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Contrasting migratory chronology and routes of Lesser Scaup: implications of different migration strategies in a broadly distributed species

Cronología migratoria contrastante y rutas del Porrón Bola: implicancias de diferentes estrategias de migración en una especie ampliamente distribuida

Laurie A. Hall [1], *Christopher J. Latty* [2], *Jeffrey M. Warren* [3], *John Y. Takekawa* [1,4] and *Susan E. W. De La Cruz* [1]

ABSTRACT. Migration allows birds to improve fitness by exploiting seasonal resource peaks and avoiding limitations. Migration strategies may differ among individuals within a species, but for all strategies, the benefit of increased fitness should outweigh the costs of migration. These costs can include increased mortality risk, time constraints in the annual cycle, and metabolic energy loss. We compared migratory chronology and routes of individuals from a broadly distributed species of waterfowl, the Lesser Scaup (*Aythya affinis*; hereafter Scaup), marked at the northern (66.51000° N, 145.98556° W) and southern (44.63778° N, 111.73694° W) extents of its breeding distribution in North America. Scaup breeding farther north in interior Alaska, USA migrated greater distances and had protracted migrations, especially in fall, compared to Scaup breeding farther south in southwest Montana, USA. During migration, Scaup breeding in Alaska used more staging and stopover areas compared to Scaup breeding in Montana. Scaup breeding in Alaska also spent less time at their breeding area and more time at their wintering areas compared to Scaup breeding in Montana. In addition, Scaup breeding in Alaska were largely absent from wintering areas in the Intermountain West that were used by Scaup breeding in Montana. These differences could have important effects on Scaup fitness and could contribute to differences in fecundity and recruitment observed across the Scaup's broad latitudinal distribution. Understanding the fitness implications of intraspecific variation in migration strategies of broadly distributed species can assist resource managers by focusing conservation efforts on specific breeding populations, informing models of disease transmission, and improving projections of species' responses to environmental change.

RESUMEN. La migración permite a las aves mejorar su eficacia biológica al aprovechar los picos estacionales de recursos y evitar limitaciones. Las estrategias migratorias pueden variar entre individuos dentro de una especie, pero para todas las estrategias, el beneficio de una mayor eficacia biológica debería superar los costos de la migración. Estos costos pueden incluir un mayor riesgo de mortalidad, limitaciones de tiempo en el ciclo anual y pérdida de energía metabólica. Comparamos la cronología migratoria y las rutas de los individuos de una especie de ave acuática ampliamente distribuida, el Porrón Bola (*Aythya affinis*; de ahora en adelante Porrones), marcada en los extremos norte (66,51000° N, 145,98556° O) y sur (44,63778° N, 111,73694° O) de su distribución reproductiva en Norteamérica. Los Porrones que se reproducen más al norte en el interior de Alaska, EUA, migraron mayores distancias y tuvieron migraciones prolongadas, especialmente en otoño, en comparación con los Porrones que se reproducen más al sur en el suroeste de Montana, EUA. Durante la migración, los Porrones que se reproducen en Alaska usaron más sitios de estadía y parada que los Porrones que se reproducen en Montana. Además, los Porrones que se reproducen en Alaska pasaron menos tiempo en su área de reproducción y más tiempo en sus áreas de invernada en comparación con los Porrones que se reproducen en Montana. Adicionalmente, los Porrones que se reproducen en Alaska estuvieron en gran medida ausentes en las áreas de invernada en el Oeste Intermontano, las cuales fueron usadas por los Porrones que se reproducen en Montana. Estas diferencias podrían tener efectos importantes en la eficacia biológica de los Porrones y podrían contribuir a las diferencias en fecundidad y reclutamiento observadas a lo largo de la amplia distribución latitudinal de los Porrones. Comprender las implicancias para la eficacia biológica de la variación intraespecífica en las estrategias migratorias de una especie ampliamente distribuida puede ayudar a los administradores de recursos a centrar los esfuerzos de conservación en poblaciones reproductivas específicas, informar modelos de transmisión de enfermedades y mejorar las proyecciones de las respuestas de las especies al cambio ambiental.

Key Words: *diving ducks; flyway; migration; North America; platform transmitter terminal (PTT); Scaup; telemetry; waterfowl*

INTRODUCTION

Migration is driven by ecological and biogeographical factors, including the spatiotemporal distribution of resources, predation, and competition (Alerstam et al. 2003). It allows birds to improve their fitness by exploiting seasonal resource peaks while avoiding limitations (Lack 1968, Alerstam et al. 2003). Migration strategies differ among species, populations, and individuals (e.g., Vardanis et al. 2011, 2016, Weimerskirch et al. 2015, Pearse et al. 2020), though most involve flights with intermittent breaks at stopover or staging areas where birds require safe roosting areas and high-quality food to refuel (Warnock 2010, Alerstam 2011, Stafford et al. 2014). Despite differences among strategies, the benefit of increased fitness should outweigh the costs, including increased mortality risk, time constraints in the annual cycle, and metabolic energy loss (Alerstam et al. 2003, Alerstam 2011). Different breeding populations of a species, particularly those with broad geographic distributions, may employ different strategies because of spatial variation in environmental conditions.

[1]San Francisco Bay Estuary Field Station, Western Ecological Research Center, U.S. Geological Survey, [2]Arctic National Wildlife Refuge, U.S. Fish and Wildlife Service, [3]Division of Scientific Resources, U.S. Fish and Wildlife Service, [4]Suisun Resource Conservation District

The Lesser Scaup (*Aythya affinis*; hereafter Scaup) is a broadly-distributed, medium-sized diving duck that breeds in boreal forests, prairie parklands, and montane wetlands from central Alaska to southern Colorado, USA and winters along the Atlantic and Pacific coasts of the USA and throughout the southern USA, Central America, and the Caribbean (Anteau et al. 2020). It is one of the most abundant waterfowl species in North America, yet it is a species of conservation concern because the population has undergone a marked decline in recent decades (Afton and Anderson 2001, Drever et al. 2012, Austin et al. 2014, U.S. Fish and Wildlife Service 2015). Habitat loss at breeding, wintering, and migratory stopover areas, increased contaminant exposure, and changing food availability are among the hypothesized causes of the decline (Afton and Anderson 2001, Custer et al. 2003, Anteau et al. 2007, DeVink et al. 2008a). Climatic warming, particularly in the boreal forest, is likely to have exacerbated the effects of these factors (Drever et al. 2012).

Scaup breeding at different latitudes could employ different migration strategies in response to heterogeneous environmental conditions that could, in turn, have important consequences for survival and reproductive success. Compared to other waterfowl, Scaup are among the latest migrants in fall and spring, adjusting their timing and routes in response to proximate factors, including temperature, precipitation, and ice conditions (Austin et al. 2002, Mallory et al. 2003, Finger et al. 2016). Scaup are also late breeders, with a more fixed and constrained nesting period compared to other waterfowl (Gurney et al. 2011, Anteau et al. 2020). These constraints result in fitness trade-offs related to the timing of migration, migration distance, and the number of stops during migration. Previous studies have suggested that reduced food availability during spring caused declines in female body condition (i.e., the spring-condition hypothesis) that resulted in reduced fecundity and recruitment, particularly for Scaup breeding at northern latitudes (Anteau and Afton 2004, 2009, DeVink et al. 2008b, Hobson et al. 2009, Arnold et al. 2016, Hammell 2016). Different migration strategies employed by Scaup breeding at different latitudes could contribute to differences in female body condition, fecundity, and recruitment observed across the species' broad latitudinal distribution.

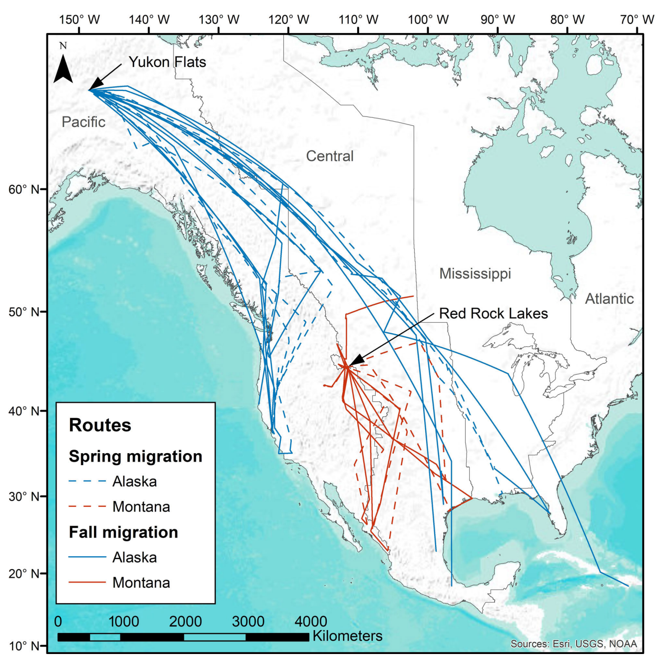
Here, we provide novel information on the migratory chronology and routes of Scaup breeding in western North America at the northern extent of the breeding distribution in Yukon Flats National Wildlife Refuge in Alaska, USA (66.51000° N, 145.98556° W) and at the southern extent of the distribution in Red Rock Lakes National Wildlife Refuge in Montana, USA (44.63778° N, 111.73694° W). Using data from Scaup marked with platform transmitter terminals (PTTs), we determined the day that each stage of the annual cycle was initiated, including spring migration departure, breeding area arrival, molting area arrival, fall migration departure, and wintering area arrival. We also calculated the mean duration of each stage. We examined Scaup routes including the use of different flyways, molting, wintering, and staging and stopover areas. In addition, we compared the winter distributions of PTT-marked Scaup to winter band recoveries from Scaup banded in Alaska and Montana. We hypothesized Scaup breeding farther north in Alaska would migrate greater distances, for longer durations, and would arrive at breeding and wintering areas later than Scaup breeding farther south in Montana.

METHODS

Study areas

Yukon Flats National Wildlife Refuge is the largest interior wetland basin in Alaska located near the northern extent of the Scaup breeding distribution (Fig. 1; hereafter Alaska). It comprises 3.3 million ha of boreal wetlands and riparian areas, with nearly 40,000 lakes (U.S. Fish and Wildlife Service 1987, Martin et al. 2009). In contrast, Lower Red Rock Lake is a 2332 ha montane wetland (2033 meters above mean sea level) within Red Rock Lakes National Wildlife Refuge in the Centennial Valley of southwest Montana located at the southern extent of the Scaup breeding distribution (Warren et al. 2013; Fig. 1; hereafter Montana). Lower Red Rock Lake is relatively shallow; nesting season water depths are typically < 1.5 m, with large open water areas interspersed with vegetation (Warren et al. 2013). Despite being situated at very different latitudes, both breeding areas have a Köppen-Geiger climate classification of Cool Continental/Subarctic characterized by extreme variability and short growing season length (U.S. Fish and Wildlife Service 1987, Gurney et al. 2011).

Fig. 1. North American Flyways (Pacific, Central, Mississippi, and Atlantic) with spring (dashed lines) and fall (solid lines) migratory routes of Lesser Scaup (*Aythya affinis*) marked with platform transmitter terminals (PTTs) at two breeding areas: Yukon Flats National Wildlife Refuge in Alaska, USA ($N^{\dagger}$ = 11; blue) in 2012 and Red Rock Lakes National Wildlife Refuge in Montana, USA ($N^{\ddagger}$ = 11; red) in 2009.
† Includes observations from one individual that was tracked for > 1 annual cycle.
‡ Includes observations from three individuals that were tracked for > 1 annual cycle.



Capture, marking, and location data collection

We captured and marked adult (after-hatch-year) female Scaup on breeding areas in Alaska (*N* = 15) and Montana (*N* = 9). In Alaska, Scaup were captured on their nests from 21 to 24 June 2012 using walk-in traps (Weller 1957). In Montana, flightless Scaup were captured from 21 to 22 August 2009 using spotlighting (Lindmeier and Jessen 1961). Battery powered PTTs (26 g; Microwave Telemetry, Inc., Maryland, USA) were surgically implanted by experienced veterinary surgeons using techniques from Olsen et al. (1992) and Mulcahy and Esler (1999). Marked birds weighed an average of 604 g (range = 542–682 g) in Alaska and 652 g (range = 610–700 g) in Montana and had no visible injuries. Duty cycles for PTTs implanted in Alaska were 3 cycles of 4 hours on and 94 hours off, 18 cycles of 2 hours on and 240 hours off, 38 cycles of 6 hours on and 92 hours off, 20 cycles of 2 hours on and 240 hours off, and 39 cycles of 6 hours on and 92 hours off (Appendix 1 Table S1). Duty cycles for PTTs implanted in Montana were 8 hours on and 72 hours off. Duty cycles for PTTs implanted in Alaska were designed to collect locations less frequently for two years compared to duty cycles for PTTs implanted in Montana, which collected locations more frequently for one year. These differences did not impact our inferences about migratory chronology and routes, except that the long-off period for PTTs deployed in Alaska limited our ability to differentiate staging and stopover areas (see "Data analysis" for more information). All Scaup were banded with U.S. Geological Survey aluminum leg bands and were aged and sexed using plumage and cloacal characteristics (Hochbaum 1942, Carney 1964).

We obtained location data including date, time, latitude, longitude, and location error class (LC) for Scaup marked in Alaska from 2012 to 2013 and for Scaup marked in Montana from 2009 to 2010 using the Argos satellite system (Collecte Localisation Satellite, Ramonville Saint-Agne, France; Hall et al. 2024). Locations were calculated from frequency Doppler shifts, and error classes included: LC-3 (< 250 m), LC-2 (250–500 m), LC-1 (500–1500 m), LC-0 (> 1500 m), and LC-A, LC-B, and LC-Z (no accuracy information available). We excluded data collected during the first seven days following surgeries to minimize potential biases in movement patterns while Scaup adjusted to transmitters (Mulcahy and Esler 1999, Lamb et al. 2020). Location data were filtered to remove outliers and retain locations with the greatest accuracy using the best hybrid Douglas Argos Filter in Movebank® (Douglas et al. 2012). Parameter values for the filter included a Maxredun of 10, a Minrate of 100, a Ratecoef of 15, and an Xmigrate of 2. Default values were used for all other filter parameters. We calculated migratory chronology using all locations retained by the Douglas Argos Filter (i.e., we did not enable the Best of Day filter) so that the timing of transitions between stages of the annual cycle could be inferred with greater accuracy (Douglas et al. 2012). To characterize migratory routes, we enabled the Best of Day filter to retain one location with the best LC during each duty cycle (Douglas et al. 2012).

We compared wintering areas of female PTT-marked Scaup to winter distributions of female Scaup banded in Alaska and Montana. We defined the wintering period using the migratory chronologies of PTT-marked Scaup breeding in Alaska, which had a longer wintering period than Scaup breeding in Montana. Accordingly, winter band recoveries ranged from ordinal day 299 to 72, which corresponded to the earliest arrival at wintering areas and the earliest spring migration departure, respectively. (Table 1). Band recoveries from 2008 to 2014 were included because this period encompassed the years during which PTT-marked Scaup were tracked and reflected contemporary climate and habitat distribution. Band recovery data were obtained from the U.S. Geological Survey Bird Banding Laboratory (Laurel, MD, USA).

Table 1. Means and ranges for the ordinal day initiated and duration (days) of different stages of the annual cycle for Lesser Scaup (*Aythya affinis*) marked with platform transmitter terminals on breeding areas at Yukon Flats National Wildlife Refuge in Alaska, USA in 2012 and at Red Rock Lakes National Wildlife Refuge in Montana, USA in 2009. The ordinal day initiated was the day of departure for spring and fall migration and the day of arrival at breeding, molting, and wintering areas. Duration was the total number of days that a scaup was migrating or occupying a breeding, molting, or wintering area.

		Ordinal day initiated			Duration (days)		
Breeding area	Stage	*N*†	Mean	Range	*N*†	Mean	Range
Alaska	Spring migration	7	89	72-102	6	57	50-67
	Breeding	6	148	139-158	1	65	
	Molting	3	215	214-216	3	50	40-59
	Fall migration	11	252	242-270	10	70	40-100
	Wintering	9	323	299-341	7	137	96-155
Montana	Spring migration	6	81	65-98	6	37	18-52
	Breeding	6	117	107-130	3	96	86-112
	Molting	6	226	218-249	4	65	56-75
	Fall migration	9	293	268-323	8	29	10-56
	Wintering	8	325	290-346	6	124	116-138

† Includes observations from individuals that were tracked for > 1 annual cycle.

Data analysis

All measurements and summary statistics were performed in R v. 4.0.4 (R Core Team 2020), unless otherwise specified. Locations retained for migratory chronology were used to determine the ordinal day (e.g., 1 Jan. 2009 = day 1 and 31 Dec. 2009 = day 365; 1 Jan. 2012 = day 1 and 31 Dec. 2012 = day 366) when each stage of the annual cycle was initiated by individual Scaup (i.e., spring migration departure, breeding area arrival, molting area arrival, fall migration departure, and wintering area arrival). The arrival date of a Scaup was estimated as the mid-point of the duty cycle prior to the individual's detection at that location. For example, if two consecutive locations were recorded 10 days apart, then we assumed a Scaup arrived at the second location five days prior to the date the Scaup was detected at that location.

We calculated the Geodesic distance for each movement segment between two consecutive locations. We used a histogram of average daily speeds (km day^{-1}) to determine a threshold for classifying movements; daily movements ≤ 20 km were classified as "local," movements > 20 km that occurred during spring or fall migration periods were classified as "migratory," and movements > 20 km that did not occur during the spring or fall migration periods were classified as "exploratory" (Edelhoff et al. 2016). We conducted visual assessments of all routes to check classifications for accuracy, and movements were reclassified as needed. Each movement segment was assigned to a stage in the annual cycle based on its distance classification (i.e., local, migratory, or exploratory) and the time of year relative to the annual cycle previously described for Scaup (Anteau et al. 2020). We then calculated the mean ordinal day of initiation and mean duration of each stage for Scaup breeding in Alaska and Montana.

Locations retained with the Best of Day filter were used to map Scaup migration routes in ArcGIS v. 10.7.1. We visually examined flyway use and inferred molting, wintering, and migratory staging and stopover areas based on movement distances and the time of year as described above for migratory chronology. We were unable to differentiate between staging (used for ≥ 7 days) and stopover (used for < 7 days) areas for PTTs deployed in Alaska because these transmitters had a long off-period in their duty cycle (Warnock 2010). Therefore, we compared the number of stops, regardless of duration, between Scaup from the two breeding areas.

We measured the Geodesic distance between the breeding area and molting and wintering areas for each Scaup in ArcGIS v. 10.7.1 and compared the mean distances between Scaup from the two breeding areas. We also compared daily speeds of Scaup from the two breeding areas. We assessed route fidelity at a regional-scale by identifying Scaup that used staging and stopover areas within a 100-km radius during both spring and fall migration. Finally, we compared wintering areas of PTT-marked Scaup to the distribution of winter band recoveries by mapping Scaup locations and calculating the percent of PTT-marked Scaup and band recoveries in each flyway. Spatial polygons for flyways were obtained from Weltzin et al. (2018).

RESULTS

Migratory chronology

We collected 8743 locations from 24 Scaup, and we retained 6412 locations from 18 Scaup (Alaska $N = 10$; Montana $N = 8$) after applying a Douglas Argos Filter and removing locations from three Scaup with PTTs that failed to transmit data according to their duty cycle and from three Scaup with tags that stopped transmitting at the breeding areas. We tracked most individuals for less than one annual cycle, but one Scaup from Alaska and three Scaup from Montana had PTTs that lasted longer than one year. Therefore, our dataset included locations for these individuals from a second year. Greater than 95% of daily movements were ≤ 20 km and were classified as local movements, whereas 4.9% of movements were > 20 km and were classified as migratory. Exploratory movements (i.e., long-distance movements that occurred outside migration seasons) were rare, constituting only 0.1% of movements.

Average departure for spring migration occurred eight days later for Scaup breeding in Alaska compared to Scaup breeding in Montana (Table 1, Fig. 2). In addition, Scaup breeding in Alaska arrived at breeding areas 31 days later than Scaup breeding in Montana (Table 1, Fig. 2). Average arrival at molting areas occurred 11 days earlier for Scaup breeding in Alaska compared to those breeding in Montana (Table 1, Fig. 2). Scaup breeding in Alaska departed for fall migration 41 days earlier than Scaup breeding in Montana, while the average day of arrival at wintering areas was similar for Scaup from both breeding areas (Table 1, Fig. 2).

Scaup breeding in Alaska had more protracted spring and fall migrations, migrating for an average of 20 more days during spring and 41 more days during fall, compared to Scaup breeding in Montana (Table 1). Scaup breeding in Alaska also spent an average of 13 more days at their wintering areas and an average of 31 fewer days at their breeding areas compared to Scaup breeding in Montana (Table 1). In addition, Scaup breeding in Alaska spent an average of 15 fewer days at their molting areas than Scaup breeding in Montana (Table 1).

Migratory routes

When the Best of Day filter was applied, 1274 locations were retained. Scaup marked with PTTs in Alaska generally migrated to wintering areas in either the Pacific ($N = 6$) or Central ($N = 3$) Flyways, but one Scaup crossed into the Mississippi Flyway, and another crossed into the Atlantic Flyway (Figs. 1, 3). Most Scaup marked with PTTs in Montana also migrated to wintering areas in the Pacific ($N = 5$) and Central ($N = 2$) Flyways, but one wintered in the Mississippi Flyway (Fig. 1, 3). A majority of Scaup migrated to wintering areas in the USA; however, approximately 30% of PTT-marked Scaup wintered in Mexico. The percentages of PTT-marked Scaup and band recoveries in each flyway during winter were similar, except our sample of PTT-marked Scaup breeding in Alaska overestimated the percentage of Scaup that wintered in the Pacific Flyway and underestimated the percentage of Scaup that wintered in the Mississippi Flyway compared to the estimates from band recoveries; however, our modest sample size precluded a thorough statistical analysis (Table 2).

Scaup breeding in Alaska migrated an average of 4987 (range = 2746–11,729; $N = 11$) km to reach their wintering areas, a much greater distance than Scaup breeding in Montana that migrated an average of only 1565 (range = 324–2459; $N = 8$) km (Fig. 1). One Scaup marked in Alaska migrated nearly 12,000 km across North America to Cuba; we assumed the bird wintered in Cuba, but the bird's exact wintering location was unknown because its PTT stopped transmitting shortly after arrival in Cuba (Fig. 1). The average latitude and longitude of wintering areas for Scaup breeding in Alaska and Montana were similar, with Scaup marked in Alaska wintering slightly northwest, on average, of Scaup marked in Montana (Table S2, Fig. 3). However, data from PTTs and band recoveries indicated that the spatial distribution of wintering areas differed between Scaup from the two breeding areas. Scaup marked in Montana wintered at intermediate latitudes and longitudes compared to Scaup marked in Alaska, which primarily wintered either northwest or southeast of Scaup marked in Montana (Fig. 3).

Most Scaup marked in Alaska (70%) and Montana (100%) used a single wintering area; however, three Scaup marked in Alaska made long-distance movements, using more than one wintering area. The first moved almost 900 km from Oaxaca, Mexico to Texas, USA and then another 900 km to Mississippi, USA between December and February (Table S2, Fig. 3). The second wintered in the California Central Valley, USA, moving 50–214 km among wetlands between January and February (Table S2, Fig. 3). The third migrated to Tamaulipas on the East Coast of Mexico where it wintered and remained through the subsequent

Fig. 2. Speeds (km day^{-1}) during the annual cycle of Lesser Scaup (*Aythya affinis*) marked with platform transmitter terminals (PTTs) at two breeding areas: (A) Yukon Flats National Wildlife Refuge in Alaska, USA ($N^{\dagger}$ = 11; blue) in 2012 and (B) Red Rock Lakes National Wildlife Refuge in Montana, USA ($N^{\ddagger}$ = 11; red) in 2009. The mean ordinal days of spring migration departure, breeding area arrival, molting area arrival, fall migration departure, and wintering area arrival are shown with dotted lines for each breeding area.
† Includes observations from one individual that was tracked for > 1 annual cycle.
‡ Includes observations from three individuals that were tracked for > 1 annual cycle.

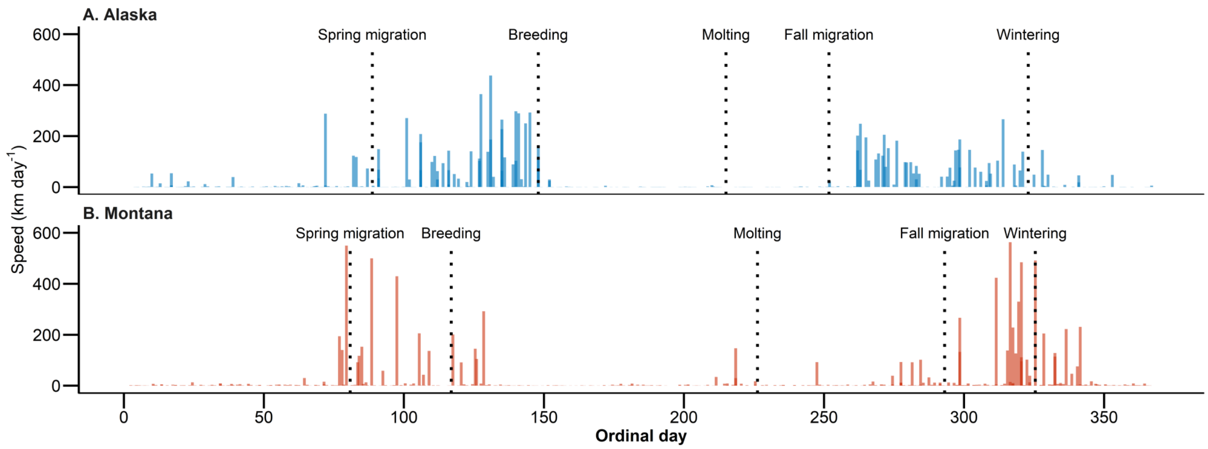


Fig. 3. North American Flyways (Pacific, Central, Mississippi, and Atlantic) with wintering areas of Lesser Scaup (*Aythya affinis*) marked with platform transmitter terminals (PTTs) at two breeding areas: Yukon Flats National Wildlife Refuge in Alaska, USA ($N^{\dagger}$ = 11; blue triangles) in 2012 and Red Rock Lakes National Wildlife Refuge in Montana, USA ($N^{\ddagger}$ = 11; red triangles) in 2009, and recovery locations of Scaup banded in Alaska (blue circles) and Montana (red circles) during 2008-2014. Some PTT-marked Scaup used more than one wintering area.
† Includes observations from one individual that was tracked for > 1 annual cycle.
‡ Includes observations from three individuals that were tracked for > 1 annual cycle.

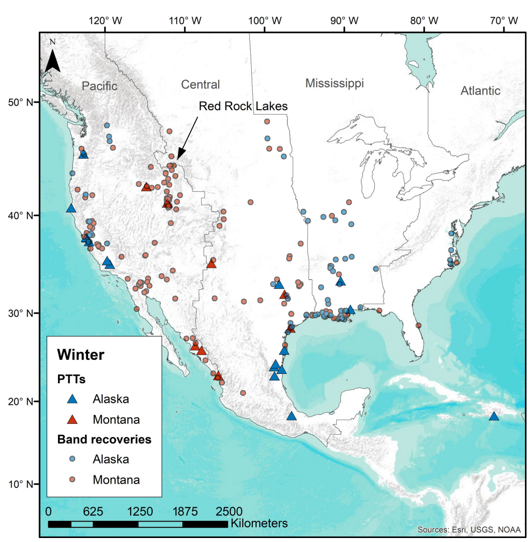


Table 2. Percentages of Lesser Scaup (*Aythya affinis*) marked with platform transmitter terminals (PTTs) and band recoveries originating in Alaska and Montana, USA that wintered in the Pacific, Central, Mississippi, and Atlantic Flyways from 2008–2014.

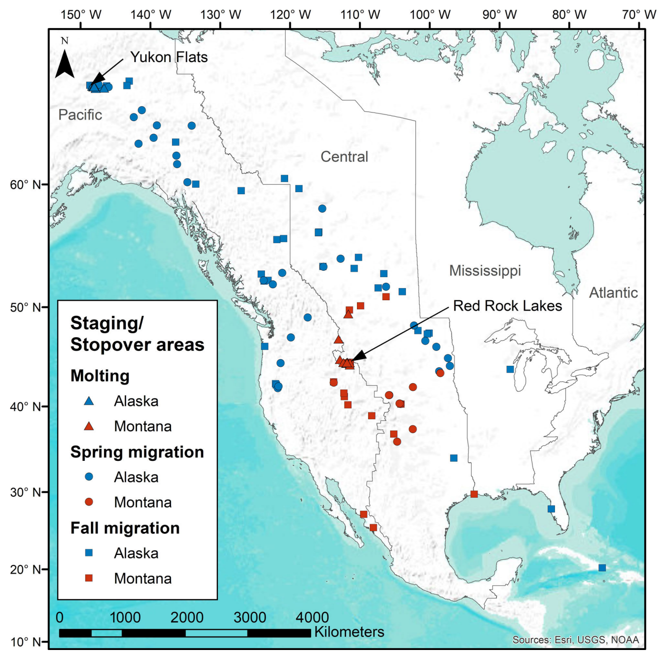
	Alaska		Montana	
	PTTs (%)	Band recoveries (%)	PTTs (%)	Band recoveries (%)
Flyway	$N^{\dagger}$ = 11	N = 78	N = 8	N = 187
Pacific	54.6	28.2	62.5	67.9
Central	27.3	15.4	25.0	20.9
Mississippi	9.1	50.0	12.5	9.6
Atlantic	9.1	6.4	0.0	1.6

† Includes observations from one individual that was tracked for > 1 annual cycle.

year. During this period, it made occasional long-distance movements (range = 84–119 km) among wetlands in Tamaulipas (Table S2, Fig. 3). In addition, one Scaup marked in Alaska had a PTT that lasted through two wintering periods, and this bird wintered in the same region, San Francisco Bay, California, USA, during both winters.

During spring migration, Scaup breeding in Alaska stopped at an average of 5 (range = 1–10; N = 6) staging and stopover areas, while Scaup breeding in Montana stopped at an average of only 1.5 (range = 1–2; N = 6) staging and stopover areas (Table S3, Fig. 4). Fifty percent of Scaup tracked for a full annual cycle (3 of 5 from Alaska and 2 of 6 from Montana) appeared to use similar routes during spring and fall migration, stopping at staging or stopover areas within 100 km of previously used stops. The greatest daily speeds we observed during spring were 437 km day^{-1} and 550 km day^{-1} from Scaup breeding in Alaska and Montana, respectively (Fig. 2).

Fig. 4. North American Flyways (Pacific, Central, Mississippi, and Atlantic) with staging and stopover areas used during molting (triangles), spring migration (circles), and fall migration (squares) by Lesser Scaup (*Aythya affinis*) marked with platform transmitter terminals (PTTs) at two breeding areas: Yukon Flats National Wildlife Refuge in Alaska, USA ($N^{\dagger}$ = 11; blue) in 2012 and Red Rock Lakes National Wildlife Refuge in Montana, USA ($N^{\ddagger}$ = 11; red) in 2009.
† Includes observations from one individual that was tracked for > 1 annual cycle.
‡ Includes observations from three individuals that were tracked for > 1 annual cycle.



Prior to departure for fall migration, most Scaup marked in Alaska (73%) and Montana (54%) molted near their breeding areas, but some dispersed to molting areas (Table S4, Fig. 4). In Alaska, Scaup that dispersed for molting moved an average of 20 (range = 18–25; *N* = 3) km, whereas Scaup breeding in Montana dispersed much farther at an average distance of 219 (range = 35–526; *N* = 4) km (Table S4, Fig. 4). In fact, two Scaup marked in Montana dispersed to molting areas > 200 km from the breeding area. In addition, one Scaup marked in Alaska used the same molting area for two consecutive years, indicating that some Scaup may exhibit fidelity to their molting areas.

During fall migration, Scaup breeding in Alaska made a greater number of stops, an average of 3.7 (range = 2–6; *N* = 11), compared to Scaup breeding in Montana that only stopped at an average of 2.2 (range = 1–4; *N* = 9) staging and stopover areas (Table S5, Fig. 4). Three Scaup marked in Alaska used Lubicon Lake in Alberta, Canada, and three used Tulebagh Lake in Alaska, USA as fall staging and stopover areas (Table S5, Fig. 4). In contrast, four Scaup marked in Montana used Henry's Lake in Idaho, USA, two used Island Park Reservoir in Idaho, USA, and two used Great Salt Lake in Utah, USA as fall staging and stopover areas (Table S5, Fig. 4). The maximum daily speed we observed was 563 km day^{-1}, recorded during fall migration from a Scaup marked in Montana (Fig. 2).

DISCUSSION

We detected differences in the timing of migration, migration distance, and the number of stops during migration for Scaup breeding at the northern extent of the range compared to Scaup breeding at the southern extent of the range. As predicted, Scaup breeding in Alaska migrated greater distances and had more protracted migrations, especially in fall, making use of more staging and stopover areas compared to Scaup breeding in Montana. Scaup breeding in Alaska also arrived at their breeding area later, spending less time at their breeding area and more time at their wintering areas compared to Scaup breeding in Montana. In addition, Scaup breeding in Alaska and Montana wintered in different regions. This intraspecific variation in migration strategies could have important implications for Scaup fitness.

Flyway use and waterfowl management

Previous studies of Scaup migration have focused on birds using the Atlantic, Mississippi, and Central Flyways (Austin et al. 2002, Finger et al. 2016, Schummer et al. 2018). Our sample of PTT-marked Scaup from western breeding areas used all four North American Flyways; thus, we present some of the first data for Scaup using the Pacific Flyway. Similar to observations from other waterfowl, Scaup breeding in the West crossed multiple flyways during migration, underscoring the importance of coordinating management efforts across flyways (Lamb et al. 2019). Further, approximately 30% of PTT-marked Scaup used the Pacific and Central Flyways to reach wintering areas in Mexico. In contrast, recent "stepped-down" regional abundance objectives from the North American Waterfowl Management Plan (NAWMP) indicated that only approximately 10% of the combined Greater and Lesser Scaup population wintered in Mexico (U.S. Department of the Interior et al. 2012, Fleming et al. 2019). Although our sample size was small, our data suggested that a substantial proportion of Lesser Scaup breeding in the West could winter in Mexico, and future revisions of NAWMP could consider increasing the proportion of Scaup wintering in Mexico when calculating regional abundance objectives.

A more complete understanding of waterfowl migration routes not only aids in conservation efforts but can also improve models of disease transmission. For example, scientists are currently tracking the spread of highly pathogenic avian influenza H5 and H5N1 through North America, and Scaup are one of several wild waterfowl known to transmit the virus (Stephens et al. 2019, McDuie et al. 2022, National Wildlife Health Center 2022, Prosser et al. 2022). The crossover we observed among flyways could increase disease transmission (National Wildlife Health Center 2022).

Trade-offs of different migration strategies

We detected differences in migration strategies between Scaup breeding in Alaska and Montana that resulted in different time constraints throughout the annual cycle. Scaup breeding at all latitudes are constrained to initiate nesting in June (Anteau and Afton 2004, Gurney et al. 2011, Anteau et al. 2020). Therefore, Scaup that arrive earlier to breeding areas at southern latitudes have more time to forage and improve their body condition prior to nesting compared to Scaup breeding farther north. However, previous studies suggested that Scaup breeding in Alaska had ample time to improve their body condition before breeding (Afton 1984, Martin 2007). In addition, Scaup can use both endogenous and exogenous resources for egg development (Afton and Ankney 1991, Esler et al. 2001, Cutting et al. 2011, 2014). This flexibility could offset the trade-off between the time of arrival at breeding areas and migration distance. In fact, Esler et al. (2001) detected limited differences in nutrient reserve use for egg development in Scaup breeding at northern compared to southern latitudes.

Heterogeneous effects of environmental change across the Scaup's broad distribution could also have differential impacts on migration strategies of Scaup breeding at northern and southern latitudes. Inter- and intraspecific variation in migration strategies have been associated with phenological shifts of different magnitudes in response to warming temperatures during spring migration (Hurlbert and Liang 2012, Usui et al. 2017). Such shifts could have disproportionate effects on Scaup breeding at different latitudes and exacerbate the demographic impacts of environmental change on Scaup (Drever et al. 2012).

In addition to differences in the time of arrival at breeding areas, our results indicated that wintering area use differed between Scaup breeding in Alaska and Montana. Scaup breeding in Alaska spent more time at wintering areas compared to Scaup breeding in Montana. Further, data from PTTs and band recoveries indicated that Scaup breeding in Alaska primarily wintered to the west or east of Scaup breeding in Montana and were largely absent from wintering areas in the Intermountain West. Scaup using wintering habitats in different regions are likely to experience different threats and may require management actions targeted to specific breeding populations (Ely et al. 2013, Ely and Meixell 2016). Assessing body condition and plasma metabolites of migrating and wintering Scaup could provide additional insight into differences in habitat quality among migration routes and the trade-offs of the different migration strategies described in our study (Smith et al. 2021).

Transmitter effects and other limitations

Although surgically implanted transmitters have low post-surgical mortality rates and are commonly used to track waterfowl, implanted transmitters can have sublethal effects on behavior that may influence long-term survival and reproductive success (Mulcahy and Esler 1999, Latty et al. 2010, Fast et al. 2011, Lamb et al. 2020). In fact, a recent study by Lamb et al. (2020) demonstrated that spring migrations of waterfowl with implanted transmitters occurred later in the first-year after marking compared to subsequent years. Thus, the implanted PTTs used in our study could have biased our migratory chronology results. However, PTT-marked Scaup from both breeding areas would likely have experienced the same level of bias, so the magnitude of differences in migratory chronology that we observed would have been minimally affected by such a bias.

Band recoveries of Scaup breeding in Alaska and Montana corroborated our inferences from PTT-marked Scaup. However, some limitations of band recovery data should be acknowledged. Namely, most band recoveries are made during waterfowl hunting seasons, which typically occur from September to January. Therefore, we limited inferences from banding data to the wintering period. In addition, banding data are subject to spatial and temporal variation in hunting intensity that influence the distribution of band recoveries. For example, waterfowl hunting and reporting of band returns could occur less frequently in foreign countries such as Mexico compared to the USA.

Another important limitation of our study was that Scaup from each breeding area were tracked during different years. The migratory chronology and routes of Scaup breeding in Alaska and Montana were likely influenced by annual variation in weather (Austin et al. 2002, Mallory et al. 2003, Finger et al. 2016). However, given the magnitude of differences we observed between migration strategies, it is unlikely these differences were the result of weather variation alone. Multi-year studies of migrating Scaup could assess the effects of weather and other drivers on annual variation in routes and improve the accuracy of migratory chronology estimates.

CONCLUSIONS

Species with broad geographic distributions may employ different migration strategies because of heterogeneous environmental conditions. Such intraspecific variation in migratory chronology and routes could result in fitness trade-offs that can have important demographic consequences and necessitate customized management actions (Ely et al. 2013, Stafford et al. 2014). Further, understanding variation in migration strategies can inform predictions of the impacts of environmental change on migratory behavior (Vardanis et al. 2016). Our study demonstrated differences in Scaup migration strategies across a broad latitudinal distribution; Scaup breeding at the northern extent of the distribution migrated longer distances, for longer durations, and made more stops compared to Scaup breeding at the southern extent of the distribution. The differences we observed in migration distance and duration resulted in different time constraints in the annual cycle of Scaup and could have important effects on Scaup fitness. Future studies of intraspecific variation in migration strategies could evaluate the fitness implications of different strategies. For example, gut content and proximate analysis could be paired with tracking data to assess differences in pre-breeding body condition among individuals with different migration strategies. Such studies could assist resource managers by focusing conservation efforts on specific breeding populations, informing models of disease transmission, and improving projections of species' responses to environmental change.

Author Contributions:

S.E.W.D. and J.Y.T. developed this research with input from C.J.L. and J.M.W. Data were collected by C.J.L. and J.M.W. L.A.H analyzed the data and wrote the manuscript with contributions from all authors. S.E.W.D., J.Y.T., C.J.L., and J.M.W. contributed resources and funding.

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Data Availability:

Data from this research are provided in Hall et al. 2024, https://doi.org/10.5066/P9QERTWN.

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APPENDIX 1

Contrasting migratory chronology and routes of Lesser Scaup: Implications of different migration strategies in a broadly distributed species

Laurie A. Hall[1], Christopher J. Latty[2], Jeffrey M. Warren[3], John Y. Takekawa[1,4], and Susan E. W. De La Cruz[1]

[1]San Francisco Bay Estuary Field Station, Western Ecological Research Center, U.S. Geological Survey, [2]Fairbanks Fish and Wildlife Field Office, U.S. Fish and Wildlife Service, [3]Division of Scientific Resources, U.S. Fish and Wildlife Service, [4]Suisun Resource Conservation District

Table S1. Timing of duty cycles for platform transmitter terminals (PTTs) used to mark Lesser Scaup (*Aythya affinis*) at Yukon Flats National Wildlife Refuge in Alaska, USA in 2012. The number of cycles for each on/off period, the number of days elapsed during the cycling, and the start and end months of each set of cycles are given.

	No. cycles	**On (hours)**	**Off (hours)**	**No. days**	**Start month**	**End month**
	3	4	94	12	Late June	Early July
	18	2	240	182	Early July	Early January
	38	6	92	155	Early January	Mid June
	20	2	240	202	Mid June	Early January
	39	6	92	159	Early January	Late July
Total	118	20	758	710		

Table S2. Wintering areas of Lesser Scaup (*Aythya affinis*) marked with platform transmitter terminals (PTTs) at two breeding areas: Yukon Flats National Wildlife Refuge (NWR) in Alaska, USA ($N^{\dagger}$ = 11) in 2012 and Red Rock Lakes NWR in Montana, USA ($N^{\ddagger}$ = 11) in 2009. N_{obs} indicates the number of observations at each area because some Scaup used more than one wintering area.
† Includes observations from one individual that was tracked for > 1 annual cycle.
‡ Includes observations from three individuals that were tracked for > 1 annual cycle.

Breeding area	N_{obs}	Wintering area	City	State/Province	Country	Latitude	Longitude
Yukon Flats NWR	3	San Francisco Bay		CA	USA	37.900	-122.343
Yukon Flats NWR	2	Central Valley	Lost Hills	CA	USA	35.539	-119.728
Yukon Flats NWR	2	La Loba Lake	San Juan	Tamaulipas	Mexico	24.361	-98.625
Yukon Flats NWR	1	Columbia River	Portland	OR	USA	45.646	-122.702
Yukon Flats NWR	1	Humboldt Bay	Eureka	CA	USA	40.738	-124.233
Yukon Flats NWR	1	Agricultural fields and fishponds	Moorhead	MS	USA	33.436	-90.465
Yukon Flats NWR	1	Lake Jacksboro	Jacksboro	TX	USA	33.095	-98.176
Yukon Flats NWR	1	Bay St. Louis		MS	USA	30.417	-89.248
Yukon Flats NWR	1	Rio Grande River	Brownsville	TX	Mexico	25.922	-97.532
Yukon Flats NWR	1	Las Adjuntos Lake	Padilla	Tamaulipas	Mexico	24.043	-98.794
Yukon Flats NWR	1	Contadera Lake	La Pesca	Tamaulipas	Mexico	23.742	-97.854
Yukon Flats NWR	1	San Lorenzo Lake	Nuevo Quintero	Tamaulipas	Mexico	22.987	-98.758
Yukon Flats NWR	1	Lake Miguel Aleman		Oaxaca	Mexico	18.329	-96.617
Yukon Flats NWR	1	Laguna del Rincon	Laguna de Cabral	Independencia	Dominican Republic	18.299	-71.238
Red Rock Lakes NWR	1	Snake River		ID	USA	42.722	-114.822
Red Rock Lakes NWR	1	Great Salt Lake		UT	USA	41.199	-112.192
Red Rock Lakes NWR	1	Rio Grande River	Corrales	NM	USA	35.251	-106.661
Red Rock Lakes NWR	1	Lake Whitney/Brazos River	Lakeside Village	TX	USA	32.036	-97.491
Red Rock Lakes NWR	1	Arnasas NWR		TX	USA	28.378	-96.756
Red Rock Lakes NWR	1	El Sabino	La Barranca	Sinaloa	Mexico	26.410	-108.688

Red Rock Lakes NWR	1	Lic Gustavo Diaz Ordaz (Bacurato)		Sinaloa	Mexico	25.885	-107.903
Red Rock Lakes NWR	1	Baluarte River		Sinaloa	Mexico	23.031	-105.790

Table S3. Spring staging and stopover areas of Lesser Scaup (*Aythya affinis*) marked with platform transmitter terminals (PTTs) at two breeding areas: Yukon Flats National Wildlife Refuge (NWR) in Alaska, USA ($N^{\dagger}$ = 11) in 2012 and Red Rock Lakes NWR in Montana, USA ($N^{\ddagger}$ = 11) in 2009. N_{obs} indicates the number of observations at each area.
† Includes observations from one individual that was tracked for > 1 annual cycle.
‡ Includes observations from three individuals that were tracked for > 1 annual cycle.

Breeding area	N_{obs}	**Spring staging/stopover area**	**City**	**State/ Province**	**Country**	**Latitude**	**Longitude**
Yukon Flats NWR	3	Klamath Region		OR	USA	42.162	-121.644
Yukon Flats NWR	2	Yukon River Region		YT	Canada	63.967	-139.077
Yukon Flats NWR	2	Nordenskiold River Region	Carmacks	YT	USA	62.000	-136.281
Yukon Flats NWR	2	Twin Lakes Region	Florence	SD	USA	45.093	-97.396
Yukon Flats NWR	1	Unnamed Lake North of Joe Guay Island		AK	USA	66.404	-147.422
Yukon Flats NWR	1	Upper Mouth Birch Creek/Yukon Flats NWR		AK	USA	66.268	-145.977
Yukon Flats NWR	2	Yukon River	Eagle	AK	USA	64.901	-141.232
Yukon Flats NWR	1	Stewart River		YT	Canada	63.949	-134.094
Yukon Flats NWR	1	Tsolmund Lake	Northway	AK	USA	62.792	-141.694
Yukon Flats NWR	1	Bennett Lake		YT	Canada	60.161	-134.694
Yukon Flats NWR	1	Wabasa River		AB	Canada	58.231	-115.385
Yukon Flats NWR	1	Hollow Lake	Hollow Lake	AB	Canada	54.248	-112.759
Yukon Flats NWR	1	Chip Lake	Northville	AB	Canada	53.574	-115.216
Yukon Flats NWR	1	Bowron Lake Provincial Park		BC	Canada	53.047	-121.113
Yukon Flats NWR	1	Temapho Lake		BC	Canada	52.411	-123.796
Yukon Flats NWR	1	East of Fraser River	Becher House	BC	Canada	52.058	-122.475
Yukon Flats NWR	1	East of Blackstrap Lake	Shields	SK	Canada	51.841	-106.266
Yukon Flats NWR	1	Pend Oreille River		OR	USA	49.050	-117.469
Yukon Flats NWR	1	Unnamed Lake	Palermo	ND	USA	48.284	-102.241
Yukon Flats NWR	1	Flat Lake	George	WA	USA	47.139	-119.888

Yukon Flats NWR	1	Apple Creek	Apple Valley	ND	USA	46.803	-100.622
Yukon Flats NWR	1	West of Grunneich Waterfowl Production Area		ND	USA	46.225	-99.057
Yukon Flats NWR	1	Lake Billy Chinook		OR	USA	44.583	-121.364
Yukon Flats NWR	1	Lutz Waterfowl Production Area	White Lake	SD	USA	43.750	-98.638
Red Rock Lakes NWR	2	Hutton Lake NWR Region		WY	USA	41.228	-105.842
Red Rock Lakes NWR	2	South Platte River		CO	USA	40.331	-104.309
Red Rock Lakes NWR	1	Stickney	Stickney	SD	USA	43.563	-98.481
Red Rock Lakes NWR	1	Snake River		ID	USA	42.566	-113.743
Red Rock Lakes NWR	1	Thompson Lake	Lakeside	NE	USA	42.087	-102.404
Red Rock Lakes NWR	1	Springfield	Springfield	CO	USA	37.480	-102.420
Red Rock Lakes NWR	1	Salt Lake	Wagon Mound	NM	USA	36.036	-104.649

Table S4. Molting areas of Lesser Scaup (*Aythya affinis*) marked with platform transmitter terminals (PTTs) at two breeding areas: Yukon Flats National Wildlife Refuge (NWR) in Alaska, USA ($N^{\dagger}$ = 11) in 2012 and Red Rock Lakes NWR in Montana, USA ($N^{\ddagger}$ = 11) in 2009. N_{obs} indicates the number of observations at each area.

† Includes observations from one individual that was tracked for > 1 annual cycle.

‡ Includes observations from three individuals that were tracked for > 1 annual cycle.

Breeding area	N_{obs}	**Molting area**	**City**	**State/Province**	**Country**	**Latitude**	**Longitude**
Yukon Flats NWR	9	Yukon Flats NWR		AK	USA	66.312	-148.321
Yukon Flats NWR	2	South of Oscar Island		AK	USA	66.189	-147.822
Red Rock Lakes NWR	7	Red Rock Lakes NWR		MT	USA	44.681	-111.789
Red Rock Lakes NWR	1	Crow Indian Lake	Lethbridge	AB	Canada	49.381	-111.649
Red Rock Lakes NWR	1	Kleinschmidt & Browns Lakes		MT	USA	46.981	-113.047
Red Rock Lakes NWR	1	Lima Reservoir		MT	USA	44.655	-112.364
Red Rock Lakes NWR	1	Island Park Reservoir		ID	USA	44.390	-111.451

Table S5. Fall staging and stopover areas of Lesser Scaup (*Aythya affinis*) marked with platform transmitter terminals (PTTs) at two breeding areas: Yukon Flats National Wildlife Refuge (NWR) in Alaska, USA ($N^{\dagger} = 11$) in 2012 and Red Rock Lakes NWR in Montana, USA ($N^{\ddagger} = 11$) in 2009. N_{obs} indicates the number of observations at each area.
† Includes observations from one individual that was tracked for > 1 annual cycle.
‡ Includes observations from three individuals that were tracked for > 1 annual cycle.

Breeding area	N_{obs}	Fall staging/stopover area	City	State/ Province	Country	Latitude	Longitude
Yukon Flats NWR	3	Tulebagh Lake Region		AK	USA	66.366	-148.640
Yukon Flats NWR	3	Lubicon Lake		AB	Canada	56.425	-115.884
Yukon Flats NWR	2	Roaring Bear Lake		AK	USA	66.361	-148.071
Yukon Flats NWR	2	Marack Lake		AK	USA	66.310	-148.259
Yukon Flats NWR	2	Moberly Lake		BC	Canada	55.901	-120.902
Yukon Flats NWR	2	Klamath Region		OR	USA	42.460	-122.056
Yukon Flats NWR	1	East of Tiinkdhul Lake		AK	USA	66.607	-143.023
Yukon Flats NWR	1	East of Yukon River		AK	USA	66.353	-143.332
Yukon Flats NWR	1	South of Upper Mouth Birch Creek/Yukon Flats NWR		AK	USA	66.332	-146.265
Yukon Flats NWR	1	West of Big Meadow Lake		AK	USA	66.185	-147.181
Yukon Flats NWR	1	Twin Lakes		AK	USA	66.167	-147.510
Yukon Flats NWR	1	West of Diamain Lake	Pelly Crossing	YT	Canada	62.895	-136.371
Yukon Flats NWR	1	Trout Lake		NT	Canada	60.425	-120.776
Yukon Flats NWR	1	Bennett Lake		YT	Canada	60.027	-133.486
Yukon Flats NWR	1	Bistcho Lake		AB	Canada	59.708	-118.716
Yukon Flats NWR	1	Niloil Lake	Coal River	BC	Canada	59.553	-126.982
Yukon Flats NWR	1	Beaver River	Beaver Crossing	AB	Canada	54.360	-110.174
Yukon Flats NWR	1	Chip Lake	Northville	AB	Canada	53.605	-115.270
Yukon Flats NWR	1	Unnamed Lake	Claysmore	AB	Canada	53.436	-110.808
Yukon Flats NWR	1	Lac Natal		SK	Canada	52.983	-106.563

Yukon Flats NWR	1	Narcosli Lake Ecological Reserve		BC	Canada	52.950	-124.108
Yukon Flats NWR	1	Rosita Lake		BC	Canada	52.413	-123.156
Yukon Flats NWR	1	Temapho Lake		BC	Canada	52.339	-123.702
Yukon Flats NWR	1	Goose Lake	Laura	SK	Canada	51.740	-107.359
Yukon Flats NWR	1	Unnamed Lake	Lestock	SK	Canada	51.404	-103.923
Yukon Flats NWR	1	North of Missouri River	White Shield	ND	USA	47.796	-101.677
Yukon Flats NWR	1	Faul Waterfowl Production Area	Goodrich	ND	USA	47.562	-100.084
Yukon Flats NWR	1	Unnamed Lake	McClusky	ND	USA	47.466	-100.328
Yukon Flats NWR	1	Columbia River		OR	USA	46.259	-123.606
Yukon Flats NWR	1	Lake Winnebago		WI	USA	43.941	-88.463
Yukon Flats NWR	1	Lake Texoma		OK	USA	34.110	-96.542
Yukon Flats NWR	1	Tampa Bay		FL	USA	27.898	-82.567
Yukon Flats NWR	1	Unnamed Lake	Sempre		Cuba	20.210	-75.282
Red Rock Lakes NWR	4	Henry's Lake		ID	USA	44.661	-111.430
Red Rock Lakes NWR	2	Island Park Reservoir		ID	USA	44.445	-111.356
Red Rock Lakes NWR	2	Great Salt Lake		UT	USA	41.454	-112.262
Red Rock Lakes NWR	1	Eyebrow Lake	Bridgeford	SK	Canada	50.947	-106.243
Red Rock Lakes NWR	1	Many Island Lake	Medicine Hat	AB	Canada	50.126	-109.891
Red Rock Lakes NWR	1	Yellow Lake	Juno	AB	Canada	49.748	-111.479
Red Rock Lakes NWR	1	Red Rock Lakes NWR		MT	USA	44.612	-111.911
Red Rock Lakes NWR	1	Snake River		ID	USA	42.649	-113.748
Red Rock Lakes NWR	1	South Platte River		CO	USA	40.262	-104.101
Red Rock Lakes NWR	1	Utah Lake		UT	USA	40.186	-111.695
Red Rock Lakes NWR	1	Juantita and Hallenbeck Reservoirs	Grand Junction	CO	USA	38.972	-108.289
Red Rock Lakes NWR	1	Bartlett Lake		NM	USA	36.904	-105.129
Red Rock Lakes NWR	1	Sabine NWR		LA	USA	29.745	-93.608
Red Rock Lakes NWR	1	Rio Mayo	Guaymitas	Sonora	Mexico	27.201	-109.445

Red Rock Lakes NWR	1	Eustaquio Balbuena		Sinaloa	Mexico	25.501	-108.054