

Movements and Habitat Use of White-Fronted Geese (Anser albifrons frontalis) During the Remigial Molt in Arctic Alaska, USA

Authors: Flint, Paul L., and Meixell, Brandt W.

Source: Waterbirds, 40(3): 272-281

Published By: The Waterbird Society

URL: https://doi.org/10.1675/063.040.0308

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Movements and Habitat Use of White-fronted Geese (Anser albifrons frontalis) During the Remigial Molt in Arctic Alaska, USA

PAUL L. FLINT* AND BRANDT W. MEIXELL

U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska, 99508, USA

*Corresponding author; E-mail: pflint@usgs.gov

Abstract.—Proposed oil and gas leasing in the National Petroleum Reserve - Alaska has raised questions about possible impacts of development on molting Greater White-fronted Geese (*Anser albifrons frontalis*) and their habitats. We used GPS transmitters to record fine-scale location data of molting and post-molt White-fronted Geese to assess patterns of movement and resource selection relative to vegetation class, year (2012, 2013), and body mass at capture. Molting White-fronted Geese were located an average of 63.3 ± 4.9 m (SE) from lakeshores. Estimated terrestrial home range size for flightless birds differed between years (2012 = 13.2 ± 2.6 km²; $2013 = 6.5 \pm 1.8$ km²), but did not vary among habitat strata or with body mass. Molting White-fronted Geese used sedge (*Carex aquatilus*) dominated low centered polygons and water more frequently than expected given proportional habitat availability, but avoided tussock tundra and wet sedge vegetation classes. Upon regaining flight, individuals tended to remain in the same general area, and the center of their home range only moved an average of 6.9 km. Greater White-fronted Geese that could fly tended to forage further from lakeshores (= 245 m), and used a larger home range (= 44.3 ± 9.5 km²) than when flightless. *Received 10 March 2017, accepted 19 April 2017*.

Key words.—Anser albifrons frontalis, flightless molt, Greater White-fronted Goose, habitat use, home range, movement rate, National Petroleum Reserve - Alaska.

Waterbirds 40(3): 272-281, 2017

Greater White-fronted Geese (Anser albifrons frontalis; hereafter, White-fronted Geese), like most waterfowl species, undergo a simultaneous molt of their primary and secondary feather tracts (i.e., remigial molt), rendering them flightless for a number of weeks as new flight feathers are grown. Waterfowl typically select specific habitat types for the flightless molt that provide some balance of the following factors: low predation risk, low probability of disturbance, open water escape areas, and an abundant, predictable food supply rich in nutrients essential for feather production (Fox et al. 1995, 2015; Fox and Kahlert 1999, 2000; Lewis et al. 2011). Consistency and predictability of habitats are likely key features because once waterfowl lose their flight feathers, they have limited ability to move in response to changing conditions.

The number of White-fronted Geese spending the summer in the National Petroleum Reserve - Alaska has been increasing in recent years (Flint *et al.* 2008). Within the Teshekpuk Lake Special Area (SA), located in the northeast portion of the National Petroleum Reserve - Alaska, the abundance of White-fronted Geese increased seven fold

between 1976 and 2005 (Derksen et al. 1982; Flint et al. 2008), becoming the most numerous goose species molting in this area (current estimates ~ 41,000; U.S. Fish and Wildlife Service, unpubl. data). Habitats in the Teshekpuk Lake SA include extensive areas of sedges and grasses along the shorelines of coastal inlets and large permafrost thaw lakes, providing molting geese with a rich food source in close proximity to open water refuges (Derksen et al. 1982; Weller et al. 1994). The area also supports relatively low densities of avian (i.e., raptors) and mammalian [e.g., Arctic fox (Vulpes lagopus)] predators and, because of its remote Arctic location, is largely free of human activities and associated disturbances.

Construction of the first oil production facility in the National Petroleum Reserve - Alaska was recently initiated, and proposals for future development of known oil and gas deposits (Nandanwar *et al.* 2016) have raised questions about the effects of disturbance on molting White-fronted Geese (Bureau of Land Management 2015). The Bureau of Land Management is required to provide conditions, restrictions, and prohibitions deemed necessary to protect wildlife and

mitigate effects of oil and gas leasing on lands they manage (Bureau of Land Management 2015). Understanding how locally abundant species select habitats and move across the landscape is required for prioritizing site selections for developments and defining appropriate operating stipulations and procedures to achieve management goals. Waterfowl, in general, can be vulnerable to disturbance during the flightless wing molt (Bergman 1973; Madsen 1984; Mosbech and Glahder 1991), and several species of geese have been shown to be sensitive to various disturbance stimuli throughout the annual cycle, including the wing molt period (Owens 1977; Ward et al. 1994; Fox et al. 2015). In particular, studies have documented spatial displacement and substantial shifts in behavior for multiple species of molting geese as a result of aircraft over-flights (Madsen 1984; Jensen 1990; Miller et al. 1994), which are regular occurrences in areas of Arctic oil and gas development.

Our goals were to quantify patterns of movement and habitat use by molting White-fronted Geese in the Teshekpuk Lake SA. We sought to describe habitat selection and primary measures of habitat use (i.e., home range sizes and movement patterns). We assessed evidence that preferred habitat was limited in either quantity or spatial distribution because development is more likely to have negative effects on birds if habitat is limited. Under a scenario of habitat limitation, we expected to see preference for an uncommon habitat type, small and slow movements within preferred patches, and large, rapid movements between patches. We hypothesized that shifts in habitat use between when birds were flightless and when they regained flight would be indicative of habitat limitation and/or preference relative to escape habitat.

METHODS

Study Area

We conducted our study within the Teshekpuk Lake SA (70° 47′ 08.01″ N, 150° 12′ 03.21″ W) during the summers of 2012 and 2013. Boggs *et al.* (2013) analyzed satellite imagery at 30-m pixel resolution

and defined and described the four dominant vegetation classes on our study area as: 1) water sedge (Carex aquatilis) low centered polygon class (i.e., Carex LCP) that occurs on low slope areas with lowcenter ice-wedge polygons. The polygon centers typically have standing water with marsh and wet sedge vegetation, primarily water sedge and tall cottongrass (Eriophorum angustifolium); 2) wet sedge class (i.e., wet sedge) that occurs on sites with 0-10% visible surface water and more than 20% cover of sedge species. Sites are flat to sloping in valley bottoms, drained lake basins, water tracks, and adjacent to streams. Patch size is small to moderate and may be linear. Sites are typically dominated by water sedge and tall cottongrass but may also be dominated or co-dominated by other Carex or Eriophorum species; 3) herbaceous-dominated tussock tundra class (i.e., tussock tundra) that occurs in valleys and slopes, and these sites are permafrost dominated, poorly drained, and underlain by mesic, silty mineral soils with a shallow surface organic layer surrounding the tussocks. Patch size is small and matrix-forming. Tussock cottongrass (E. vaginatum) is the primary tussock former in most stands, but Bigelow's sedge (C. bigelowii) may dominate some sites. Shrubs in the over-story are less than 25% cover; and 4) water class that included the large lakes identified in the National Hydrography Dataset (U.S. Geological Survey 2013) as well as smaller wetlands and flooded habitats.

Capture and Marking

We captured flightless White-fronted Geese by herding them into corral traps with a helicopter. From the flock captured on each lake, we selected one adult male and one adult female (that had recently dropped their primaries) and marked these birds with neck collars containing global positioning system (GPS) recording transmitters (Telemetry Solutions). Marked birds were released back into molting flocks. Detailed data on individual molting White-fronted Geese are difficult to collect because birds respond to visual and audible observer disturbance by retreating to open water, even when observers are great distances (> 1 km) away (P. L. Flint, pers. obs). To avoid these observer effects, we used GPS transmitters that collected location data on programmable intervals and offloaded data remotely. This allowed us to collect data on habitat use patterns of White-fronted Geese without our presence altering their behavior. During 2012, we marked 21 White-fronted Geese from 4-8 July and during 2013, we marked 32 White-fronted Geese from 7-11 July. We monitored transmitter-marked birds throughout the flightless molt and during the period immediately after they regained flight. Both years of our study experienced high rates of transmitter failure, as verified by sudden loss of transmitter signals from flightless individuals (i.e., birds that could not move out of our reception range) and transmitters that could be located but would not offload data. As such, we had cases with incomplete data for the entire flightless period, and our effective sample size was reduced.

GPS transmitters had a predicted location error range of 3 m. Transmitters were glued to standard plastic neck collars, and the entire assembly weighed 80-85 g. Transmitters were programmed to obtain a GPS fix every 4 hr; remote download of location data was obtained via UHF radio transmission. We downloaded transmitter data twice per season (28 July and 11 August 2012, 30 July and 11 August 2013) from fixed-wing aircraft equipped with wing-mounted antennas that maintained an altitude as high as possible given weather conditions (typically > 300 m). We had a single case where a bird died and the collar apparently remained in the same location for 9 days. During this period, 51 locations were recorded with an average deviance of 3 m and a maximum of 9 m. We believe the accuracy of our locations was within the predicted range.

Data Analyses

We quantified patterns of White-fronted Goose movement and habitat use during, and immediately following, their flightless molt period, requiring that we separate molt data (i.e., flightless) from post-molt data (i.e., flighted). To differentiate these two stages, we used an algorithm based on the assumption that movement rates of White-fronted Geese were substantially reduced during the flightless period. Our algorithm, similar to one described by Lewis et al. (2010), identified the dates that movement rates distinctly increased beyond what had been measured for a given flightless bird, allowing us to objectively define dates of molt termination for each transmitter-marked individual. Because birds were flightless at the time of marking, the movement rates over the next several weeks provided a robust measure of the mean and variance in movement rates for flightless individuals. The algorithm used a running average, and associated variance, for each individual in an iterative sequential fashion to search for the first day that observed movement exceeded that measured while flightless. All subsequent analyses of GPS location data were divided into the periods of molt and post-molt.

We measured four variables indicative of habitat use and movements of molting White-fronted Geese: 1) distance to lakeshore; 2) movement rate; 3) total home range; and 4) terrestrial home range. We also assessed use of specific habitats within home ranges by comparing the proportion of GPS locations that occurred in a given vegetation class (i.e., proportion used) in relation to the total proportion of each vegetation class available. To quantify distance to shore (m), we measured the minimum distance from each land-based point location to the nearest lakeshore as defined by the National Hydrography Dataset (U.S. Geological Survey 2013). We considered distance to lakeshore indicative of distance from potential escape habitat (i.e., open water). To quantify movement rate (m/hr), we measured the straight-line distance and time elapsed between successive GPS point locations, thus producing N-1 estimates of movement rate per individual, where N is the total number of point locations. For our estimates of home range, we calculated 95% fixed kernel home ranges with least squares cross-validation (Kernohan

et al. 2001) using the Animal Movement extension in ArcView (Hooge and Eichenlaub 1997). We used all of an individual's GPS locations (i.e., land and water) in our entire home range calculations. Because estimates of home range sizes are sensitive to the number of locations obtained per transmitter (Seaman et al. 1999), and because some of our transmitters failed before the completion of molt, we included the number of days sampled in our analyses. Terrestrial home ranges were calculated by removing large bodies of water as identified using the National Hydrography Dataset (U.S. Geological Survey 2013) from the 95% home range isopleth. Thus, terrestrial home ranges account for the fact that birds tend to forage around the perimeter of large lakes, and thereby exclude large expanses of open water. Whereas estimates of entire home range depict the total area encompassing GPS locations, estimates of terrestrial home range provide a clearer description of the habitats used for foraging.

Our evaluation of variation in movement and habitat use patterns of molting White-fronted Geese consisted of repeated locations every 4 hr from marked individuals and a suite of characteristics measured one time for each individual. Therefore, assessment of the effect of a given variable required first calculating the amount of variation that occurred among individuals; this established the maximum degree of variation that could be explained by individual characteristics. If significant variation occurred among individuals, then a model where characteristics were used in place of the individual identifier were examined to assess potential relationships. For home range, each individual had one estimate, thus not requiring a repeated-measures design. We considered the following explanatory variables: year, body mass, habitat strata, and vegetation class. Year included the two years (2012, 2013) in which GPS transmitters were deployed. Body mass (g) was measured at the time birds were captured and marked with transmitters and was included to assess potential effects of body condition on patterns of use. Habitat stratum was a categorical variable defined as coastal, inland, or upland. Coastal habitats were characterized by the occurrence of saltwater or saltwater intrusion, elevations ≤ 1.5 m, and salt-tolerant plant communities; inland habitats lacked saltwater intrusion, occurred at intermediate elevations (> 1.5 m to \leq 4 m), and were characterized by predominantly freshwater plant communities; and the upland stratum was defined by freshwater habitat and elevations > 4 m (Flint et al. 2008; Fig. 1).

To assess habitat selection within home ranges, we used a GIS coverage of vegetation classifications (Boggs et al. 2013; Fig. 1). Using these defined habitats, we calculated the proportion of each vegetation class that occurred within each bird's terrestrial home range (i.e., excluding large water bodies) and used these estimates as the proportional availability by vegetation class. We also classified each GPS point location in terms of vegetation class and calculated the proportion of all locations for an individual in each class. We estimated the selection coefficient for each vegetation class as proportional use minus proportional availability. If birds use

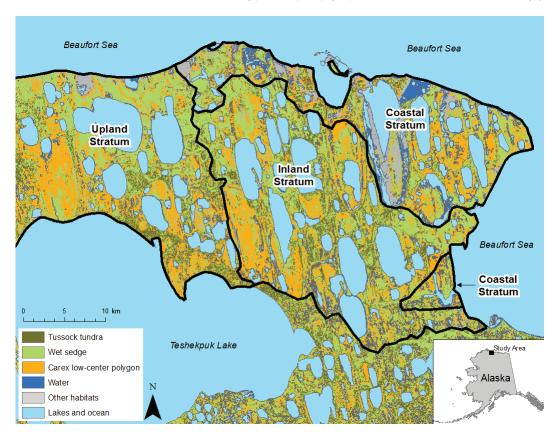


Figure 1. Molting goose region of the Teshekpuk Lake Special Area in Arctic Alaska. The overall area was dominated by four habitat types. Strata used in analyses are identified.

habitats randomly (i.e., in proportion to their availability), then the expected selection coefficient is 0. We tested if selection coefficients were significantly different from 0 using a randomization test. We randomly selected individual birds with replacement until the original sample size was obtained, then recalculated the availability and use of each vegetation class for each sample and estimated the selection coefficients. We repeated this process 100 times for each group and determined if the 95% CI for the population of selection coefficients included 0. We conducted this analysis for both molting and post-molt terrestrial home ranges.

RESULTS

Forty-four GPS transmitters operated for the majority of the molt period; 31 remained functional and provided information during the immediate post-molt period when birds could fly. There was no relationship between estimated home range size and the number of days that transmitters operated. The mean

number of GPS locations per individual during molt was 156 ± 8.1 and 118 ± 4.7 in 2012 and 2013, respectively. The average flightless period was 30.1 ± 0.8 days (Range = 27-34) and 29.0 ± 0.4 days (Range = 26-32) in 2012 and 2013, respectively. On average, point locations of flightless White-fronted Geese were 64 ± 5 m from the nearest lakeshore. However, the distribution of land-based locations collected by transmitters relative to the nearest lakeshore was skewed; only 19% of locations were > 100 m and 31% were < 20 m from shore (Table 1). Only 14% of the variation in distance to lakeshore occurred among individuals. A model using the mean value of distance to lakeshore for each bird explained little of the among-individual variation ($r^2 = 0.09$), and there was no variation in distance to lakeshore by year (F_{139}) = 0.17, P = 0.69), stratum ($F_{2.39}$ = 1.68, P = 0.21), or body weight at capture ($F_{1.39}$ = 0.57,

P = 0.57). Once individuals regained flight, mean distance to lakeshore increased to 248 \pm 8 m.

White-fronted Geese moved an average of 128 ± 5 m/hr while flightless (Table 1). Because travel patterns between successive point locations are unknown, our estimates of movement rates represent minimums. Only 5% of the variation in movement rate occurred among individuals. A model using the average value of movement rate per individual explained 33% of the variation among individuals, with movement rate varying by year ($F_{1,36} = 9.33, P < 0.01$) and stratum ($F_{2.36} = 3.43$, P = 0.04), but not by body mass at capture ($F_{1.36} = 1.23$, P = 0.28). Parameter estimates indicated that Whitefronted Geese molting within the intermediate inland strata moved at rates 38 ± 29 m/hr faster than those in coastal habitats. Parameter estimates for year indicated that Whitefronted Geese moved 40 ± 13 m/hr faster in 2012 than in 2013.

The average entire home range used by flightless White-fronted Geese was $20.7 \pm 4.2 \text{ km}^2$ in 2012 and $9.9 \pm 1.7 \text{ km}^2$ in 2013. The mean terrestrial home range size used by flightless White-fronted Geese was $13.2 \pm 2.6 \text{ km}^2$ in 2012 and $6.5 \pm 1.1 \text{ km}^2$ in 2013 (Table 2; Fig. 2). Terrestrial home range size

only varied by year $(F_{1,37} = 6.99, P = 0.01)$ and not with body mass $(F_{1,37} = 1.51, P = 0.23)$, stratum $(F_{2,37} = 0.70, P = 0.50)$, or number of days monitored $(F_{1,37} = 1.31, P = 0.26)$.

When using all available points (i.e., all individuals combined) to estimate a single home range, three vegetation classes and water dominated the landscape and accounted for > 95% of the area (Table 3). Taking this as the landscape-scale definition of availability, the habitat composition of individual home ranges appeared to be a random sample of available habitats. Within molting terrestrial home ranges, we found evidence of selection for Carex LCP and water, but avoidance of tussock tundra and wet sedge classes. Wet sedge was the most common vegetation class within home ranges (45%), but only about 25% of locations occurred within this class. As such, wet sedge meadows were commonly used, but were used less than their availability on the landscape.

We monitored movements and habitat use for a brief period after marked individuals regained flight (average 7.2 days in 2012 and 4.3 days in 2013). As expected, movement rate, escape distance, and home range all increased once birds began to fly (Tables 1 and 2). Individuals did not move far when

Table 1. Summary statistics for movement rate and escape distance of White-fronted Geese marked with GPS transmitters in the Teshekpuk Lake Special Area in Arctic Alaska, 2012-2013. Movement rate is the straight line distance between successive GPS locations with time spans < 12 hr. Distance to lakeshore is measured from each GPS location to the shoreline of the nearest mapped wetland.

	2	012	2013		
Metric	Molt	Fly	Molt	Fly	
Movement rate (m/hr)					
Average	148.0	372.1	117.2	255.3	
Median	96.0	159.6	75.2	101.2	
Minimum	0.0	0.7	0.0	0.0	
Maximum	1,226.1	8,227.3	1,145.4	5,437.8	
SD	154.7	821.2	75.2	443.8	
Count	2,599	433	3,415	541	
Distance to lakeshore (m)					
Average	70.1	236.9	61.1	256.5	
Median	47.2	176.7	40.5	165.7	
Minimum	0.0	0.0	0.0	0.0	
Maximum	970.5	1,105.1	1,068.4	1,679.2	
SD	90.1	241.4	83.7	273.2	
Count	2,624	441	3,590	587	

Table 2. Summary statistics for home range size of White-fronted Geese marked with GPS transmitters in the Teshekpuk Lake Special Area in Arctic Alaska, 2012-2013. Entire home range is the 95% fixed kernel home range. Terrestrial home range is the entire home range with large expanses of open water removed.

	2012				2013					
	Molt		Fly		N	ſolt	Fly			
Metric	Entire	Terrestrial	Entire	Terrestrial	Entire	Terrestrial	Entire	Terrestrial		
Average	20.7	13.2	69.0	48.2	9.9	6.5	59.4	42.6		
Median	13.6	8.7	17.3	15.3	6.2	4.2	32.4	22.1		
Minimum	3.2	2.3	2.0	1.8	0.8	0.6	0.8	0.8		
Maximum	55.6	31.6	220.2	149.7	38.7	26.4	224.1	167.9		
SD	4.2	2.6	86.0	58.2	1.7	1.17	1.9	50.8		
Count	17	17	9	9	27	27	21	21		

they regained flight; average distance between centroids of molting and post-molt home range was 6.9 km. Within home ranges, there was an increase in the use of wet sedge habitats and a decrease in use of water once birds regained flight (Table 3). Otherwise, there was little change in the habitat

composition of home ranges between molting and post-molting birds (Table 3).

DISCUSSION

White-fronted Geese molt along a wide range of lake sizes across a gradient of habi-

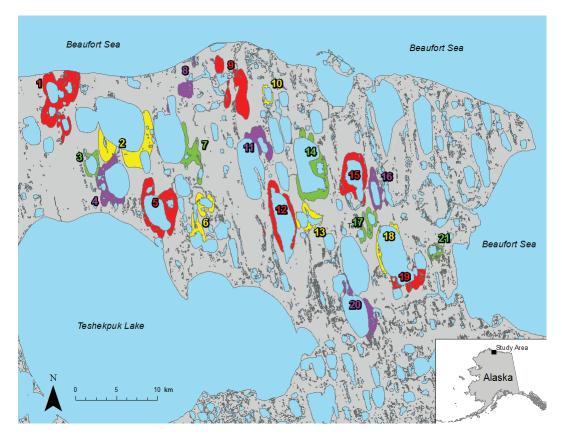


Figure 2. A sample of 21 molting White-fronted Goose terrestrial home ranges estimated from birds marked with GPS data logging transmitters within the Teshekpuk Lake Special Area in Arctic Alaska, 2012-2013. Each color and number combination denotes a different individual.

Table 3. Habitat use and availability comparisons for White-fronted Geese marked with GPS transmitters during the flightless wing molt in the Teshekpuk Lake Special Area in Arctic Alaska, 2012-2013. Vegetation classes are defined by Boggs et al. (2013) and Carex LCP is an abbreviation for Carex aquatilis low centered polygon. Used is the percentage of GPS locations that occurred within each vegetation class; bold in the Used column indicates significant difference between Used and Available for that vegetation class in that year. Available is the percentage of each vegetation class that occurred within home ranges of marked birds; bold in the Available column indicates significant difference between the proportions of vegetation classes within home ranges compared to overall availability. Overall Available is the percentage of each vegetation class occurring within the entire study area. The 95% confidence intervals (CI) are based on bootstrap resampling.

		2012						Overall			
Status	Vegetation Class	Used (%)	95% CI	Available	95% CI	1	Used (%)	95% CI	Available (%)	95% CI	Available (%)
Molt											
	Wet sedge	27.5	20.4-32.4	45.0	39.2-50.9		22.8	18.8-26.8	3 43.5	37.1-48.9	45.3
	Carex LCP	41.7	34.4-46.6	32.9	26.1-38.2		41.1	35.1-46.5	34.8	30.2-41.1	31.2
	Tussock tundra	5.8	2.8-9.7	12.1	8.1-15.3		6.3	4.2-8.5	11.7	9.1-14.1	14.1
	Water	14.6	11.6-18.6	5.5	4.0 - 7.0		21.1	16.4-25.2	6.5	4.6 - 8.0	4.6
Post-molt											
	Wet sedge	38.7	28.3-48.5	45.2	36.8-53.5		33.2	26.0-39.5	47.5	39.8-55.0	42.3
	Carex LCP	41.4	33.5-49.9	32.9	26.0-41.3		42.9	38.0-47.4	33.1	26.3-39.1	32.9
	Tussock tundra	7.6	2.3-16.5	12.5	6.5-17.1		7.8	4.0-11.8	9.5	6.8-12.3	13.1
	Water	5.3	2.4 - 8.7	4.8	3.5-6.3		8.4	3.2-14.	45.4	3.7-7.2	6.2

tat strata within the Teshekpuk Lake SA. We found little evidence of selection for specific vegetation classes or patterns of movement among these strata, and there was no major shift in habitat use between the flightless molt and when individuals regained flight. The most commonly used vegetation classes are widely distributed and comprise > 75% of the landscape. Hence, White-fronted Geese molting in the Teshekpuk Lake SA appear to be habitat generalists, and there is no indication that foraging habitat is limiting. Molting Black Brant (Branta bernicla nigricans) in the Teshekpuk Lake SA showed a clear shift from freshwater to coastal estuaries upon regaining flight, suggesting that coastal areas provided superior habitat as compared to that used during molt (Lewis et al. 2011). Conversely, molting Whitefronted Geese tended to remain in the same general area when they regained flight, but used habitats further from open water once the constraint of running to escape habitat had been removed. For the metrics of movement rate and distance to escape habitat, the majority of the variation occurred within individuals. As such, individuals have considerable flexibility to adjust their movement rate and escape distance as localized conditions vary, but it is unclear what factors may influence the within-individual variation in movement rate and escape distance. The number of White-fronted Geese molting in the Teshekpuk Lake SA has increased seven fold in recent years (Flint *et al.* 2008). We interpret the increase in numbers along with the broad extent of the commonly used vegetation classes to indicate that White-fronted Geese are habitat generalists with no indication that habitat is limiting.

Average home range size of molting birds was considerably larger in 2012 than 2013, which corresponded with higher movement rates in 2012. It is possible that the higher movement rates and larger home ranges are indicative of lower forage quality in 2012. That is, birds were forced to move faster and farther in search of adequate forage. We have no data on mass loss or other parameters that would validate this explanation. Certainly, 2012 was considerably warmer than 2013 in Arctic Alaska (Van Hemert et al. 2015). Under warmer conditions, Arctic plants may produce higher biomass of slightly lower quality (i.e., % nitrogen) forage (Doiron et al. 2014). Alternatively, under relatively warmer conditions, there may have been little advantage for roosting to

conserve energy (Fox et al. 2015) such that birds spent more time moving because there was little cost to that behavior. Lewis et al. (2011) also found annual variation in movement rates of molting Black Brant in the Teshekpuk Lake SA, but reported the opposite pattern where birds moved faster in a colder year. Given these opposing patterns for two species molting in the same area, we suspect that our relationship between movement rate and temperature is spurious. Other factors that we have no data on, such as predator numbers or disturbance, may be more important determinants of movement rates and home range size.

White-fronted Geese used somewhat larger home ranges during the flightless period than did sympatric Black Brant (Lewis et al. 2011). However, Black Brant were also typically found much closer to the water (i.e., 31 m) than White-fronted Geese. This difference is likely a consequence of body size and associated vulnerability to fox predation as well as forage requirements. Black Brant, being completely unable to defend against foxes, are constrained to a much narrower swath of land along the margin of waterbodies, resulting in a smaller home range. Further, larger body size may infer less specific forage requirements, allowing White-fronted Geese to forage further from water. Thus, larger home range size for White-fronted Geese compared to Black Brant may be the result of species-specific requirements for escape and foraging habitats.

Flightless White-fronted Geese were located within close proximity to shore in all habitat types. Of the > 6,200 land-based GPS locations obtained from flightless birds, only 19% were > 100 m from the shore of a mapped lake. Small bodies of water that are unmapped could also function as escape habitat. As such, we believe it is rare that molting White-fronted Geese are found more than 100 m from water. Similarly, Greylag (A. anser), Pink-footed (A. brachyrhynchus), and Barnacle (B. leucopsis) geese were all shown to feed within 150 m of shore during the flightless molt (Madsen and Mortensen 1987; Fox and Kahlert 2000). Kristiansen and Jarrett (2002) reported that both molt-

ing Greenland White-fronted (A. a. falvirostris) and Canada (B. canadensis) geese rarely fed > 60 m from shore. The consistency of this behavior across multiple goose species and diverse molting areas suggests relatively rigid molting habitat requirements, namely ample food resources adjacent to open water. Moreover, the consistency of this behavior suggests that proximity to shore is driven by a common selective pressure. Fox and Kahlert (2000) found that Greylag Geese on a small island commonly fed far from shore while flighted, yet remained exclusively near shore during the flightless molt. Given that most species of flightless geese readily take to open water when disturbed, Fox and Kahlert (2000) concluded that proximity to shore is driven by predation risk, as opposed to food availability. Similarly, while many of the vegetation classes (and presumably the same forage plant species) used by Whitefronted Geese are located close to wetland shorelines in the Teshekpuk Lake SA, these habitats also commonly occur at distances > 100 m from shore (Markon and Derksen 1994; Boggs et al. 2013). Once birds regained flight, they used the same habitat types, but were found further from lakeshores of mapped wetlands.

The area within the Teshekpuk Lake SA that is used by molting White-fronted Geese is dominated by a few vegetation classes. The most common are identified as Carex LCP and wet sedge (Boggs et al. 2013). The detailed descriptions of these classes identifies both as being dominated by water sedge and tall cottongrass with the primary difference being that Carex LCP consists of patterned ground where the majority of the polygon may be flooded. Wet sedge habitat consists of either high-centered polygons, where the margins of the polygons are flooded, or nonpatterned ground. As such, there is likely little difference in forage plant species between these two vegetation classes, but rather a difference in how water is distributed within these habitats. Greater than 63% of GPS locations occurred in these two vegetation classes, and we infer that these plants likely represent the dominant forage for molting White-fronted Geese in the Teshekpuk Lake

SA. The finding that wet sedge habitat was used significantly less than available should not be used to infer that this vegetation class was completely avoided; it was in fact the second most commonly used habitat. Preference for the Carex LCP vegetation class when it contains the same forage plant species as wet sedge habitats may indicate that the wet sedge class occurred further away from escape habitat (i.e., open water). Use of the wet sedge vegetation class increased once birds regained flight, supporting the idea that the avoidance during molt was related to escape. We found no indication that home ranges were selected to target a specific subset of vegetation classes. Further, there was little change in the proportional representation of vegetation classes or patterns of use of vegetation classes between molting and flighted home ranges. Thus, we see little indication of habitat-based limitation for molting White-fronted Geese.

Molting Black Brant in the Teshekpuk Lake SA only remained flightless for about 3 weeks, and were able to fly before primaries were fully grown (Taylor 1996). Because birds in our study were marked after they had already lost their flight feathers, we were surprised that most of our marked sample remained apparently flightless for < 4 weeks. We suspect that this represents a case where White-fronted Geese could have flown earlier, but chose not to. Black Brant molting in the Teshekpuk Lake SA showed a clear pattern where they shifted habitat types as soon as they could fly (Lewis et al. 2011). As such, Black Brant may have had a reason to fly as soon as possible. In contrast, molting Whitefronted Geese showed little evidence of a shift in habitat use once they regained flight. Therefore, the relatively longer duration of the apparent flightless period we estimated for White-fronted Geese may indicate that there was little reason or incentive for birds to fly before their wings were fully developed.

Our results demonstrate that flightless White-fronted Geese maintain fairly small home ranges across a gradient of habitats, suggesting that suitable habitat for this species is widely distributed in the Teshekpuk Lake SA. The only constraint we could document

was the apparent need to molt within 100 m of a wetland (i.e., potential escape habitat). White-fronted Geese appear to focus their activity in areas dominated by water sedge and tall cottongrass, and show some preference for polygonal patterned ground. A comparison of forage plant nutrient quality between habitat types would be useful for explaining our results. Given the apparent widespread availability of suitable habitat in the National Petroleum Reserve - Alaska together with the total potential area available to molting White-fronted Geese, the effect of a limited number of localized displacements resulting from disturbance/development would not likely be measureable at the population level.

Acknowledgments

This work was part of the U.S. Geological Survey's (USGS) Changing Arctic Ecosystem Initiative and was supported by funding from the Wildlife Program of the USGS Ecosystem Mission Area. The Bureau of Land Management provided financial and logistical support. Aerial support was provided by Pollux Aviation and Arctic Air Alaska. We thank T. Lewis and J. Terrenzi for assistance with GIS based analyses and numerous technicians for assistance with goose captures and aerial telemetry. Comments on a draft of this manuscript were provided by T. Fox, J. Pearce, D. Nigro and three anonymous reviewers. Use of trade, product, or company names is solely for descriptive purposes and does not imply endorsement by the U.S. Government. All applicable ethical guidelines for the use of birds in research have been followed, including those presented in the Ornithological Council's "Guidelines to the Use of Wild Birds in Research." All procedures were approved by the USGS Alaska Science Center Animal Care and Use Committee (2011-10), and were authorized under USGS Bird Banding and Marking Permit (20022), U.S. Fish and Wildlife Service scientific permit (MB789758), and Bureau of Land Management permit (BLM AK FF09571). Data presented in this paper are publicly available via the USGS Alaska Science Center at https://doi.org/10.5066/F7PR7TG8.

LITERATURE CITED

Bergman, R. D. 1973. Use of southern boreal lakes by post-breeding Canvasbacks and Redheads. Journal of Wildlife Management 37: 160-170.

Boggs, K., T. V. Boucher, T. T. Kuo, D. Fehringer and S. Guyer. 2013. Vegetation map and classification: Northern, Western and Interior Alaska. Alaska Natural Heritage Program, University of Alaska Anchorage, Anchorage, Alaska. http://accs.uaa.alaska.edu/vegetation-ecology/vegetation-map-northern-western-and-interior-alaska/, accessed 26 April 2017.

- Bureau of Land Management. 2015. Supplemental environmental impact statement for the Alpine satellite development plan for the proposed Greater Mooses Tooth One development project. Record of Decision. Unpublished report, U.S. Department of the Interior, Bureau of Land Management, Anchorage, Alaska.
- Derksen, D. V., W. D. Eldridge and M. W. Weller. 1982. Habitat ecology of Pacific Black Brant and other geese moulting near Teshekpuk Lake, Alaska. Wildfowl 33: 39-57.
- Doiron, M., G. Gauthier and E. Levesque. 2014. Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore. Journal of Ecology 102: 508-517.
- Flint, P. L., E. J. Mallek, R. J. King, J. A. Schmutz, K. S. Bollinger and D. V. Derksen. 2008. Changes in abundance and spatial distribution of geese molting near Teshekpuk Lake, Alaska: interspecific competition or ecological change? Polar Biology 31: 549-556.
- Fox, A. D. and J. Kahlert. 1999. Adjustments to nitrogen metabolism during wing moult in Greylag Geese, *Anser anser*. Functional Ecology 13: 661-669.
- Fox, A. D. and J. Kahlert. 2000. Do moulting Greylag Geese *Anser anser* forage in proximity to water in response to food availability and/or quality? Bird Study 47: 266-274.
- Fox, A. D., P. L. Flint, W. L. Hohman and J.-P. L. Savard. 2015. Waterfowl habitat use and selection during the remigial moult period in the northern hemisphere. Pages 131-168 in Ecology and Conservation of Waterfowl in the Northern Hemisphere (E. C. Rees, R. M. Kaminski and E. B. Webb, Eds.). Wildfowl Special Issue 4, Wildfowl and Wetlands Trust, Slimbridge, Gloucestershire, U.K.
- Fox, A. D., J. Kahlert, H. Ettrup, H. Nilsson and J. P. Hounisen. 1995. Moulting Greylag Geese *Anser anser* on the Danish island of Saltholm; numbers, phenology, status and origins. Wildfowl 46: 16-30.
- Hooge, P. N. and B. Eichenlaub. 1997. Animal movement extension to Arc-View v. 1.1. Unpublished report, U.S. Department of the Interior, Geological Survey, Alaska Biological Science Center, Anchorage, Alaska.
- Jensen, K. C. 1990. Responses of molting Pacific Brant to experimental aircraft disturbance in the Teshekpuk Lake Special Area, Alaska. Ph.D. Thesis, Texas A&M University, College Station.
- Kernohan, R. E., B. A. South and S. S. Walls. 2001. Analysis of animal space use and movements. Pages 125-166 in Radio Tracking and Animal Populations (J. J. Millspaugh and J. M. Marzluff, Eds.). Academic Press, San Diego, California.
- Kristiansen, J. N., and N. S. Jarrett. 2002. Inter-specific competition between Greenland White-fronted Geese Anser albifrons flavirostris and Canada Geese Branta canadensis interior moulting in West Greenland: mechanisms and consequences. Ardea 90: 1-13.

- Lewis, T. L., P. L. Flint, J. A. Schmutz and D. V. Derksen. 2010. Pre-moult patterns of habitat use and moult site selection by Brant Geese *Branta bernicla nigri*cans: individuals prospect for moult sites. Ibis 152: 556-568
- Lewis, T. L., P. L. Flint, D. V. Derksen and J. A. Schmutz. 2011. Fine scale movements and habitat use of Black Brant during the flightless wing molt in Arctic Alaska. Waterbirds 34: 177-185.
- Madsen, J. 1984. Study of the possible impact of oil exploration on goose populations in Jameson Land, East Greenland. Norsk Polarinstitutt Skrifter 181: 141-151
- Madsen, J. and C. E. Mortensen. 1987. Habitat exploitation and interspecific competition of moulting geese in East Greenland. Ibis 129: 25-44.
- Markon, C. J. and D. V. Derksen. 1994. Identification of tundra land cover near Teshekpuk Lake, Alaska using SPOT satellite data. Arctic 47: 222-231.
- Miller, M. W., K. C. Jensen, W. E. Grant and M. W. Weller. 1994. A simulation model of helicopter disturbance of molting Pacific Black Brant. Ecological Modeling 73: 293-309.
- Mosbech, A. and C. Glahder. 1991. Assessment of the impact of helicopter disturbance on moulting Pink-footed Geese Anser brachyrynchus and Barnacle Geese Branta leucopsis in Jameson Land, Greenland. Ardea 79: 233-238.
- Nandanwar, M. S., B. J. Anderson, T. Ajayi, T. S. Collett and M. V. Zyrianova. 2016. Evaluation of gas production potential from gas hydrate deposits in National Petroleum Reserve Alaska using numerical simulations. Journal of Natural Gas Science and Engineering 36: 760-772.
- Owens, N. W. 1977. Responses of wintering Brent Geese to human disturbance. Wildfowl 28: 5-14.
- Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raideke and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63: 739-747.
- Taylor, E. J. 1996. Molt of Black Brant (*Branta bernicla nigricans*) on the Arctic Coastal Plain, Alaska. Auk 112: 904-919.
- U.S. Geological Survey. 2013. National hydrography geodatabase: the national map. U.S. Geological Survey, Reston, Virginia. http://viewer.nationalmap. gov/viewer/nhd.html?p=nhd, accessed 25 April 2017.
- Van Hemert, C., P. L. Flint, M. Udevitz, J. Koch, T. Atwood, K. Oakley and J. M. Pearce. 2015. Forecasting wildlife response to rapid warming in the Alaskan Arctic. BioScience 65: 718-728.
- Ward, D. H., R. A. Stehn and D. V. Derksen. 1994. Response of staging Brant to disturbance at the Izembek Lagoon, Alaska. Wildlife Society Bulletin 22: 220-228.
- Weller, M. W., K. C. Jensen, E. J. Taylor, M. W. Miller, K. S. Bollinger, D. V. Derksen, D. Esler and C. J. Markon. 1994. Assessment of shoreline vegetation in relation to use by molting Black Brant Branta berni-