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ORIGINAL ARTICLES

Snow cover and snow goose *Anser caerulescens caerulescens* distribution during spring migration

Jerry W. Hupp, Amy B. Zacheis, R. Michael Anthony, Donna G. Robertson, Wallace P. Erickson & Kelly C. Palacios

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Arctic geese often use spring migration stopover areas when feeding habitats are partially snow covered. Melting of snow during the stopover period causes spatial and temporal variability in distribution and abundance of feeding habitat. We recorded changes in snow cover and lesser snow goose *Anser caerulescens caerulescens* distribution on a spring migration stopover area in south-central Alaska during aerial surveys in 1993-1994. Our objectives were to determine whether geese selected among areas with different amounts of snow cover and to assess how temporal changes in snow cover affected goose distribution. We also measured temporal changes in chemical composition of forage species after snow melt. We divided an Arc/Info coverage of the approximately 210 km^2 coastal stopover area into 2-km^2 cells, and measured snow cover and snow goose use of cells. Cells that had 10-49.9% snow cover were selected by snow geese, whereas cells that lacked snow cover were avoided. In both years, snow cover diminished along the coast between mid-April and early May. Flock distribution changed as snow geese abandoned snow-free areas in favour of cells where snow patches were interspersed with bare ground. Snow-free areas may have been less attractive to geese because available forage had been quickly exploited as bare ground was exposed, and because soils became drier making extraction of underground forage more difficult. Fiber content of two forage species increased whereas non-structural carbohydrate concentrations of forage plants appeared to diminish after snow melt, but changes in nutrient concentrations likely occurred too slowly to account for abandonment of snow-free areas by snow geese.

Key words: Alaska, Anser caerulescens caerulescens, forage nutritional quality, lesser snow geese, migration, resource selection, snow cover

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During spring migration, arctic geese often follow the northward progression of snow melt and use stopover areas shortly after open water and bare ground first become available (Ryder 1967, Cooper 1978, Lincoln 1979, Raveling 1979a, Wege & Raveling 1983). Geese may closely follow breakup of ice and snow in order to arrive on nesting areas soon after nest sites become available. Geese that initiate nests early typically have larger clutches and a longer time available to rear broods (Cooch 1961, Barry 1962, Cooper 1978, MacInnes & Dunn 1988, MacInnes, Dunn, Rusch, Cooke & Cooch 1990, Cooke, Rockwell & Lank 1995). Early-nesting geese are also more likely to hatch young when forage quality on nesting areas is highest (Sedinger & Raveling 1986). Another advantage of using migration stopover areas shortly after bare ground becomes available is that newly-emerged plants often have high nutritional value (Drent, Ebbinge & Weijand 1979, Raveling 1979a, Owen & Gullestad 1984, Fox, Gitay, Boyd & Tomlinson 1991). Selective exploitation of high quality forage on stopover areas (Boudewijn 1984, Prop & Deerenberg 1991, Kristiansen, Fox, Stroud & Boyd 1998) may be important for some goose species to build endogenous reserves of lipid and protein used during nesting (Ankney & MacInnes 1978, Ankney 1982, Raveling 1979b, Ebbinge & Spaans 1995).

Geese can arrive at migration areas when snow still covers some of the feeding habitat (Wege & Raveling 1983, Prevett, Marshall & Thomas 1985, Fox et al. 1991). Because geese cannot exploit plants beneath snow, access to forage can be limited depending on stage of snow melt. Melting of snow during the stopover period creates spatial and temporal variability in habitat conditions and provides geese with a choice of feeding at the most recently exposed sites or using those that have been snow-free for longer periods. Although there are widespread observations of geese using migration areas during spring snow melt, distribution of geese relative to snow cover has rarely been assessed and patterns of foraging following snow melt are poorly studied (although see Fox et al. 1991). Such data would help biologists predict where geese are likely to occur within a stopover area and when they are likely to use feeding habitats.

We examined the influence of snow cover on the distribution of lesser snow geese *Anser caerulescens caerulescens* at a spring migration stopover area in south-central Alaska. Our objectives were to determine whether snow geese selected among areas that had different amounts of snow cover and whether flock distribution changed as snow melt progressed. We also assessed whether snow melt influenced temporal patterns of use at a site. Because nutritional quality of plants may change rapidly in spring, we examined temporal changes in chemical composition of forage to determine if geese derived a nutritional benefit by exploiting areas immediately after snow melt.

Methods

Study area

Snow geese that nest on Wrangel Island, Russia and winter in the Fraser and Skagit river valleys of British Columbia and Washington migrate along the North Pacific coast in spring and use Upper Cook Inlet (UCI), Alaska, as a stopover area (Kerbes, Meeres & Hines 1999). Approximately 50,000 snow geese occur in the Fraser and Skagit river wintering area (Kerbes et al. 1999) and up to 32,000 snow geese have been observed to simultaneously occur in UCI (W.I. Butler, Jr. & R.E. Gill, Jr., unpubl. report). Due to turnover of birds, only a portion of the population is present in UCI at one time. Snow geese are present in UCI for 2-3 weeks in late April and early May.

Geese use three salt marshes that occur along approximately 130 km of coast in northern and western UCI (Fig. 1). Salt marsh vegetation is restricted to areas within 1-3 km of the coast. Distribution of plant communities within marshes varies according to soil moisture

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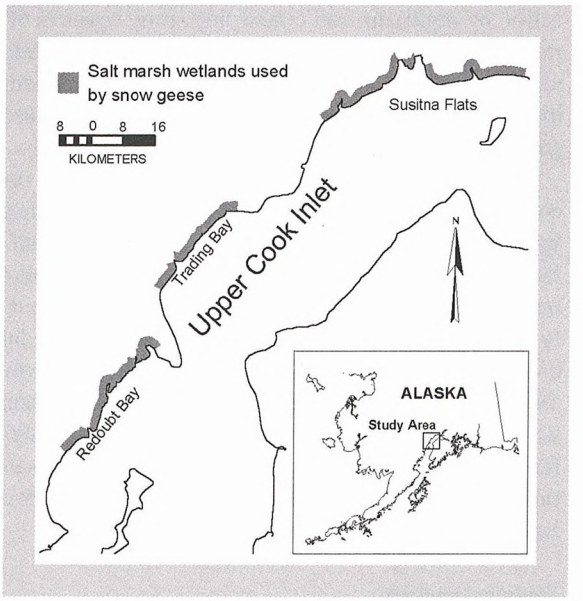

Figure 1. Location of the Cook Inlet, Alaska study area (inset). Distribution of salt marsh wetlands used by lesser snow geese during spring migration stopover on the north and west coast of Upper Cook Inlet. Unshaded areas are rocky or forested coast.

and salinity gradients (Vince & Snow 1984). The outer coastal fringe of salt marshes frequently consists of *Puccinellia* spp. and *Triglochin maritimum*. Slightly inland from the coast are often a sedge meadow community dominated by *Carex ramenskii* and *T. maritimum* and a forb meadow community that consists of *Plantago maritima*, *Potentilla egedii*, *T. maritimum*, and *C. ramenskii*. Sedge meadow and forb meadow communities can extend up to 1.5 km inland and both are used by snow geese (Zacheis, Hupp & Ruess 2001). Flocks also periodically use areas of *C. lyngbyaei* situated up to 2 km inland from the coast. Most (69%) of the snow goose diet is underground forage including roots of *P. maritima* and *T. maritimum*, and rhizomes of *C. ramenskii* (Zacheis et al. 2001). They also consume non-photosynthetic lower stems of *C. ramenskii* and *C. lyngbyaei* shoots. Marshes are completely snow or ice covered during winter, although some melting usually occurs before geese arrive in mid-April. Most of the coastal habitat is tidally flooded only during extreme tides.

Snow cover and snow goose distribution

Field methods

We used a Cessna 185 aircraft to conduct aerial surveys of coastal wetlands in Susitna Flats, Trading Bay and Redoubt Bay (see Fig. 1) during snow goose migration. Once snow geese were observed on reconnaissance flights, we surveyed flock distribution at 2-4 day intervals until geese departed the region. We conducted six aerial surveys between 17 April and 3 May in 1993 and six surveys between 21 April and 6 May in 1994. On the outbound portion of each survey, the pilot flew a zig-zag search pattern at 300 m above ground level (AGL) over coastal wetlands while two observers looked for snow goose flocks on the ground. Flocks were easily observed against dark areas of bare ground. During daylight hours snow geese spent 60-70% of the day feeding and did not depart feeding areas between feeding bouts (J.W. Hupp, pers. obs.). We therefore assumed that flocks seen on the ground were on feeding areas. The pilot flew the aircraft directly over each observed flock. Unlike some populations (Davis & Wisely 1974, Bélanger & Bédard 1989), snow geese that migrated through UCI usually did not flush in response to aircraft. A forward observer estimated flock size and determined when the flock was directly beneath the aircraft. At that time a second observer recorded aircraft location on a laptop computer linked to a Global Positioning System (GPS) receiver (Anthony & Stehn 1994). The GPS tracking system updated aircraft location at one second intervals.

We used an S-video camera vertically mounted over

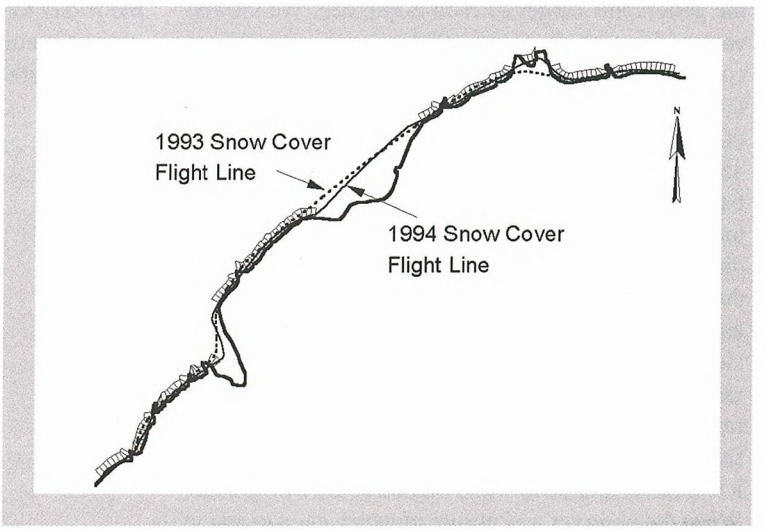

Figure 2. Division of coastal wetlands of Upper Cook Inlet, Alaska into 2-km² cells. Use of each cell by lesser snow geese during spring migration (April-May) was determined from aerial surveys during 1993-1994. Snow cover in each cell was estimated from aerial video images obtained along coastal flight lines.

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a belly port in the aircraft to record snow and ice cover in coastal wetlands during the return portion of each survey. We flew slightly inland along a route that paralleled the coastline at 1,000 m AGL, and continuously operated the video camera to capture images of snow cover in wetlands. The camera lens was set on wide angle (8 mm focal length) with a 1/1000 second shutter speed. In 1994, we used a Horita GPS Video Titler to record latitude and longitude of the aircraft on the video image. Latitude and longitude were not recorded on video images in 1993. The pilot used the GPS tracking system to follow the same route during each survey. Routes differed slightly between years (Fig. 2).

Spatial and temporal analysis of goose distribution and snow cover

We analyzed spatial distribution of snow cover and geese using a geographic information system (Arc/Info). In areas of salt marsh up to 2 km from the coast, we drew irregularly-shaped, but equal-sized 2-km^2 cells that conformed to the coastline (see Fig. 2). We determined the spatial extent of salt marshes from aerial imagery. The inland boundary of cells was 2 km from the coast because in most areas salt marsh habitat did not occur further inland and because 96% of flocks were <2 km from the coast. Snow goose flock locations, as determined by the GPS tracking system, were superimposed on the coverage and the presence or absence of flocks in each 2-km^2 cell was determined for each survey. We also measured distance of all flocks to the coastline.

We used video images to measure snow cover near the geographic center of each 2-km^2 cell. We viewed each video tape from the 1994 surveys on a 52-cm colour monitor and paused the video on frames where the latitude and longitude were closest to the centers of the cells. Each video frame covered approximately 450 × 600 m. Location error was ±110 m (SE = 8.0) based on comparison of estimated latitude and longitude of 62 landmarks on video images to known coordinates determined with a precision GPS receiver during field visits. We visually estimated percent snow and ice cover on the paused video frame as one of five classes (0, 0.1-9.9, 10-49.9, 50-89.9, 90-100%) and assigned the 2-km^2 cell to that class. We used broad mid-range classes to reduce the number of categories considered in our analysis of resource selection, and to make it less likely that a cell was assigned to the wrong class. When the observer was unsure of which class to assign a cell, the video frame was digitized, and snow and ice cover were classified and measured with image processing software. We verified accuracy of visual classification by digitizing and classifying snow cover in 60 randomly-selected video frames where we also made visual estimates. We did not include non-vegetated, intertidal mud flats when estimating snow cover because geese did not feed in those areas.

Because aircraft latitude and longitude were not recorded on the 1993 imagery, we selected sample frames by matching images to the 1994 videos. There was sufficient overlap of images to identify common landmarks on >80% of 1993 video frames. Landmarks were clearly visible because of an abundance of ponds and tidal creeks in the coastal wetlands of UCI (Vince & Snow 1984, Lawson, Bigl, Bodette & Weyrick 1995). When we could not locate a common landmark because of differences in flight lines, we estimated an image's location by counting the number of frames between two landmarks at known locations.

Statistical analysis

We considered all 2-km^2 cells on the study area to be available to geese. Used cells were those in which at least one snow goose flock was present. We calculated resource selection ratios (Manly, McDonald & Thomas 1993) for each year to determine if use of a snow cover class differed from its availability. Geese selected for a snow cover class when use of the class was disproportionately greater than its availability, and selected against a class when use was disproportionately less than availability. We defined u_{ij} as the number of cells used within the i^{th} snow cover class on the j^{th} survey day, t_j as the total number of cells used on the j^{th} survey day, a_{ij} as the proportion of cells surveyed on the j^{th} day that had snow class i, and $\bar{a}_i$ was the mean proportion of cells in snow class i across all days. The selection ratio for the i^{th} snow cover class was estimated as:

$$\hat{R}_i = \frac{\left(\frac{\bar{u}_i}{\bar{t}}\right)}{\bar{a}_i} \quad (1)$$

where,

$$\bar{u}_i = \frac{\sum_{j=1}^{d} u_{ij}}{d} \quad (2),$$

$$\bar{t} = \frac{\sum_{j=1}^{d} t_j}{d} \quad (3)$$

and, where d was the number of days.

We transformed the estimator using $\ln(\hat{R}_i)$, built con-

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fidence intervals for $\ln(\hat{R}_i)$, and exponentiated the endpoints of the intervals for $\hat{R}_i$. The variance of $\ln(\hat{R}_i)$ was approximated by the estimator:

$$var(\ln(\hat{R}_i)) \cong \frac{1}{d}\left[\frac{s^2_{\bar{u}_i}}{\bar{u}_i^2}+\frac{s^2_{\bar{t}}}{\bar{t}^2}+\frac{s^2_{\bar{a}_i}}{\bar{a}_i^2}-2\left(\frac{cov(\bar{u}_i,\bar{t})}{\bar{u}_i\bar{t}}\right)\right] \quad (4),$$

where s^2 was the sample variance. These formulas were used to construct approximate 100(1-α)% confidence intervals for $\hat{R}_i$:

$$e^{\ln(\hat{R}_i) \pm 2\sqrt{var(\ln(\hat{R}_i))}} \quad (5).$$

Formulas based on log transformation of ratios and corresponding variances yielded confidence intervals with lower limits greater than 0, whereas approximate confidence intervals based on the untransformed ratios yielded lower limits less than 0. Furthermore, confidence intervals based on log-transformed ratios and corresponding variance had wider intervals than corresponding intervals based on the untransformed ratios. Selection for a particular snow cover class occurred when the lower limit of the confidence interval was >1, and selection against a snow cover class occurred when the upper limit of the confidence interval was <1.

Upon identifying the snow cover classes primarily used by geese, we examined temporal changes in their availability. We used Spearman correlation analysis to determine if there was a relationship between Julian dates of surveys and the numbers of 2-km² cells in snow cover classes primarily used by geese. We conducted a separate analysis for each of the three salt marshes to determine if temporal trends were the same across areas. We also examined whether the spatial distribution of geese changed over time. We sequentially numbered the linearly arranged 2-km² cells, and used a Mann-Whitney test (Conover 1980) to determine if the distribution of cells used during the early part of migration (surveys 1-3) differed from those used during the latter part of migration (surveys 4-6).

Changes in forage chemistry following snow melt

We examined acid detergent fiber (ADF), nitrogen and total non-structural carbohydrate (TNC) concentrations of major forage items (Zacheis et al. 2001) at three times after snow melt to assess temporal changes in chemical composition. We selected sample sites in an approximately 10 km² area of Susitna Flats where geese had been observed during aerial surveys. Each site was a 6-10 m² plot in a relatively homogeneous patch of a particular forage. Sites were separated by >100 m and were marked the summer before sampling when we could determine plant species composition. In spring, we built exclosures around each site to prevent feeding by geese. We collected *C. lyngbyaei* shoots, *C. ramenskii* shoots and rhizomes, and *T. maritimum* shoots at four sites at 1, 10 and 20 days following snow melt in 1995. We removed green material on the upper part of *C. lyngbyaei* and *C. ramenskii* shoots so that analysis was based only on the basal portion that snow geese consumed. *P. maritima* roots were collected at four locations across the same time sequence following snow melt in 1997. We collected sufficient material for nutrient analysis at each site and measured biomass (g dry mass /m²) in two randomly placed 0.25 × 0.25-m quadrats during each sample period.

We dried samples to a constant mass at 60°C and measured ADF (Van Soest 1982) and percent nitrogen of subsamples. We used a LECO CNS 2000 autoanalyser to measure nitrogen. Because of the small amount of new plant growth available after snow melt, we had to pool the remaining material within each time period and species in order to obtain sufficient material for analysis of TNC (Smith 1981). Therefore measurement of TNC was not replicated across sites within a time period. We analysed changes in ADF, nitrogen and biomass across time periods with a repeated measures analysis of variance. Data were analysed in SAS using PROC MIXED, with an autoregressive order one covariance structure within plots (Littell, Milliken, Stroup & Wolfinger 1996). Significance levels for ADF and nitrogen were assessed at the 0.025 level to adjust for multiple hypotheses tests based on chemical analysis of the same plant samples.

Table 1. Numbers of snow geese and flocks observed during aerial surveys of coastal salt marshes in Upper Cook Inlet, Alaska during spring migration in 1993 and 1994.

Survey date		Observed number of Flocks	Geese
1993	April 17	7	1430
	April 20	14	4230
	April 22	28	12965
	April 26	17	8490
	April 29	15	6590
	May 3	1	68
1994	April 21	28	3279
	April 25	28	7725
	April 27	43	11925
	April 29	50	17295
	May 2	24	7835
	May 6	18	5010

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Table 2. Numbers of 2-km² cells available (A) in each of the five categories of snow cover, and the number of cells used by snow geese (U) during aerial surveys of coastal wetlands in Upper Cook Inlet, Alaska during 1993-1994.

	Number of cells in 1993													
Category of	17 April		20 April		22 April		26 April		29 April		3 May		Total	
snow cover (%)	A	U	A	U	A	U	A	U	A	U	A	U	A	U
0	6	0	24	3	32	4	39	2	64	2	83	0	248	11
0.1 - 9.9	27	6	16	2	17	4	29	3	21	1	9	0	119	16
10 - 49.9	11	0	22	5	20	6	19	7	8	4	3	1	83	23
50 - 89.9	29	1	28	2	26	9	9	2	3	3	1	0	96	17
90 -100	23	0	6	1	1	0	0	0	0	0	0	0	30	1
Total	96	7	96	13	96	23	96	14	96	10	96	1	576	68

	Number of cells in 1994													
Category of	21 April		25 April		27 April		29 April		2 May		6 May		Total	
snow cover (%)	A	U	A	U	A	U	A	U	A	U	A	U	A	U
0	4	0	21	7	29	2	35	2	48	1	69	1	206	13
0.1 - 9.9	25	10	11	4	15	2	20	4	25	4	21	2	117	26
10 - 49.9	7	1	16	4	19	6	19	7	12	3	6	3	79	24
50 - 89.9	27	7	30	4	28	8	22	9	17	4	6	0	130	32
90 -100	42	0	27	1	14	2	9	4	3	0	3	0	98	7
Total	105	18	105	20	105	20	105	26	105	12	105	6	630	102

Results

Selection of snow cover classes

We observed 82 snow goose flocks on surveys in 1993 and 191 flocks in 1994 (Table 1). In both years, numbers peaked between 22 and 29 April as new flocks arrived, and then diminished as geese left UCI. Median distance of all flocks from the coastline was 400 and 500 m in 1993 and 1994, respectively. Average flock size was 412 (SE = 57) in 1993 and 294 (SE = 22) in 1994.

We measured snow cover on 96 2-km² cells during each survey in 1993. The flight line followed the coast more closely in 1994 than in 1993 and we measured snow cover on 105 cells in 1994 (see Fig. 2). In 1993, 75 (91%) of the flocks occurred on 2-km² cells for which we had snow cover estimates and 45 cells were used at least once (Table 2). In 1994, 149 (78%) flocks occurred on cells for which we had snow cover estimates and 59 cells were used at least once (see Table 2). Flocks that fell outside the boundaries of cells primarily occurred >2 km inland or were near the mouths of large rivers where the flight lines did not closely follow the coast and we lacked estimates of snow cover. Those flocks were not considered in the analysis of snow cover selection.

In both years ≥80% of used cells were in three snow cover classes (0.1-9.9, 10-49.9, 50-89.9%), and geese selected for areas that had 10-49.9% snow cover (Fig. 3). In 1994 geese also selected for cells that had 50-89.9% snow cover. Less than 7% of use occurred in areas that had ≥90% snow cover although use did not significantly differ from availability. In both years

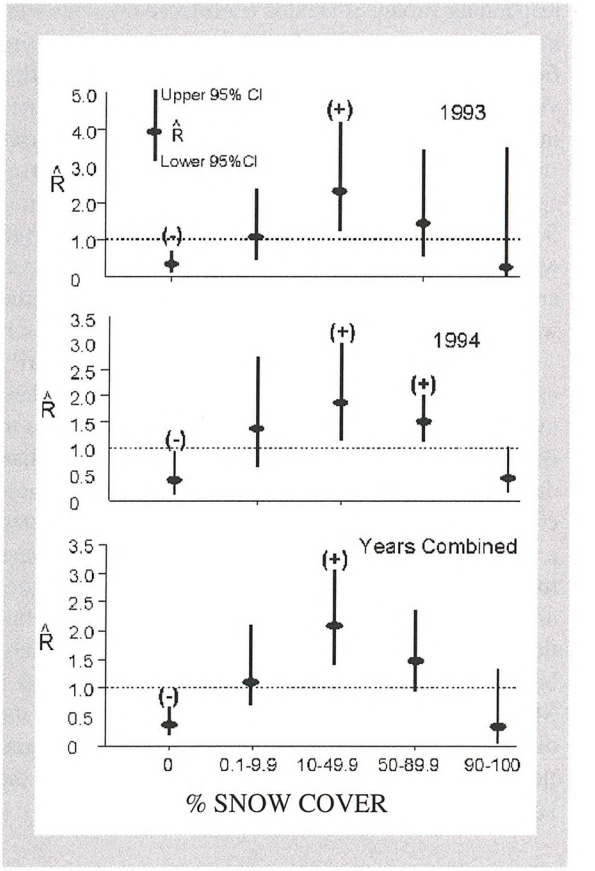

Figure 3. Selection of snow cover classes by lesser snow geese during spring migration in Upper Cook Inlet, Alaska, during 1993-1994. Selection ratios ($\hat{R}$) and associated 95% confidence intervals (CI) were based on use and availability of each snow cover class, as measured during aerial surveys of 2-km² cells in coastal wetlands. Snow geese selected a snow cover class (+) if the lower limit of the 95% CI was >1 and avoided a class (-) if the upper limit of the 95% CI was <1.

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geese selected against cells that lacked snow (see Fig. 3) even though snow-free areas were widely available after the initial survey. Because of similarities in selection ratios between years, log-normal ratios based on used cells from the two years were averaged, then back transformed to give a single selection ratio for each category of snow cover. Variances were combined in the log-normal scale (var((X+Y)/2) = (1/4)(var(X) + var(Y)). The 95% confidence intervals were calculated in the log-normal scale, then back-transformed to get confidence limits in the original scale. The combined results indicated that snow geese selected for cells with 10-49.9% snow cover and selected against areas that lacked snow cover (see Fig. 3).

Temporal changes in snow cover and snow goose distribution

Snow cover diminished rapidly during the study period in both years. Only 6 and 4% of cells lacked snow during the initial surveys in 1993 and 1994, respectively. However, 86% of cells were snow-free 17 days later on the final survey in 1993, and 66% lacked snow after 16 days on the final survey in 1994 (see Table 2). Snow geese used cells during a relatively short duration when snow was interspersed with bare ground. Among used cells, 65 and 53% were used on only one survey in 1993 and 1994, respectively. Average duration between first and last observed use of a cell was 2.6 days (SE = 0.4) in 1993 and 3.3 days (SE = 0.4) in 1994. In both years, last observed use of a cell occurred an average of 4 days (SE = 0.7) before we determined the cell to be snow-free.

We examined temporal changes in availability of cells with 0.1-89.9% snow cover because ≥80% of use occurred in that range. Temporal patterns of snow melt differed among different regions of the study area. At Susitna Flats and Trading Bay, there was a negative correlation between survey date and the number of cells with 0.1-89.9% snow cover in both years (Fig. 4). Those areas had patchy snow cover during early surveys but were snow-free during later surveys. Conversely, at Redoubt Bay in the southern portion of the study area there was no correlation between survey date and number of cells with 0.1-89.9% snow cover in 1993, although their availability was greatest during the mid part of migration. In 1994, there was a positive correlation between availability of cells with 0.1-89.9% snow cover and survey date (see Fig. 4). Most cells in

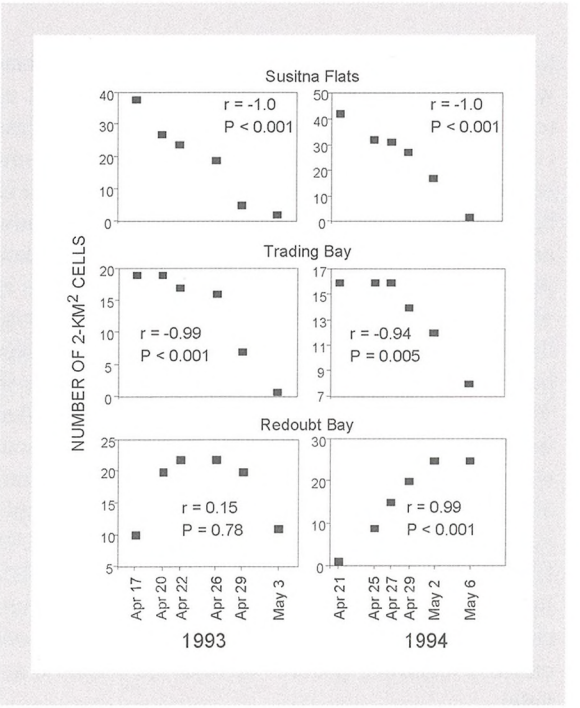

Figure 4. Numbers of 2-km² cells with 0.1-89.9% snow cover for each survey date in the three wetland regions of Upper Cook Inlet, Alaska. A Spearman rank correlation (r) shows the relationship between Julian date and numbers of cells with 0.1-89.9% snow cover for each region.

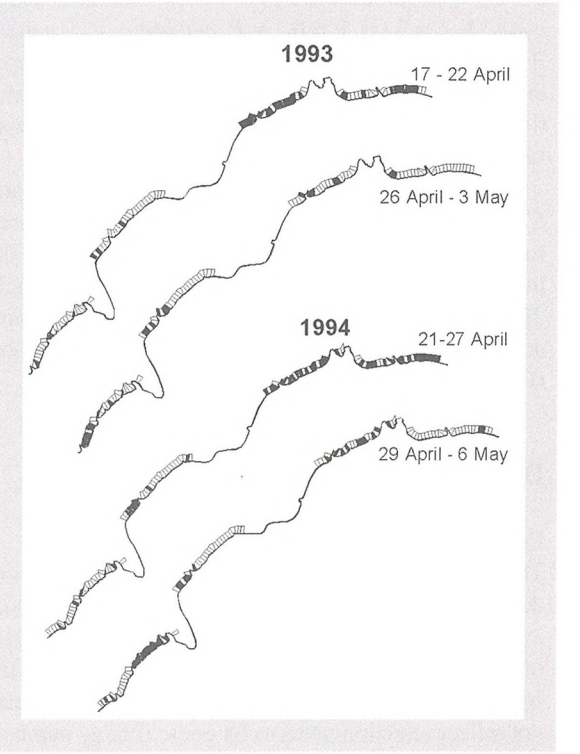

Figure 5. Distribution of 2-km² cells used (shaded) by snow geese during early and late periods of migration in Upper Cook Inlet, Alaska.

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Redoubt Bay had ≥90% snow cover during early surveys but areas of patchy snow cover became more available as melting occurred during mid and late migration. As the amount of habitat likely to be used diminished over time in northern portions of the study area, availability was greater during the mid or latter part of migration in Redoubt Bay.

The spatial distribution of snow goose flocks also changed over time (Mann-Whitney test: 1993; χ^2 = 10.3, df = 1, P = 0.001; 1994; χ^2 = 15.2, df = 1, P < 0.0001). In both years geese primarily used cells in the northern portion of the study area during the early part of migration, but used areas in the southern portion during the latter surveys (Fig. 5).

Changes in forage chemistry following snow melt

ADF of *C. ramenskii* shoots and rhizomes ($F_{2,4}$ = 12.4, P = 0.02) and *C. lyngbyaei* shoots ($F_{2,6}$ = 12.0, P = 0.01) increased over the 20 days following snow melt (Fig. 6). ADF of *T. maritimum* shoots increased slightly although the change was not significant ($F_{2,6}$ = 6.63, P = 0.03) given our rejection criteria. There was no change in ADF of *P. maritima* roots over time ($F_{2,6}$ = 0.77, P = 0.50; see Fig. 6). Nitrogen content did not change for any forage species (*T. maritimum*: $F_{2,6}$ = 0.79, P = 0.49; *C. ramenskii*: $F_{2,6}$ = 1.00, P = 0.42; *C. lyngbyaei*: $F_{2,6}$ = 3.00, P = 0.13; *P. maritima*: $F_{2,6}$ = 3.29, P = 0.11). TNC appeared to decrease in each forage species following snow melt (see Fig. 6), however, statistical significance could not be determined because samples were not replicated.

Biomass of *T. maritimum* ($F_{2,6}$ = 11.4, P = 0.009) and *C. lyngbyaei* shoots ($F_{2,6}$ = 48.8, P ≤ 0.001) increased following snow melt (see Fig. 6), with most of the increase occurring on 11-20 days following snow melt. There was no change in biomass of *C. ramenskii* shoots and rhizomes ($F_{2,6}$ = 4.31, P = 0.07) or *P. maritima* roots ($F_{2,6}$ = 0.58, P = 0.59).

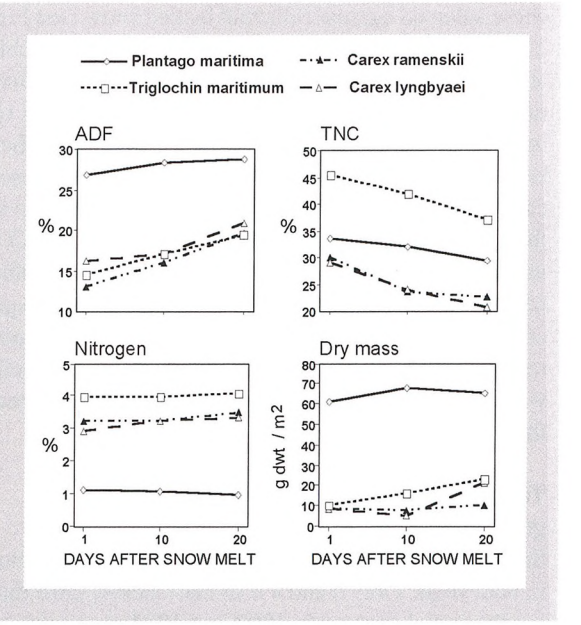

Figure 6. Change in biomass (g dry mass/m²) and acid detergent fiber (ADF), total non-structural carbohydrate (TNC) and nitrogen concentrations (% dry mass) of major snow goose forage species following snow melt in Upper Cook Inlet, Alaska. Analysis was based on roots of *Plantago maritima*, shoots and rhizomes of *Carex ramenskii*, and shoots of *Triglochin maritimum* and *Carex lyngbyaei*, collected at four exclosed sites for each species, and three times following snow melt. Biomass and concentrations of ADF and nitrogen were averaged across sites, whereas sites were pooled to estimate TNC.

Discussion

Potential bias in resource selection analysis

The outcome of resource selection analyses is dependent upon definitions of use and availability (Johnson 1980). We weighted all used cells equally regardless of the numbers of geese present and considered the entire study area as available to geese. Our analysis may not reflect selection patterns by geese if large numbers of cells were used by relatively few birds, or if some cells were not used because habitat features unrelated to snow made them unsuitable. To assess the former bias we conducted an analysis in which we defined u_{ij} (equation 2) as the number of geese seen in snow class i on the j^{th} survey, and t_j (equation 3) as the total number of birds seen on survey j. We again found that in both years geese selected against areas without snow and for areas with 10-49.9% snow cover. To evaluate the second possible bias we conducted an analysis in which we only considered available cells to be those that were used at least once by geese during the 2-year period. Results were again the same as the analysis in which the entire study area was available, except that we did not observe selection against areas without snow in 1994. Bias resulting from cells lacking suitable habitat was unlikely because the main forage species were widely distributed (A.B. Zacheis & J.W. Hupp, pers. obs.). Because results with different definitions of use and availability provided similar outcomes, we believe our analysis was robust and conclusions regarding patterns of resource selection are valid.

Patterns of resource selection

Snow geese primarily used areas with 0.1-89.9% snow

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cover, and were most likely to select areas with 10-49.9% snow cover. They selected against snow-free areas and only 7% of used cells had ≥90% snow cover. Areas with ≥90% snow cover typically had narrow bands of bare ground along the coast where high tides melted snow. Those areas may have been infrequently used because the small amount of bare ground was often dominated by *Puccinellia*, which snow geese in UCI rarely consumed (Zacheis et al. 2001). As melt progressed, snow patches became interspersed with bare ground. Habitat quality initially improved because larger areas of bare ground provided more foraging opportunities, and melting exposed inland plant communities where forage species were more abundant. Areas with intermediate snow cover may also have been favoured because melt water saturated the exposed ground and likely made grubbing for underground forage easier (Alisauskas, Ankney & Klass 1988, Hupp & Robertson 1998). Melt water usually drained from an area within 3-5 days after snow melt and geese may have been less likely to use snow-free areas because soils were too dry (J.W. Hupp, pers. obs.).

Snow geese may also have selected for areas with intermediate snow cover in order to exploit bare ground before forage was depleted by conspecifics. Snow geese primarily consumed underground material (Zacheis et al. 2001) that plants could not rapidly replace. Even the above ground parts of plants added little biomass in the first 10 days after snow melt and could probably not quickly replace tissue consumed by geese. Once an area had been fed upon, forage abundance was likely reduced for the remainder of the migration period. Zacheis et al. (2001) observed a 26% reduction in biomass of the main snow goose forage, *P. maritima* roots, following exploitation at Susitna Flats. Geese can consume large amounts of forage on migration areas (Drent et al. 1979, Bédard & Gauthier 1989, Hupp, White, Sedinger & Robertson 1996) and snow geese can reduce forage abundance through grubbing (Smith & Odum 1981, Giroux & Bédard 1987, Boyd 1995, Hupp, Robertson & Schmutz 2000). Therefore the first flocks to exploit a site when snow cover was still present likely found more profitable foraging conditions than subsequent flocks that delayed foraging until an area was completely snow free.

Temporal patterns of use and changes in spatial distribution

Snow cover changed quickly in spring, affecting duration of use at individual cells and distribution of flocks among cells. Most cells were used only during a 2-3 day period when snow patches were interspersed with open ground. Flocks often abandoned used cells shortly before snow had completely melted. Thus the pattern of exploitation was one of brief, but intense use at a site followed by a rapid movement from the area once snow melted. Flocks that left a used cell either departed UCI or moved to other areas where snow was interspersed with open ground. Snow geese are highly mobile and flock distribution can quickly shift in response to habitat changes across large areas (Robertson, Brackney, Spindler & Hupp 1997). Elsewhere, migrating geese may use stopover areas for longer periods (3-7 weeks) when growing plants can replace material consumed by geese (Prins, Ydenberg & Drent 1980) or where biomass of forage is much higher than on our study area (Giroux & Bédard 1988).

Snow melt was not uniform across the study area. The area of habitat likely to be used diminished over time at Susitna Flats and Trading Bay, but not in Redoubt Bay. That was because coastal mountains were closer to the coast in the southern portion of the study area. Snowfall was typically heavier in Redoubt Bay and evening shading slowed snow melt. During the early surveys, areas of intermediate snow cover were more available in Susitna Flats and Trading Bay whereas most areas of Redoubt Bay had ≥90% snow cover. During the later surveys, northern portions of the study area were often snow free, whereas melt had progressed in Redoubt Bay making the area more attractive to geese. As a result of spatial differences in timing of snow melt, favourable snow conditions occurred across a limited amount of the study area at a given time, and we never observed snow geese on ≥30% of the 2-km^2 cells during a single survey. As the distribution of favourable foraging conditions changed, the flock distribution shifted from the northern part of the study area to the south.

Temporal changes in forage quality

Nutritional quality of forage species appeared to diminish after snow melt. ADF of the two *Carex* species increased whereas TNC concentrations of all forage species apparently declined. Metabolizability of goose forage can be inversely correlated with fiber content (Prop & Vulink 1992, Gadallah & Jefferies 1995, Petrie, Drobney & Graber 1998) whereas TNC is highly digestible (Marriott & Forbes 1970, Coleman & Boag 1987, Buchsbaum, Wilson & Valiela 1986, Amat, Garcia-Criado & Garcia-Ciudad 1991, McWilliams 1993). TNC probably diminished due to mobilization of nutrients from underground parts and lower stems of plants (White 1973), whereas the increase in ADF of the *Carex* species was likely due to addition of new cell wall

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material during growth (Bailey 1973, Jones & Wilson 1987).

Spatial and temporal patterns of foraging by geese may be affected by declining nitrogen concentrations of green shoots as spring growth progresses (Fox et al. 1991). However, we found no evidence of temporal changes in nitrogen. Snow geese primarily consumed non-photosynthetic tissues in which nitrogen concentrations may be less likely to change during spring growth.

Forage quality was highest immediately after snow melt and diminished during the subsequent 20 days. Therefore there was at least a slight nutritional advantage for geese to arrive in UCI shortly after snow melt began. Geese that arrived in UCI may have bypassed snow-free areas if they associated higher forage quality with the presence of snow cover. However, following their arrival we doubt that changes in flock distribution were a result of diminishing forage quality. Because most 2-km^2 cells were used only for 2-3 days, changes in quality during that brief period were probably not sufficient to cause a shift in resource selection. Geese probably abandoned previously used areas due to reductions in forage availability and soil moisture following snow melt rather than diminishing forage quality.

Conservation implications

Petroleum and natural gas development is ongoing in UCI and further resource development on salt marsh wetlands is possible. Our study demonstrates the importance of conserving salt marsh habitats throughout the stopover area. Because snow cover varies within years as melt progresses, and among years depending on timing of snow melt, wetland habitats need to be maintained throughout the coastal region to ensure that feeding areas are available under a variety of snow conditions.

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