Migratory connectivity and variation in migration phenology within the Pacific population of Barrow's Goldeneye (Bucephala islandica)

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ABSTRACT. Effective management of migratory animals requires an understanding of individual movement patterns throughout the annual cycle. We used satellite transmitters to track adult Barrow's Goldeneye (Bucephala islandica) captured at five wintering sites, one breeding site, and one molting site from across the species' geographic range in western North America. The data were analyzed to assess the strength of migratory connectivity and determine latitudinal and sex effects on migration phenology. At the range-wide scale, migratory connectivity was high; cluster analyses showed subpopulations aggregated at each stage of the annual cycle. Barrow's Goldeneye from all wintering latitudes traveled north and east to breed. Compared to females, males traveled farther north to molt and consequently traveled longer distances when returning to their wintering areas. Wintering latitude had little effect on migration distance but a large effect on the phenology of migration. Individuals that wintered at northern latitudes arrived on their wintering areas earlier and departed later than individuals that wintered farther south. Individuals that wintered at northern latitudes also arrived on and left their inland breeding areas later but left their molting sites earlier than individuals that wintered farther south. Sex also influenced the phenology of migration at all sites: males left their mates during incubation and consequently spent less time on breeding areas and more time on their molting and fall staging areas. The high level of migratory connectivity observed in this study suggests that the subpopulation of Barrow’s Goldeneye in south-central Alaska is demographically independent from subpopulations in southeast Alaska and British Columbia, and could be managed separately.

Connectivité migratoire et variation de la phénologie de migration au sein de la population du Pacifique du Garrot d'Islande (Bucephala islandica)

RÉSUMÉ. Une gestion efficace de la faune migratrice passe par une compréhension de la tendance des déplacements individuels tout au long du cycle annuel. Au moyen d’émetteurs satellites, nous avons suivi des Garrots d’Islande (Bucephala islandica) adultes capturés à cinq sites d'hivernage, un site de reproduction et un site de mue dans l’ensemble de l'aire de répartition géographique de l'espèce dans l'Ouest de l'Amérique du Nord. Nous avons analysé les données de façon à évaluer la force de la connectivité migratoire et à déterminer les effets de la latitude et du sexe sur la phénologie de migration. À l'échelle de l'aire de répartition, la connectivité migratoire était élevée; les analyses par grappes ont montré que les sous-populations se regroupaient à chaque étape du cycle annuel. Les Garrots d’Islande de diverses latitudes d'hivernage ont voyagé vers le nord et l'est pour se reproduire. Comparativement aux femelles, les mâles se sont déplacés plus au nord pour muer et ont donc parcouru de plus grandes distances pour retourner dans leurs zones d'hivernage. La latitude d'hivernage a eu peu d'effets sur la distance de migration, mais a eu un effet important sur la phénologie de la migration. Les individus qui hivernent à des latitudes nordiques arrivent plus tôt sur leurs aires d'hivernage et en repartent plus tard que les individus qui hivernent plus au sud. Les individus qui ont hiverné aux latitudes nordiques sont également arrivés et ont quitté leurs aires de nidification intérieures plus tard, mais ont quitté leurs sites de mue plus tôt que les individus qui ont hiverné plus au sud. Le sexe a également influé sur la phénologie de migration à tous les sites: les mâles ont quitté les femelles pendant l’incubation et ont donc passé moins de temps sur les aires de nidification et plus de temps sur leurs aires de mue et leurs haltes migratoires automnales. Le niveau élevé de connectivité migratoire observé dans cette étude indique que la sous-population de Garrots d’Islande du Centre-Sud de l’Alaska est démographiquement indépendante des sous-populations du Sud-Est de l’Alaska et de la Colombie-Britannique, et pourrait être gérée séparément.

Key Words: annual cycle; Barrow's Goldeneye; Bucephala islandica; latitude; migratory connectivity; phenology; satellite telemetry

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INTRODUCTION

Migratory animals carry out different stages of the annual cycle in geographically distinct areas, sometimes separated by thousands of kilometers. This geographic separation among annual cycle stages and the different conditions encountered at each stage complicate efforts to understand drivers of changes in abundance or distribution (Newton 2008, Harrison et al. 2011, Marra et al. 2015). In addition, a lack of understanding of migratory connectivity precludes understanding dynamics that may be specific to subpopulations and how they influence overall population dynamics of a migratory species. We define “population” broadly as a geographical unit incorporating the entirety of a species’ range or a significant and distinct portion thereof. We consider subpopulations to be discrete units within populations, defined by genetic or demographic criteria, including the degree of migratory connectivity. Determining whether structure exists within populations—i.e., whether subpopulations occur—in combination with a spatially explicit understanding of seasonal factors that affect demographic traits (i.e., vital rates) of subpopulations is necessary for applying conservation prescriptions at appropriate scales, seasons, and locations (Esler 2000).

The term migratory connectivity refers to the degree and scale of consistency in affiliations of groups of individuals among wintering, breeding, and molting sites. Quantifying migratory connectivity, annual site fidelity, and the timing of annual cycle events can help reveal where and how factors influence populations (Webster and Marra 2005, Harrison et al. 2011, Bauer et al. 2016). The extent to which individuals from discrete breeding or non-breeding areas remain in sympatry throughout the annual cycle (strength of connectivity) and have similar demographic/vital rates can influence subpopulation trends and has important implications for management and conservation (Marra et al. 2006, Gilroy et al. 2016). For species with high migratory connectivity, subpopulations are demographically independent, with abundance dynamics driven by factors specific to each subpopulation. For example, Kramer et al. (2018) demonstrated that Golden-winged Warblers (*Vermivora chrysoptera*) have high migratory connectivity and that declines in abundance observed in the Appalachian Mountains were associated with habitat loss on wintering areas in South America for the specific Appalachian-breeding subpopulation. For unstructured populations, dynamics are coherent at the population level, with effects of drivers of abundance being expressed across the entire population (Esler 2000).

Important drivers of variation in vital rates can occur during any stage of the annual cycle. Most studies of migratory birds focus on breeding areas (Marra et al. 2015), and some researchers argue that factors that affect productivity, juvenile survival, and subsequent recruitment are key drivers of population dynamics (Sillett and Holmes 2005, Hogan et al. 2013b, Rushing et al. 2016). However, because mortality rates can be extremely high during migration (Sillett and Holmes 2002, Loonstra et al. 2019), other researchers suggest that migration is a demographically important stage of the annual cycle (e.g., Lok et al. 2015, Robinson et al. 2020). Finally, conditions on wintering areas, which can influence both adult and juvenile survival (Taylor and Stutchbury 2016) and affect timing of spring migration and subsequent breeding performance (Marra et al. 1998), can also influence population dynamics (Woodworth et al. 2017, Wilson et al. 2018). The relative effects of each annual cycle stage are likely life history and species dependent, and could vary among demographically discrete subpopulations within a species. Determining the importance of each stage relative to population dynamics is difficult because events and conditions during one stage can influence individual performance in a subsequent stage (termed carryover effects) (Harrison et al. 2011, Marra et al. 2015). Therefore, understanding the degree of population structuring throughout the year and across a species’ range is needed to understand seasonal and carryover effects.

The timing of annual cycle stages can vary widely among subpopulations of the same species, and this variation can influence subpopulation dynamics (Dunn and Winkler 1999). In particular, timing of breeding can determine individual reproductive success and can shape phenotypic differences in reproductive traits among subpopulations (Verhulst and Nilsson 2008, Lany et al. 2015). In temperate North America, individuals that breed farther north tend to breed later than their southern counterparts; this can lead to northern breeding individuals experiencing shorter time periods for reproduction and greater temporal constraints across the remainder of the annual cycle (Winkler et al. 2014, Gow et al. 2019). Additionally, for many migratory bird species, males or pairs that arrive on breeding areas relatively early can secure higher quality breeding territories (Morbey and Ydenberg 2001). Many species are advancing their breeding initiation dates in response to a warming climate, and this can have both positive and negative reproductive consequences (Dunn et al. 2011, Bouret et al. 2015). For example, Møller et al. (2008) demonstrated that species that are unable to adapt their timing of migration become mismatched with their food resources, and as a result, experience declines in fecundity and subsequently abundance. However, whether and how differences in the timing of stages among subpopulations at different latitudes, and among sexes, carry over to influence subsequent timing events in the annual cycle are poorly understood (Conklin et al. 2010, Briedis et al. 2016, Gow et al. 2019). Studies that use tracking technology can establish annual cycle timing of events as a baseline against which future climate scenarios can be compared.

Advances in technology allow researchers to track spatial and temporal movement patterns of animals for extended periods and over broad geographic scales (Joo et al. 2020). This has facilitated the discovery of unknown migration routes, helped identify critical stopover locations and wintering areas, and provided insight on timing of transitions between stages of the annual cycle. For instance, by using both geolocators and satellite transmitters, Hooijmeijer et al. (2014) identified three distinct migration routes used by Black-tailed Godwits (*Limosa limosa*), and critical sites on each route. Using satellite telemetry, Lamb et al. (2021) identified the core breeding area for Atlantic Black Scoters, which was previously undescribed. Lemke et al. (2013) used geolocators to track migration of Great Reed Warblers (*Acrocephalus arundinaceus*) and found that they 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 to describing movements of individuals from a single breeding or wintering location (e.g., Bobek et al. 2008, Lemke et al. 2013), a
**Table 1.** Number of adult male and female Barrow’s Goldeneye marked with platform terminal transmitters and retained in analyses of movement throughout the annual cycle (AB: Alberta; AK: Alaska; BC: British Columbia).

| Year | Capture site       | Annual cycle stage | Number marked | Number retained |
|------|--------------------|--------------------|---------------|----------------|
|      |                    | Male              | Female        | Male           | Female        |
| 2006 | Riske Creek, BC    | Breed             | 23            | 17             |
| 2007 | Riske Creek, BC    | Breed             | 15            | 15             |
|      | Vancouver, BC      | Winter            | 10            | 5              |
| 2008 | Riske Creek, BC    | Breed             | 10            | 10             |
| 2009 | South-central AK   | Winter            | 19            | 6              |
|      | Riske Creek, BC    | Breed             | 10            | 6              |
|      | Cardinal Lake, AB  | Molt              | 20            | 14             |
| 2010 | Cardinal Lake, AB  | Molt              | 18            | 16             |
| 2011 | Vancouver, BC      | Winter            | 10            | 10             |
|      | Riske Creek, BC    | Winter            | 2             | 1              |
| 2012 | Juneau, AK         | Winter            | 23            | 21             |
| 2013 | South-central AK   | Winter            | 5             | 4              |
| 2014 | Kitimat, BC        | Winter            | 19            | 15             |
| 2015 | Vancouver, BC      | Winter            | 8             | 8              |
| Total|                    |                   | 180           | 141            |

small number of individuals from a few locations (e.g., Robert et al. 2002, English et al. 2017), or only one sex or age class (e.g., De La Cruz et al. 2009, Meattey et al. 2018, but see Knight et al. 2018, Kramer et al. 2018).

Satellite transmitters (platform terminal transmitters [PTTs]) have been deployed to study aspects of the wintering ecology (Willie et al. 2019), molt (Hogan et al. 2011), and movement patterns of the sea duck Barrow’s Goldeneye (*Bucephala islandica*) in the Pacific Northwest since 2006 (Boyd and Esler 2014). In this study, we deployed PTTs on adult Barrow’s Goldeneye wintering from southern British Columbia to south-central Alaska, an area that encompasses most of the winter range of this species in western North America. We also deployed PTTs at a key breeding site in south-central British Columbia and a key molting site in northwest Alberta. We consider all these individuals to be members of the Pacific population of Barrow’s Goldeneye, based on our definition of population. The data generated over the course of this research provide a rare opportunity to examine large-scale patterns of migratory connectivity across the range and throughout the annual cycle of this population, and to assess if distinct subpopulations exist. The data also allow for an assessment of sex and latitude effects on timing of transitions between stages of the annual cycle.

We quantify the strength of migratory connectivity for the Pacific population of Barrow’s Goldeneye among the three key stages of the annual cycle (wintering, breeding, and molting) and use cluster analysis to determine if observed connectivity depends on a consistent aggregation of individuals in distinct regions (Ambrosini et al. 2009). In addition to describing migratory connectivity, we evaluate how sex and latitude influence the timing of transitions between stages of the annual cycle. In contrast to many other birds, waterfowl often pair on wintering areas (Savard 1985, Bluhm 1988), so we did not expect to find sex-related differences in timing of departure from wintering areas or arrival on breeding areas, but expected that sex differences in parental care (female Barrow’s Goldeneye rear ducklings alone on breeding ponds) (Eadie et al. 2020) would result in sex differences in timing of departure from breeding areas. We also expected that latitudinal differences would lead to variation in timing of breeding and thus migration from the coast to inland breeding areas in spring and back to the coast in fall. We discuss the implications of our results for the delineation and management of subpopulations of Pacific Barrow’s Goldeneye.

**METHODS**

**Study species and study design**

Barrow’s Goldeneye have a discontinuous world distribution (Eadie et al. 2020). The Pacific population in the northwest region of North America supports ~90% of the global estimate of about 200,000 birds, with ~60% breeding and wintering in British Columbia, Canada (Eadie et al. 2020). Barrow’s Goldeneye also occur in northeastern North America (~5200 birds) (Robert and Savard 2006) and Iceland (~2000 birds) (Gardarsson 1978), which we also consider discrete populations.

We collected movement data for Barrow’s Goldeneye in western North America from 2006 to 2017 based on after-hatch-year (AHY) individuals implanted with PTTs (Table 1). We captured birds using a variety of capture methods (mist nets, drive traps, and floating mist nets) at four wintering regions throughout their Pacific range (Kachemak Bay, Alaska, 59.61°N, -151.35°W and Prince William Sound, Alaska, 60.38°N, -147.71°W; Juneau, Alaska, 58.25°N, -134.34°W; Kitimat, British Columbia, 53.52°N, -129.26°W; and Indian Arm near Vancouver, British Columbia, 49.38°N, -122.88°W), one breeding site (Riske Creek, British Columbia, 52.0°N, -122.5°W), and one molting location (Cardinal Lake, Alberta, 56.22°N, -117.78°W) (Table 1). We combined wintering birds captured in Kachemak Bay and Prince William Sound, which are separated by only 260 km, because we considered them to be wintering in the same region, termed south-central Alaska. 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 a PTT (26–38 g Microwave Telemetry and Telonics transmitters) in the
coelomic cavity of each Barrow's Goldeneye, following standardized methods described in Mulcahy and Esler (1999). PTT duty cycles were programmed to transmit locations for 2–6 hours every 3–4 days. Data (latitude, longitude, location error index, date, 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 satellites as they move relative to a PTT. Locations are assigned an accuracy class, as follows: 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). Location accuracy 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).

**Data management**

We downloaded Barrow’s Goldeneye PTT data previously stored on the Movebank data repository (http://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 by enabling the “Best of Day” filter. 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, Sesson 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 a Barrow’s Goldeneye could travel in a 24-hour 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 known to be < 50 km within a stationary period of the annual cycle (i.e., remigial molt). Hatch-year birds were marked in only one capture location, so analyses were restricted to AHY birds.

**Defining stages of the annual cycle**

Barrow's Goldeneye winter primarily in coastal waters and occasionally on inland lakes and rivers that remain ice-free. We defined the date of arrival on wintering areas as the day an individual switched from making directional daily movements of > 100 km to non-directional daily movements of < 100 km. We defined the date of departure from a wintering area as the day an individual left the coast and moved > 100 km inland. Following De La Cruz et al. (2009), where the time interval between locations before and after arrival/departure was greater than 1 day, we estimated arrival and departure dates using the median date between locations before and after arrival/departure.

Barrow’s Goldeneye may molt on their breeding areas or at separate, distant locations (Eadie et al. 2020). Like most waterfowl, Barrow’s Goldeneye undergo remigial molt in late summer to early fall, which renders the birds flightless for a little more than 1 month (Hogan et al. 2013). We defined the date of arrival on molting areas as the day the birds arrived at a location and remained stationary for > 30 days (i.e., made no overland movements estimated to be > 1 km). If these criteria identified two potential molt sites, the site occupied during the most likely period for remigial molt (Hogan et al. 2013a, Eadie et al. 2020) was defined as the molting site. Following remigial molt, we defined an individual’s date of departure from its molting site as the first day with overland directional movements of > 1 km toward the coast. Again, where necessary, we estimated arrival and departure dates using the median date between locations before and after arrival/departure.

Sex ratios of adult sea ducks are heavily male biased (Rodway et al. 2015), so some males will be unpaired and may move directly from their wintering areas to a molting site. We assessed the possibility that some males in our sample were unpaired, and did not assign males a breeding location if their putative "breeding" area was (i) within 200 km of a known molting site used by several thousand individuals (van de Watering and Cooke 2000, Hogan et al. 2011), (ii) outside the assumed breeding range of the species (based on the Sea Duck Joint Venture map: https://seaduckjv.org/meet-the-sea-ducks/barrows-goldeneye/) and the breeding range indicated by the female PTT data, or (iii) in habitat unsuitable for a cavity-nesting sea duck (i.e., no large trees).

For each individual, we calculated the total length of stay within its wintering, breeding, and molting areas as the difference between the estimated departure date and the arrival date at each location plus 1 day. The extra day accounted for the fact that a bird could have been present in the area on the assumed day of arrival or the assumed day of departure (De La Cruz et al. 2009, Meattey et al. 2018). We determined the geographic center of an individual’s wintering, breeding, and molting area by calculating the mean-center centroid of the locations obtained for each stage of the annual life cycle using ArcGIS Pro version 2.4.3 (Esri 2020). Centroids were calculated using only locations obtained during a single wintering, breeding, or molting period spanning one annual cycle.

**Statistical analyses**

**Migratory connectivity**

We quantified the strength of migratory connectivity between wintering and breeding areas, breeding areas and molting sites, and molting sites and wintering areas using Mantel tests that
measure the correlation between two matrices (Ambrosini et al. 2009). The matrices contained pairwise straight-line geodesic distances between the mean-center centroids for all individuals for each stage of the annual cycle. Because the distribution of Barrow's Goldeneye in the Pacific population was not spatially clustered, we chose to quantify migratory connectivity using Mantel correlations rather than the MC Index (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 molting and breeding locations, we calculated Pearson's correlation coefficient for the latitude and longitude of each stationary period (wintering, breeding, and molting).

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 molting stages (“distribution pattern transfer”) (see Besag and Diggle 1977) or because subpopulations or groups of individuals aggregate during each stage of the annual cycle (e.g., Cedar Waxwings [Bombycilla cedrorum]) (see Cohen et al. 2018). To assess the importance of these two processes, we performed a cluster analysis using the mean-center 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 (Esri 2020). HDBSCAN is a data-driven, density-based clustering algorithm that allows clusters to vary in shape and density, and assigns individuals to a cluster when centroids concentrate in a region, and leaves individuals unassigned (i.e., labeled as noise) if their centroids have no or few near neighbors. The minimum number of individuals per cluster in HDBSCAN is three. The larger the minimum number of individuals per cluster, the more conservative the clustering; clusters will be restricted to progressively denser areas with more individuals being unassigned. Following Meattey et al. (2018), we set the minimum number of individuals per cluster to be five, which identified biologically relevant clusters in our data.

**Timing of annual cycle stages**

We used a series of generalized linear models fitted assuming Gaussian distributions to examine sex and latitude effects on (i) the timing of arrival on and departure from the wintering areas, breeding areas, and molting sites, (ii) the length of stay at each location, and (iii) the distance traveled during each migration (wintering–breeding, breeding–molting, and molting–wintering). We confirmed the assumptions of homoscedasticity and normality using visual inspection of residual plots. 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 mean-center centroid for all 197 individuals. We focused on wintering origins because waterfowl typically pair on wintering areas, and subsequently exhibit strong mate (Bluhm 1988, Savard and Eadie 1989) and wintering site fidelity (Willie et al. 2019), and because most of our captures occurred on wintering sites. Thus, wintering latitude is generally representative of where a 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 data set. The statistical analyses used to examine sex and winter capture site effects are summarized in Appendix 1. Means are provided with standard deviations unless stated otherwise, and all statistical analyses were performed using the software R version 3.6.1 (R Core Team 2016).

Previous research suggested that waterfowl implanted with transmitters could experience changes in behavior and delays in the timing of migration (Hoojimijer et al. 2014, Lamb et al. 2020). We compared the behavior of individuals in the year they were tagged with their behavior the following year and found that tagging tended to delay departure and arrival in the stage subsequent to marking (see Results). Therefore, we controlled for this effect by (i) excluding the first 14 days of capture from spatial analyses (Esler et al. 2000, Lamb et al. 2020), (ii) not using the first year of data, when a second year was available (Meattey et al. 2018), and (iii) including a transmitter effect variable in models that examined the timing and duration of migration, denoting whether an individual had been tagged in the period prior to departure from one stage and arrival at the next.

**RESULTS**

We used data from 271 adult Barrow’s Goldeneye deployed with satellite transmitters (Table 1). We excluded data from 57 individuals because their transmitters provided invalid locations ($n = 6$) or the bird died or the transmitter failed within 14 days of implantation ($n = 51$). Differentiating mortality from radio failure is difficult, although temperature and voltage variation from transmissions can offer clues. In this case, up to 31 of the excluded individuals showed potential for mortality (11.4% of marked birds), which is a considerably higher mortality rate than that shown in other cases (1.5% for implanted Harlequin Ducks [Histrionicus histrionicus]; Mulcahy and Esler 1999). Many of these individuals were associated with particularly cold capture conditions in Alaska; future studies should consider these findings in efforts to reduce post-surgery mortality. The filtered data set therefore included data from 214 (male = 141; female = 73) adult birds (Table 1). On average, these birds were tracked for 346 days (range: 18–1171) and provided 82 locations (range: 4–307) per individual. Most 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 areas, 179 birds on their breeding areas, and 199 birds at molting sites.

We identified six males that migrated from their wintering areas directly to a molting site. We also identified an additional five males that moved to staging sites close to their molting sites that were outside the known breeding range, where Barrow’s Goldeneye breeding females (including satellite-tagged females) have never been observed and where there are no large-diameter trees that provide nesting cavities typically required by Barrow’s Goldeneye. For these individuals, attributes associated with breeding areas were not calculated or analyzed.

**Migratory connectivity**

Both male and female Barrow’s Goldeneye exhibited high degrees of migratory connectivity between each stage of the annual cycle (Table 2). In other words, locations during each annual cycle stage were correlated with locations during the rest of the year, which...
Sex indicates that the Pacific population has significant structuring. Females had stronger migratory connectivity than males, especially from breeding to molting (Table 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 groupings was low (south-central Alaska: \( r_m = 0.16, P = 0.05 \); Vancouver: \( r_m = 0.03, P = 0.38 \) (Fig. 1), thereby indicating a lack of correlation among locations across annual cycle stages at this scale. These results demonstrate that migratory connectivity is scale dependent and that the structure observed in the Pacific population is at a regional, not local, scale.

Table 2: Migratory connectivity of adult male and female Barrow’s Goldeneye between different stages of the annual cycle. Migratory connectivity was estimated using Mantel correlations \( (r_m) \) and is reported along with the 95% CI and sample size (\( N \)). Mantel correlation \( r_m \) values range from -1.0 to 1.0, where -1.0 indicates low connectivity and 1.0 indicates high connectivity.

| Stage          | Sex | \( r_m \) | 95% CI    | \( N \) | \( P \) |
|---------------|-----|----------|-----------|--------|-------|
| Winter-breed  | M   | 0.86     | 0.84, 0.90| 86     | <0.001|
| Winter-breed  | F   | 0.90     | 0.89, 0.88| 68     | <0.001|
| Breed-molt    | M   | 0.58     | 0.54, 0.62| 101    | <0.001|
| Breed-molt    | F   | 0.90     | 0.88, 0.93| 57     | <0.001|
| Molt-winter   | M   | 0.65     | 0.61, 0.68| 113    | <0.001|
| Molt-winter   | F   | 0.79     | 0.75, 0.84| 61     | <0.001|

Spatial groupings at regional scales were apparent for both males and females (Fig. 1 and 2). The overlay of clusters and lines of movements highlight the fact that birds close to one another in one stage were also near each other in the subsequent stage (Table A1.1); this explained the strong correlation between pairwise distance matrices. The distinct clusters of wintering Barrow’s Goldeneye revealed the spatial structure of our four winter capture regions along the coast, one breeding capture site in south-central British Columbia, and one molting capture site in northwest Alberta. Four molting clusters coincided with breeding clusters, indicating that females that were raising broods remained in their breeding ponds to molt (Fig. 2 [panels 5–6]). Both Fig. 1 and Fig. 2 show complete spatial segregation of birds captured in south-central Alaska and birds captured in southern British Columbia throughout the annual cycle.

Birds tended to move in a northerly direction to breed, traveling 370 ± 216 km from their wintering areas to breeding areas (Fig. 1 and 2). Birds that wintered at northern sites bred farther north, which resulted in a correlation between an individual’s wintering latitude and breeding latitude \( (r_{winter-breed latitude} = 0.81, P < 0.001) \). Post-breeding birds migrated farther north to molt, with males traveling farther than females (males: 812 ± 433 km; females: 237 ± 296) (Fig. 1 and 2, Table A1.1). We speculate that post-breeding movements of females were related to their reproductive success; i.e., successful females likely molted at or near their brood-rearing location, whereas unsuccessful females migrated north to molt. Birds that bred in south-central Alaska typically moved in a northeast direction to molt, whereas those that bred near Juneau traveled north, and all southern counterparts moved either north or northeast. Breeding longitude was a strong predictor of molting longitude \( (r_{breed-molt longitude} = 0.91, P < 0.001) \). Similarly, breeding latitude was a predictor of molting latitude \( (r_{breed-molt latitude} = 0.65, P < 0.001) \). Birds returned to coastal sites to winter, moving in a south-southwest direction. Males traveled farther than females at this stage of the annual cycle, having molted at higher latitudes than females from the same wintering areas (males: 1090 ± 366 km; females: 536 ± 384) (Fig. 1 and 2, Table A1.1). The longitude and latitude of molting sites were strong predictors of longitude and latitude of wintering sites \( (r_{molt-winter longitude} = 0.91, P < 0.001; r_{molt-winter latitude} = 0.66, P < 0.001) \). Due to the high degree of interannual winter site fidelity documented in all age and sex classes of Barrow’s Goldeneye (Willie et al. 2019), relationships between breeding to subsequent wintering areas were essentially the same as those for wintering to breeding areas.

Annual cycle phenology and migration strategies

Transmitter effects on the timing of migration

Birds tagged on their wintering areas departed 14.2 ± 2 days later in the year they were tagged than in the following year (paired \( t = 5.40, n = 45, P < 0.0001 \)), and their arrival on breeding areas was delayed 12.9 ± 2 days (paired \( t = 4.30, n = 38, P = 0.0001 \)). Birds tagged on their breeding areas departed 9.2 ± 1 days later in the year they were tagged than the following year (paired \( t = 2.74, n = 11, P = 0.02 \)), but they arrived at their molt location only 4.1 ± 1 days later (paired \( t = 1.15, n = 13, P = 0.27 \)). Birds tagged at their molt location departed 8.9 ± 0.5 days later in the year they were tagged than the following year (paired \( t = 1.47, n = 9, P = 0.18 \)) but arrived at their wintering areas at the same time (0.00 ± 0 days; paired \( t = 0, n = 6, P = 1.0 \)).

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 3). Our models indicated that both males and females that wintered at northern latitudes along the south-central Alaskan coast (60º N) arrived on their wintering areas on average 31 ± 12 days earlier and departed on spring migration 16 ± 10 days later (Fig. 3), and thus spent more time on their wintering areas, than birds that overwintered at more southerly locations (50ºN) (Fig. 4, Table 3). There were no sex differences in timing of arrival at, or departure from, wintering areas (Table 3).

Winter latitude and sex combined to influence timing of arrival and departure from breeding areas. Male and female Barrow’s Goldeneye that bred at northern latitudes arrived on breeding areas on average 11 ± 8 days later and departed 18 ± 15 days later than birds that bred at southern latitudes (Fig. 3). Although both sexes arrived on the breeding areas at approximately the same time, after accounting for latitude (Fig. 3, Table 3), males departed breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their breeding areas for molting sites on average 37 ± 18 days before females. Males, consequently, spent less time (37 ± 9 days) on their
Fig. 1. Annual cycle migratory connectivity of adult male Barrow’s Goldeneye ($n = 151$) that migrated from wintering to breeding (1,4), breeding to molting (2,3), and molting to wintering (3,6) 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.

molting areas than birds that wintered at more southern latitudes (Fig. 4, Table 3). On average, males arrived on molting areas 29 ± 6 days before, and departed 1 ± 8 days after, females (Fig. 3 and 4, Table 3). 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 molting) and on migration between these annual stages (Fig. 3 and 4).

DISCUSSION

Migratory species with breeding and wintering ranges that span 25 degrees latitude would be expected to adjust the timing of annual cycle stages to latitudinal gradients in climatic conditions (e.g., Both et al. 2004, Gow et al. 2019). Latitudinal variation in the timing of each stage may also carry over to later stages if the timing of breeding or molting and/or the length of time individuals spend at a given location depend on events that take place at earlier stages of the annual cycle (van Wijk et al. 2017, Gow et al. 2019). Consistent with this hypothesis, we found that wintering latitude influences not only when Barrow’s Goldeneye leave their wintering area but also timing of arrival on their breeding area and timing of departure from breeding and molting areas. Winter latitude, consequently, had large effects on the amount of time Barrow’s Goldeneye allocated to each stage of the annual cycle; individuals that wintered in south-central Alaska spent on average 60 days more in their wintering area and 25 days less in their molting area than individuals that wintered near Vancouver, British Columbia. Our study therefore highlights how migratory connectivity and the spatial structure of wide-ranging species can drive intraspecific variation in the phenology of annual cycles.

Sex differences in the timing of stages in the annual cycle of migratory birds may be driven by differences in benefits of early arrival on the breeding areas (e.g., Morbey and Ydenberg 2001), uniparental care (e.g., Whitfield and Tomkovich 1996), or differential migration of males and females (e.g., Cristol et al. 1999). Barrow’s Goldeneye pair on wintering areas (Savard 1985), which leads to males and females arriving on their breeding areas 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 during the period after arrival on breeding areas to after departure from molting areas. Consequently, females spent on average 40 more days on their breeding areas (generally consistent with the brood-rearing period) and therefore 40 fewer days on molting areas compared to males. Females were also less likely to travel long distances to more northerly molting sites, likely due to constraints imposed by caring for young. Females that did not remain on breeding ponds but migrated early and molted at areas > 100 km to the north were likely individuals that did not breed at all or were failed breeders. Females with broods are highly attentive and will remain with their brood through the summer and into fall unless another hen adopts the brood or the ducklings are predated (Eadie et al. 2020). Females and males, however, spent a similar amount of time on their wintering areas, after accounting for effects of latitude.

Satellite tracking studies that span the entire annual cycle can focus on periods of the year in which relatively little research has been conducted. We have shown that post-breeding Barrow’s Goldeneye males can travel on average 812 ± 433 km and females
Fig. 2. Annual cycle migratory connectivity of adult female Barrow’s Goldeneye ($n = 78$) that migrated from wintering to breeding (1,4), breeding to molting (2,3), and molting to wintering (3,6) 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.

Fig. 3. Wintering latitude and sex effects on the date of arrival, departure, and distance traveled by adult Barrow’s Goldeneye to the subsequent stage for wintering (1,4,7), breeding (2,5,8), and molting stages (3,6,9).

237 ± 296 km (Fig. 1 and 2, Table A1.1) to reach their molting area. Known molting areas for Barrow’s Goldeneye include the Old Crow Flats in the Yukon, and Cardinal Lake and Great Slave Lakes in Alberta (Hogan et al. 2011). Our results highlight the potential for other important molting locations to exist east of the Alaska border, the northernmost areas of the Northwest.

Fig. 4. Sex and latitude effects on arrival to, departure from, and length of stay for adult Barrow’s Goldeneye on wintering, breeding, and molting areas. Northern latitudes include individuals wintering at latitudes of 60º degrees; southern latitudes include individuals wintering at latitudes of 50º degrees. Spaces between the arrows represent time spent during migration. (Painting of Barrow’s Goldeneye © Peter Forstner [see Figure A2.1]).
Table 3. Summary of generalized linear models examining sex, latitude, and transmitter effects on (i) the timing of arrival on and departure from the wintering areas, breeding areas, and molting sites, (ii) the length of stay (LOS) at each location, (iii) the distance traveled during each migration (wintering-breeding, breeding-molting, and molting-wintering). The explanatory variable of “latitude” is the latitude of the wintering areas mean-center centroid for all 197 individuals. The “argosfilter” package in R studio was used to measure the straight-line geodesic distances between consecutive centroids.

| Variable | Metric | Latitude | Sex | Transmitter effect | Latitude*sex | Full model |
|----------|--------|----------|-----|--------------------|--------------|------------|
|          |        | F = | df | P = | F = | df | P = | F = | df | P = | Adj. r² | F = | df | P = |
| Winter   |        |     |     |     |     |     |     |     |     |     |       |     |     |     |
| Winter   |        | 103.7 | 1.94 | <0.001 | 1.02 | 1.94 | 0.31 | 0.08 | 1.94 | 0.78 | 4.43 | 1.94 | 0.04 | 0.52 | 27.3 | 4.94 | <0.001 |
|          |        | 51.9  | 1.157 | <0.001 | 0.23 | 1157 | 0.63 | 24.7 | 1.157 | <0.001 | 0.34 | 1.157 | 0.56 | 0.31 | 19.3 | 4.157 | <0.001 |
| Winter   |        | 123.6 | 1.94 | <0.001 | 1.58 | 1.94 | 0.21 | 10.7 | 1.94 | 0.001 | 2.36 | 1.94 | 0.13 | 0.58 | 34.6 | 1.94 | <0.001 |
| Breed    |        | 22.3  | 1.113 | <0.001 | 0.001 | 1113 | 0.98 | 1.29 | 1.113 | 0.26 | 0.88 | 1.113 | 0.35 | 0.15 | 6.11 | 4.113 | <0.001 |
|          |        | 5.03  | 1.109 | 0.03 | 100.8 | 1109 | <0.001 | 0.13 | 1.109 | 0.72 | 7.49 | 1.109 | 0.007 | 0.49 | 28.4 | 4.84 | <0.001 |
| Winter   |        | 0.33  | 1.109 | 0.57 | 95.3 | 1109 | <0.001 | 0.68 | 1.109 | 0.41 | 4.95 | 1.109 | 0.03 | 0.46 | 25.3 | 4.109 | <0.001 |
| Molt     |        | 0.05  | 1.84 | 0.83 | 46.5 | 1.84 | <0.001 | 1.14 | 1.84 | 0.29 | 0.01 | 1.84 | 0.95 | 0.33 | 11.9 | 4.84 | <0.001 |
|          |        | 38.8  | 1.99 | <0.001 | 0.05 | 1.99 | 0.83 | 8.7 | 1.99 | 0.004 | 0.1 | 1.99 | 0.76 | 0.3 | 11.9 | 4.99 | <0.001 |
| Winter   |        | 11.1  | 1.84 | 0.001 | 16.7 | 1.84 | <0.001 | 3.57 | 1.84 | 0.06 | 0.25 | 1.84 | 0.62 | 0.24 | 7.9 | 4.84 | <0.001 |
| Distance |        | 0.45  | 1.155 | 0.5 | 0.58 | 1155 | 0.45 | 1.23 | 1.155 | 0.27 | 4.48 | 1.155 | 0.04 | 0.02 | 1.68 | 4.155 | 0.16 |
|          |        | 59.2  | 1.102 | 0.17 | 59.2 | 1102 | <0.001 | 0.28 | 1.102 | 0.6 | 1.32 | 1.102 | 0.25 | 0.36 | 15.7 | 4.102 | <0.001 |
|          |        | 1.32  | 1.91 | 0.25 | 48.2 | 1.91 | <0.001 | 7.23 | 1.91 | 0.009 | 1.73 | 1.91 | 0.19 | 0.36 | 14.6 | 4.91 | <0.001 |

Territories, and due west of Great Slave Lake. This highlights the potential for disturbance and environmental change in the North to influence Barrow’s Goldeneye populations.

Measuring migratory connectivity across large spatial scales—i.e., species’ ranges—has been argued to be vital for understanding factors that drive trends in abundance of migratory birds (Knight et al. 2018, Kramer et al. 2018). We demonstrate, using satellite tracking data from across the Pacific Barrow’s Goldeneye distribution in western North America, that migratory connectivity of Barrow’s Goldeneye is high, and that structure is evident across regional scales but not smaller scales. From a management perspective, our results indicate that events or stressors in one region of the Pacific coast or inland region of the Pacific Northwest would lead to regional geographic variation in vital rates and subsequent subpopulation trends (Marra et al. 2006). In addition, latitudinal and sex differences in phenology of spring and fall migration will influence how the timing of stressors affects each regional subpopulation.

Studies that have quantified avian migratory connectivity provide evidence that individuals often mix without respect to geography as they move from one stage of the annual cycle to the next. Finch et al. (2017) reported that 18 of 28 long-distance migrants exhibited weak, diffuse migratory connectivity. Comparable studies on sea ducks, not included in the review by Finch et al. (2017), also report low levels of migratory connectivity between breeding and wintering areas for some species (Oppel et al. 2008, Takekawa et al. 2011, Meatley et al. 2018, but see Petersen and Flint 2002). In contrast, we found that Barrow’s Goldeneye have high migratory connectivity throughout the entire annual cycle. Several authors have suggested that differences in migratory connectivity that have been detected across species are a consequence of the scale at which studies are conducted, with studies conducted at larger spatial scales being more likely to capture the occurrence of spatially structured populations (Gilroy et al. 2016, Finch et al. 2017, Knight et al. 2018). Our results support this argument. Migratory connectivity measured over the Barrow’s Goldeneye Pacific population range was high, whereas migratory connectivity measured at smaller geographic scales—i.e., within regions—was low. Studies that are limited to a small portion of a species’ distribution (e.g., Hallworth et al. 2015) may therefore underestimate the strength of connectivity that exists at population-wide scales.

Studies that fully describe migratory connectivity can aid in delineation of subpopulations and in more effective management of migratory species (Webster et al. 2002, Meatley et al. 2018, Lamb et al. 2019, Bowman et al. 2021). We have shown that adult Pacific Barrow’s Goldeneye are somewhat structured, with high migratory connectivity at regional scales through all stages of the annual cycle. South-central Alaska and southern British Columbia had entirely distinct clusters, which demonstrates a nearly complete separation at a broad geographic scale. Band recovery data also suggest that discrete subpopulations occur at that same scale (Pearce et al. 2014). We might expect this high level of migratory connectivity of adult Barrow’s Goldeneye when combined with high breeding and wintering site fidelity to result in distinct genetic structuring. Pearce et al. (2014) found this pattern in mitochondrial DNA, with strong structuring in haplotypes evident among Barrow’s Goldeneye from Alaska, British Columbia, Quebec, and Iceland, consistent with our direct measures of demographic structure. However, a recent study found little to no nuclear genetic structure across the Pacific
population (Brown et al. 2020). The authors suggested that this 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 areas, in contrast to juvenile females (e.g., Boyd et al. 2009, Pearce and Petersen 2009, Bentzen and Powell 2015). Boyd et al. (2009) showed that juvenile male Barrow’s Goldeneye had significantly lower return rates to their natal area compared to juvenile females, and hence higher dispersal probabilities.

CONCLUSION
Our results show regional clustering across all annual cycle stages, indicating demographic structuring of the Pacific Barrow’s Goldeneye population. However, putting distinct boundaries around subpopulations can be challenging, particularly in a population with a continuous distribution. We suggest that the Pacific Barrow’s Goldeneye subpopulations function as expected by an isolation-by-distance model of population structure (Zink 1997). Birds sampled in neighboring regions show some degree of spatial overlap in annual distributions, whereas birds sampled from regions at each end of the continuous distribution (i.e., Alaska and southern British Columbia) show no spatial overlap in their annual distributions. Within the Pacific Barrow’s Goldeneye population distribution, strong regional migratory connectivity indicates that subpopulations function largely independently (i.e., population trends in Alaska and southern British Columbia may not reflect overall population trends) and could be considered discrete population units. Although south-central Alaska appears to be completely separate from all other regions, we recognize that deployment of transmitters in the area between south-central and southeastern Alaska (Juneau) likely would have resulted in more overlapping movements, consistent with an isolation-by-distance model. Nevertheless, our data support significant levels of demographic independence among subpopulations at broad regional scales. Therefore, management activities (e.g., harvest management, habitat enhancement) could be applied at appropriate corresponding spatial scales to affect population dynamics of a subpopulation of interest.

Responses to this article can be read online at: https://www.ace-eco.org/issues/responses.php/2195

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Avian Conservation and Ecology 17(2): 7
http://www.ace-eco.org/vol17/iss2/art7/

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Acknowledgments:
Funding and/or support for this research was provided by Environment and Climate Change Canada, the U.S. Geological Survey, the U.S. Fish and Wildlife Service, the Alaska Department of Fish and Game, the Alberta North American Waterfowl Management Plan Partnership, the Alberta Conservation Association, Ducks Unlimited Canada, the Natural Sciences and Engineering Research Council, and the North American Sea Duck Joint Venture. We also appreciate the institutional support provided by the Gitga’at Guardian Watchmen Program, Centre for Wildlife Ecology at Simon Fraser University, and the Pacific Wildlife Foundation. The following individuals assisted with the captures: E. Anderson, N. Barton, D. Bradbeer, A. Breault, J. Brooks, R. Butler, K. Chernoff, N. Clyde, J. Cragg, A. Crupi, S. Davis, K. Devitt, R. Dickson, T. Donnelly, T. DiMarzio, R. Foster, G. Grigg, D. Groves, R. Hermanutz, D. Hogan, J. Hupp, I. Iverson, E. Jaschke, J. Jennings, A. Lebeau, E. Lok, R. MacVicar, M. Mafei, D. Marks, J. McDonald, M. Merriam, T. Morgan, A. Olsen, J. Olsen, E. Palm, M. Petrola, J. Pierce, J. Provencher, D. Rand, G. Raven, J. Reed, C. Rice, A. Robinson, D. Rosenberg, R. Scott, D. Sherrill, K. Smith, R. Stayne, K. Tingen, B. Uher-Koch, C. Van Stratt, M. Willis, M. Wilson, K. Wright, C. Wohl, and R. Worcester. We thank J. Barrett, S. L. Lee, M. Willie, and C. E. Fuss for their assistance with Argos data management and GIS support. We also thank D. Douglas for expert assistance with data management in Movebank. In addition to co-author M. McAdie, we thank the following veterinarians who performed surgical implants: K. Doty, D. Mulcahy, and P. Tuomi. We thank Paul Flint, John Eadie, and Scott Gilliland for their constructive feedback on this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not represent endorsement by the U.S. Government. This work was conducted in accordance with Environment and Climate Change Canada Scientific Permit to Capture and Band Migratory Birds 10673P and U.S. Fish and Wildlife Service Federal Fish and Wildlife Permit #MB789758. Capture and surgical procedures followed prescribed guidance by the Simon Fraser University Animal Care and Use Committee (Animal Care and Use Protocol 1121B-06). The Argos PTT data used in this study are accessible through Movebank in the Data Repository file “Migration Patterns of Pacific Sea Ducks”. https://www.movebank.org/cms/webapp/gwt_fragment?page=studies,study=1441422788

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Acknowledgments:
Funding and/or support for this research was provided by Environment and Climate Change Canada, the U.S. Geological Survey, the U.S. Fish and Wildlife Service, the Alaska Department of Fish and Game, the Alberta North American Waterfowl Management Plan Partnership, the Alberta Conservation Association, Ducks Unlimited Canada, the Natural Sciences and Engineering Research Council, and the North American Sea Duck Joint Venture. We also appreciate the institutional support provided by the Gitga’at Guardian Watchmen Program, Centre for Wildlife Ecology at Simon Fraser University, and the Pacific Wildlife Foundation. The following individuals assisted with the captures: E. Anderson, N. Barton, D. Bradbeer, A. Breault, J. Brooks, R. Butler, K. Chernoff, N. Clyde, J. Cragg, A. Crupi, S. Davis, K. Devitt, R. Dickson, T. Donnelly, T. DiMarzio, R. Foster, G. Grigg, D. Groves, R. Hermanutz, D. Hogan, J. Hupp, I. Iverson, E. Jaschke, J. Jennings, A. Lebeau, E. Lok, R. MacVicar, M. Mafei, D. Marks, J. McDonald, M. Merriam, T. Morgan, A. Olsen, J. Olsen, E. Palm, M. Petrola, J. Pierce, J. Provencher, D. Rand, G. Raven, J. Reed, C. Rice, A. Robinson, D. Rosenberg, R. Scott, D. Sherrill, K. Smith, R. Stayne, K. Tingen, B. Uher-Koch, C. Van Stratt, M. Willis, M. Wilson, K. Wright, C. Wohl, and R. Worcester. We thank J. Barrett, S. L. Lee, M. Willie, and C. E. Fuss for their assistance with Argos data management and GIS support. We also thank D. Douglas for expert assistance with data management in Movebank. In addition to co-author M. McAdie, we thank the following veterinarians who performed surgical implants: K. Doty, D. Mulcahy, and P. Tuomi. We thank Paul Flint, John Eadie, and Scott Gilliland for their constructive feedback on this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not represent endorsement by the U.S. Government. This work was conducted in accordance with Environment and Climate Change Canada Scientific Permit to Capture and Band Migratory Birds 10673P and U.S. Fish and Wildlife Service Federal Fish and Wildlife Permit #MB789758. Capture and surgical procedures followed prescribed guidance by the Simon Fraser University Animal Care and Use Committee (Animal Care and Use Protocol 1121B-06). The Argos PTT data used in this study are accessible through Movebank in the Data Repository file “Migration Patterns of Pacific Sea Ducks”. https://www.movebank.org/cms/webapp/gwt_fragment?page=studies,study=1441422788
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### Table A1.1. Summary of mean and standard deviations of timing of migration based on sex and winter capture location.

| Variable | Metric       | Vancouver Mean/SD | Kitimat Mean/SD | Juneau Mean/SD | South-central AK Mean/SD | Vancouver Mean/SD | Kitimat Mean/SD | Juneau Mean/SD | South-central AK Mean/SD |
|----------|--------------|-------------------|-----------------|---------------|--------------------------|-------------------|----------------|---------------|--------------------------|
|          |              | Range             | Range           | Range         | Range                    | Range             | Range          | Range         | Range                    |
| Winter   | Arrive       | Nov 05 ± 7        | [Oct 30-Nov 16] | Oct 20 ± 8    | Oct 08 ± 8               | Nov 07 ± 7        | Oct 28 ± 16    | Oct 16 ± 11   | Oct 21 ± 0               |
|          |              | [Mar 13-Apr 22]   | [Mar 21-May 14] | [May 11 ± 13] | [Apr 17-May 16]          | [Mar 30-May 22]   | [Apr 06-May 17] |                |                          |
|          | Depart       | Apr 07 ± 13       | [Apr 18-May 29]| May 01 ± 9    | Apr 21 ± 9               | Apr 27 ± 17       | Apr 28 ± 26    | May 02 ± 14   | May 08 ± 8               |
| Breed    | Arrive       | Apr 23 ± 10       | [Mar 30-May 08]| May 06 ± 3    | Apr 26 ± 13              | May 04 ± 11       | May 06 ± 8     | May 09 ± 8    | Apr 23-May 17            |
|          |              | [Apr 14-Jun 08]   | [May 16 ± 26]   | [Jun 19 ± 21] | [Jun 17 ± 24]            | [Apr 19-May 22]  | [Jul 16 ± 10]  | Jul 07 ± 23   | Jul 18 ± 14              |
|          | Depart       | May 27 ± 11       | [May 26-Aug 31]| Jun 19 ± 21   | Jul 23 ± 24              | [May 31-Jun 09]   | [Jun 09-Aug 01]| [Jun 01-Jul 30]| [Jun 22-Aug 05]          |
|          | LOS (days)   | 31 ± 11           | [20-79]         | 40 ± 24       | 42 ± 27                  | 87 ± 26           | 73 ± 12        | 62 ± 23       | 70 ± 19                  |
|          |              | [10-58]           | [20-45]         |              | [22-61]                  | [27-145]          | [53-84]        | [29-90]       | [37-104]                |
| Molt     | Arrive       | Jul 26 ± 29       | [Jun 27 ± 16]   | Jun 06 ± 21   | Jul 26 ± 16              | Jul 29 ± 15       | Jul 25 ± 13    | Jul 27 ± 8    | Jul 27 ± 21              |
|          |              | [May 12-Aug 01]   | [Jun 03-Jul 16]| [Jun 13-Aug 9]| [Jun 26-Jul 21]          | [Jul 01-Aug 12]   | [Jul 01-Aug 08]| [Jul Aug 18] | [Jul 22-Aug 21]          |
|          | 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              |
|          | LOS (days)   | 81 ± 42           | [Aug 21-Oct 04]| [Aug 11-Oct 06]| [Aug 25-Sep 15]          | [Sep 12-Oct 24]   | [Sep 18-Nov 01]| [Sep 25-Oct 22]| [Jul 21-Oct 08]          |
|          |              | [29-176]          | [56-109]        | [24-106]      | [56-91]                  | [32-101]          | [47-109]       | [35-90]       | [29-71]                  |
| Distance | Winter (km)  | 287 ± 90          | 480 ± 109       | 321 ± 189     | 431 ± 119                | 365 ± 140         | 431 ± 310      | 397 ± 178     | 397 ± 178                |
|          |              | [183-927]         | [86-1235]       | [107-714]     | [320-600]                | [187-703]         | [191-1249]     | [62-469]      | [222-577]               |
| Breeding | Winter (km)  | 786 ± 333         | 1078 ± 321      | 778 ± 366     | 274 ± 246                | 347 ± 371         | 261 ± 238      | 93 ± 149       | 68 ± 11                  |
|          |              | [701-1927]        | [1129-1750]     | [487-1305]    | [327-945]                | [210-1656]        | [239-1692]     | [156-564]     | [247-518]               |
| Molt (km)| Winter (km)  | 1088 ± 373        | 1451 ± 264      | 1173 ± 167    | 723 ± 280                | 692 ± 398         | 713 ± 453      | 347 ± 152     | 352 ± 131                |
|          |              | [701-1927]        | [1129-1750]     | [487-1305]    | [327-945]                | [210-1656]        | [239-1692]     | [156-564]     | [247-518]               |

**Appendix 1.** Supplemental analysis based on winter capture location.
Table A1.2  Summary of generalized linear models examining sex, winter capture location, and transmitter effects on i) the timing of arrival and departure on wintering areas, breeding areas and molting sites, ii) the length of stay (LOS) at each location, iii) the distance traveled during each migration (wintering-breeding, breeding-molting, and molting-wintering).

| Variable | Metric                | Winter Capture Location | Sex | Transmitter Effect | Winter Capture Location*Sex | Full Model |
|----------|-----------------------|-------------------------|-----|--------------------|----------------------------|------------|
| Winter   | Arrive                | F= 40 df = 3,93 P < 0.001 | F= 2.25 df = 1.93 P = 0.14 | NA NA NA | 2.24 3.93 0.09 | 0.55 18.4 7.93 | <0.001 |
|          | Depart                | F= 12.3 df = 1.120 P < 0.001 | F= 0.25 df = 1.120 P = 0.62 | 20 1.120 <0.001 | 1.72 3.120 0.17 | 0.3 7.8 8.120 | <0.001 |
|          | LOS (days)            | F= 34.7 df = 3.65 P < 0.001 | F= 1.36 df = 1.65 P = 0.28 | 12.3 1.65 <0.001 | 2.08 3.65 0.11 | 0.61 15.5 8.65 | <0.001 |
| Breed    | Arrive                | F= 11.8 df = 3.120 P < 0.001 | F= 0.1 df = 1.120 P = 0.75 | 9.06 1.120 0.003 | 0.82 3.120 0.49 | 0.23 5.88 8.120 | <0.001 |
|          | Depart                | F= 0.73 df = 3.103 P = 0.54 | F= 102.7 df = 1.103 <0.001 | NA NA NA | 3.71 3.103 0.01 | 0.5 16.6 7.103 | <0.001 |
|          | LOS (days)            | F= 1.81 df = 3.94 P = 0.15 | F= 76.4 df = 1.94 <0.001 | NA NA NA | 1.99 3.94 0.12 | 0.44 12.6 7.94 | <0.001 |
| Molt     | Arrive                | F= 0.16 df = 3.94 P = 0.92 | F= 59.6 df = 1.94 <0.001 | NA NA NA | 0.22 3.94 0.88 | 0.35 8.68 7.94 | <0.001 |
|          | Depart                | F= 11.1 df = 3.102 <0.001 | F= 7.63 df = 1.102 0.007 | NA NA NA | 0.88 3.102 0.45 | 0.25 6.23 7.102 | <0.001 |
|          | LOS (days)            | F= 3.51 df = 3.86 P = 0.02 | F= 8.44 df = 1.86 0.005 | NA NA NA | 0.23 3.86 0.87 | 0.12 2.81 7.86 | 0.01 |
| Distance travelled (km) | Winter to Breed | F= 0.69 df = 3.120 P = 0.56 | F= 0.59 df = 1.120 0.44 | 1.15 1.120 0.29 | 1.61 3.120 0.19 | 0.005 1.08 8.120 | 0.38 |
|          | Breed to Molt         | F= 2.52 df = 3.96 P = 0.06 | F= 56.8 df = 1.96 <0.001 | NA NA NA | 2.28 3.96 0.08 | 0.38 10.2 7.96 | <0.001 |
|          | Molt to Winter        | F= 8.61 df = 3.94 <0.001 | F= 88.7 df = 1.94 <0.001 | NA NA NA | 3 3.94 0.03 | 0.54 17.7 7.94 | <0.001 |

The above results are limited to individuals captured on their wintering areas.
Appendix 2. Supplemental materials

Table A2.1 Evaluation of observed migratory connectivity of adult male and female Barrow’s Goldeneye for each stage of the annual cycle. Density-based cluster analysis determined whether connectivity depends on aggregation of individuals or on rigid transference of distribution patterns between areas. Noise points are individuals that were not assigned to a cluster.

| 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           |
| Molt M    | 137 | 6  | 19         | 7-47           |
| Molt F    | 62  | 4  | 20         | 7-14           |
Figure A2.1 Original oil painting of a Barrow’s Goldeneye breeding pair by ©Peter Forstner. Frame hand-carved by ©House of Maes. This painting was used to create Figure 4 with permission from the artist ©Peter Forstner.