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Changes in abundance and spatial distribution of geese molting near Teshekpuk Lake, Alaska: interspecific competition or ecological change?

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Abstract Goose populations molting in the Teshekpuk Lake Special Area of the National Petroleum Reserve—Alaska have changed in size and distribution over the past 30 years. Black brant (*Branta bernicla nigricans*) are relatively stable in numbers but are shifting from large, inland lakes to salt marshes. Concurrently, populations of greater white-fronted geese (*Anser albifrons frontalis*) have increased seven fold. Populations of Canada geese (*Branta canadensis* and/or *B. hutchinsii*) are stable with little indication of distributional shifts. The lesser snow goose (*Anser caerulescens caerulescens*) population is proportionally small, but increasing rapidly. Coastline erosion of the Beaufort Sea has altered tundra habitats by allowing saltwater intrusion, which has resulted in shifts in composition of forage plant species. We propose two alternative hypotheses for the observed shift in black brant distribution. Ecological change may have altered optimal foraging habitats for molting birds, or alternatively, interspecific competition between black brant and greater white-fronted geese may be excluding black brant from preferred habitats. Regardless of the causative mechanism, the observed shifts in species distributions are an important consideration for future resource planning.

Keywords Alaska · Black brant · Canada geese · Greater white-fronted goose · Habitat change · Interspecific competition · Molting · Snow geese · Teshekpuk Lake

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Introduction

Annually, four species of geese—black brant (*Branta bernicla nigricans*), greater white-fronted geese (*Anser albifrons frontalis*), Canada geese (*Branta hutchinsii* and/or *B. canadensis*), and lesser snow geese (*Chen caerulescens caerulescens*) —migrate to the Teshekpuk Lake Special Area (TLSA) in the National Petroleum Reserve—Alaska to molt their flight feathers (King and Hodges 1979). Molting birds use a series of large, wind-oriented thaw lakes within historic shorelines of much larger, drained lake basins (Derksen et al. 1979, 1982). During the molt, geese feed on grasses and sedges along the shorelines of these lake basins (Derksen et al. 1979; Weller et al. 1994). Weller et al. (1994) hypothesized that geese select lakes for molt based on forage plant availability and found a correlation between black brant numbers and the abundance of moss/peat shoreline, which is assumed to be the preferred habitat type. Comparable analyses of habitat preference have not been conducted for other species of geese molting in this area.

Changes in the arctic climate in recent decades have resulted in physical and ecological changes at landscape levels (Overpeck et al. 1997; Serreze et al. 2000; Sturm et al. 2001; Jorgensen et al. 2006). Arctic lake systems are changing in response to permafrost dynamics (Weller and Derksen 1979; Smol et al. 2005; Smith et al. 2005) and Beaufort Sea coastline erosion has increased as seasonal summer pack ice extent has declined (Kobayashi et al. 1999; Serreze et al. 2003; Mars and Houseknecht 2007). These changes in freshwater and marine systems may have led to modification of habitats available to molting geese in the TLSA. Using 27 years of aerial survey data, we analyzed long-term trends in population size and distribution of geese molting in the TLSA. We present these data as

temporal and spatial trends and propose hypotheses to explain the observed patterns.

Methods

Aerial surveys

Surveys were conducted in mid-July and were timed to occur when the maximum proportion of the population was flightless. Surveys were conducted from 1976 to 1978, and from 1982 to 2005 (i.e., no surveys were conducted from 1979 to 1981). The survey area included approximately 196 lakes and several creeks, bays, as well as near-shore coastline segments (Fig. 1). Lakes were assigned unique identification numbers, which remained consistent on all surveys. Lake identification numbers were printed on 1:63,360 or 1:250,000 scale maps which were used for aircraft navigation. Observations of geese were assigned to the lake (identification number) at which they were observed. Surveys were flown in fixed-winged, float-equipped aircraft at 45–75 m above ground level and at airspeeds of 130–190 km/h. Surveys were flown when surface winds were less than 40 km/h.

Shorelines of large lakes were flown so that any feeding or loafing geese on land would be observed and recorded. The surfaces of large lakes were flown in a systematic fashion providing 100% coverage of the lake. For smaller lakes, a flig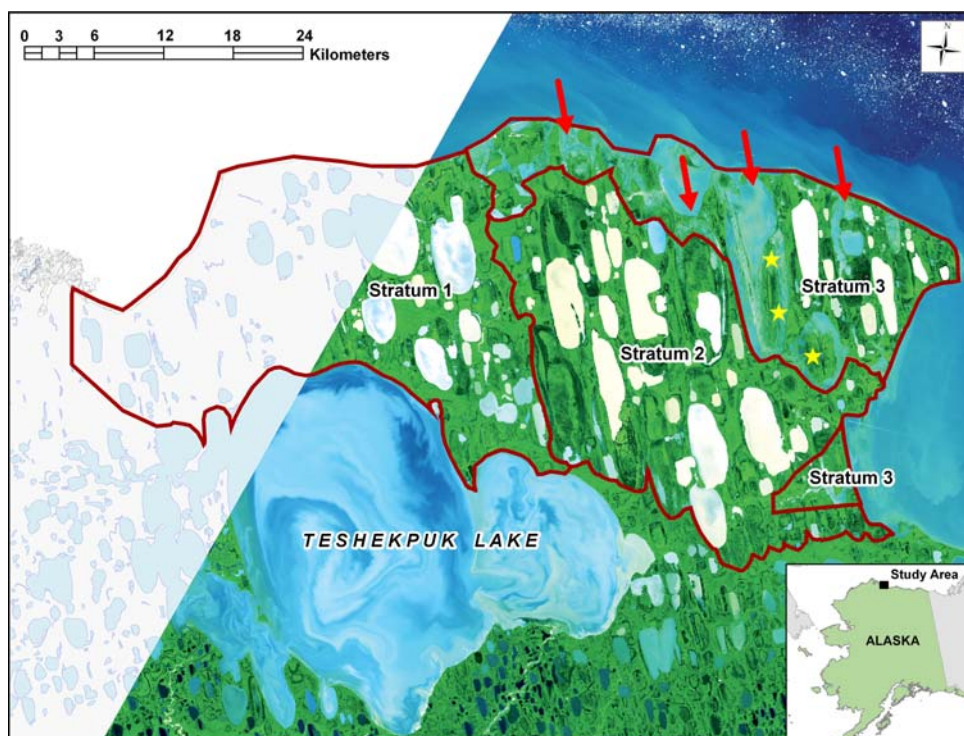ht path over or around the lake provided an unrestricted view of the entire lake and shoreline. Observations of geese were recorded on magnetic tape or laptop computers as lake identification number, species, age (adults or goslings), and flock size.

Geese in small flocks (<25) were individually counted. For larger flocks of geese (>25), ocular estimation was used to assign numeric values to flock size. This was accomplished by estimating subsets of a flock and adding them together for the recorded estimate. The size of the subset was proportional to the size of the flock. For example, a flock recorded as 212 geese would be estimated by adding the number of birds in subsets of 50 (i.e., 50 + 50 + 50 + 50 + 12). A very large flock of geese (e.g., 1,800) would be estimated by adding subsets of 100 or 200, and would be counted several times to produce an accurate estimate.

Habitat stratification

Three broad strata were defined based on habitat characteristics (Fig. 1). We used three physiognomic characteristics to define boundaries among these strata: (1) ground and aerial observations of salt water intrusion, (2) high resolution digital elevation data, and (3) a vegetation classification map (Markon and Derksen 1994). In general, stratum three is characterized by the occurrence of salt-water intrusion and was demarcated using a combination of elevation data (less than 1.5 m and which partially identifies the Simpsonian [70–80 ka] marine transgression) and the

Fig. 1 Aster satellite image of a portion of the Teshekpuk Lake Special Area (70.47°N, 152.52°). This image was taken in August of 2000, 3 days after a major storm with a high tidal surge. Discoloration within lakes was caused by suspended sediments from wind-generated waves. Areas without green coloration indicate no Aster data. Strata boundaries are depicted with *red* lines. *Red arrows* indicate locations with regular salt water intrusion and *stars* indicate areas of observed salt-killed tundra

northeast edge of the lowland moist sedge-shrub tundra. Stratum 2 was demarcated on the south by the elevation data (less than 4 m and corresponding to the Pelukian [120–130 ka] marine transgression) and on the west by a major stream drainage and the associated moist sedge meadow tundra class from Markon and Derksen (1994). Stratum 1 included the remainder of the study area generally corresponding to elevations greater than 4 m.

Statistical analyses

Overall population trajectories

We ran models to quantify overall (i.e., pooled across strata) time trends within species that considered adults and juveniles separately. Models examined included intercept only, linear trend, polynomial, and 2- and 3-parameter models of exponential growth. We used the constraint that intercept terms were >0 to keep the models biologically relevant. Models were fit using program SAS (SAS Institute 2004). Small sample bias adjusted Akaike's information criterion (AICc) values were calculated for each model (Burnham and Anderson 2002). The best approximating model for each species was selected based on AICc values. The same non-linear model fit procedures were applied to counts of juveniles for each species.

Changes in distributions

Using the best models defined above for adults of each species as a baseline, we considered additional models, which included parameters allowing differences in population trends among strata indicating changes or shifts in distribution. For linear models this is functionally analyses of covariance with year as a covariate and strata as a factor. Variation among trajectories was assessed by including the interaction between year and strata in the model. For non-linear models, strata-specific terms were added to rate functions. Support for each model was assessed using AICc.

Results

Overall patterns of abundance

The number of molting geese counted in the TLSA ranged from 18,525 to 90,191 between 1976 and 2005. Black brant and Canada goose populations were best described with intercept only models (Fig. 2), indicating no change in population size through time (Table 1). Greater white-fronted geese were best fit with a second order polynomial model where the squared term was positive. Thus, greater white-fronted goose populations increased geometrically (Fig. 2).
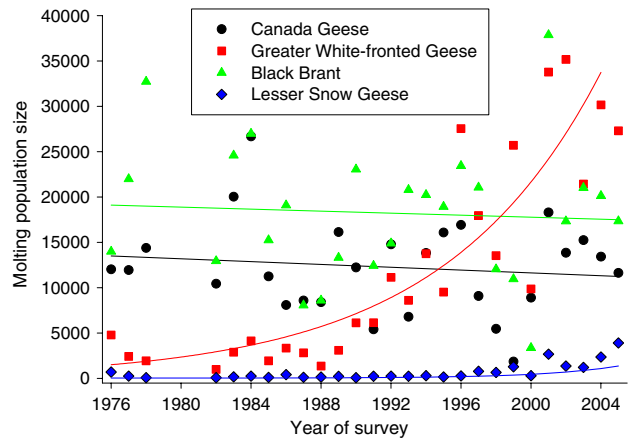

Fig. 2 Molting population trends by species across the Teshekpuk Lake Special Area, Alaska

All models for greater white-fronted geese indicated rapid population growth and only varied slightly in the shape of the non-linear function (Table 1). Lesser snow geese were best fit with a two parameter exponential model (Fig. 2). Lesser snow goose populations were comparatively smaller than the other species, but increased exponentially. All models for lesser snow geese indicated non-linear population growth and only varied in the shape of the growth function (Table 1).

Evidence of changes in distributions

For black brant and Canada geese these analyses are functionally equivalent to ANCOVA with stratum as a class variable. There was strong support for variation in black brant trends among strata (Table 2). The number of black brant counted in stratum 2 declined, coincident with increases in stratum 3 during the study period (Fig. 3). For greater white-fronted geese we considered three models where there was a stratum effect on the year and the year^2 terms simultaneously, as well as the year and year^2 terms independently. There was strong support for variation in greater white-fronted goose trends among strata (Table 2) with models having strata level variation in either the year or the year^2 parameter receiving similar support. Overall, greater white-fronted geese increased in all strata with the greatest rate of increase in stratum 2 (Fig. 4). There was only weak evidence of variation in Canada goose trends across strata (Table 2). For lesser snow geese we modeled strata-specific rate parameters in the exponential term. There was strong support for variation in lesser snow goose trends across strata (Table 2). Lesser snow geese increased in all strata with the greatest increase in stratum 3. The combination of species-specific differences in numerical trends and relative distributions among strata resulted in

Table 1 Candidate models used to examine overall trends in population size for each species of geese molting in the Teshekpuk Lake Special Area, Alaska

Species	Model structure	# par[a]	AICc[b]	ΔAICc[c]
Black brant	Intercept	2	484.9	0
	Intercept year	3	487.4	2.4
	Intercept year year^2	4	488.8	3.9
	Intercept + exp($a \times$ year)	3	487.4	2.5
	Intercept + ($a \times$ exp($b \times$ year))	4	490.1	5.2
Greater white-fronted geese	Intercept	2	506.3	36.0
	Intercept year	3	477.3	7.0
	Intercept year year^2	4	470.3	0
	Intercept + exp($a \times$ year)	3	491.8	21.5
	Intercept + ($a \times$ exp($b \times$ year))	4	473.5	3.2
Canada geese	Intercept	2	464.8	0
	Intercept year	3	466.9	2.1
	Intercept year year^2	4	469.3	4.5
	Intercept + exp($a \times$ year)	3	_[d]	_[d]
	Intercept + ($a \times$ exp($b \times$ year))	4	469.6	4.8
Lesser snow geese	Intercept	2	372.6	41.9
	Intercept year	3	360.9	30.2
	Intercept year year^2	4	342.7	12.0
	Intercept + exp($a \times$ year)	3	330.7	0
	Intercept + ($a \times$ exp($b \times$ year))	4	333.3	2.6

[a] Number of parameters in each model

[b] Akaike's Information Criterion value adjusted for small sample size

[c] Difference in AICc value for each model relative to the lowest AICc for each species. Thus, ΔAICc = 0 indicates the most parsimonious model for each species

[d] Model failed to converge

Table 2 Candidate models used to assess variation in population trajectories among strata for each species of geese molting in the Teshekpuk Lake Special Area, Alaska

Species	Model structure	# par[a]	AICc[b]	ΔAICc[c]
Black brant	Intercept stratum year year $\times$ stratum	7	1323.7	0
	Intercept stratum year	5	1331.1	7.4
Greater white-fronted geese	Intercept stratum year year^2 year $\times$ stratum year$^2 \times$ stratum	10	1276.3	4.7
	Intercept stratum year year^2 year $\times$ stratum	8	1271.8	0.3
	Intercept stratum year year^2 year$^2 \times$ stratum	8	1271.5	0
	Intercept stratum year year^2	6	1289.5	17.9
Canada geese	Intercept stratum year year $\times$ stratum	7	1240.5	0
	Intercept stratum year	5	1241.1	0.6
Lesser snow geese	Intercept + exp(($b + c \times$ stratum1 + $d \times$ stratum2) $\times$ year)	5	893.8	0
	Intercept + exp($b \times$ year)	3	926.6	32.8

[a] Number of parameters in each model

[b] Akaike's information criterion value adjusted for small sample size

[c] Difference in AICc value for each model relative to the lowest AICc for each species. ΔAICc = 0 indicates the most parsimonious model for each species

dramatic changes in proportional species distributions within strata across time (Fig. 4).

Evidence of increases in local productivity

The numbers of juveniles counted in the TLSA increased during our study for all species (Fig. 5). For juvenile black brant three models had similar AIC values (Table 3) including intercept only, linear increase and simple exponential increase. Thus, there was no strong trend in juvenile brant numbers, but there was some support for a slight increase through time. For juvenile greater white-fronted geese, Canada geese and lesser snow geese numbers were all increasing exponentially (Table 3). All models for trends in these three species indicated non-linear increases in population size of juveniles and only varied slightly in the shape of the non-linear function.
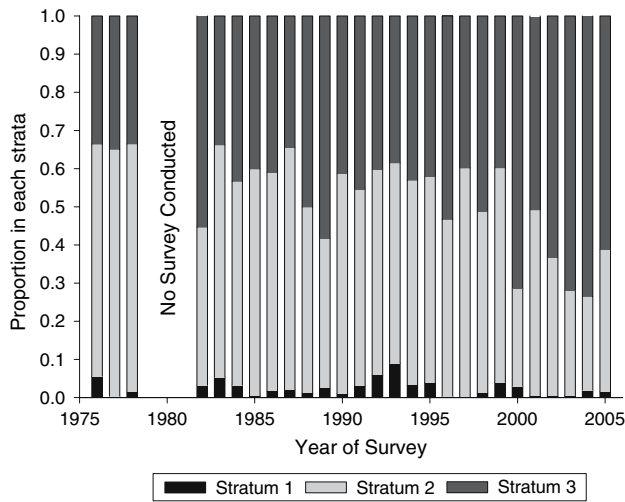
Fig. 3 The proportion of molting black brant counted in each stratum within the Teshekpuk Lake Special Area, Alaska has varied among years. There has been a shift in distribution from stratum 2 to stratum 3 during the period of study
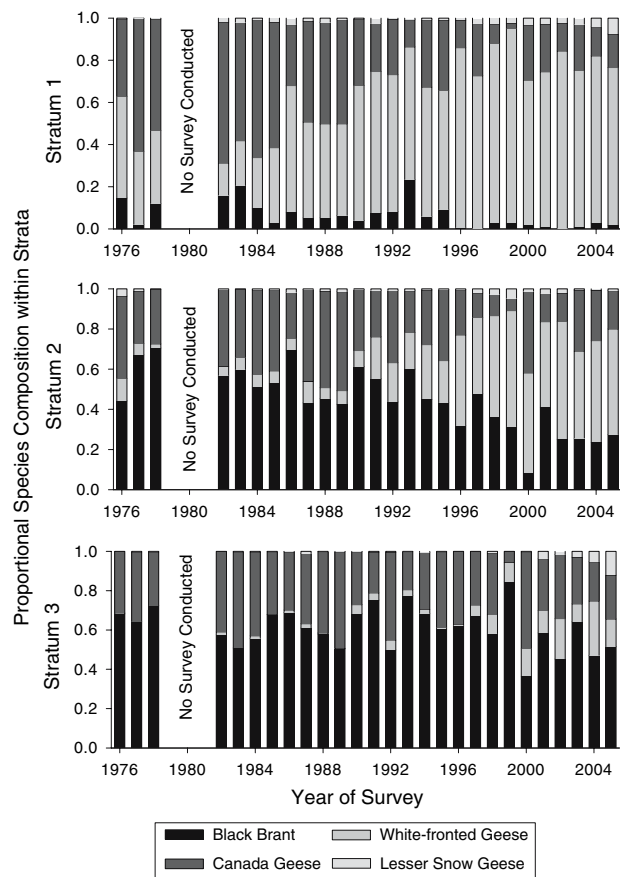

Fig. 4 The proportional species composition of the molting population within the Teshekpuk Lake Special Area, Alaska by year and strata shows the trend towards numerical dominance of greater white-fronted geese in strata 1 and 2
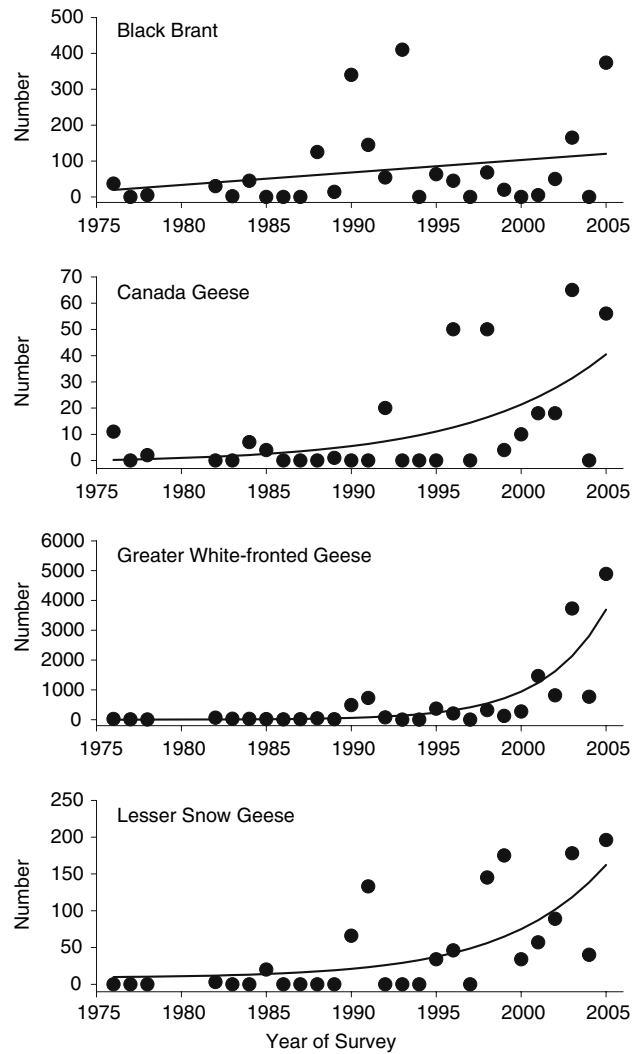

Fig. 5 Trends in number of goslings observed for each species across all strata within the Teshekpuk Lake Special Area, Alaska. Gosling counts for all species show a pattern of increase in recent years

Discussion

Over a 30-year time span of aerial survey data, goose populations and their use of habitats in the TLSA have changed. Greater white-fronted goose populations have increase seven fold while the relatively stable numbers of molting black brant have shifted in terms of spatial distribution. The area with the highest rate of population increase for greater white-fronted geese corresponds with the area where black brant populations are declining most rapidly. Breeding, as indexed by the number of goslings observed, has increased for all four species.

Data reported here are observational and the analyses correlational. As such, we have no ability to infer cause and effect relationships. However, patterns observed suggest

Table 3 Candidate models used to examine overall trends in population size for juveniles of each species of geese molting in the Teshekpuk Lake Special Area, Alaska

Species	Model structure	# par[a]	AICc[b]	ΔAICc[c]
Black brant	Intercept	2	261.0	0
	Intercept year	3	261.8	0.8
	Intercept year year^2	4	264.5	3.5
	Intercept + exp(a × year)	3	261.8	0.8
	Intercept + (a × exp(b × year))	4	—[d]	—[d]
Greater white-fronted geese	Intercept	2	384.2	29.5
	Intercept year	3	376.5	21.9
	Intercept year year^2	4	369.1	14.5
	Intercept + exp(a × year)	3	354.6	0
	Intercept + (a × exp(b × year))	4	354.7	0.03
Canada geese	Intercept	2	164.2	8.8
	Intercept year	3	158.7	3.3
	Intercept year year^2	4	157.8	2.4
	Intercept + exp(a × year)	3	155.4	0
	Intercept + (a × exp(b × year))	4	158.1	2.7
Lesser snow geese	Intercept	2	228.1	13.8
	Intercept year	3	216.6	2.3
	Intercept year year^2	4	216.5	2.2
	Intercept + exp(a × year)	3	214.3	0
	Intercept + (a × exp(b × year))	4	216.3	2.1

[a] Number of parameters in each model

[b] Akaike's information criterion value adjusted for small sample size

[c] Difference in AICc value for each model relative to the lowest AICc for each species. Thus, ΔAICc = 0 indicates the most parsimonious model for each species

[d] Model failed to converge

several hypotheses that may explain these patterns. Previous researchers considered the question of why geese molt at particular sites and they concluded that forage quality and availability and presence of escape habitat likely influenced distributions of molting geese (Hohman et al. 1992; Reed et al. 2003). Weller et al. (1994) hypothesized that for black brant, ice pans on the deeper, large lakes in the TLSA represented escape habitat from mammalian predators such as arctic foxes (*Alopex lagopus*) during the flightless period. However, the observed shift of black brant to more coastal, saline-influenced habitats would seem to question the importance of ice as escape habitat because we never observed lakes in stratum 3 to maintain ice during the flightless period. Therefore, we suggest that the overall shift in distribution for molting black brant represents a change in optimal foraging conditions across the molting area. Such changes in optimal foraging conditions may result from a decline in forage quality or availability in stratum 2, an increase in stratum 3, or some combination thereof. We hypothesize that the causative factors driving such change are (1) interspecific competition between black brant and greater white-fronted geese has reduced forage availability in stratum 2, and/or (2) salt water intrusion and associated plant succession have enhanced foraging conditions for black brant in stratum 3. Either of these hypotheses could act independently, or both could function simultaneously. Inherent in both of these hypotheses is the assumption that nutrient acquisition by geese is limiting.

The interspecific competition hypothesis implies that black brant are being forced out of preferred molting habitats to less optimal locations. Similarly, Nilsson et al. (2001) concluded that changes in molting distribution of graylag geese (*Anser anser*) were caused by intraspecific competition. Nack and Andersen (2006) concluded that increasing populations of lesser snow geese displaced brood rearing Canada geese from preferred habitats in Hudson Bay, Canada. We hypothesize that a similar interaction may be occurring between black brant and greater white-fronted geese on the TLSA. The interspecific competition hypothesis is supported by the analyses demonstrating that black brant are moving out of stratum 2 coincident with white-fronted geese showing substantial increases in this stratum. This hypothesis assumes that these species either compete directly for forage, or that some form of interference competition exists between taxa. Derksen et al. (1979) reported that black brant, greater white-fronted geese, and Canada geese all fed in moss/peat habitat zones around lakes. However, greater white-fronted geese also used emergent *Arctophila fulva*, and greater white-fronted geese and Canada geese foraged in upland habitats. Further, historically, most greater white-fronted geese molted in stratum 1 where moss/peat habitat used by black brant is sparse (Derksen et al. 1979; Weller and Derksen 1979; Markon and Derksen 1994). Thus, of these three species, black brant appear to be the least flexible in terms of their habitat requirements; whereas greater white-fronted geese have the ability to use habitats apparently avoided by black brant.

Generalist species frequently out-compete specialists as generalists can shift to alternative habitats when conditions become limiting (Richmond et al. 2005). Further, black brant are the smallest of the four species of geese molting in the TLSA. As such, black brant would require higher quality forage than the other species, as they are less able to effectively utilize low quality foods (Demment and Van Soest 1985; Sedinger 1997). Thus, black brant would be more sensitive to reductions in availability of high quality forage than other species. Estimating the degree of overlap in forage selection among species, or other forms of competition, are essential to assessing the viability of this hypothesis.

The enhanced foraging conditions hypothesis implies that successional changes in plant communities have altered optimal foraging habitat for molting birds. Coastline erosion has occurred most dramatically in stratum 3 where several large lake systems have been breached and inundated with salt–water at an unknown point in the past (MacCarthy 1953; Mars and Houseknecht 2007; Fig. 1). Evidence of salt–water intrusion is apparent with extensive areas of salt-killed tundra. However, associated with this salt–water intrusion, there is evidence of succession to salt-tolerant plant species such as *Puccinellia phraganodes*, and *Carex subspathacia* (PLF pers. obs.). In other areas of Alaska, black brant forage extensively on these plant species during nesting and brood rearing (Sedinger et al. 2001; Person et al. 2003; Ward et al. 2005). Thus, long-term ecological change may have altered optimal foraging habitats and the shift in habitat use by molting black brant may represent optimal habitat selection in a changing environment. Assessment of forage plant quality and availability among areas is required to determine the viability of this hypothesis.

The distributional changes we documented occurred over a 30-year period. Given that these birds are flightless during the period when competition or other nutrient constraints are imposed, the shifts in distribution we documented occurred among, not within, years. Bollinger and Derksen (1996) reported homing rates to specific lakes >94%, implying that black brant are highly traditional in selection of lakes for molt. The observed changes in distribution suggest that the apparent low rates of dispersal are directional across strata. Birds exposed to sub-optimal conditions during molt in year i, may be less likely to show fidelity to sites in years $\geq i + 1$. This mechanism would result from the process described in the interspecific competition hypothesis. An alternative mechanism explaining shifts in distribution is that birds may investigate the entire TLSA prior to initiation of molt and then select specific lakes for molt based on forage conditions encountered during these explorations. This mechanism fits with the enhanced foraging conditions hypothesis. Thus, understanding the mechanisms that drive distributional shifts may yield clues as to the underlying processes influencing long term changes among strata.

The increasing trend in numbers of juvenile white-fronted geese, Canada geese, and snow geese makes it clear that either breeding effort or breeding success has increased in this area. Interestingly, one of the primary hypotheses for why geese undertake a molt migration is to avoid intraspecific competition with brood flocks (Hohman et al. 1992; O'Briain et al. 1998). The increase in brood flocks in the TLSA would seem to support the overall hypothesis that habitat conditions have changed making this area attractive to breeding as well as molting birds. Alternatively, increases in high arctic season length associated with broad scale climate change may have relaxed breeding season length constraints for geese at this latitude. Thus, increases in breeding propensity and/or success may not be strictly related to foraging conditions during the period of use by non- and failed-breeding birds.

In its 1998 Record of Decision, the Bureau of Land Management excluded most of the TLSA from leasing for petroleum development due, in part, to use by large numbers of molting geese. However, in 2006 the U.S. Department of the Interior proposed changing this status to allow leasing and associated development. The TLSA is unique and there are no other known areas that support large numbers of four species of molting geese across the circumpolar Arctic (Derksen et al. 1979). This portion of the Arctic Coastal Plain is subject to dynamic habitat change associated with coastal erosion and thermokarst lake processes (Mars and Houseknecht 2007). Our results demonstrate that the abundance and spatial distribution of the goose populations have changed substantially through time. Regardless of the causative factors driving the observed shifts, these goose populations are dynamic and we expect further changes in abundance and distribution to occur. Understanding the causative mechanisms driving the observed changes would facilitate prediction of areas which might be most important to molting geese in the future and thereby aid future management planning. Accordingly, additional research designed to establish cause and effect relationships and validate or refute our hypotheses regarding changing goose distributions is necessary.

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