requires baseline information on the distribution of marine birds to support decision-making during a marine pollution incident. Barrow's goldeneye wintering at latitudes in southern British Columbia overlap with areas that experienced significant ship traffic and had high predicted probabilities of chronic oil pollution (William and O'Hara 2010; Fox et al. 2016). The variation in the timing of transitions means different response planning is required depending on the latitude where an oil spill occurred. A longer wintering period at northern latitudes, like south-central Alaska, meant that northern birds were more likely prone to events or impacts on the wintering grounds than individuals wintering farther south. Nevertheless, individuals wintering in British Columbia would likely be impacted by any spills that happened between November and May.

Recent assessment of population trends in British Columbia suggest slight differences in estimated population declines in the Salish Sea and the northern Pacific coast regions (Ethier et al. 2020). Variation in population trends at this scale are unlikely due to differences in where individuals at these locations breed and moult because we found that migratory connectivity measured at this scale was relatively low. Similarly, any oil spill in the Salish Sea would be expected to have diffuse effects on the British Columbia breeding population. However, long-distance migrants with high degrees of migratory connectivity have been shown to be sensitive to environmental changes that could lead to a mismatch in the timing between their migration phenology and environmental conditions (Visser and Both 2005). Climate-driven departure decision that result in individuals arriving on breeding grounds that are still frozen could contribute to declining population trends in both the Salish Sea and the northern Pacific coast of BC.

3.4. References

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Appendix.

Supplemental Tables and Figure

Table A.1 Mean and standard deviations of timing of migration and migratory behavior based on winter capture location.

		Males				Females			
		Vancouver	Kitimat	Juneau	South-central AK	Vancouver	Kitimat	Juneau	South-central AK
Variable	Metric	Mean/Sd Range	Mean/Sd Range	Mean/Sd Range	Mean/Sd Range	Mean/Sd Range	Mean/Sd Range	Mean/Sd Range	Mean/Sd Range
Winter	Arrive	Nov 05 ± 7	Oct 20 ± 18	Oct 08 ± 8	Oct 08 ± 7	Nov 07 ± 6	Oct 28 ± 16	Oct 16 ± 11	Oct 21 ± 0
		[Oct 30-Nov 16]	[Oct 10-Nov 10]	[Oct 01-Oct 26]	[Oct 02-Oct 19]	[Oct 30-Nov 15]	[Sep 30-Nov 10]	[Sep 28-Oct 26]	[Oct 21-Oct 21]
	Depart	Apr 07 ± 13	Apr 19 ± 24	May 11 ± 13	May 01 ± 9	Apr 21 ± 9	Apr 27 ± 17	May 02 ± 14	May 08 ± 8
		[Mar 13-Apr 22]	[Mar 21-May 14]	[Apr 18-May 29]	[Apr 17-May 16]	[Mar 31-May 04]	[Mar 30-May 22]	[Apr 06-May 17]	[Apr 29-May 13]
	Length of Stay (days)	151 ± 12	176 ± 42	218 ± 16	205 ± 9	165 ± 10	175 ± 12	199 ± 10	190 ± 55
		[136-164]	[131-216]	[193-241]	[192-212]	[150-175]	[155-183]	[176-205]	[180-308]
Breed	Arrive	Apr 23 ± 10	May 09 ± 15	May 10 ± 11	May 06 ± 3	Apr 26 ± 13	May 04 ± 11	May 06 ± 8	May 09 ± 8
		[Mar 30-May 08]	[Apr 14-Jun 13]	[Apr 18-May 29]	[May 04-May 08]	[Mar 31- May 26]	[Apr 19-May 22]	[Apr 29-May 20]	[Apr 23-May 17]
	Depart	May 27 ± 11	Jun 16 ± 26	Jun 19 ± 21	Jun 17 ± 24	Jul 23 ± 24	Jul 16 ± 10	Jul 07 ± 23	Jul 18 ± 14
		[May 10-Jun 19]	[May 26-Aug 31]	[May 25-Aug 19]	[May 31-Jun 04]	[Jun 09-Sep 28]	[Jun 01-Jul 30]	[Jun 09-Aug 01]	[Jun 22-Aug 05]
	Length of Stay (days)	34 ± 11	38 ± 16	40 ± 24	42 ± 27	87 ± 26	73 ± 12	62 ± 23	70 ± 19
		[10-58]	[20-79]	[20-45]	[22-61]	[27-145]	[53-84]	[29-90]	[37-104]
Moult	Arrive	Jul 26 ± 29	Jun 27 ± 16	Jul 06 ± 21	Jun 26 ± 16	Jul 29 ± 15	Jul 25 ± 13	Jul 28 ± 7	Jul 27 ± 21
		[May 12-Aug 01]	[Jun 03-Jul 21]	[Jun 13-Aug 19]	[May 26-Jul 21]	[Jul 01-Aug 22]	[Jul 01-Aug 08]	[Jul 18-Aug 09]	[Jun 22-Aug 23]
	Depart	Sep 25 ± 32	Sep 15 ± 16	Sep 11 ± 16	Sep 06 ± 6	Oct 03 ± 12	Oct 03 ± 15	Sep 22 ± 21	Sep 17 ± 23
		[Jun 29-Nov 06]	[Aug 21-Oct 04]	[Aug 11-Oct 06]	[Aug 25-Sep 15]	[Sep 12-Oct 24]	[Sep 18-Nov 01]	[Aug 25-Oct 22]	[Jul 21-Oct 08]
	Length of Stay (days)	81 ± 42	79 ± 18	67 ± 25	73 ± 10	65 ± 20	68 ± 21	56 ± 20	52 ± 16
		[29-176]	[56-109]	[24-106]	[56-91]	[32-101]	[47-109]	[35-90]	[29-71]
Number of stops taken on migration	Winter to Breed	1 ± 1	1 ± 1	1 ± 1	0 ± 1	1 ± 1	1 ± 1	1 ± 2	0 ± 1
		[0-2]	[0-2]	[0-2]	[0-1]	[0-2]	[0-2]	[0-3]	[0-1]
	Breed to Moult	2 ± 2	2 ± 2	1 ± 1	1 ± 1	1 ± 1	1 ± 1	1 ± 1	0 ± 0
		[0-4]	[0-4]	[0-2]	[0-2]	[0-2]	[0-2]	[0-2]	[0-1]
	Moult to Winter	2 ± 1	2 ± 2	0 ± 1	1 ± 1	2 ± 1	1 ± 1	1 ± 1	1 ± 1
		[0-3]	[0-4]	[0-1]	[0-2]	[0-3]	[0-2]	[0-2]	[0-2]

		Males				Females			
		Vancouver	Kitimat	Juneau	South-central AK	Vancouver	Kitimat	Juneau	South-central AK
Variable	Metric	Mean/Sd Range	Mean/Sd Range	Mean/Sd Range	Mean/Sd Range	Mean/Sd Range	Mean/Sd Range	Mean/Sd Range	Mean/Sd Range
Stopover length of stay (days)	Winter to Breed	9 ± 8 [2-29]	17 ± 15 [3-41]	6 ± 2 [4-8]	5 ± 0 [5-5]	12 ± 9 [4-29]	7 ± 4 [3-12]	12 ± 9 [4-24]	5 ± 0 [5-5]
	Breed to Moult	13 ± 10 [2-38]	8 ± 5 [3-19]	12 ± 14 [3-49]	9 ± 5 [4-12]	16 ± 16 [4-45]	6 ± 3 [3-11]	11 ± 10 [4-28]	20 ± 0 [20-20]
	Moult to Winter	16 ± 14 [3-47]	15 ± 12 [3-38]	17 ± 7 [5-29]	14 ± 3 [8-16]	16 ± 10 [4-42]	10 ± 8 [4-25]	20 ± 12 [5-45]	16 ± 6 [12-20]
Distance travelled (km)	Winter to Breed	287 ± 90 [183-527]	480 ± 309 [86-1235]	321 ± 189 [107-714]	431 ± 119 [320-600]	365 ± 140 [187-703]	431 ± 310 [191-1249]	262 ± 145 [62-469]	399 ± 178 [222-577]
	Breed to Moult	786 ± 333 [470-1698]	1078 ± 321 [447-1432]	779 ± 366 [0-1105]	274 ± 246 [3-573]	347 ± 371 [5-1396]	261 ± 238 [2-757]	93 ± 149 [1-477]	68 ± 11 [55-76]
	Moult to Winter	1088 ± 373 [701-1927]	1451 ± 264 [1129-1750]	1173 ± 167 [487-1305]	723 ± 280 [327-945]	692 ± 398 [210-1656]	713 ± 453 [239-1692]	347 ± 152 [156-564]	352 ± 131 [247-518]
Total duration spent on migration (days)	Winter to Breed	11 ± 10 [0-33]	15 ± 14 [0-44]	15 ± 6 [8-25]	10 ± 2 [8-12]	12 ± 9 [0-33]	8 ± 6 [0-19]	21 ± 9 [8-29]	9 ± 1 [8-9]
	Breed to Moult	15 ±13 [0-42]	17 ± 7 [6-28]	19 ± 14 [8-53]	23 ± 18 [10-54]	16 ± 15 [0-50]	13 ± 13 [0-44]	17 ± 11 [8-37]	17 ± 11 [9-24]
	Moult to Winter	17 ± 17 [0-56]	14 ± 12 [0-41]	25 ± 9 [8-47]	24 ± 11 [9-45]	21 ± 11 [0-41]	11 ± 8 [0-28]	29 ± 15 [0-49]	27 ± 14 [14-57]

Table A.2 **Results of anova and linear regressions tests for latitudinal and sex differences of various timing and migratory behavior variables. P values less than 0.05 are colored in red.**

		Winter Capture Location		Sex		Winter Capture Location* Sex		Full Model Stats		
Variable	Metric	$F_{[x1,x2]}$	P =	$F_{[x1,x2]}$	P =	$F_{[x1,x2]}$	P=	adjusted r^2	$F_{[x1,x2]}$	P =
Winter	Arrive	$F_{[3, 93]} = 57.0$	< 0.001	$F_{[1, 93]} = 10.6$	< 0.001	$F_{[3, 93]} = 0.94$	0.42	0.64	$F_{[7, 93]} =26.4$	< 0.001
	Depart	$F_{[3, 107]} = 18.4$	< 0.001	$F_{[1, 107]} = 3.08$	0.82	$F_{[3, 107]} = 5.43$	0.05	0.37	$F_{[7, 107]} = 10.7$	< 0.001
	Length of Stay (days)	$F_{[3, 83]} = 63.9$	< 0.001	$F_{[1, 83]} = 3.32$	0.07	$F_{[3,83]} = 5.71$	< 0.001	0.70	$F_{[7, 83]} = 30.3$	< 0.001
Breed	Arrive	$F_{[3, 87]} = 10.6$	< 0.001	$F_{[1, 87]} = 0.01$	0.98	$F_{[3, 87]} = 0.95$	0.42	0.23	$F_{[7, 87]} = 4.96$	< 0.001
	Depart	$F_{[3, 79]} = 2.39$	0.07	$F_{[1, 79]} = 84.6$	< 0.001	$F_{[3, 79]} = 4.84$	< 0.001	0.54	$F_{[7, 79]} = 15.2$	< 0.001
	Length of Stay (days)	$F_{[3, 79]} = 2.95$	0.03	$F_{[1, 79]} = 84.4$	< 0.001	$F_{[3, 79]} = 2.84$	0.04	0.52	$F_{[7, 79]} = 14.5$	< 0.001
Moult	Arrive	$F_{[3, 100]} = 0.27$	0.85	$F_{[1, 100]} = 61.9$	< 0.001	$F_{[3, 100]} = 0.46$	0.71	0.35	$F_{[7, 100]} = 9.15$	< 0.001
	Depart	$F_{[3, 90]} = 4.40$	< 0.001	$F_{[1, 90]} = 8.82$	< 0.001	$F_{[3, 90]} = 0.33$	0.80	0.14	$F_{[7, 90]} = 3.29$	< 0.001
	Length of Stay (days)	$F_{[3, 90]} = 1.51$	0.22	$F_{[1, 90]} = 8.34$	< 0.001	$F_{[3, 90]} = 0.16$	0.92	0.06	$F_{[7, 90]} = 1.91$	0.07
Probability of stopping	Winter to Breed	$F_{[3, 87]} = 1.06$	0.37	$F_{[1, 87]} = 0.19$	0.66	$F_{[3,87]} = 1.29$	0.28	0.01	$F_{[7, 87]} = 1.03$	0.41
	Breed to Moult	$F_{[3, 87]} = 0.98$	0.40	$F_{[1, 87]} = 4.99$	0.03	$F_{[3,87]} = 1.48$	0.23	0.05	$F_{[7, 87]} = 1.77$	0.10
	Moult to Winter	$F_{[3, 87]} = 0.32$	0.81	$F_{[1, 87]} = 3.76$	0.06	$F_{[3,87]} = 4.06$	< 0.001	0.10	$F_{[7, 87]} = 2.41$	0.03
Stopover length of stay (days)	Winter to Breed	$F_{[3, 45]} = 0.51$	0.60	$F_{[1, 45]} = 0.04$	0.85	$F_{[3, 45]} = 3.20$	0.05	0.05	$F_{[7, 45]} = 1.49$	0.21
	Breed to Moult	$F_{[3, 61]} = 2.73$	0.07	$F_{[1, 61]} = 0.01$	0.91	$F_{[3, 61]} = 0.29$	0.75	0.02	$F_{[7, 61]} = 1.22$	0.31
	Moult to Winter	$F_{[3, 77]} = 0.88$	0.42	$F_{[1, 77]} = 0.06$	0.80	$F_{[3, 77]} = 0.71$	0.50	-0.02	$F_{[7, 77]} = 0.65$	0.67
Number of stops on migration	Winter to Breed	$F_{[3, 87]} = 0.55$	0.65	$F_{[1, 87]} = 0.01$	0.93	$F_{[3,87]} = 1.12$	0.35	-0.02	$F_{[7, 87]} = 0.72$	0.66
	Breed to Moult	$F_{[3, 87]} = 1.58$	0.20	$F_{[1, 87]} = 8.82$	< 0.001	$F_{[3,87]} = 1.57$	0.20	0.11	$F_{[7, 87]} = 2.61$	0.02
	Moult to Winter	$F_{[3, 87]} = 0.74$	0.53	$F_{[1, 87]} = 1.67$	0.20	$F_{[3,87]} = 2.78$	0.04	0.05	$F_{[7, 87]} = 1.75$	0.11
Distance travelled (km)	Breed to Moult	$F_{[3, 87]} = 1.58$	0.20	$F_{[1, 87]} = 8.82$	< 0.001	$F_{[3,87]} = 1.57$	0.20	0.11	$F_{[7, 87]} = 2.61$	0.02
	Moult to Winter	$F_{[3, 87]} = 0.74$	0.53	$F_{[1, 87]} = 1.67$	0.20	$F_{[3,87]} = 2.78$	0.04	0.05	$F_{[7, 87]} = 1.75$	0.11
	Moult to Winter	$F_{[3, 83]} = 7.13$	< 0.001	$F_{[1, 83]} = 83.7$	< 0.001	$F_{[3, 83]} = 3.11$	0.03	0.54	$F_{[7,83]} = 16.4$	< 0.001
Total duration migration (Days)	Winter to Breed	$F_{[3, 71]} = 1.94$	0.13	$F_{[1, 71]} = 1.88$	0.17	$F_{[3, 71]} = 2.17$	0.09	0.08	$F_{[7.71]} = 2.03$	0.06
	Breed to Moult	$F_{[3, 65]} = 0.02$	0.89	$F_{[1, 65]} = 0.03$	0.87	$F_{[3, 65]} = 0.17$	0.92	0.01	$F_{[7, 65]} = 1.16$	0.99
	Moult to Winter	$F_{[3, 112]} = 4.76$	< 0.001	$F_{[1, 112]} = 0.34$	0.56	$F_{[3, 112]} = 0.71$	0.55	0.08	$F_{[7, 112]} = 2.39$	0.03

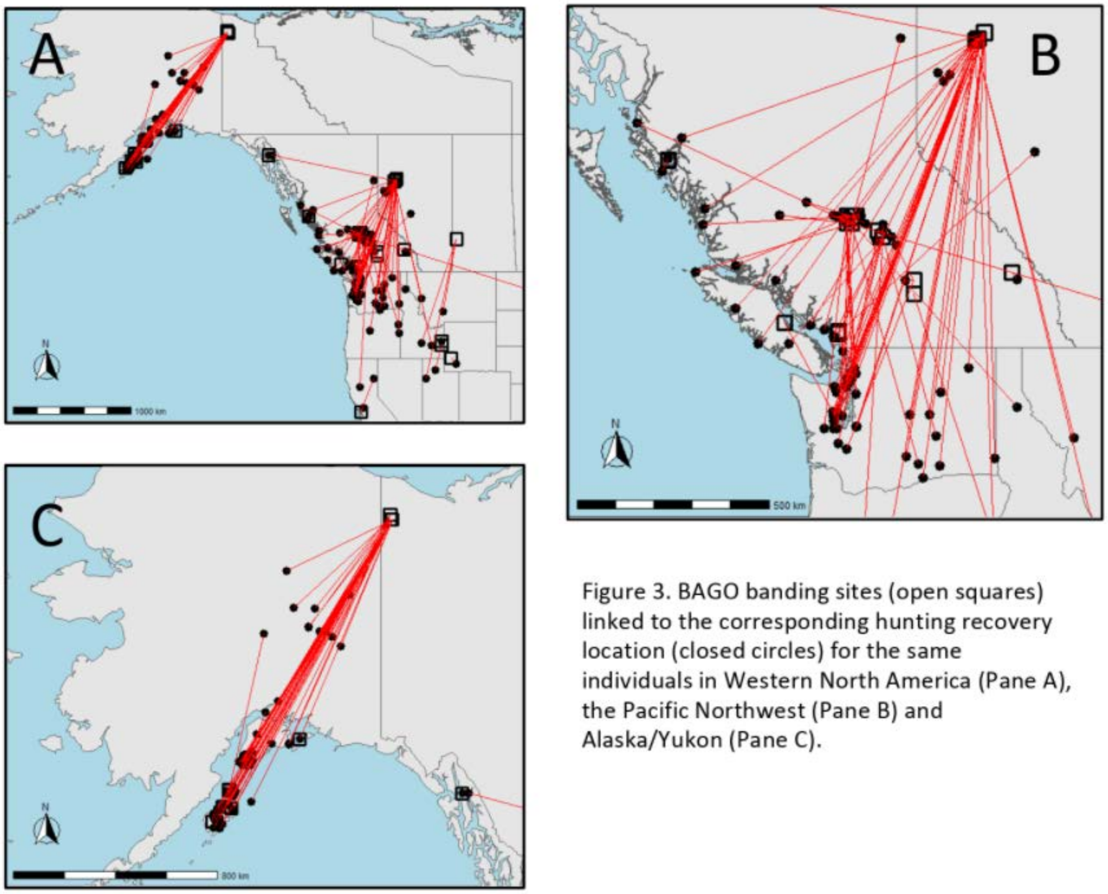

Figure 3. BAGO banding sites (open squares) linked to the corresponding hunting recovery location (closed circles) for the same individuals in Western North America (Pane A), the Pacific Northwest (Pane B) and Alaska/Yukon (Pane C).

Figure A.1 Barrow’s goldeneye banding sites (open squares) linked to the corresponding hunting recovery locations(closed circles) for the same individuals in Western North America (Pane A), the Pacific Northwest (Pane B) and Alaska/Yukon (Pane C). Maps were generated by Nik Clyde and Sean Boyd at Environment & Climate Change Canada (2020; unpublished).