

# Population dynamics of breeding shorebirds in Arctic Alaska

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Shorebird populations were monitored in 9 of 11 years between 1981 and 1991 near Prudhoe Bay, north Alaska, USA. Weather, predation, habitat changes and events away from the breeding grounds were considered as possible determinants of population change. Densities of Semipalmated Sandpiper *Calidris pusilla*, Dunlin *C. alpina* and Red Phalarope *Phalaropus fulicaria* (the most common philopatric species) fluctuated synchronously, although these species overwinter in widely disparate areas. This suggests that population regulation occurs in the breeding areas. Population trends of these species were correlated with hatching success two years earlier. Hatching success was determined primarily by the intensity of nest predation by arctic foxes. Shorebird eggs were an alternative prey used by foxes following crashes in microtine rodent (lemming) populations. These fluctuations in productivity have long-term implications on population size. Adverse weather on the breeding grounds had its greatest effect on nest initiation; in years of delayed snow-melt or cold temperatures, birds nested later. However, in most years, a proportion of shorebirds on the breeding grounds did not attempt to nest. Non-breeding appeared to be related to the severity of the weather. Occasional catastrophic population changes may be attributable to climatic events, but the best-documented cases have occurred away from the breeding areas. For example, phalarope densities were lower following the El Niño in 1982–83.

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Se observaron las poblaciones de aves costeras durante 9 de los 11 años comprendidos entre 1981 y 1991 en las cercanías de Prudhoe Bay, en el norte de Alaska, EE.UU. Como posibles determinantes del cambio poblacional se analizaron factores tales como las condiciones climáticas, la conducta predatoria, los cambios de hábitat y los sucesos alejados de los criaderos. La densidad de los playeros semipalmados *Calidris pusilla*, las alondras de mar *C. alpina* y los falaropos rojos *Phalaropus fulicaria* (las especies filopátricas más comunes) fluctuaron sincrónicamente, a pesar de que esas especies pasan el invierno en zonas muy separadas. Ello parece indicar que la regulación de la población ocurre en los criaderos. Las tendencias poblacionales de esas especies se correlacionaron con el éxito de la incubación dos años antes. El éxito en materia de incubación se determinó principalmente en base a la intensidad de la predación de los nidos por parte de los zorros del Ártico. Los huevos de las aves costeras fueron una presa alternativa de los zorros como resultado de las abruptas disminuciones de las poblaciones de roedores micrótidos (lemmings o ratón de Noruega). Esas fluctuaciones en la productividad tienen implicaciones a largo plazo para el volumen de la población. Las condiciones climáticas adversas sobre los criaderos tuvieron su mayor efecto sobre el inicio de la nidificación; en años en que se retrasa el deshielo o que las temperaturas son frías, las aves anidaron más tarde. Sin embargo, en la mayoría de los años, se observó en los criaderos cierto porcentaje de aves costeras que no trataron de anidar. La evitación de la reproducción parecía estar relacionada con la incoherencia de las condiciones climáticas. Los ocasionales cambios catastróficos en la población podrían obedecer a las condiciones climáticas, pero los casos mejor documentados han ocurrido en puntos alejados de los criaderos. Por ejemplo, la densidad de los falaropos fue inferior después de El Niño en 1982–83.

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Les populations d'oiseaux de rivage de la région de Prudhoe Bay dans le nord de l'Alaska, aux États-Unis, ont été étudiées au cours de neuf des onze années de la période 1981–1991. Ont été considérés comme agents potentiels de changement de la population : les conditions météorologiques, la prédation, la modification des habitats et des phénomènes se produisant à l'extérieur des aires de reproduction. Les densités de Bécasseau semipalmé *Calidris pusilla*, de Bécasseau variable *C. alpina* et de Phalarope roux *Phalaropus fulicaria*, les espèces philopatriques les plus courantes, ont fluctué de façon synchrone, même si ces espèces hivernent dans des régions très variées. Cela semble indiquer que la régulation des populations se produit dans les aires de reproduction. On a établi, pour ces espèces, des corrélations entre les tendances démographiques et le succès d'éclosion, déterminé deux ans auparavant, essentiellement en fonction de l'intensité de la prédation des nids par les renards arctiques. En effet, les renards se sont nourris d'oeufs d'oiseaux de rivage après l'effondrement des populations de Microtinés (lemmings). Ces fluctuations de productivité ont des effets à long terme sur la taille des populations. Les conditions météorologiques défavorables à la reproduction ont l'effet le plus important au moment de la construction des nids; ainsi, lorsque la fonte des neiges est tardive ou que le temps est

particulièrement froid, les oiseaux nidifient plus tard que d'habitude. Toutefois, la plupart des années, une portion des oiseaux de rivage n'a pas cherché à nidifier; on pense que cela tient aux rigueurs du climat. Il arrive à l'occasion que des changements catastrophiques de population soient attribuables à des phénomènes climatiques, mais les cas les mieux étudiés se sont produits à l'extérieur des aires de reproduction. Les densités de phalaropes, par exemple, étaient plus faibles après le passage d'El Niño en 1982–1983.

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## Introduction

This review summarizes information on the fluctuations in bird use at a study area near Prudhoe Bay along the Beaufort Sea coast of the Alaska North Slope (Figure 1). This study area, the Point McIntyre Reference Area (PMRA), is near the Prudhoe Bay oilfield but is relatively isolated from oilfield facilities. Field sampling was conducted during nine summers between 1981 and 1991 (no sampling was undertaken in 1983 and 1985). The study plots were originally established as part of a control area for a study to monitor the effects of an oilfield expansion 4 km to the east. The layout of the plots was determined by that study; however, sampling in this area continued long after its original role was ended. This sampling has provided a time series of data showing natural variations in populations of birds using coastal tundra along the central Beaufort Sea. The variables used to quantify bird use included nest densities, timing of nest initiation, nest success and breeding season bird densities.

In this paper, temporal changes in shorebird densities and nesting biology are described, and trends in nest densities are correlated with several environmental (snow cover and temperature) and biotic variables in order to determine the factors causing population fluctuations. Space limitations prevent a complete presentation of all the analyses conducted and discussion of the results. This summary provides an overview of the study and some of the more interesting findings.

## The breeding bird community

The species composition of breeding birds near Prudhoe Bay was dominated by shorebirds (Figure 2). Population levels of all species in the tundra bird community were monitored and trends determined. Data summaries of the ten most numerous nesting species (eight of which were shorebirds) are presented below. These species were King Eider *Somateria spectabilis*, Lesser Golden-Plover *Pluvialis dominica*, Semipalmated Sandpiper *Calidris pusilla*, Pectoral Sandpiper *C. melanotos*, Dunlin *C. alpina*, Stilt Sandpiper *C. himantopus*, Buff-breasted Sandpiper *Tryngites subruficollis*, Red-necked Phalarope *Phalaropus lobatus*, Red Phalarope *P. fulicaria* and Lapland Longspur *Calcarius lapponicus*.

These ten species accounted for 92% of the approximately 4,500 nests (600 from this investigation) that we have found on study plots in the Prudhoe Bay area. The results and discussion concentrate primarily on shorebirds, but data on the King Eider and Lapland Longspur are also included in the summary tables.

## Methods

### Birds and nests

The results obtained from ten study plots (each measuring 100 m × 1,000 m [or 10-ha plots], for a total area of 1 km<sup>2</sup>) provided most of the information for this report. The habitat composition was not considered when these plots were originally established, except that large, deep lakes were avoided.

All the results presented herein are based on data obtained during breeding season censuses. In our sampling protocol, the breeding season comprised Census Periods 2–5 (Table 1). All plots were censused during each period (2–5; note that Census Period 1 occurs prior to most nesting activity), and an attempt was made to locate every nest that might be associated with any of the birds using the plots. To aid in nest location, a rope was dragged (50-m swaths) by two biologists in order to flush right-sitting birds during Census Periods 3 and 4. Additional visits were scheduled to monitor nests. As hatching approached, an attempt was made to visit the nests every other day.

Following the completion of monitoring, three parameters (hatching success, nest initiation date and re-nest status) were determined for each nest. A nest was considered to be successful if at least one egg hatched. Evidence used in evaluating *nest success* included (1) the length of time the nest had been active since initiation, (2) evidence of predation (broken eggs, fox scats or urine), (3) the presence of hatching eggs, chicks or egg bits (tiny fragments remaining from hatching) and (4) re-nesting attempts. If the outcome of a nest attempt could not be determined by these criteria, the reproductive success was coded as *unknown*.

The *nest initiation date* was the date the first egg was laid. This date could rarely be determined directly. If the nest was found during egg laying, the initiation date was determined by subtracting one

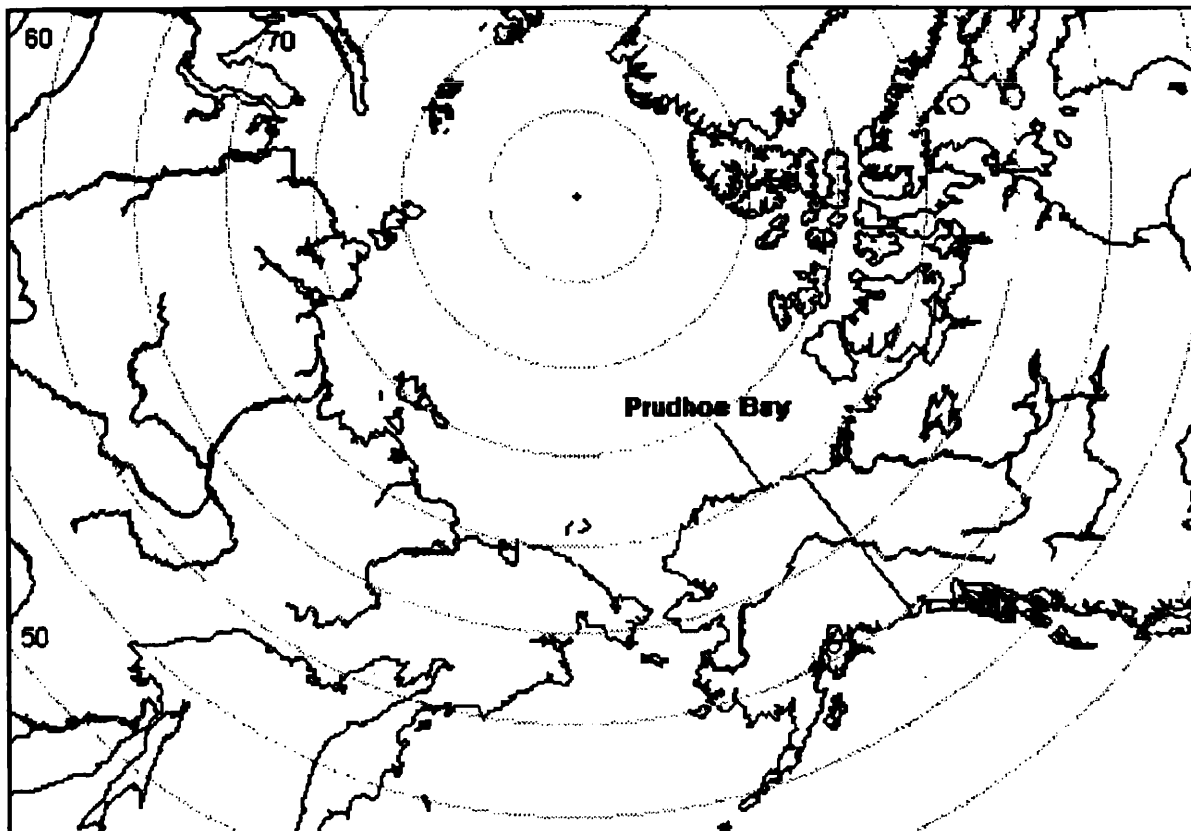


Figure 1. Polar view of the Arctic showing location of Prudhoe Bay, Alaska, where sampling for this study took place.

day for each egg back to the first egg, assuming that one egg is laid each day. For nests found during the incubation period, the date of initiation was estimated only for those having a known hatching date. The initiation date was derived by back-calculating from the hatching date and subtracting the average incubation period and the clutch size to the first egg.

A *re-nest* was a second nesting effort by a pair of birds that failed a prior attempt. A nest initiated shortly after another one failed in the same general location (within approximately 100 m) indicated re-nesting. Such nests were excluded from the analysis of densities and nest initiation dates.

### Environmental measures

Temperature measurements were obtained from records at Deadhorse Flight Service Station, approximately 20 km SSW of the PMRA, where weather measurements were recorded hourly. These records were averaged to provide a daily value. Depending on the specific analyses, these data were further summarized to provide an overall measure for the breeding season as a whole (1 June – 18 July) or for particular census periods of interest. Temperature deviation, as used in the analyses, was the difference between average temperature on a given day and the average temperature for that date for the years 1981–1991

(including 1983 and 1985). Each deviation was added to yield a cumulative value that indicated the total energy input (in degree-days) up to that date (from 1 June) relative to other years. An 'average' year would have a negative value.

Starting in 1986, snow cover estimates were made during the censuses. The percentage of tundra covered in each 50 m × 50 m unit of the plots (40 estimates per plot per visit) was estimated and recorded during maintenance activities and censuses. Differences in the timing of melt among years were evaluated by comparing the percent snow cover during Census Periods 2 and 3.

### Statistical analyses

The principal analytical techniques used in this report examined changes in densities of birds or nests among years. Nest densities were based on the numbers of nests found in the plots (excluding re-nests) each year. Annual densities of birds were determined by averaging the four censuses conducted during each breeding season. Changes in density over years were evaluated using the Friedman test. The sample units (ten plots) were considered to be blocks subjected to nine treatments (years). Calculations of nest initiation dates and nest success are based on information from all nests monitored in the reference area. The Kruskal-Wallis test was used to detect significant differences

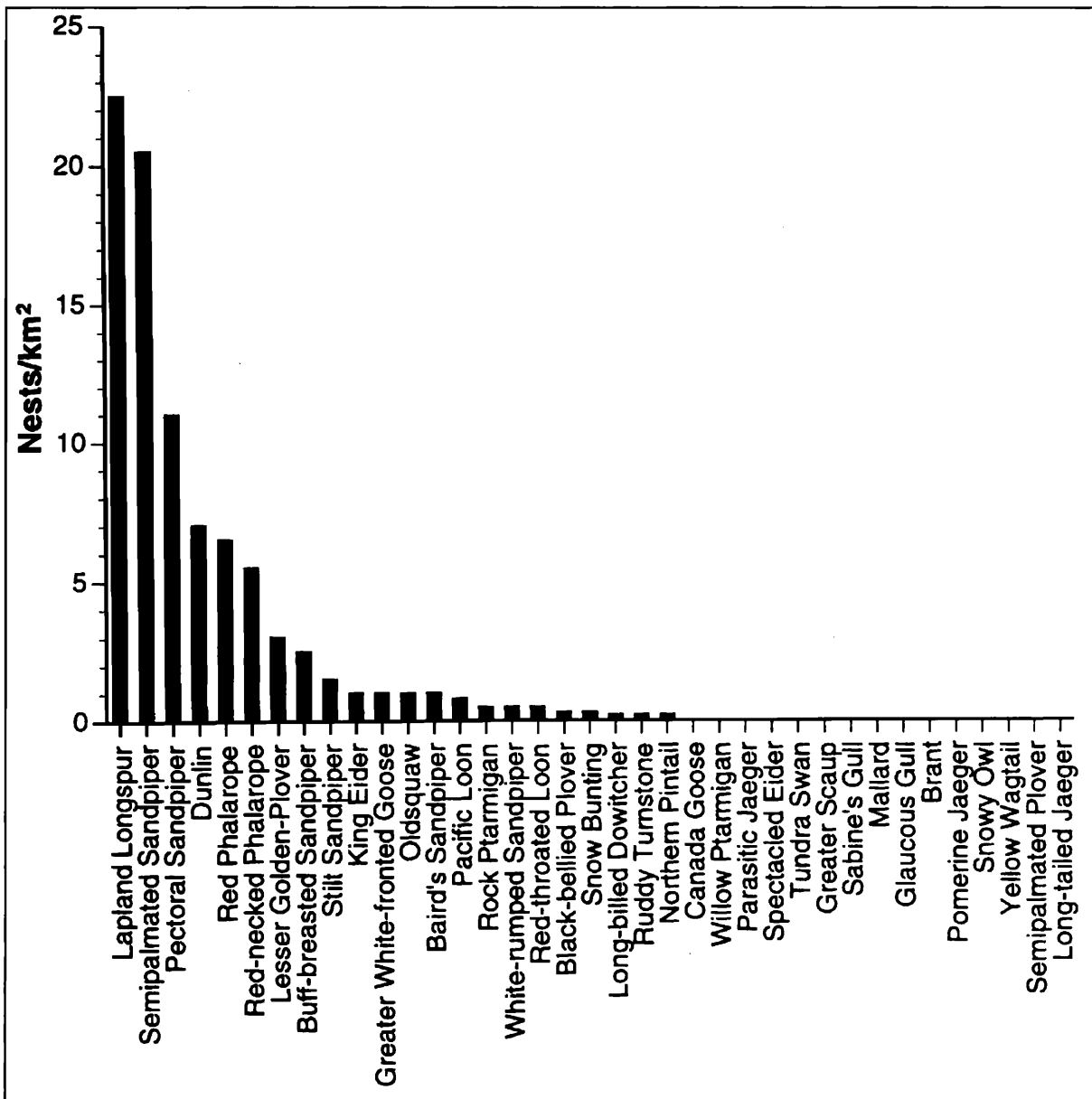


Figure 2. Species composition of the Prudhoe Bay area tundra bird community based on nests on over 200 study plots scattered throughout the region. The PMRA is the subset of these plots that received the most continuous sampling and contributed 13% of the total nests studied.

Table 1. Plot census periods for determining breeding season bird densities.

Period	Timing	Dates
2	Early June	9–13 June
3	Mid-June	14–27 June
4	Early July	28 June – 10 July
5	Mid-July	11–18 July

in nest initiation dates among years, and the  $\chi^2$  goodness-of-fit test was used to test for differences in nest success among years. Pearson correlation coefficients were used to document covariation

among measures of the environment, nest variable and measures of bird abundance.

A significance level of  $p = 0.05$  was used for all tests except the screening of correlations among bird and environmental variables, where a more restrictive criterion of  $p = 0.01$  was used.

## Results and discussion

### Nest densities

Among-year differences in nest densities were significant only for Pectoral Sandpiper and Lapland Longspur (Table 2). The Pectoral Sandpiper was the most variable species. Much of this variability

**Table 2.** Nest densities in Point McIntyre Reference Area, 1981–1991. Test results (probabilities) of Friedman analyses for among-year changes in nest density are listed. In all cases, the degrees of freedom for the test statistics are 8 (9 years - 1).

Species	Nest densities (no. of nests/km <sup>2</sup> )										p
	1981	1982	1984	1986	1987	1988	1989	1990	1991		
King Eider	2	3	0	3	1	1	0	0	2	0.951	
Lesser Golden-Plover	1	3	1	2	2	3	3	3	4	0.974	
Semipalmated Sandpiper	12	13	12	11	10	11	15	19	10	0.237	
Pectoral Sandpiper	7	1	7	4	7	9	3	33	6	0.006	
Dunlin	8	8	10	3	6	5	9	10	8	0.469	
Stilt Sandpiper	0	0	1	1	0	1	0	0	3	0.997	
Buff-breasted Sandpiper	2	3	0	0	1	0	0	2	1	0.952	
Red-necked Phalarope	0	0	0	0	0	2	1	3	2	0.938	
Red Phalarope	10	9	4	3	2	5	6	11	6	0.321	
Lapland Longspur	15	10	22	20	6	22	6	13	22	0.008	
Totals	57	50	57	47	35	59	43	94	64	–	

**Table 3.** Median dates of nest initiation within the Point McIntyre Reference Area. Test results (probabilities) of Kruskal-Wallis analyses for among-year changes in the median date of nest initiation are listed.

Species	Median date of nest initiation										p
	1981	1982	1984	1986	1987	1988	1989	1990	1991		
King Eider					21 June						
Lesser Golden-Plover	16 June	13 June	15 June	22 June	26 June	24 June	23 June	1 June	18 June	0.054	
Semipalmated Sandpiper	15 June	21 June	11 June	18 June	14 June	15 June	22 June	4 June	14 June	0.000	
Pectoral Sandpiper	15 June	29 June	16 June	23 June	24 June	24 June	15 June	8 June	17 June	0.000	
Dunlin	11 June	18 June	11 June	15 June	14 June	12 June	11 June	7 June	9 June	0.003	
Stilt Sandpiper			10 June		16 June		14 June	2 June	13 June	0.253	
Buff-breasted Sandpiper	14 June	28 June	23 June		2 July			3 July	1 July	0.317	
Red-necked Phalarope		28 June		25 June	23 June	22 June	18 June	6 June	18 June	0.160	
Red Phalarope	19 June	23 June	14 June		21 June	16 June	20 June	10 June	21 June	0.002	
Lapland Longspur	14 June	16 June	10 June	18 June	20 June	13 June	12 June	9 June	16 June	0.000	

resulted from the exceptionally high nest density of 1990. Pectoral Sandpipers are thought to be nomadic, changing nesting areas between years for unknown reasons (Pitelka 1959). Because their regional abundances can fluctuate considerably among years, it is not unexpected that large inter-annual changes in density were recorded. The magnitude of their invasion into the Prudhoe Bay area in 1990 was of greater amplitude than any fluctuation previously experienced.

Although not showing statistically significant differences among years, several species exhibited more gradual, but regular, density shifts. The common philopatric shorebirds, such as Semipalmated Sandpiper, Dunlin and Red Phalarope, are most notable in this regard. Following the presentation of major trends in other aspects of the breeding status of these species, density fluctuations of site-tenacious species and correlations among nest densities and other measures are also discussed.

### Nest initiation

Nesting is often thought to occur in a highly synchronous fashion in the Arctic. However, median nest initiation dates were found to vary considerably among species (Table 3). For example, median initiation dates in 1990 encompassed the period from 1 June to 3 July (Lesser Golden-Plover and Buff-breasted Sandpiper, respectively). Within species, there was also considerable variability as to when nest initiation occurred across years. Lesser Golden-Plovers, for example, initiated their nests 25 days earlier in 1990 than in 1987. Five species exhibited significant variability among years in the timing of nesting (Table 3).

Years promoting early or late nesting tended to affect many species in unison. Except for the Buff-breasted Sandpiper, all other species had their earliest nest initiation in 1990. Four pairs of initiation dates were significantly correlated with each other: Lesser Golden-Plover with Stilt Sandpiper ( $r = 0.992$ ,  $p = 0.001$ ), Pectoral Sandpiper

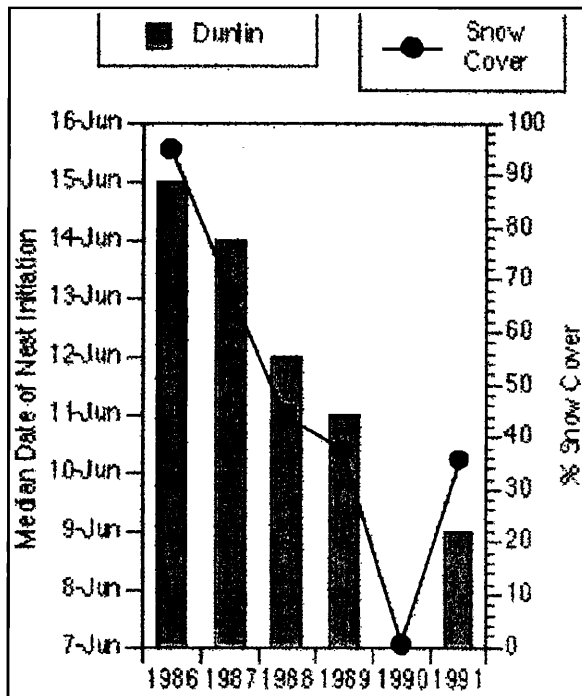


Figure 3. Trend in nest initiation dates of Dunlin in relation to percent snow cover during early (9-13) June.

with Dunlin ( $r = 0.911$ ,  $p = 0.001$ ), Pectoral Sandpiper with Red-necked Phalarope ( $r = 0.960$ ,  $p = 0.001$ ) and Dunlin with Red-necked Phalarope ( $r = 0.920$ ,  $p = 0.003$ ). The species in these correlations included both early- and intermediate-season nesters. The timing of nest initiation of the late-nesting Buff-breasted Sandpiper was not in synchrony with any of these species. Conspicuously absent from this group are some of the most common nesting species: Lapland Longspur, Semipalmated Sandpiper and Red Phalarope.

Snow-melt was thought to be the environmental factor of greatest potential influence on nest initiation, but the short time series of this parameter prevented as rigorous a statistical evaluation of its importance as was possible for the other environmental variables. Dunlin nest initiation data and snow cover exhibited a significant relationship ( $r = 0.955$ ,  $p = 0.003$ ), with initiation being late in years of delayed snow-melt (Figure 3). Most species (except the late-nesting Buff-breasted Sandpiper) had relatively high correlations between nest initiation date and snow cover, and several of these will no doubt prove statistically significant as the period of monitoring becomes longer.

### Nest success

Nesting success varied both among species and among years (Table 4). Statistically significant differences among years were detected for the Semipalmated Sandpiper and the Lapland Longspur and for all species combined ( $c = 38.990$ ,

30.592 and 54.067, respectively;  $p < 0.001$  for all tests). Nest success, especially that of Semipalmated Sandpiper, was lowest in 1986. A single best year was not as evident, although both 1981 and 1988 had, overall, high nest success.

Semipalmated Sandpiper nest success was correlated with the success of all the species pooled ( $r = 0.964$ ,  $p < 0.001$ ; Figure 4). The significance of this correlation suggests that nest success varies (relatively) synchronously across all species. Because Semipalmated Sandpipers accounted for only 19% of the total nests monitored, there is a minor element of self-correlation; the greater proportion of the total success did not involve this species. For most species taken individually, our annual measures of nest success in the PMRA are variable owing to small samples. This correlation showed that patterns of variation in our best-monitored species were mirrored in all species combined. Variations in nest success were more or less synchronous for all species, and the measure for all species pooled best characterized conditions for a given year.

Many factors may influence nest success; these include predation (by arctic fox *Alopex lagopus*, jaegers, Glaucous Gull *Larus hyperboreus*, Common Raven *Corvus corax* and others), desertion (perhaps weather-related) and trampling by caribou. Trends in nest success were not found to be significantly correlated with any environmental or biotic variable. The largest single source of nest loss appeared to be nest predation by arctic foxes. My working hypothesis, the 'Alternative Prey Hypothesis' first advanced by Summers & Underhill (1987), is that arctic fox population levels fluctuate in response to the availability of their primary prey, which in this study are presumed to be lemmings. Following precipitous declines in lemming abundance, arctic foxes switch to alternative food sources, in particular bird nests. This leads to episodic periods of low nest success until fox populations decrease or the availability of the primary prey increases.

### Breeding season populations

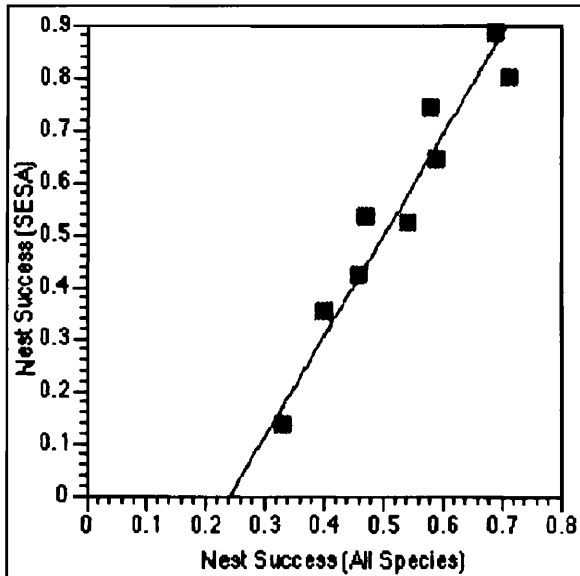
#### Densities

The population densities of five of the ten species under study varied significantly between years. These species were Pectoral Sandpiper, Buff-breasted Sandpiper, Red-necked Phalarope, Red Phalarope and Lapland Longspur (Table 5). The nest densities of the Pectoral Sandpiper and Lapland Longspur also varied significantly between years (Table 2), and the changes found here probably reflect changes in breeding effort.

Breeding season population densities of three species (Pectoral Sandpiper, Buff-breasted Sandpiper and Red Phalarope) were strongly correlated

**Table 4.** Proportion of nests hatching at least one egg in the Point McIntyre Reference Area, 1981–1991. Only species of which at least 100 nests were monitored are detailed.

Nest success	% of nests hatching $\geq 1$ egg									
	1981	1982	1984	1986	1987	1988	1989	1990	1991	All years
Semipalmated Sandpiper	0.80	0.35	0.52	0.13	0.74	0.88	0.42	0.64	0.53	0.60
Pectoral Sandpiper	0.83	0.75	0.56	0.50	0.44	0.77	0.75	0.58	0.41	0.57
Dunlin	0.33	0.36	0.38	0.60	0.66	0.70	0.42	0.53	0.45	0.50
Lapland Longspur	0.90	0.41	0.56	0.51	0.72	0.67	0.31	0.66	0.61	0.59
All species	0.71	0.40	0.54	0.33	0.58	0.69	0.46	0.59	0.47	0.54

**Figure 4.** Semipalmated Sandpiper (SESA) nest success in relation to nest success over all species.

with the densities of their nests ( $r = 0.937$ ,  $p < 0.001$ ;  $r = 0.815$ ,  $p = 0.007$ ;  $r = 0.983$ ,  $p < 0.001$ ; respectively). Perhaps the most significant feature of these correlations is that similar relationships were not found for other species. That a relationship exists between bird densities and nest densities is often assumed in population assessments based on bird counts alone (*e.g.* line transects), but, as evidenced here, this may not always be a valid assumption. The only species showing this relationship were those with the most variable abundances in the Prudhoe Bay area. Two of these species, the Pectoral Sandpiper and Buff-breasted Sandpiper, are nomadic and exhibit little philopatry. The Red Phalarope, although somewhat philopatric, owes its variability to a dramatic population decrease in the mid-1980s. Both species of phalaropes decreased markedly in abundance between 1982 and 1984 (there was no sampling in 1983), corresponding to the severe El Niño that may have induced losses on the wintering grounds. None of the species exhibiting a high correlation between nest and bird densities is monogamous, and all have uniparental incubation systems. *A priori*, these species might have been expected to

have the weakest correlations between nest and bird densities, because early departure of the non-incubating birds affected census results. The importance of mating systems in these correlations is uncertain.

Most species that are philopatric, and thus have more stable numbers, showed little relationship between bird and nest densities. This lack of relationship between birds and nests of most philopatric species suggested that non-breeding birds were present in some years. This prompted the use of a non-breeding index as an analytical tool for understanding patterns of density variation in nests and birds.

#### *The non-breeding index*

The non-breeding index is defined here as the ratio of the number of birds counted during the breeding season per nest found. Ideally, this index might be expected to be close to 2 if there was an equal sex ratio, if all nests were found and if all birds were breeding. In practice, some deviation from 2 would be expected because of the overlap of migration and nesting. For example, many shorebirds commence migration prior to fledging of their young or even the hatch of their eggs. This is particularly true of species with uniparental care, such that one sex, female phalaropes for example, may be absent during some breeding season censuses. Hence, an index less than 2 might be expected. Disproportionate sampling of nesting and foraging habitats or failure to locate some nests could also contribute to departures from an index value of 2. However, within a species, the index should remain relatively stable over years if most birds were nesting. Our results revealed that non-breeding indices were not constant over years; they showed considerable variability (Table 6). In the two common monogamous species, the Semipalmated Sandpiper and the Dunlin, the minimum value of the index was 1.8; this is close to the expected value of 2 if all birds nested.

Several correlations were found involving non-breeding indices, but they were not strongly associated with any single class of measurement. Findings of potential biological significance

**Table 5.** Average breeding season density of birds in the Point McIntyre Reference Area. Test results (probabilities) of Friedman analyses for among-year changes in breeding season bird density are listed.

Species	No. of birds/km <sup>2</sup>									p
	1981	1982	1984	1986	1987	1988	1989	1990	1991	
King Eider	3.8	10.5	4.3	1.3	1.8	1.5	3.3	2.0	2.25	0.158
Lesser Golden-Plover	16.5	8.8	6.3	6.0	5.5	5.3	3.3	6.3	11.0	0.106
Semipalmated Sandpiper	30.3	30.5	28.3	23.5	30.5	34.0	28.0	33.5	27.5	0.240
Pectoral Sandpiper	38.3	22.5	29.5	17.0	30.0	36.5	18.5	65.8	22.8	0.000
Dunlin	23.3	25.3	20.8	17.0	18.8	16.0	17.3	20.3	14.5	0.072
Stilt Sandpiper	0.0	0.3	1.0	2.8	2.0	2.8	3.3	2.3	1.75	0.136
Buff-breasted Sandpiper	8.8	14.0	3.8	4.3	4.3	4.3	0.5	5.8	1.25	0.001
Red-necked Phalarope	10.3	2.8	5.0	1.5	2.8	5.5	6.8	18.0	9.0	0.024
Red Phalarope	21.3	20.0	5.3	3.5	3.8	7.3	10.5	28.0	6.5	0.000
Lapland Longspur	92.5	67.3	71.3	57.0	44.0	72.5	31.3	54.5	58.5	0.000

**Table 6.** Yearly non-breeding index scores for the Point McIntyre Reference Area. Empty cells indicate that no nest was found that year.

Species	Non-breeding index score (no. of birds/no. of nests)								
	1981	1982	1984	1986	1987	1988	1989	1990	1991
King Eider	1.9	3.5		0.4	1.8	1.5			1.1
Lesser Golden-Plover	16.5	2.9	6.3	3.0	2.8	1.8	1.1	2.1	2.8
Semipalmated Sandpiper	2.5	2.3	2.4	2.1	3.1	3.1	1.9	1.8	2.8
Pectoral Sandpiper	5.5	22.5	4.2	4.3	4.3	4.1	6.2	2.0	3.8
Dunlin	2.9	3.2	2.1	5.7	3.1	3.2	1.9	2.0	1.8
Stilt Sandpiper			1.0	2.8		2.8			0.6
Buff-breasted Sandpiper	4.4	4.7			4.3			2.9	1.3
Red-necked Phalarope						2.8	6.8	6.0	4.5
Red Phalarope	2.1	2.2	1.3	1.2	1.9	1.5	1.8	2.6	1.1
Lapland Longspur	6.2	6.7	3.2	2.9	7.3	3.3	5.2	4.2	2.7

included the following: (1) weather appeared to be important to Semipalmated Sandpipers, because non-breeding was correlated with low temperature ( $r = -0.874$ ,  $p = 0.002$ ; Figure 5), (2) non-breeding by Dunlins was associated with low nest densities ( $r = -0.874$ ,  $p = 0.002$ ), but (3) non-breeding was associated with high breeding season bird densities for both the Lesser Golden-Plover ( $r = 0.836$ ,  $p = 0.005$ ) and the Red Phalarope ( $r = 0.865$ ,  $p = 0.003$ ).

These results indicate that reductions in nesting effort may arise from environmental factors such as temperature. However, high non-breeding scores should not always be viewed as having negative implications for breeding. In the case of the Lesser Golden-Plover and the Red Phalarope, these indices increased with breeding season bird densities and, in the case of the Red Phalarope, with nest densities (which were correlated with bird densities). In these cases, adult birds apparently made greater use of the area, perhaps for staging prior to migration.

The non-breeding indices and the presence of non-breeding birds are important for several reasons. First, they highlight the use of the Arctic

Coastal Plain by birds for purposes other than nesting. Among arctic shorebirds, the presence of non-breeding birds on the breeding grounds is rarely considered. In contrast to waterfowl, especially geese, where subadult birds return to the Arctic, even though they do not nest, non-breeding shorebirds are frequently thought to remain in their wintering ranges. Occasional sightings of non-breeding shorebirds in the Arctic have been reported during extreme conditions when nesting fails to take place. However, our results suggest that a variable proportion of non-breeding birds may be present in many years.

Second, the presence of non-breeding birds helps to explain why population densities and nesting densities are so poorly correlated for many species during the breeding season. Nest densities and population densities correlated only for those species with the greatest fluctuations in their use of the area, most notably the nomadic species, including Pectoral and Buff-breasted sandpipers. The other species, including most of the philopatric species, are predominantly represented by monogamous species. Evidently, variations in



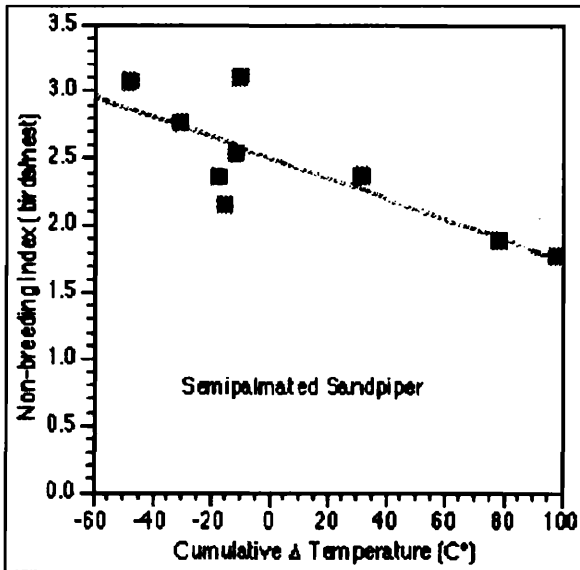


Figure 5. Semipalmated Sandpiper non-breeding index in relation to breeding season temperatures.

environmental variables can exert a considerable influence on the nesting effort of these species, resulting in a lack of synchronization between densities of birds and nests.

**Variation in nest densities of North Slope shorebirds**

In this section, the data series describing annual trends in nest densities is compared with trends found for other measures of nesting and environmental conditions in order to find common

patterns. Two approaches were taken. First, a specific hypothesis, that breeding density is determined by prior nest success, was investigated. Support for this hypothesis would indicate that changes in nest density reflected actual population changes, at least for philopatric species. Second, the roles of environmental conditions and non-breeding, as determinants of nesting densities, were evaluated. If fluctuations in nest density were related to weather or non-breeding, these density changes may not necessarily have had population-level implications.

*Nest success as a predictor of future nest densities*

The major changes in nest densities, such as those for the Pectoral Sandpiper, are the easiest to detect with statistical verification. However, additional and more subtle density changes also occur. Nest density trends of the three most common philopatric species — the Semipalmated Sandpiper, the Dunlin and the Red Phalarope — appeared to change synchronously (Figure 6). The similarities in those trends suggested that some common factor was contributing to density changes in all three species. Semipalmated Sandpipers winter in coastal South America, primarily along the coast of Suriname (Morrison & Ross 1989). Dunlin from Alaska’s Arctic Coastal Plain spend the winter around the South China Sea and the Sea of Japan (MacLean & Holmes 1971). Red Phalaropes are marine birds during the winter, and those nesting in Alaska are thought to winter at sea off Peru and Chile (Marchant, Hayman & Prater 1986). Because these birds migrate to such different areas, it is

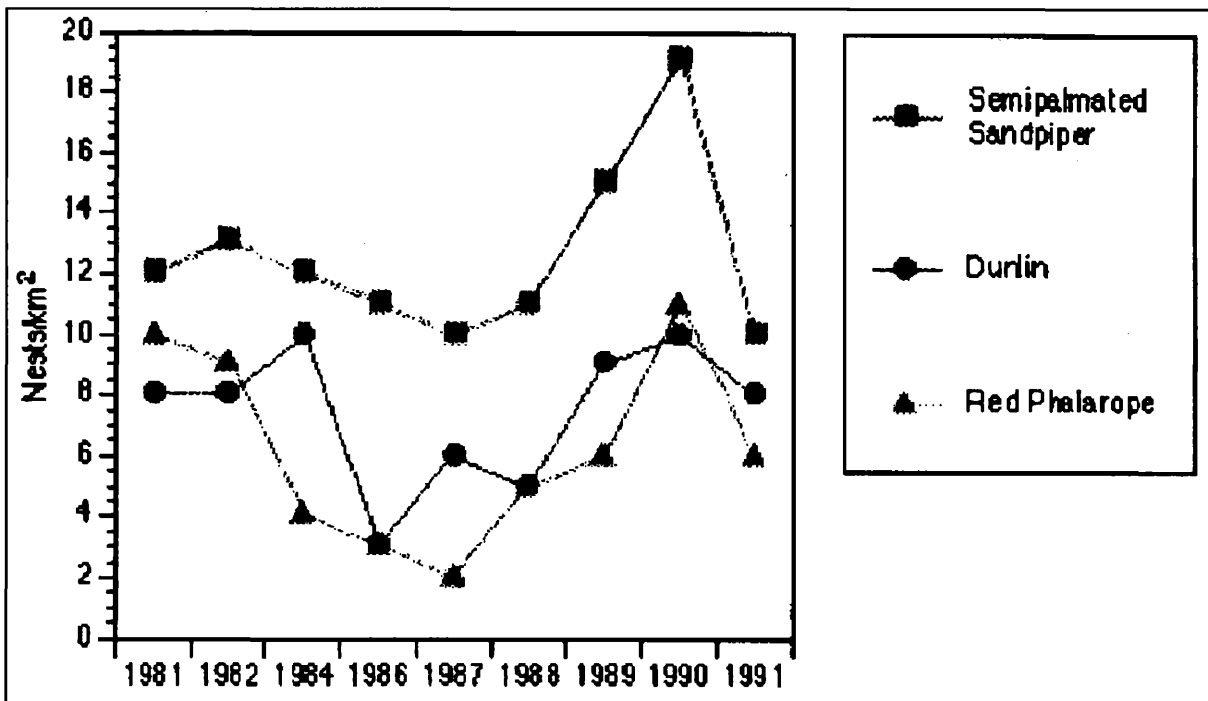


Figure 6. Trends in nest densities of the common philopatric shorebirds in the PMRA.

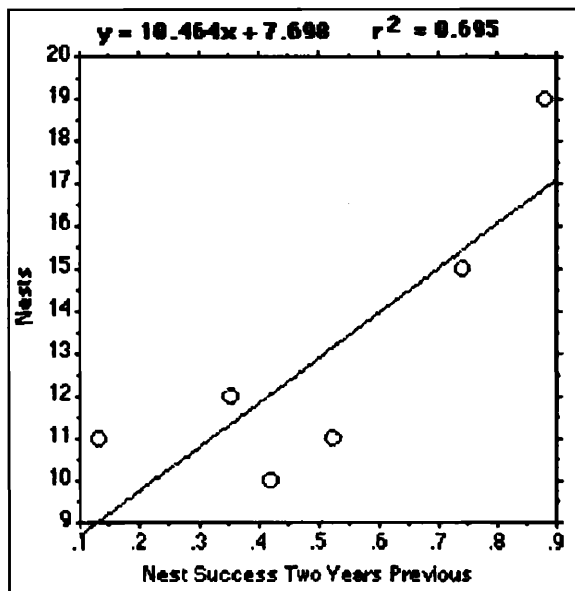


Figure 7. Results of regression of Semipalmated Sandpiper nest density on their nest success two years earlier.

unlikely that the synchronous population trends can be attributable to factors operating on the separate wintering grounds. These species occur together only on the breeding grounds; therefore, the cause for their parallel changes in abundance most likely occurs where they nest.

Recruitment appears to be a factor in determining the direction of nest density changes. Nest densities of the Semipalmated Sandpiper were significantly correlated with nest success two years earlier (Figure 7;  $F_{1,4} = 0.097$ ,  $p = 0.04$ ,  $r = 0.833$ ). Dunlin and Red Phalaropes were not sufficiently numerous to provide reliable estimates of nest success for individual species. However, evidence presented earlier indicated that the trends in nest success appeared to vary in parallel across all species. If nest success is a leading indicator of nest densities, as appears to be the case, we would expect similar patterns in density fluctuations across all site-tenacious species. This was indeed the pattern that we observed. It is simplistic to expect nest densities to be entirely dependent on nest success. Realistically, nest success should (with all other things being equal) influence the direction of change but not the absolute value. The breeding population in any year ( $y$ ) would depend on population size during the preceding year ( $y-1$ ) with some allowance for mortality ( $m$ ) plus recruitment of new birds into the breeding population. Recruitment would depend on the nesting population two years earlier ( $y-2$ ) times nest success in that year to give production of young. Some allowance needs to be made for survival ( $s$ ) before entering the breeding population. Additional allowances need to be made for such factors as partial non-breeding during years of adverse weather. Because of non-breeding,

nests $_{[y-1]}$  may underestimate the size of the breeding population, especially as population size is used to calculate the survivorship component of the model described above. Eventually, we hope to incorporate all these factors into a model of population trends. At present, nest success alone appears to explain a large amount of the annual fluctuations in nest densities.

Other shorebird populations may be regulated by nest success. Sanderling *Calidris alba*, Curlew Sandpiper *C. ferruginea* and Ruddy Turnstone *Arenaria interpres* populations wintering in South Africa follow a three-year cycle (Summers & Underhill 1987; Summers *et al.* 1987). The major component of these changes was the proportion of first-year birds (*i.e.* nest success during the preceding summer). This cycle correlated with fox and lemming abundances on the Taimyr Peninsula in Russia, where many of these shorebirds breed. Following crashes in lemming populations, the foxes apparently preyed on bird nests, thus resulting in low nest success and low proportions of young birds on the wintering grounds.

Our results agree with the hypothesis that nest success is determined by variable predation rates and that success in turn drives the rate of recruitment, which determines the size of the breeding populations of philopatric shorebirds. Field studies are now in progress to ascertain that trends in nest success in the PMRA indeed correspond with changes in microtine abundance.

#### Influences of environmental factors

##### Snow

Our results have shown that nest initiation was delayed during years of persistent snow cover, especially for the Dunlin (Figure 3), as shown for this species and others in earlier studies. Meltøfte (1985), in Greenland, found a strong negative correlation between Dunlin nest initiation and early June snow cover. He concluded that delayed nesting resulted from poor feeding conditions and increased risk of nest predation. Nest initiation by Greater Golden-Plovers *Pluvialis apricaria* was also influenced by snow-melt (Byrkjedal 1980). Before nesting, the birds apparently waited until a considerable amount of snow-free area was available. Significantly greater predation on artificial nests occurred early in the season, when predators (primarily red foxes *Vulpes vulpes*) could systematically search restricted snow-free areas for nests. Byrkjedal (1980) concluded that vulnerability to predation was the factor ultimately controlling the timing of nest initiation.

##### Temperature

Temperature, as represented by the cumulative deviation from average temperature summed over the entire breeding season, was the best environmental predictor of nest densities. In particular, the

nest density of the Semipalmated Sandpiper was positively correlated with temperature ( $r = 0.906$ ,  $p = 0.001$ ). A related result was that the non-breeding index of Semipalmated Sandpipers was inversely related to breeding season temperatures (Figure 5). In aggregate, these relationships suggested that fewer Semipalmated Sandpipers attempted nesting in cold years. The birds were present but not all nesting.

In an average year ( $\Delta\text{temp.} = 0$ ), the non-breeding index is approximately 2.5 (Figure 5), which suggests that on the order of 20% of Semipalmated Sandpipers do not nest (assuming that an index of 2.0 represents complete nesting). This could be interpreted as indicating that the Prudhoe Bay area is colder than optimum for breeding Semipalmated Sandpipers. If so, higher nest densities would be expected in warmer areas. Regional comparisons are difficult, because most study areas differ more than in temperature alone. Much higher densities, approximately 50 nests/km<sup>2</sup>, have been recorded from subarctic areas such as in Churchill, Manitoba (Gratto, Morrison & Cooke 1985). However, even there, Gratto-Trevor (1991) reported years when fewer than half of the Semipalmated Sandpipers present actually nested.

The numbers of non-breeding Dunlin and Semipalmated Sandpipers were examined in relation to the annual temperature summaries shown in Figure 8. As reported earlier, the incidence of non-breeding in Semipalmated Sandpipers increased in association with lower temperatures. The data for Dunlin indicated a similar relationship, the principal difference being that this species had higher non-breeding indices (especially in 1986). The Dunlin is an earlier-nesting species than the Semipalmated Sandpiper and thus may be more affected by adverse conditions such as delayed snow-melt.

The negative association between nest densities and non-breeding or weather for species such as the Semipalmated Sandpiper and Dunlin indicates that we can expect some error in our measures of both current and past population sizes based on nest densities. For the Dunlin, nest density was very low in 1986 owing to the high incidence of non-breeders. These birds were still part of the population in 1987 and allowed for an apparent increase in nest density greater than might have been predicted based on recruitment alone.

Environmental factors appeared to have a pronounced influence on some measures of nesting. Our data suggest that temperature was the best predictor of variability in breeding biology for a given year; however, the timing of snow-melt also appeared to be important. These environmental factors are related (as snow tends to melt earlier when temperatures are above average), but the

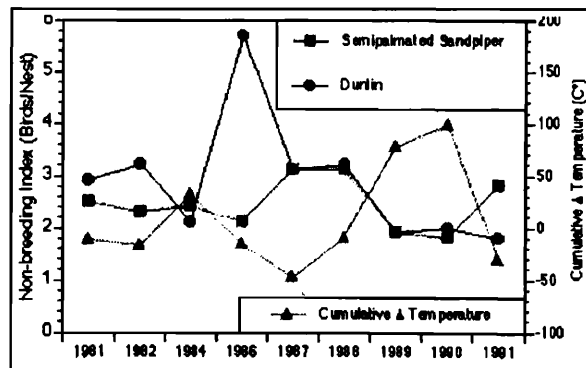


Figure 8. Trends in non-breeding indices of Semipalmated Sandpiper and Dunlin and of annual cumulative temperature deviations (1 June - 18 July).

analyses indicated that the shorebird population data correlated better with temperature over the entire breeding season than with temperature up to when most of the snow had melted (end of Census Period 2). Therefore, the influence of temperature appears to extend beyond its role in snow-melt. Environmental conditions exerted their greatest influence on the timing of nest initiation and the related measure of non-breeding (the ultimate in delayed initiation) as measured by the non-breeding index. Under conditions that we would expect to be adverse, *i.e.* delayed snow-melt or cold temperatures, nesting is delayed or not attempted.

#### Other correlates of nest density

Several correlations were found between nest densities and variables other than environmental measures. Predominant in these relationships were correlations involving Pectoral Sandpiper nest densities. The numbers of Pectoral Sandpipers have long been known to vary markedly from year to year at breeding locations (Pitelka 1959), but explanations for this variation have been elusive. The nest density of the Pectoral Sandpiper was highly correlated with four measurements describing tundra bird breeding biology: Semipalmated Sandpiper nest initiation, Red Phalarope nest initiation, Pectoral Sandpiper density and Red-necked Phalarope density.

Two correlations involved nest initiation. High nest densities of Pectoral Sandpipers corresponded to years of early nesting by Semipalmated Sandpipers and Red Phalaropes. Two independent correlations with nest initiation suggested that the conditions favourable for early nesting also favoured settling by Pectoral Sandpipers. Of interest are the species involved in these correlations. Besides the Pectoral Sandpiper, four species were common breeding birds in the PMRA: the Dunlin, the Semipalmated Sandpiper, the Red Phalarope and the Lapland Longspur. The Dunlin and the Lapland Longspur are early-nesting species whose nest initiations appear to be strongly influenced by the timing of snow-melt. The Semipalmated Sandpiper and the

Red Phalarope, along with the Pectoral Sandpiper, are mid-season nesters. Nesting of these species is not as affected by snow-melt and, in the case of the Semipalmated Sandpiper, appears to be influenced by temperature. The abundance of nesting Pectoral Sandpipers appears to be related to whatever regulates the timing of these mid-season nesters. In all cases, the relationship was greatly influenced by the outlying data point corresponding to the high 1990 nest density, but the same general trends appeared to be present even when that data point was excluded.

#### Summary

In summary, several interesting associations between nest densities and other measures were detected. Correlations involving environmental measures were infrequently detected directly; only the correlation between the Semipalmated Sandpiper and temperature met our criterion for statistical significance. Species having the greatest among-year variability in nest densities, especially nomadic species such as the Pectoral Sandpiper, were found to have significant correlations between bird and nest densities. This was not found for other species. The lack of correlation implies that nest and bird densities were out of synchrony, with the only possible conclusion that some birds that were not associated with nests were present. The non-breeding index, a measure of surplus birds, was found to vary inversely with nest densities of the early-nesting Dunlin, indicating that there were excess non-breeding birds during years of low nesting densities. This excess probably accounted for the rapid rebounds we recorded after years of nesting depressions. Reductions in nesting effort appeared to be related to environmental factors: low temperatures in the case of the Semipalmated Sandpiper and persistent snow cover for the Dunlin. Although the factor or factors that induced high nesting densities of Pectoral Sandpipers remain unknown, high nest densities of this species were correlated with early nesting in the Semipalmated Sandpiper and the Red Phalarope, two other species characterized by mid-season nest initiation dates.

#### Conclusions

Arctic shorebirds are sometimes characterized as having two breeding strategies (Pitelka, Holmes & MacLean 1974). One group comprises *conservative* species, such as Semipalmated Sandpiper and Dunlin, which have stable breeding densities, with breeding birds spaced relatively uniformly so that the birds can expect to find the resources they need within their 'territories'. The second group includes *opportunistic* species, such as Pectoral Sandpiper, which are nomadic and alter their local abundances markedly in response to changing environmental conditions. Our results supported a general dichotomy of philopatric versus nomadic species

but otherwise indicated that the breeding biology of these tundra birds is somewhat more complicated. Our results showed that the nesting populations of conservative species were much more variable than has been previously reported. Indications are that these species do not regulate their densities by spacing behaviour but rather that these populations are perpetually recovering from population depression caused by poor recruitment. The magnitudes of the population fluctuations are significant — on the order of two- to three-fold — although the densities of these species are still much more stable than those of the nomadic species.

Environmental conditions were also found to be important in the population dynamics of tundra birds. The most important role was in causing birds to forego breeding during years of adverse conditions. Our results indicated a much greater degree and regularity of non-breeding in arctic shorebirds than has been previously reported. Snow cover and temperatures appeared to be important environmental conditions influencing the incidence of nesting. The abundance of nomadic species appeared to be related to conditions that promoted early nesting.

In summary, our preliminary findings indicate that populations of philopatric shorebirds were regulated by recruitment, with episodic years of intense nest predation followed, two years later, by population depressions due to low recruitment. The trends predicted by this relationship are moderated by the influences of environmental conditions that discourage a variable proportion of the breeding population from attempting to nest each year.

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