ARCTIC
VOL. 69, NO. 1 (MARCH 2016) P. 19 – 28
http://dx.doi.org/10.14430/arctic4544

Habitat Use and Foraging Patterns of Molting Male Long-tailed Ducks in Lagoons of the Central Beaufort Sea, Alaska

Paul L. Flint,[1,2] John A. Reed,[1] Deborah L. Lacroix[1,3] and Richard B. Lanctot[1,4]

(*Received 15 April 2015; accepted in revised form 27 August 2015*)

ABSTRACT. From mid-July through September, 10 000 to 30 000 Long-tailed Ducks (*Clangula hyemalis*) use the lagoon systems of the central Beaufort Sea for remigial molt. Little is known about their foraging behavior and patterns of habitat use during this flightless period. We used radio transmitters to track male Long-tailed Ducks through the molt period from 2000 to 2002 in three lagoons: one adjacent to industrial oil field development and activity and two in areas without industrial activity. We found that an index to time spent foraging generally increased through the molt period. Foraging, habitat use, and home range size showed similar patterns, but those patterns were highly variable among lagoons and across years. Even with continuous daylight during the study period, birds tended to use offshore areas during the day for feeding and roosted in protected nearshore waters at night. We suspect that variability in behaviors associated with foraging, habitat use, and home range size are likely influenced by availability of invertebrate prey. Proximity to oil field activity did not appear to affect foraging behaviors of molting Long-tailed Ducks.

Key words: *Clangula hyemalis*; disturbance; diurnal; home range; radio telemetry

RÉSUMÉ. De la mi-juillet jusqu’au mois de septembre, de 10 000 à 30 000 hareldes kakawis (*Clangula hyemalis*) se servent des systèmes de lagunes du centre de la mer de Beaufort pour la mue de leurs rémiges. On en sait peu au sujet de leurs comportements et de leurs habitudes de recherche de nourriture pendant cette période sans vol. À l’aide d’émetteurs radio, nous avons suivi des hareldes kakawis mâles pendant la période de mue des années 2000 à 2002 dans trois lagunes : une adjacente à des travaux de mise en valeur industrielle du pétrole et deux, dans deux zones où il n’y a pas d’activité industrielle. Nous avons constaté que pendant la période de mue, l’indice du temps consacré à la recherche de nourriture augmentait de manière générale. La recherche de nourriture, l’utilisation de l’habitat et la taille du domaine vital affichaient des tendances semblables, bien que ces tendances variaient beaucoup d’une lagune à l’autre et d’une année à l’autre. Malgré la présence continuelle de lumière du jour pendant la période visée par l’étude, les oiseaux avaient tendance à se servir des zones extracôtières pour s’alimenter pendant la journée, et le soir venu, ils se reposaient dans les eaux littorales protégées. Nous soupçonnons que la variabilité des comportements de recherche de nourriture, d’utilisation de l’habitat et de la taille du parcours vital est vraisemblablement influencée par la disponibilité de proies invertébrées. La proximité de l’activité des champs de pétrole ne semblait pas exercer d’influence sur le comportement d’alimentation des hareldes kakawis en mue.

Mots clés : *Clangula hyemalis*; perturbation; diurne; domaine vital; radiotélémesure

Traduit pour la revue *Arctic* par Nicole Giguère.

INTRODUCTION

From mid-July through September, Long-tailed Ducks (*Clangula hyemalis*) are the most abundant waterbird along the Beaufort Sea coast (Dickson and Gilchrist, 2002; Fischer and Larned, 2004; Johnson et al., 2005). During this period, 10 000 to 30 000 Long-tailed Ducks congregate in protected lagoons in northern Alaska for a 3 – 4 week post-breeding molt (Fischer and Larned, 2004; Johnson et al., 2005). During this molt, all flight feathers are dropped simultaneously, rendering the ducks flightless. Long-tailed ducks meet a portion of the high energetic demands of feather regrowth by feeding during the molt period (Howell, 2002). Thus, a better understanding of foraging behavior patterns and habitat use during the molt period is important because abiotic factors that adversely affect foraging rates and availability of suitable habitat could influence subsequent demographic trends. This topic is of particular interest because Long-tailed Duck populations have experienced substantial declines (Flint, 2013; Bowman et al., 2015) and have been considered an indicator species of the effects of oil field activity on waterbirds along the Beaufort Sea coast (Johnson et al., 2005).

---

[1] U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA
[2] Corresponding author: pflint@usgs.gov
[3] Ecofish Research, Suite 906 - 595 Howe Street, Vancouver, British Columbia V6C 2T5, Canada
[4] U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road, Anchorage, Alaska 99503, USA

Little is known about patterns of foraging and habitat use by individual molting Long-tailed Ducks in the lagoons of the Beaufort Sea. Observations suggest that molting ducks concentrate in the waters near barrier islands and that there is a diurnal pattern of habitat use, with ducks observed near the islands at night and moving into the lagoons during the day (Ward and Sharp, 1974). Johnson (1984) analyzed stomach samples from Long-tailed Ducks in Simpson Lagoon and concluded that these ducks were opportunistic feeders, generally preying on organisms in accordance with availability. The primary forage items were mysids, amphipods, and bivalves (> 85% of the diet). Griffiths and Dillinger (1981) conducted repeated, systematic sampling for invertebrates in Simpson Lagoon and reported that mysids and amphipods were most abundant in the central portion of the lagoon, but were highly variable in space and time both within seasons and among years. Thus, Long-tailed Ducks may have access to high-quality food, but they must adapt to potentially large variation in prey abundance during the flightless period. In general, prey availability influences habitat selection and foraging rates of wintering sea ducks, and studies have demonstrated that when prey abundance is high, ducks spend less time foraging and feed over a smaller area (Kirk et al., 2007, 2008; Lewis et al., 2007).

Industrial activity along the central Beaufort Sea coast has steadily increased since the discovery of oil and gas near Prudhoe Bay, Alaska, in the 1970s. Coastal activity expanded in 1999 with the construction of Northstar, the first offshore oil production facility in Arctic Alaska. As oil field expansion continues, so does interest in the potential effects of human activity on the wildlife species that rely on these coastal areas at critical life history stages (Johnson et al., 2005). Previous consideration of the effects of human disturbance on molting Long-tailed Ducks focused on helicopter overflights (Ward and Sharp, 1974) and underwater seismic survey activity (Lacroix et al., 2003). Ward and Sharp (1974) saw brief behavioral changes of molting Long-tailed Ducks immediately following low-level (100 m) overflights. Lacroix et al. (2003) found little evidence for a trend of movement away from boat-based seismic survey activity or in the level of diving behavior (viewed as a surrogate for feeding). Other investigators have attempted to look more broadly at the influence of proximity to oil field development on molting Long-tailed Ducks by comparing aerial counts (Fischer and Larned, 2004; Johnson et al., 2005) and movement patterns (Flint et al., 2004) of ducks in waters adjacent to the oil fields and in control areas away from development. These studies have found little effect.

Our objective was to describe the patterns of foraging and habitat use of molting Long-tailed Ducks in lagoons of the Beaufort Sea. We studied radio-tagged ducks across multiple lagoons that differed in their exposure to industrial development and activity. We hypothesized that patterns of habitat use would be correlated with foraging behavior. We also suspected that if an effect of industrial disturbance existed, it would be realized as displacement from preferred habitats or changes in the foraging rate (time spent foraging).

METHODS

Study Area

We studied Long-tailed Ducks in three lagoons (Simpson, Maguire, and Flaxman) located between the Colville and Canning Rivers (70˚15′–30′ N, 150˚30′–45′ W) in the central Beaufort Sea, Alaska (Fig. 1) from 2000 to 2002. The Simpson Lagoon area is formed by the band of barrier islands between Spy Island and Long Island. We considered this to be an industrial area because Simpson Lagoon is adjacent to the Prudhoe Bay oil field, where several drill pads and processing facilities exist along the shoreline, and the two-hectare NorthStar offshore oil field facility is located less than 6 km away (Fig. 1). The Maguire and Flaxman Island Lagoons were considered control areas because of the absence of oil field development or activity on the few existing drill sites in the area (Johnson et al., 2005).

Both lagoon areas are protected by low, discontinuous, barrier islands and are shallow (average depth of 2 m) with relatively uniform flat bottoms (Griffiths and Dillinger, 1981). Substrate near the mainland and barrier islands is primarily sand, whereas the substrate in the center of the lagoons is mud and detritus (Griffiths and Dillinger, 1981). The prevailing wind direction is onshore (i.e., northeast) so that the barrier islands create an area of protected water on the lagoon side (Johnson et al., 2005). While daylight was continuous at the start of our study, it diminished rapidly, thus reducing day length by the end of the sampling period. We considered observations collected between 2100 and 0400 to be "night" data.

Captures and Monitoring

In 2000, 2001, and 2002, we captured molting Long-tailed Ducks in corral traps deployed near known roost sites in Simpson Lagoon, the Maguire Islands, and Flaxman Island (Fig. 1). We marked 287 males (68 in 2000, 102 in 2001, and 117 in 2002) with 12 g subcutaneously anchored VHF radio-transmitters (Peitz et al., 1995). We determined duck locations and apparent foraging patterns in 2000 and 2001 on the basis of triangulation from peak-null Yagi antenna systems mounted on rotating towers in each lagoon (Fig. 1). We varied the times when towers were occupied by observers to obtain a uniform sample across the 24 h diurnal cycle. On an hourly basis, observers monitored each transmitter simultaneously from two (in 2000) or three (in 2001) antenna towers in each lagoon.

Data on apparent foraging patterns were also collected in 2000–02, using automated receivers placed throughout the lagoon systems (Fig. 1). Automated receivers scanned through all transmitter frequencies sequentially and recorded the pulse rate of each transmitter over a 45 sec interval. No pulses were recorded for birds beyond the receiving range of the tower. We classified low pulse rates (> 0 but ≤ 53/min) as diving behavior (because of the underwater attenuation of signals) and higher rates

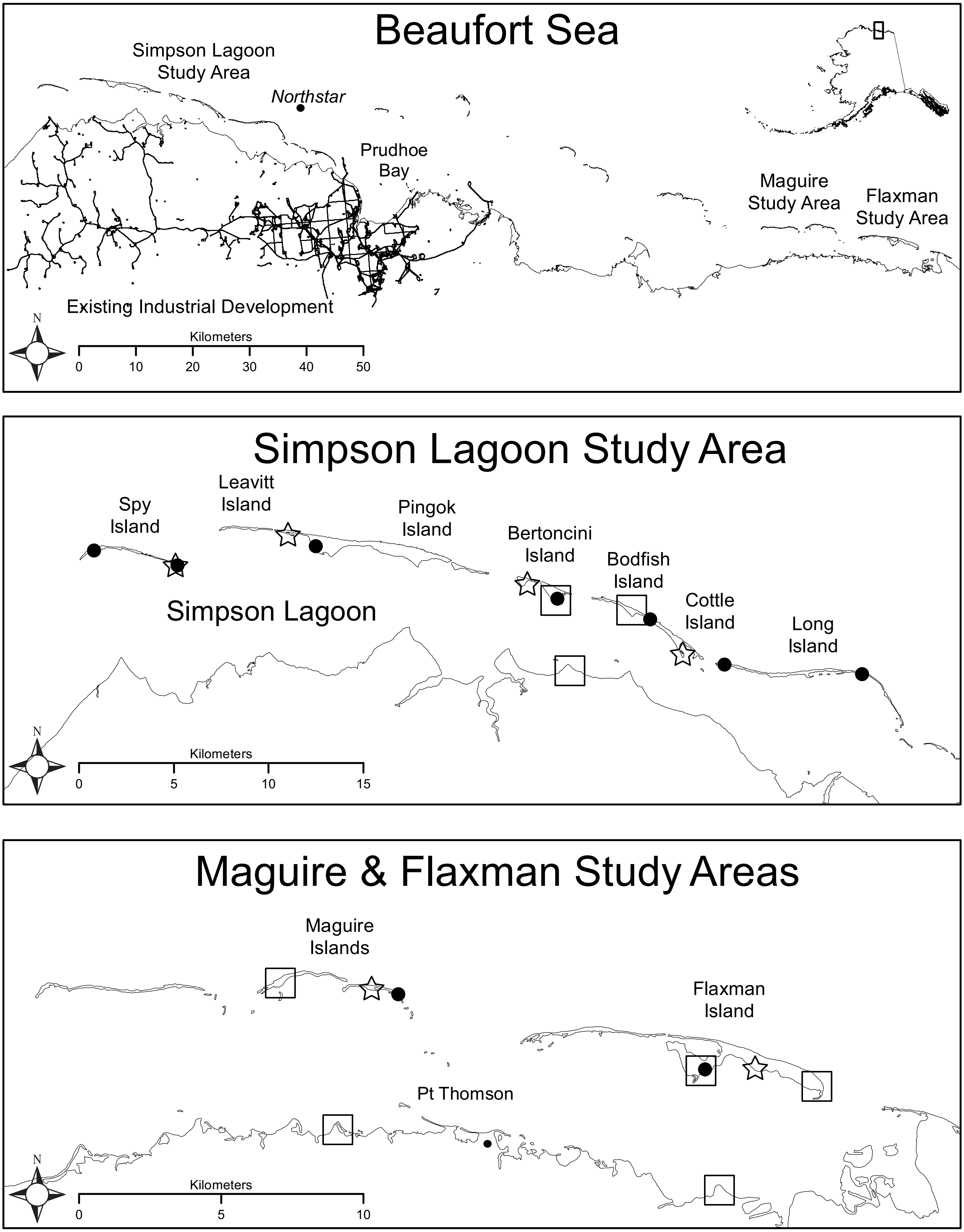

FIG. 1. Location of three lagoons of the central Beaufort Sea, Alaska. Top panel shows the location of lagoons in relation to oil fields and associated industrial development. Lower panels show the distribution of 1) triangulation telemetry receivers (open squares), 2) automated telemetry receivers (solid circles), and 3) Long-tailed Duck capture sites (open stars).

(≈ 60/min) as all non-diving behaviors combined (Lacroix et al., 2003). Further details regarding automated receivers are presented in Lacroix et al. (2003) and Flint et al. (2004).

Habitat Use

When detected simultaneously from more than one receiver, a duck's location was calculated by triangulation (White and Garrott, 1990). We overlaid these locations on GIS coverage of each lagoon. Locations were categorized into four habitat classes: island (within 300 m), mainland (within 300 m), open lagoon (> 300 m from either the island or the mainland shoreline), and ocean (> 300 m offshore from islands). The 300 m boundary was established to generally correspond with habitat classes defined by Johnson et al. (2005). From locations determined from three bearings, we eliminated those with error polygons above the 95th percentile (0.71 km^2). Locations determined from two bearings are inherently less precise, so we set their maximum acceptable error polygon size at 1 km^2. We consider these polygon size limits to be sufficiently precise for our analyses because 1) the median error polygon for all locations was only 0.11 km^2; 2) the location with the highest probability of being correct within an error polygon is the calculated location; 3) error polygon size increases with distance from antennas and, since our greatest need for precision was for birds near habitat boundaries, the proximity of receivers to the nearshore habitats reduced the likelihood of misclassification; and 4) error-polygon shapes are elongated toward receivers when the calculated location is between receivers, and this elongation parallels the 300 m habitat boundary in our study. Thus, even imprecisely calculated locations are likely to be correctly categorized by habitat type, and the few inaccurately assigned locations should be unbiased. Additionally, as an index of home range size, we calculated minimum convex polygon size using the program Animal Movement (Hooge and Eichenlaub, 2000) for all ducks with five or more fixed locations on at least three calendar days (i.e., $n \geq 15$). This minimum sample size was justified because there was no relationship between sample size and home range size estimates for individuals with 15 or more samples (Börger et al., 2006).

Foraging Behavior

Apparent foraging behavior was recorded by observers and by automated receivers. Observers recorded foraging activity on the basis of signal patterns at the triangulation towers. Long-tailed Ducks feed on epibenthic invertebrates by diving, causing transmitter signals to disappear (Lewis et al., 2007). Consequently, signals from foraging ducks were marked by a series of 10–30 s breaks in transmission, whereas signals from non-foraging ducks were continuous strings of regular pulses (1/s). We assumed that diving behavior indicated foraging (as opposed to escape behavior).

Statistical Analysis

Our techniques resulted in two data sets that differed in sample size and detail. The automated data loggers recorded apparent behavior continuously during the molt period in all three years, but these observations are not associated with locations (i.e., habitat). In contrast, the triangulation data set yields both apparent behavior and location in 2000 and 2001, but contains far fewer observations spread across dates and times of day. Accordingly, our analyses were structured to use available data. We addressed the question of time spent foraging across years, lagoons, and time of day using both data sets. Subsequent analyses that examined patterns of habitat use and foraging within specific habitats used only the triangulation data set. For the automated data set, we modeled changes through time by including date; for the smaller triangulation data set, we partitioned date into two 10-day sampling periods representing early and late molt stage because ducks had little flight feather regrowth when marked in late July (mean 9th primary = 23.6 ± 1.3 [SE] mm, ≈ 15% of full primary length). On 10 August 2000, our triangulation study was cut short by a major storm that caused substantial shoreline erosion and damaged or destroyed most of our tracking towers. As a result, we had few observations during the second sampling period in 2000.

We present our results for foraging behavior and habitat use as the proportion of all birds remotely located in each lagoon and sample period. For analyses comparing use of habitat types, we pooled habitats into near-shore (within 300 m of island or mainland) and offshore (> 300 m from shore in either the lagoon or ocean) because of small sample sizes. Prior to statistical analyses, proportions were arcsine square root transformed and plotted to check for normality. We used analysis of variance models to compare the effects of various parameters on foraging and habitat use. We also used analysis of variance models to assess factors influencing home range size. We used AICc to select the most parsimonious model among the candidate models considered (Burnham and Anderson, 2002). We report Akaike weights as indicators of evidence in favor of a particular model in the candidate model set. We calculated the relative importance of nearshore and offshore habitats for feeding by multiplying the proportion of time spent feeding in each habitat by the proportion of total time spent in each habitat and standardizing these to total 100%. This metric can be thought of as the proportion of all apparent foraging estimated to occur in each habitat type.

RESULTS

We recorded locations of marked Long-tailed Ducks from 1 to 13 August 2000 and from 1 to 23 August 2001. We determined 2297 locations by triangulation in 2000 and 4782 in 2001 (Table 1). Additionally, automated receivers

TABLE 1. Number of radio-equipped Long-tailed Ducks during their remigial molt along lagoons of the central Beaufort Sea, Alaska, in August of 2000 – 02. Sampling dates and sampling effort (hours) are also shown.

Year		Simpson Lagoon	Maguire Lagoon	Flaxman Lagoon	Totals
2000	Number of transmitters	18	25	25	68
Triangulation sampling:					
	Sampling dates (August)	1–10	1–8	2–13	
	Sampling (hours)	129	47	91	267
	Total fixed locations	872	492	933	2297
Automated data recording:					
	Sampling dates (August)	1–9	2–9	1–15	
	Total observations	11115	29673	11844	52632
2001	Number of transmitters	39	32	31	102
Triangulation sampling:					
	Sampling dates (August)	10–23	6–18	1–23	
	Sampling (hours)	168	87	162	417
	Total fixed locations	717	1106	2959	4782
Automated data recording:					
	Sampling dates (August)	2–22	2–22	3–22	
	Total observations	10197	3054	4879	18130
2002	Number of transmitters	59	29	28	
Automated data recording:					
	Sampling dates (August)	2–22	5–12	4–17	
	Total observations	7284	990	3430	11704

TABLE 2. Models used to assess variation in proportion of time Long-tailed Ducks spent foraging during their remigial molt in lagoons along the central Beaufort Sea, Alaska, in 2000–02. Data are from both triangulation locations and automated data receivers across years and lagoons (n = 326 data points).

Model[1]	K[2]	AICc	ΔAICc	r^2	Model likelihood	AIC weight
area year day day2 area*year area*year*day	20	−1131.8	0	0.37	1	0.25
area year day area*year area*year*day	19	−1130.9	0.9	0.36	0.650	0.17
area year day day2 area*year*day	16	−1130.8	0.9	0.35	0.626	0.16
area year day area*year*day	15	−1130.8	1.0	0.34	0.606	0.15
area year day day2 area*year*day2	16	−1130.4	1.4	0.35	0.496	0.13
area year day day2 area*year	12	−1129.8	2.0	0.33	0.368	0.09
area year day area*year	11	−1127.6	4.2	0.32	0.123	0.03
area year day area*day	9	−1126.5	5.3	0.31	0.070	0.02
area year day day2 area*year area*year*day area*year*day2	28	−1118.4	13.4	0.38	0.001	< 0.001
area year day year*day	9	−1110.0	21.7	0.27	< 0.001	< 0.001
year day year*day	7	−1106.9	24.9	0.26	< 0.001	< 0.001
year day	5	−1106.5	25.3	0.24	< 0.001	< 0.001
area day area*day	7	−1079.8	52.0	0.19	< 0.001	< 0.001
day	3	−1062.8	69.0	0.13	< 0.001	< 0.001
intercept	2	−1021.4	110.3	0	< 0.001	< 0.001

[1] Area represents lagoons (i.e., Simpson, Flaxman, and Maguire), year is calendar year (i.e., 2000, 2001, 2002), day is a continuous variable for day of year, day2 is a non-linear term of day^2.

[2] K = number of parameters; AICc = the small sample Akaike Information Criterion; AIC weights are the relative model likelihoods.

recorded 52 632 observations at three sites in 2000, 18 130 observations at eight sites in 2001, and 11 704 observations at eight sites in 2002. The large variation in sample sizes from year to year is the result of changes in the recording and receiving equipment.

Foraging Behavior Based on Triangulation and Automated Receiver Data

The most parsimonious model for the proportion of ducks foraging at each lagoon showed non-linear relationships through time (Table 2). Despite considerable model selection uncertainty, there was a consistent pattern of an increase in time spent foraging through the early molt period, with a slight decline at the end of the molt period in some years. Inclusion of the non-linear term had little effect on the variance explained; however, in all cases where models differed only by the squared term, the non-linear model was preferred (Table 2). There was unequivocal support for different patterns of time spent foraging across lagoons and years (Table 2).

Foraging Behavior and Habitat Use Based on Triangulation

The more detailed data set based on triangulation had little model selection uncertainty, and the proportion of ducks located while foraging varied with lagoon, year, time of day, and early or late sampling period (Fig. 2, Table 3). Birds spent more time feeding in offshore habitats than in nearshore habitats, although this variable explained only about 2% of the residual variation (Table 3). A diurnal foraging pattern was evident in all areas in both years. Ducks tended to forage during the day and roost at night (Fig. 3).

Habitat use varied by year and lagoon (Fig. 2). The most supported models included a year by lagoon interaction term (Table 4). With two exceptions (Maguire in 2000 and Flaxman in 2001), a greater proportion of ducks used offshore habitats (especially lagoon centers as opposed to ocean areas) between 0900 and 2100 (52.5% of all locations) and nearshore habitats (especially near islands as opposed to mainland) between 2100 and 0900 (63.0% of all locations; Fig. 4). However, at Maguire in 2000 and Flaxman in 2001, the proportion of locations in each habitat varied little through the day (Fig. 4). Relative importance values for foraging in offshore habitats in 2000 and 2001 were 0.57 and 0.66 for Simpson Lagoon, 0.64 and 0.36 for Flaxman Lagoon, and 0.27 and 0.78 for Maguire Lagoon. Relative habitat importance values for feeding were highest for offshore areas, except for Maguire in 2000 and Flaxman in 2001.

Mean (± SE) home range sizes ranged from 4.4 ± 0.9 km^2 to 21.5 ± 2.8 km^2. As with foraging and habitat use, analysis of variance showed a significant year by lagoon interaction ($F_{2,123} = 11.7$, $p < 0.0001$). Home range size between years was similar for Simpson and Flaxman Lagoons, but different in Maguire Lagoon (Fig. 2). The small home range sizes at Maguire in 2000 were associated with lower foraging rates and limited use of offshore habitats.

Although habitat use varied widely by year and lagoon, most locations were in the nearshore areas around islands and in open lagoon habitats (Fig. 4). Only 1.5% of all locations from Simpson Lagoon were in mainland habitat, compared to 11.6% for Maguire and 13.8% for Flaxman locations.

DISCUSSION

Our results show substantial variation in the schedule and percentage of time spent foraging by male Long-tailed Ducks (Fig. 2). Variation among lagoons and years likely reflects variation in foraging success (i.e., successful capture and consumption of prey) and in the determinants of that success, such as prey abundance and distribution (Fox et al., 2014). This idea is supported by the similar patterns of foraging behavior, frequency of use of open lagoon habitats, and home range sizes within years (Fig. 2). We suspect that when foraging success and prey availability were high, ducks did not need to spend much time foraging and thus did not move to less protected open lagoons in search of prey. Conversely, when prey availability was low, foraging effort increased and home range size expanded as ducks spent more time seeking prey in the lagoons. Griffiths and Dillinger (1981) demonstrated, from repeated invertebrate

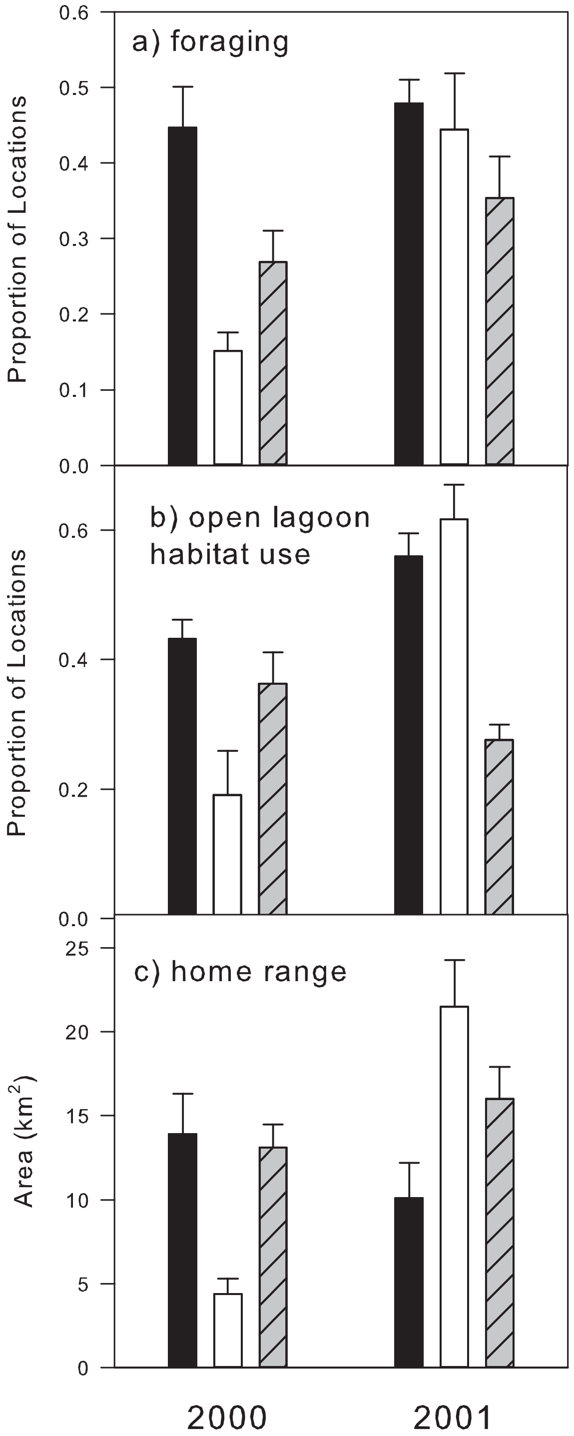

FIG. 2. Proportion of Long-tailed Ducks located by triangulation that were a) foraging, and b) in the lagoon habitat, as well as c) the mean home range size (area of minimum convex polygon) of birds in each lagoon. Data are presented as yearly means (+ SE) for the Simpson (black bars), Maguire (white), and Flaxman (gray hatched) Lagoons of the central Beaufort Sea, Alaska, 2000–01.

TABLE 3. Models used to assess variation in proportion of time Long-tailed Ducks spent foraging during their remigial molt in lagoons along the central Beaufort Sea, Alaska, in 2000–01. Data are from triangulation location towers and are assessed across different habitat types (n = 481 data points).

Model[1]	K[2]	AICc	ΔAICc	r^2	Model likelihood	AIC weight
area year period time habitat area*year*period	17	−1440.6	0	0.39	1	0.789
area year period time habitat year*time*period	25	−1437.1	3.5	0.40	0.171	0.135
year period time habitat year*time*period	23	−1435.9	4.7	0.40	0.094	0.074
area year period time habitat area*time*period	39	−1427.0	13.6	0.43	0.001	< 0.001
area year time habitat area*year*time	38	−1424.4	16.2	0.42	< 0.001	< 0.001
area year period time habitat area*year*time	39	−1424.2	16.4	0.42	< 0.001	< 0.001
area period time habitat area*time*period	38	−1416.1	24.5	0.41	< 0.001	< 0.001
area year period time habitat area*year*time*period	55	−1400.5	40.1	0.44	< 0.001	< 0.001
area year period time area*year*time*period	54	−1386.4	54.2	0.42	< 0.001	< 0.001
area year period habitat area*year*period	12	−1245.6	195.1	0.07	< 0.001	< 0.001

[1] Area represents lagoons (i.e., Simpson, Flaxman, and Maguire), year is calendar year (i.e., 2000, 2001), time is time of day in 4-hour blocks, period is early and late (i.e., first 10 days and last 10 days of sampling), habitat is nearshore and offshore as defined in text.

[2] K = number of parameters; AICc = the small sample Akaike Information Criterion; AIC weights are the relative model likelihoods.

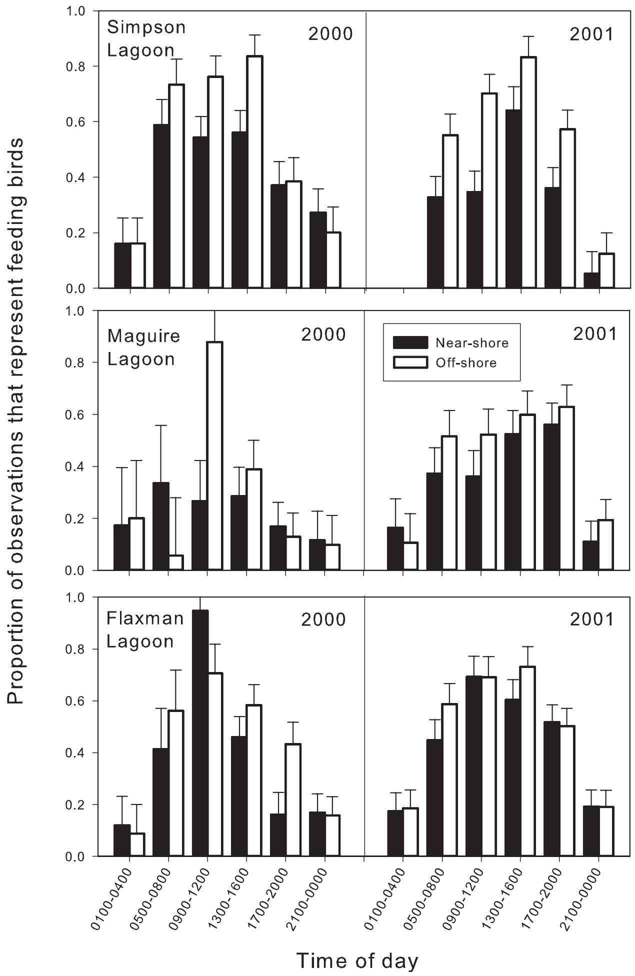

FIG. 3. Diurnal foraging patterns of Long-tailed Ducks along three lagoons of the central Beaufort Sea, Alaska, 2000–01. Bars represent the mean (+ SE) daily percentage of triangulated locations in which ducks were diving during 4-hour blocks. Nearshore is defined as within 300 m of the barrier islands or mainland, and offshore, as more than 300 m from shore in either the lagoon or the ocean.

sampling at various stations in Simpson Lagoon, that abundance of Long-tailed Duck prey is highly variable both within and among years. Further, studies of other sea duck species (i.e., scoters) have shown that birds spent less time foraging when food was more abundant (Kirk et al., 2007; Lewis et al., 2007). In addition, Kirk et al. (2008) found that scoters with more consistently available food had smaller foraging ranges. Although we were unable to assess foraging success and prey distribution directly, the fact that both prey and Long-tailed Duck behaviors show high levels of variation suggests that a correlation may exist.

Although habitat use patterns varied, ducks tended to use open lagoon habitats (offshore) during the day and nearshore habitats (near islands and mainland) at night (Fig. 5). This pattern is consistent with general observations from other studies (Johnson et al., 2005). Our conclusions on diving behavior derived from recorded pulse rates of individual transmitters also indicate that Long-tailed Ducks tended to forage during the day and roost at night (Fig. 3). As a result, most feeding took place in the open lagoon habitat, and most roosting was done near shore, where the islands and mainland spits provide protection from prevailing winds and associated waves. Exceptions to this pattern were Maguire Lagoon in 2000 and Flaxman Lagoon in 2001, where birds showed the usual diurnal pattern in foraging activity, but no diurnal pattern in habitat use was observed. We suspect that in this case, ducks found sufficient prey in the nearshore habitats, so they did not need to swim to offshore habitats to forage. Overall, environmental conditions (e.g., prey distribution and wind protection) appeared to strongly influence habitat use; birds moved away from roosting habitats only as far as necessary to obtain adequate food. The pattern of habitat use that we observed, in which birds foraged offshore during the day and roosted near shore at night, is similar to that of wintering Long-tailed Ducks at Nantucket Shoals (White et al., 2009). In contrast, Jones (1979) found the opposite pattern for wintering Long-tailed Ducks in Scotland, where birds fed near shore during the day and roosted offshore at night, presumably to avoid

TABLE 4. Models used to assess variation in the proportion of Long-tailed Duck locations in different nearshore habitats during their remigial molt along lagoons of the central Beaufort Sea, Alaska, in 2000–01. Locations are based on triangulation towers (n = 246 data points).

Model[1]	K[2]	AICc	ΔAICc	r^2	Model likelihood	AIC weight
area year time period area*year*period	16	−704.0	0	0.43	1	0.999
area year time area*year*time	37	−675.6	28.4	0.48	< 0.001	< 0.001
area year period area*year*period	11	−675.4	28.6	0.33	< 0.001	< 0.001
area year time period area*year*time	38	−672.8	31.2	0.48	< 0.001	< 0.001
area year time period year*time*period	24	−639.4	64.6	0.31	< 0.001	< 0.001
area year time period area*year*time*period	54	−635.1	68.9	0.50	< 0.001	< 0.001
year time period year*time*period	22	−631.2	72.8	0.27	< 0.001	< 0.001
area year time period area*time*period	38	−615.2	88.8	0.35	< 0.001	< 0.001
area time period area*time*period	37	−612.9	91.1	0.33	< 0.001	< 0.001

[1] Area represents lagoons (i.e., Simpson, Flaxman, and Maguire), year is calendar year (i.e., 2000, 2001), time is time of day in 4-hour blocks, period is early and late (i.e., first 10 days and last 10 days of sampling).

[2] K = number of parameters; AICc = the small sample Akaike Information Criterion; AIC weights are the relative model likelihoods.

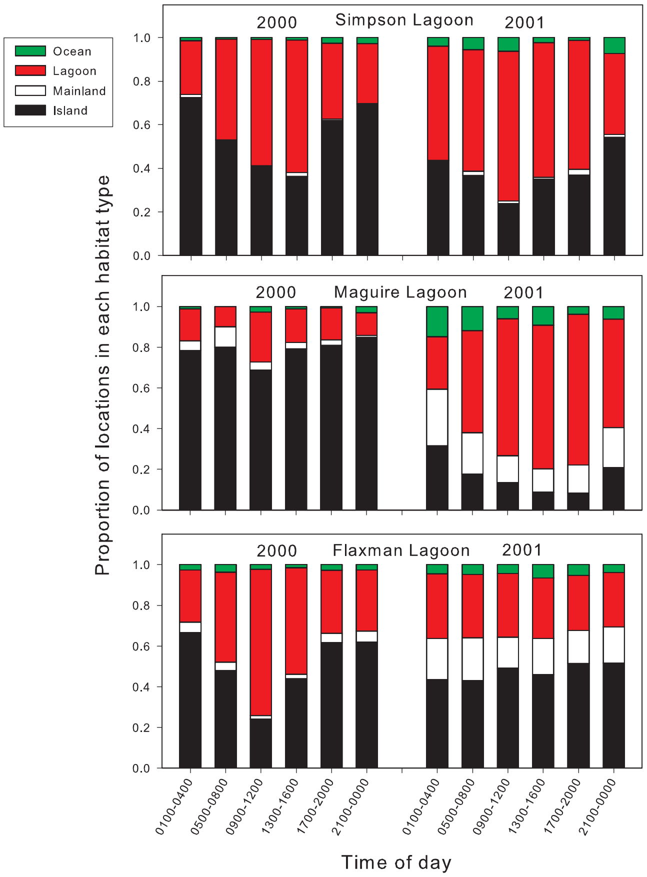

FIG. 4. Diurnal patterns of habitat use by Long-tailed Ducks along three lagoons of the central Beaufort Sea, Alaska, 2000–01. Bars represent the mean daily proportion of triangulated locations within each habitat type. Habitats are defined as in Figure 3.

predators. Thus, patterns of habitat use are likely related to both energetics and predation risk. In our study area, few predators were observed pursuing molting Long-tailed Ducks, so patterns of habitat use were likely due primarily to energetics and foraging habitat suitability.

Our data demonstrate that foraging behavior and habitat use are correlated, but at the same time, these parameters show a high degree of intra-annual variation among lagoons and interannual variation within lagoons. Together, these data provide strong, though indirect, evidence that the invertebrate prey base of Long-tailed Ducks in the Beaufort Sea is highly variable and somewhat unpredictable (Griffiths and Dillinger, 1981). At the Maguire study site, for example, time spent foraging and lagoon habitat use doubled and home range size quadrupled between 2000 and 2001 (Figs. 2 and 3). We speculate that food was less available at Maguire Lagoon in 2001. Long-tailed ducks appear to have adapted to variable habitat conditions with highly flexible foraging behavior (Hogan et al., 2013). Howell (2002) found no evidence of geographic variation in body condition of Long-tailed Ducks molting in these lagoons, which suggests that the ducks were able to compensate behaviorally for the putative variation in food availability (at least within the range of conditions encountered during our study).

Flint et al. (2004) found that Long-tailed Ducks in these lagoons consistently congregated in protected locations, but individuals were likely to move independently among congregations. This pattern suggests that food must have been distributed more or less evenly through the lagoons; otherwise, low-quality foraging locations would have been abandoned. Our results support the idea that on a finer scale (i.e., within a few such congregation sites), food quality and quantity are likely highly variable, and ducks adjust their behavior accordingly. Furthermore, the relatively consistent distributions of Long-tailed Ducks across the lagoons (Johnson et al., 2005) suggest that variation in food availability must not be predictable. That is, specific areas are not consistently better in terms of prey availability, so that there is no trend toward selection for (or abandonment of) specific molting locations.

Even in our most parameterized models, there was considerable unexplained variation (all r^2 values < 0.5, Tables 2–4). Some specific variables not considered in our analyses may explain this variation, or perhaps there is simply considerable random variation in behavior. Failure to consider important variables can influence our conclusions only if the missing variables were correlated with those we analyzed. That is, when multi-colinearity exists, inclusion or exclusion of parameters can influence the effect size and support for variables in the model. General environmental variables like wind speed and waves may have influenced behavior (Johnson et al., 2005), but such conditions were relatively consistent among lagoons and were not likely to be correlated with variables in our model (such as time of day). Overall, we do not believe the r^2 of our models invalidates our conclusions because the patterns we report from detailed data on marked individuals agree with general historical descriptions. Relatively low r^2 values are not uncommon in behavioral studies of free-ranging wild animals; nonetheless, we caution against extrapolating our results or using our data to make predictions regarding behavior.

If proximity to industrial development affected foraging or habitat use, we should have seen parallel patterns at the Maguire and Flaxman Lagoons (the non-industrial areas) that contrasted with the Simpson Lagoon (the area adjacent to oil field activity). Only mainland habitat use by Long-tailed Ducks followed this pattern: in both years, we recorded significantly more locations in the mainland habitat at Maguire and Flaxman Lagoons than at Simpson Lagoon (Fig. 4, Table 4). This pattern has also been documented during aerial surveys (Fischer and Larned, 2004; Johnson et al., 2005). However, the difference in use of mainland habitat may be related not to industrial infrastructure, but to the abundance of protective sand spits along the mainland in the Maguire and Flaxman Lagoons and the relative dearth of such areas along the mainland in the Simpson Lagoon (Johnson et al., 2005). Long-tailed Ducks appear to prefer protected waters on the lee side of landforms for roosting. Because the differences in nearshore use across lagoons may be driven primarily by roosting habitat availability, our results should not be interpreted as a test of whether proximity to industrial development affects the behavior of Long-tailed Ducks during molt. Indeed, previous studies have also not detected human disturbance effects on large-scale movements or diving behavior of molting Long-tailed Ducks in the Beaufort Sea (Lacroix et al., 2003; Fischer and Larned, 2004; Johnson et al., 2005). In the time since our data were collected, permanent processing facilities have been established on Spy Island (the western edge of Simpson Lagoon) and at Point Thompson (the eastern edge of Flaxman Lagoon), both of which are close to areas used by molting Long-tailed Ducks (Fig. 1). Replication of aerial surveys in the area (see Fischer and Larned, 2004; Johnson et al., 2005), as well as more fine-scaled behavioral observations near these developments, would perhaps be a better test of the effects of industrial development on the distribution, habitat use, and foraging behavior of molting Long-tailed Ducks.

ACKNOWLEDGEMENTS

The U.S. Geological Survey - Outer Continental Shelf Program provided funding for this research. We received extensive logistical support from BP Exploration Alaska Inc., ExxonMobil Production Co., Oasis Environmental Inc., LGL Alaska Research Associates, Cape Smythe Air, Air Logistics of Alaska, ERA Aviation, and Alaska Clean Seas. For additional logistical help, we thank M. Barker, W. Cullor, D. Derksen, L. Harms, F. Hand, L. Noel, J. Pearce, M. Petersen, B. Reynolds, C. Rock, G. Spencer, W. Streever, and L. Thorsteinson. Pilots J. Sarvis, K. Karns, E. Akola, G. Dobson, and B. Stone were particularly helpful. This project would not have been possible without the efforts of numerous field assistants. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., and Coulson, T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75(6):1393–1405. http://dx.doi.org/10.1111/j.1365-2656.2006.01164.x

Bowman, T.D., Silverman, E.D., Gilliland, S.G., and Leirness, J.B. 2015. Status and trends of North American sea ducks: Reinforcing the need for better monitoring. In: Savard, J.-P.L., Derksen, D.V., Esler, D., and Eadie, J.M., eds. Ecology and conservation of North American sea ducks. Studies in Avian Biology (no. 46). Boca Raton, Florida: CRC Press. 1–27.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. New York: Springer-Verlag.

Dickson, D.L., and Gilchrist, H.G. 2002. Status of marine birds of the southeastern Beaufort Sea. Arctic 55(Supp.1):46–58. http://dx.doi.org/10.14430/arctic734

Fischer, J.B., and Larned, W.W. 2004. Summer distribution of marine birds in the western Beaufort Sea. Arctic 57(2):143–159. http://dx.doi.org/10.14430/arctic491

Flint, P.L. 2013. Changes in size and trends of North American sea duck populations associated with North Pacific oceanic regime shifts. Marine Biology 160(1):59–65. http://dx.doi.org/10.1007/s00227-012-2062-y

Flint, P.L., Lacroix, D.L., Reed, J.A., and Lanctot, R.B. 2004. Movements of flightless Long-tailed Ducks during wing molt. Waterbirds 27(1):35–40. http://dx.doi.org/10.1675/1524-4695(2004)027[0035:MOFLDD]2.0.CO;2

Fox, A.D., Flint, P.L., Hohman, W.L., and Savard, J.-P.L. 2014. Waterfowl habitat use and selection during the remigial moult period in the Northern Hemisphere. Wildfowl Special Issue 4:131–168.

Griffiths, W.B., and Dillinger, R.E. 1981. Beaufort Sea barrier island–lagoon ecological process studies: Final report, Simpson Lagoon: Invertebrates. In: Environmental Assessment of the Alaskan Continental Shelf, Final Reports of Principal Investigators, Biological Studies 8. Boulder, Colorado: NOAA/BLM Outer Continental Shelf Environmental Assessment Program. 198 p.

Hogan, D., Esler, D., and Thompson, J.E. 2013. Variation in body mass and foraging effort of Barrow's Goldeneyes (*Bucephala islandica*) during remigial molt. The Auk 130(2):313–322. http://dx.doi.org/10.1525/auk.2013.12048

Hooge, P.N., and Eichenlaub, B. 2000. Animal movement extension to Arcview, Version 2.0. Anchorage: Alaska Science Center – Biological Science Office, U.S. Geological Survey.

Howell, M.D. 2002. Molting dynamics of male Long-tailed Ducks on the Beaufort Sea. MSc thesis, Auburn University, Auburn, Alabama.

Johnson, S.R. 1984. Prey selection by Oldsquaws in a Beaufort Sea lagoon, Alaska. In: Nettleship, D.N., Sanger, G.A., and Springer, P.F., eds. Marine birds: Their feeding ecology and commercial fisheries relationships. Proceedings of the Pacific Seabird Group Symposium, Seattle, Washington, 1982. Ottawa: Canadian Wildlife Service Special Publication. 12–19.

Johnson, S.R., Noel, L.E., Gazey, W.J., and Hawkes, V.C. 2005. Aerial monitoring of marine waterfowl in the Alaskan Beaufort Sea. Environmental Monitoring and Assessment 108(1):1–43. http://dx.doi.org/10.1007/s10661-005-3958-5

Jones, P.H. 1979. Roosting behavior of Long-tailed Ducks in relation to possible oil pollution. Wildfowl 30:155–158.

Kirk, M.K., Esler, D., and Boyd, W.S. 2007. Foraging effort of Surf Scoters (*Melanitta perspicillata*) wintering in a spatially and temporally variable prey landscape. Canadian Journal of Zoology 85(12):1207–1215. http://dx.doi.org/10.1139/Z07-105

Kirk, M.K., Esler, D., Iverson, S.A., and Boyd, W.S. 2008. Movements of wintering surf scoters: Predator responses to different prey landscapes. Oecologia 155(4):859–867. http://dx.doi.org/10.1007/s00442-007-0947-0

Lacroix, D.L., Lanctot, R.B., Reed, J.A., and McDonald, T.L. 2003. Effect of underwater seismic surveys on molting male Long-tailed Ducks in the Beaufort Sea, Alaska. Canadian Journal of Zoology 81(11):1862–1875. http://dx.doi.org/10.1139/z03-185

Lewis, T.L., Esler, D., and Boyd, W.S. 2007. Foraging behaviors of Surf Scoters and White-winged Scoters during spawning of Pacific herring. The Condor 109(1):216–222. http://dx.doi.org/10.1650/0010-5422(2007)109[216:FBOSSA]2.0.CO;2

Pietz, P.J., Brandt, D.A., Krapu, G.L., and Buhl, D.A. 1995. Modified transmitter attachment for adult ducks. Journal of Field Ornithology 66(3):408–417.

Ward, J., and Sharp, P.L. 1974. Effects of aircraft disturbance on moulting sea ducks at Herschel Island, Yukon Territory, August 8 1973. In: Gunn, W.W.H., Richardson, W.J., Schweinsburg, R.E., and Wright, T.D., eds. Chapter 2: Studies on terrestrial bird populations, moulting sea ducks and bird productivity in the Western Arctic, 1973. Arctic Gas Biological Report Series Vol. 29. 54 p.

White, G.C., and Garrott, R.A. 1990. Analysis of radio-tracking data. San Diego: Academic Press, Inc.

White, T.P., Veit, R.R., and Perry, M.C. 2009. Feeding ecology of Long-tailed Ducks *Clangula hyemalis* wintering on the Nantucket Shoals. Waterbirds 32(2):293–299. http://dx.doi.org/10.1675/063.032.0209