

Phenological advancement in arctic bird species: relative importance of snow melt and ecological factors

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Abstract Previous studies have documented advancement in clutch initiation dates (CIDs) in response to climate change, most notably for temperate-breeding passerines. Despite accelerated climate change in the Arctic, few studies have examined nest phenology shifts in arctic breeding species. We investigated whether CIDs have advanced for the most abundant breeding shorebird and passerine species at a long-term monitoring site in arctic Alaska. We pooled data from three additional nearby sites to determine the explanatory power of snow melt and ecological variables (predator abundance, green-up) on changes in breeding phenology. As predicted, all species (semipalmated sandpiper, *Calidris pusilla*, pectoral sandpiper, *Calidris melanotos*, red-necked phalarope, *Phalaropus lobatus*, red phalarope, *Phalaropus fulicarius*,

Lapland longspur, *Calcarius lapponicus*) exhibited advanced CIDs ranging from 0.40 to 0.80 days/year over 9 years. Timing of snow melt was the most important variable in explaining clutch initiation advancement (“climate/snow hypothesis”) for four of the five species, while green-up was a much less important explanatory factor. We found no evidence that high predator abundances led to earlier laying dates (“predator/re-nest hypothesis”). Our results support previous arctic studies in that climate change in the cryosphere will have a strong impact on nesting phenology although factors explaining changes in nest phenology are not necessarily uniform across the entire Arctic. Our results suggest some arctic-breeding shorebird and passerine species are altering their breeding phenology to initiate nesting earlier enabling them to, at least temporarily, avoid the negative consequences of a trophic mismatch.

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Introduction

Global temperatures have increased by 0.6° over the past 100 years (IPCC 2007), and the rate of warming has doubled in just the last four decades (Walther et al. 2002). Overwhelming evidence suggests climate changes are influencing the activities of a wide range of animal and plant species in various ways. Worldwide, organisms are experiencing range boundary shifts, changes in flowering, migration and breeding phenology, and alteration in community structure (Parmesan and Yohe 2003; Root et al. 2003). Climate change is occurring at twice the global average in the Arctic with respect to temperate regions

(IPCC 2007). The most dramatic biological responses to climate changes are expected to occur in the Arctic where positive biological feedbacks are likely to exacerbate abiotic changes (Hinzman et al. 2005) leading to rapid and potentially intractable phase shifts in arctic climate (Hinzman et al. 2013). Not surprisingly, climate-mediated changes at the population, community, and ecosystem scales appear more intensified at high latitudes (Post et al. 2009) and may be a harbinger of greater changes to come at lower latitudes. However, relative to temperate regions, there is a paucity of studies examining biological responses to climate change in arctic regions and how organisms in this region will respond to broad-scale environmental changes remains unclear.

Compared to lower latitudes, arctic summers are short and typified by a rapid thaw and snow melt; a brief growing season ensues before an early return to frigid conditions. Over the past three decades across the circumpolar Arctic, accelerated warming and expansion of the growing season has led to greater growth of trees and extension of shrubs into tundra habitats (Myneni et al. 1997; Sturm et al. 2005). The implications for such changes on the phenology of migratory animals that use arctic regions as breeding grounds are only beginning to be investigated (Høye et al. 2007; Post and Forschhammer 2008). Information from other systems suggests animals that are unable to adjust their breeding season in response to climate-driven changes in the environment risk lower reproductive success through a mismatch in food resource availability (Visser and Both 2005; Drever et al. 2012). Further, trophic mismatch during the breeding season has been proposed as a mechanism linking climate change to declining populations across diverse animal taxa (Durant et al. 2007; Thackeray et al. 2010). Negative effects of trophic mismatch are most likely for species with complex annual life cycles that migrate long distances to breed and for species that depend on resources available on the breeding grounds for successful reproduction (Both et al. 2010; Miller-Rushing et al. 2010), especially income breeders (Klaassen et al. 2001). For these reasons, animals that breed in the Arctic may be particularly vulnerable, and there is already evidence that trophic mismatch is affecting arctic and subarctic breeding species (Post and Forschhammer 2008; Gaston et al. 2009). Among arctic breeders, however, it is not clear that species will have the genetic or phenotypic flexibility to shift their reproductive behavior to track phenological changes in the environment, as the specific factors driving reproductive phenology for many species are poorly understood.

Many factors, including migration strategy (Both and Visser 2001), food availability (Weidinger and Král 2007), population size (Dunn 2004), body mass (Crick and Sparks 1999), habitat requirements (Travis 2003), and predation (Wiklund 1984; Visser and Both 2005), can influence when

animals breed. For breeding birds, nest predation is the primary source of nest failure (Martin 1993) including at arctic sites (Liebezeit et al. 2009) and can play a key role influencing nesting chronology (Morton 1971; Wiklund 1984). In the Arctic, predator levels can fluctuate dramatically both seasonally and spatially (Smith et al. 2007), sometimes in response to prey population booms (Angelstam et al. 1984), and the compressed summer season limits breeding attempts for many species (Martin and Wiebe 2004). At high latitudes, nest predation pressure could delay nesting as predator search efforts may be more successful in partially snow covered ground (Byrkjedal 1980). Conversely, in years of high predator abundance, birds may initiate nesting earlier as the value of potential re-nesting would exceed both the energetic and predation risks associated with early breeding (Smith et al. 2010; “predator/re-nest hypothesis”). While these studies indicate predation may influence clutch initiation timing, other climatic factors, namely timing of snow cover melt, may be equally or more important in influencing breeding phenologies at high latitudes (Meltote et al. 2007a, b; Thackeray et al. 2010; Grabowski et al. 2013; “climate/snow hypothesis”).

In this study, we investigate whether shifts in breeding phenology have occurred in arctic nesting birds in Alaska and test the predator/re-nest and climate/snow hypotheses directly. We examine clutch initiation timing in five different species [Lapland longspur (*Calcarius lapponicus*), pectoral sandpiper (*Calidris melanotos*), red phalarope (*Phalaropus fulicarius*), red-necked phalarope (*Phalaropus lobatus*), and semipalmated sandpiper (*Calidris pusilla*)] at a long-term monitoring site (Prudhoe Bay) and three other nearby sites in the central portion of the Arctic Coastal Plain of Alaska. These species were the most abundant passerine and shorebird species nesting at all study sites (Liebezeit et al. 2009; J. Liebezeit, unpublished data). Despite notable differences in reproductive strategy (Lapland longspur and semipalmated sandpiper: monogamous, phalaropes: polyandrous, pectoral sandpiper: polygynous) and migration distance (<5,000 to >13,000 km) among the five species (Poole et al. 2003), we expected that nesting phenology for all species has advanced at a similar rate—climate warming is accelerated in the Arctic, and the bulk of studies from temperate regions indicate a general pattern of earlier clutch initiation across diverse taxa (Winkler et al. 2002; Both et al. 2004). In particular, trends of increased climate warming in western portions of the Arctic relative to those across Eurasia might mean nesting phenology of species in the western Arctic is advancing at a greater rate than observed elsewhere (Smith et al. 2004; Meltote et al. 2007b). Under the predator/re-nest hypothesis, we predicted that increasing predator abundance would result in earlier nesting as the value of potential re-

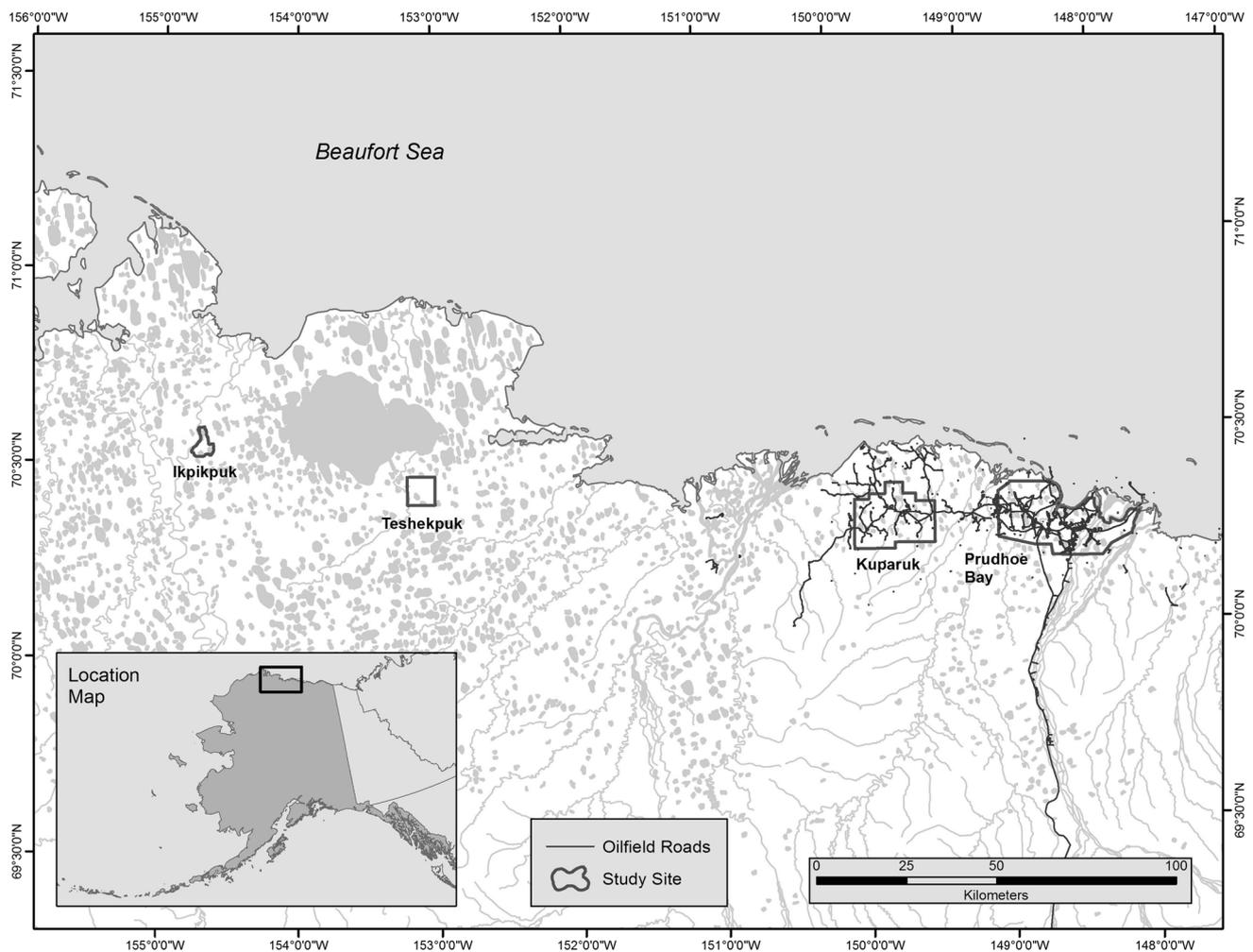


Fig. 1 Map of the study sites located on the Arctic Coastal Plain of Alaska

nesting would exceed the energetic risks of early breeding (Smith et al. 2010); under the climate/snow hypothesis, we anticipated that timing of snow melt would be the most important mechanism affecting clutch initiation as this will likely determine when nest sites and food resources become available (Melfoite et al. 2007a, b; Høye et al. 2007), particularly as these species are income breeders dependent on invertebrate prey on the breeding grounds for production of eggs (Meijer and Drent 1999; Morrison and Hobson 2004).

Materials and methods

Study sites

Data were collected for 2–9 years from 2002 to 2011 at four study sites located along a similar latitudinal gradient ($\sim 70^\circ$) spanning 250 km of the central portion of the

Arctic Coastal Plain (Fig. 1; Table 1). The study sites were originally established as part of previous and ongoing nest survivorship studies. At each site, we randomly or systematically established 10-ha study plots (12–24 plots per site). At oil field sites (Prudhoe, Kuparuk), plots were located >100 m from human infrastructure to reduce potential effects of disturbance and habitat modification (Troy 2000). All sites were in Low arctic tundra habitat characterized by a mosaic of dry or moist upland tundra, often with high densities of cottongrass tussocks (*Eriophorum* spp.), moist or wet meadows of graminoids or low shrubs, aquatic marshes dominated by sedges (*Carex* spp.) or pendant grass (*Arctophila fulva*), and lakes and ponds. The topography was generally flat, with elevations typically <50 m. Microtopographic features included high- and low-centered polygons, strangmoor/disjunct polygon ridges, hummocks, tussocks, and frost boils (Walker et al. 1980). Climatic conditions during the pre-laying and nesting period (21 May to 30 June) were similar between

Table 1 Avian nest phenology study sites, location, size, number of study plots, and years sampled on the Arctic Coastal Plain of Alaska

Site	Latitude/ longitude	Study site size (km ²)	# of 10-ha plots	Years sampled
Prudhoe Bay oil field	70°17'N, 148°32'W	509.0	12 ^a	2003–2011
Kuparuk oil field	70°18'N, 149°41'W	319.9	24	2002–2004
Teshkepkuk	70°25'N, 153°07'W	71.6	18 ^b	2005–2008
Ikpikpuk	70°33'N, 154°42'W	27.1	12	2010–2011

^a 24 in 2004

^b Only 16 sampled in any given year

sites with little within-year variation in daily temperatures (J. Liebezeit, unpublished data).

Field methods and variable preparation

We conducted four standardized nest searches using both rope-drag and behavioral techniques on each plot per year from early June to early July, following methodology adapted from Troy (unpublished report). We also included nests found incidentally later in the season while monitoring previously discovered nests; these accounted for <2 % of all nests included in the analyses. Nest locations for all species were recorded with a global positioning system (GPS) and were marked by a wooden tongue depressor placed within 5 m of the nest. We included nests discovered both within and off the plot in the analyses. We did not trap and color-mark birds on these study plots so we assumed that a nest initiated shortly after another failed within approximately 100 m of another of the same species indicated a re-nest. These accounted for only 3 % of all nests observed (2.1 % shorebirds; 5.1 % passerines). We defined clutch initiation as the date when the first egg was laid. This event was rarely observed and so clutch initiation date (CID) was calculated from nest age estimates obtained by (1) assuming 1 day for each egg laid when nests were discovered during the laying stage; (2) using published nesting-stage lengths (Poole et al. 2003) if hatch date was known; (3) judging nestling development (passerines only; Hussell and Montgomerie 2002); or (4) using the egg flotation method (Liebezeit et al. 2007).

We conducted three predator surveys on each plot annually during the early, mid, and late portions of the breeding season. Each survey consisted of three 10-min point counts separated by >200 m on the plot centerline, and each count conducted at least 30 min apart (Ralph et al. 1993). We recorded all detections of documented or suspected potential nest predators (see Liebezeit et al. 2009 for a list of predator species)

within 300 m of the point count station. Predator surveys were conducted between approximately 0800 and 2000 hour. For the analyses, we summarized the seasonal activity of potential nest predators in each plot by averaging the number of predator species detections per 30-min time period (=PRED). We only included predators known to prey on shorebird and passerine nests at these sites based on camera evidence (Liebezeit and Zack 2008; J. Liebezeit unpublished data), primarily including both red and arctic fox (*Vulpes vulpes*, *Vulpes lagopus*) and jaegers (*Stercorarius* spp).

At the start of each field season, we estimated the percentage of tundra covered by snow to the nearest 5 % within each 50-m × 50-m grid of each study plot at all sites during repeated visits. We then calculated an annual index for timing of snow melt (=SNOW) at each site by averaging the first day that plots were observed with <5 % snow cover across the entire site. We used the 5 % cutoff as it had the highest predictive power in subsequent analyses.

We used remotely sensed satellite data to derive yearly estimates of start of season time (=SOST) and early season vegetative growth. Normalized Difference Vegetation Index (NDVI) data from the Earth Resources Observation and Science (EROS) Moderate Resolution Imaging Spectroradiometer (MODIS) processing system were used to derive seasonal vegetation characteristics. The eMODIS NDVI dataset is created at the U.S. Geological Survey EROS Center (U.S. Geological Survey 2011) using the standard MODIS level 1B data as input. These data provide significantly improved geometric accuracy over the standard MODIS product for Alaska (Ji et al. 2010). Time series eMODIS NDVI data at 250 m spatial resolution were temporally smoothed using a weighted least-squares regression technique (Swets et al. 1999) to minimize contamination due to atmospheric perturbations that impact the satellite signal. We then derived phenological metrics on a per-pixel basis using a delayed moving average technique developed by Reed et al. (1994). Phenology metrics are measured by identifying critical points along the seasonal NDVI curve that represent biophysical processes of the target vegetation. We extracted day-of-year estimates for SOST for each eMODIS pixel and summarized these at the study site level (rather than plot level) as this scale was deemed to be more representative of inter-annual variability while minimizing individual pixel noise. NDVI-based phenology data provide a consistent measure of annual vegetation green-up and are strongly related to arctic tundra biomass (Epstein et al. 2012).

Statistical analyses

Statistical analyses were performed using SAS[®] version 9.3 (SAS Inc., Cary, NC) and entailed two approaches. First, to determine whether breeding phenology has shifted

Table 2 Total number of nests found of the target species/species groups and clutch initiation dates ($\pm 1SD$) across all years per site

Species	Prudhoe bay (2003–2011)		Kuparuk (2002–2004)	
	<i>n</i>	Mean CID ($\pm SD$)	<i>n</i>	Mean CID ($\pm SD$)
Lapland longspur	228	June 6 \pm 6.0	154	June 6 \pm 6.1
Semipalmated sandpiper	292	June 10 \pm 4.5	85	June 10 \pm 3.9
Pectoral sandpiper	160	June 12 \pm 5.3	115	June 12 \pm 5.4
Phalaropes	140	June 16 \pm 6.3	45	June 15 \pm 5.5
Species	Teshekpuk (2005–2008)		Ikpikpuk (2010–2011)	
	<i>n</i>	Mean CID ($\pm SD$)	<i>n</i>	Mean CID ($\pm SD$)
Lapland longspur	287	June 7 \pm 4.4	61	June 9 \pm 5.1
Semipalmated sandpiper	66	June 12 \pm 3.9	107	June 12 \pm 3.3
Pectoral sandpiper	91	June 14 \pm 4.5	44	June 13 \pm 3.6
Phalaropes	84	June 14 \pm 4.9	38	June 16 \pm 5.8

Assumed re-nesting attempts not included

for four arctic-breeding bird taxa, we focused our analyses on Prudhoe Bay because this site had the most comprehensive temporal coverage. Secondly, to test the predator/re-nest and climate/snow hypotheses at a broader spatial scale, we combined data from all four sites and compared competing models. Due to confounding effects of year and site, we could not assess phenological shift using this larger dataset. For both sets of analyses, we used general linear mixed models (PROC MIXED) to evaluate relationships between CID and variables of interest. These types of models take advantage of correlation among blocks of observations (covariance), thus enabling us to account for dependence among groups of birds at the plot level (random effects), while examining the specific influence of other fixed effects on CID (Littell et al. 2006).

The restricted maximum likelihood method was used to compute marginal log-likelihood values for each model, and an information-theoretic approach to model selection was employed, with models ranked based on 2nd-order Akaike's Information Criterion (AIC_c ; Burnham and Anderson 2002; SAS Institute Inc. 2008). The same covariance structure (random effect of plot) was retained for all models to ensure that model selection results were directly comparable, and a Kenward-Roger correction was applied in computing denominator degrees of freedom. Inference concerning fixed effects was based on precision (85 % confidence interval) of the regression coefficient (β), as this interval is more compatible with an information-theoretic approach. When wide confidence intervals indicated imprecise parameter estimates, the variable was deemed uninformative—models with uninformative parameters were considered to be unsupported and were not taken into account when interpreting results (Arnold 2010).

Phenological shift

To assess annual variation in CID at Prudhoe Bay, we included data from four avian taxa with a range of life histories ($n > 10$ nests per species per year), including Lapland longspur ($n = 228$), semipalmated sandpiper ($n = 292$), and pectoral sandpiper ($n = 160$). Sample sizes were smaller for red phalarope ($n = 65$) and red-necked phalarope ($n = 75$). Because these species have similar life histories (Rubega et al. 2000; Tracy et al. 2002), however, we combined data from both into a single grouping (phalaropes, $n = 140$). For each taxa, we developed an a priori set of candidate models that represented CID as a function of our key fixed effect of interest, year. In addition, to evaluate a possible nonlinear effect of year due to cyclical predator population dynamics (e.g., Gilg et al. 2009), we included a model with a quadratic term ($year^2$) in our candidate set.

Predator/re-nest and climate/snow hypotheses

To evaluate the relative support for a relationship between CID and key explanatory variables—predator abundance, timing of snow melt, and timing of spring green-up—across a larger geographic area, we included data from all four sites, with species groupings as described for Prudhoe Bay: Lapland longspur ($n = 730$), pectoral sandpiper ($n = 410$), phalaropes ($n = 307$), and semipalmated sandpiper ($n = 550$). We included mean daily temperature during the pre-laying and nesting period in initial Prudhoe Bay models, but it did not have any explanatory power so it was excluded from subsequent analyses. We began our analyses by evaluating

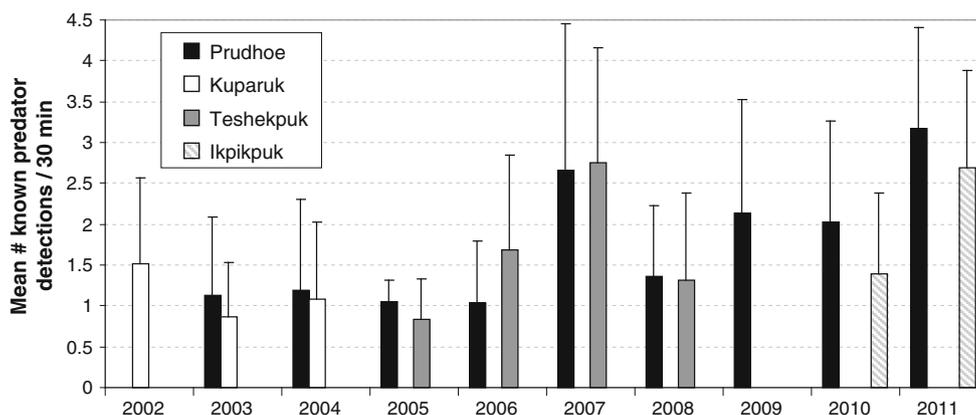
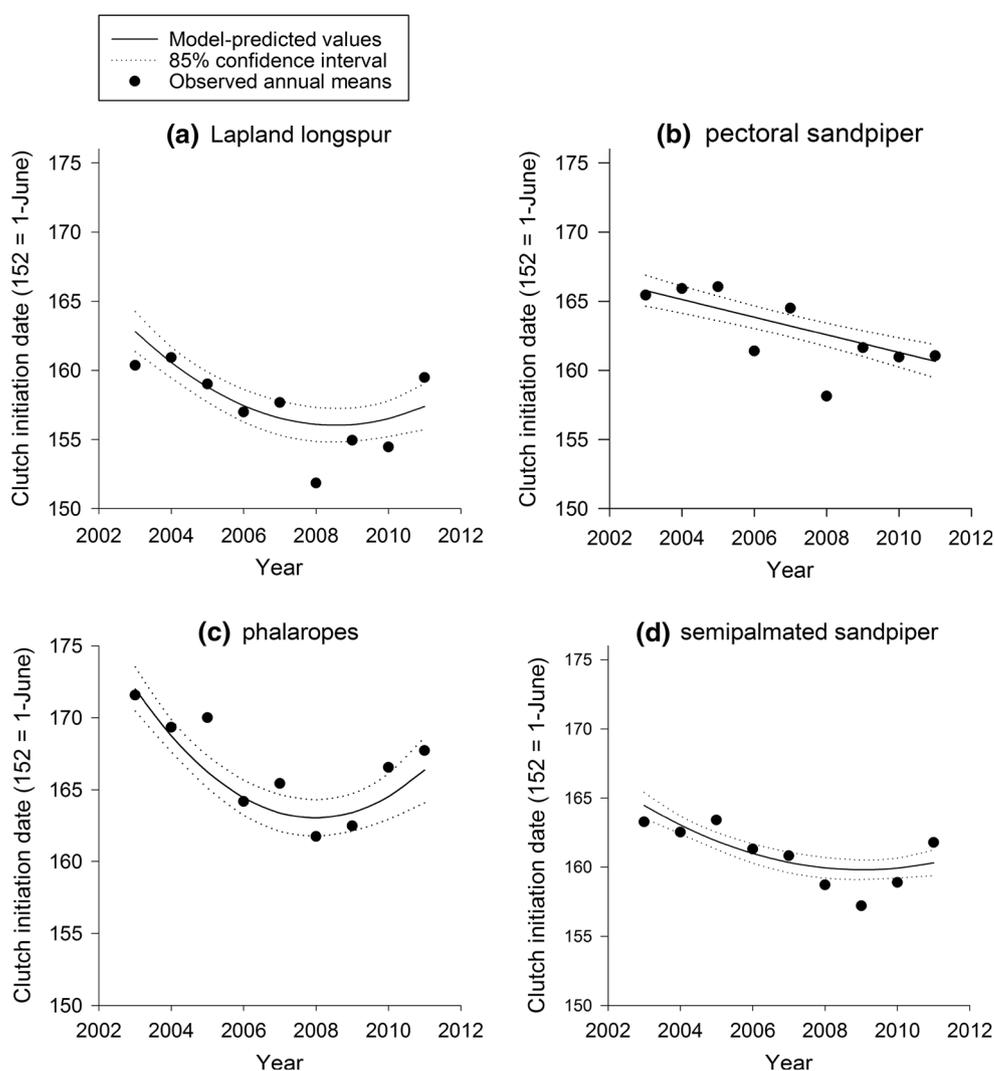


Fig. 2 Mean number (+1 SD) of detections per 30 min period of known shorebird and passerine nest predators in the region across all study sites and years

Fig. 3 Observed and model-predicted clutch initiation date values bound by 85 % confidence intervals for the five target species at the Prudhoe Bay Oilfield site, 2003–2011



correlations among our three key variables of interest (annual site means for PRED, SNOW, and SOST) (PROC CORR). Then, for each taxa, we constructed candidate model sets that represented CID as a function of site, and

the annual site means for PRED, SNOW, and SOST. Models with additive combinations of explanatory variables that were correlated (SNOW, SOST) were not considered.

Table 3 Rank of linear mixed models evaluating annual variation in clutch initiation date for avian taxa at the Prudhoe Bay study site in Low arctic Alaska

	Explanatory variables		Model selection criteria		
	Year	Year ²	Deviance	ΔAIC_c	w_i
Lapland longspur ($n = 228$)	✓	✓	1,419.8	0.0	0.96
	✓		1,427.1	6.2	0.04
			1,464.7	41.7	0.00
Pectoral sandpiper ($n = 160$)	✓		965.3	0.0	0.79
	✓	✓	966.8	2.6	0.21
			987.6	20.1	0.00
Phalaropes ($n = 140$)	✓	✓	878.0	0.0	1.00
	✓		892.5	13.4	0.00
			912.7	31.4	0.00
Semipalmated sandpiper ($n = 292$)	✓	✓	1,685.5	0.0	0.79
	✓		1,689.2	2.6	0.21
			1,712.5	23.8	0.00

Taxon is listed in the first column; number of nests included in each model set is listed in parentheses. For each taxon, the ✓ indicates which explanatory variables were included in the model set as fixed effects—no ✓ = intercept only model. To account for block effects, plot (not shown) was included as a random factor in all models. Models are ranked by differences in AIC, corrected for sample size (ΔAIC_c), w_i = Akaike weight

Results

Observers discovered 2,457 nests of the five target species on or near study plots across all years and sites. Of these, 75 were determined to be re-nesting attempts and were excluded from further analyses. CIDs for the one passerine (Lapland longspur) were earlier than all shorebirds, and phalaropes tended to initiate nests later than the two other shorebird species (Table 2).

Predator indices

We included seven known nest predator species in our analyses. The most frequently detected species included parasitic and long-tailed jaegers (*Stercorarius parasiticus*, *Stercorarius longicaudus*; 51.2 and 27.4 % respectively), followed by common raven (*Corvus corax*; 6.6 %), arctic ground squirrel (*Urocitellus parryii*; 5.7 %), arctic fox (4.9 %), snowy owl (*Bubo scandiacus*; 3.3 %), and red fox (0.9 %). Frequency of predator detections fluctuated noticeably across sites and years (Fig. 2). Years of highest predator detections occurred in 2007 and 2011 (Fig. 2).

Phenological shift

Consistent with other studies, we noted a uniform progression of earlier CIDs for all species assessed at the

Prudhoe Bay site across nine consecutive field seasons. For three of the four groups, this relationship was nonlinear (Fig. 3) as the best models included both year and the quadratic year effect (Table 3).

Predator/re-nest and climate/snow hypotheses

Consistent with our prediction of the climate/snow hypothesis, snow melt timing (SNOW) was an important factor explaining timing of clutch initiation for four of the five species across all sites (Table 4; Fig. 4). Parameter estimates indicated that for semipalmated sandpipers, the effect of snow on CID ($\beta_{\text{SNOW}} = 0.47$; 85 % CI 0.38–0.56) was smaller than observed for Lapland longspur ($\beta_{\text{SNOW}} = 0.77$; 85 % CI 0.67–0.86) or phalaropes ($\beta_{\text{SNOW}} = 0.73$; 85 % CI 0.57–0.90). Pectoral sandpipers differed in that the most-supported model suggests that timing of breeding is influenced by spring green-up (SOST); however the effect size is small ($\beta_{\text{SOST}} = 0.20$; 85 % CI 0.13–0.27), indicating spring green-up is a poor predictor of CID for pectoral sandpipers. Our prediction that years of high predator abundance would result in earlier nesting (predator/re-nest hypothesis) was not supported for any species (Table 4).

Discussion

In this paper, we provide documentation of advancement in breeding phenology for four shorebird species and one passerine species that nest in the Low Arctic. Because four of the five species we examined exhibited a nonlinear trend in CID advancement, we are unable to enumerate a precise rate of advancement as beta values from models that include a quadratic term are difficult to interpret biologically (Blums et al. 2005). However, inspection of Fig. 3 indicates an advancement ranging from 4 to 7 days over 9 years (approximate rate: 0.4–0.8 days/year). We are aware of only one other published study to document CID advancement for bird species in the Low Arctic. On Herschel Island, Yukon, Canada, Grabowski et al. (2013) documented earlier clutch initiation in four species (two shorebird and two passerine) although this trend was significant only for Baird's sandpipers (*Calidris bairdii*) (approximate CID rate: 0.52 days/year; 12 days over 23 years). At a High Arctic site in NE Greenland, Dunlin (*Calidris alpina*), Ruddy Turnstone (*Arenaria interpres*), and Sanderling (*Calidris alba*) had significantly earlier CID with a rate of change from 0.40 to 1.0 days/year over a 10-year period (1995–2005) (Melfotte et al. 2007a; Høye et al. 2007). Smith et al. (2010) reported significant differences in CID between sites for the same shorebird

Table 4 Rank of top linear mixed models explaining variation in CID for avian taxa at four sites in Low arctic Alaska

	Explanatory variables				Model selection criteria		
	SITE	SNOW	SOST	PRED	Deviance	ΔAIC_c	w_i
Lapland longspur ($n = 730$)	✓	✓			4,375.8	0.0	1.00
	✓		✓		4,408.9	33.1	0.00
	✓				4,503.6	126.8	0.00
	✓			✓	4,503.9	128.1	0.00
Pectoral sandpiper ($n = 410$)	✓		✓		2,460.0	0.0	0.84
	✓	✓			2,463.8	3.8	0.13
	✓			✓	2,466.3	6.3	0.04
	✓				2,472.5	11.4	0.00
Phalaropes ($n = 307$)	✓	✓			1,903.7	0.0	0.91
	✓		✓		1,908.3	4.6	0.08
	✓				1,938.9	34.1	0.00
	✓			✓	1,939.4	35.7	0.00
Semipalmated sandpiper ($n = 550$)	✓	✓			3,068.0	0.0	1.00
	✓		✓		3,092.5	24.5	0.00
	✓				3,120.7	51.6	0.00
	✓			✓	3,121.2	53.2	0.00

Taxon listed in the first column; number of nests in each model is listed in parentheses. The ✓ indicates the explanatory variables included in the model as fixed effects—year was not included due to confounding effects with site. To account for block effects, plot (not shown) was included as a random factor in all models. Models are ranked by differences in AIC, corrected for sample size (ΔAIC_c). SNOW = average date, across plots, when snow cover dropped below 5 %, SOST = estimated date of spring green-up, as indicated by NDVI, w_i = Akaike weight

species in central arctic Canada, but they did not examine advancement in CID overall (P. Smith, pers. comm.).

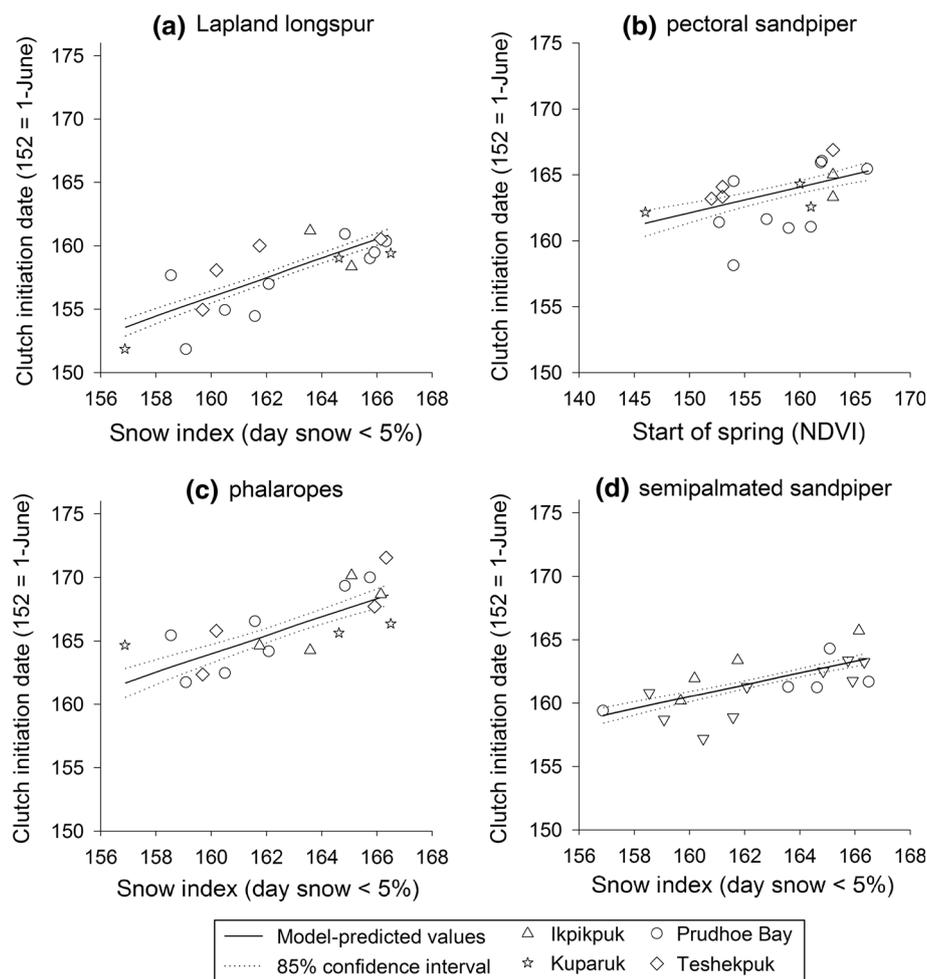
CID advancement documented in this study corresponds with the previously mentioned arctic studies with all sharing a rate generally >0.50 days/year. In contrast, previous studies examining breeding phenology of long-distance migrants (primarily passerines) at temperate latitudes report CID advancement typically <0.40 days/year (Crick and Sparks 1999; Both et al. 2004; Dunn and Winkler 2010). In general, our findings, and those of previous arctic studies examining CID change in shorebirds and passerines, suggest a more rapid breeding advancement (for long-distance migrants) compared to lower latitudes concomitant with the accelerated rate of climate changes at high latitudes (IPCC 2007).

Timing of snow melt was the most important variable in explaining clutch initiation advancement for four of the five species. This finding confirms previous evidence that shorebird clutch initiation is closely linked to snow melt (Green et al. 1977; Meltofte et al. 2007a; Smith et al. 2010; Grabowski et al. 2013). In one exception, Meltofte et al. (2007a) found that food (i.e., arthropod) abundance had the strongest effect on timing of clutch initiation, while snow cover showed increasing importance in years of later snow melt. In our study, we did not have food abundance data available so we were unable to test its importance with respect to breeding phenology. However, activity of

surface dwelling arthropods is correlated with temperature in arctic tundra environs (Tulp and Schekkerman 2008) and so it is likely food abundance would also be correlated with snow melt in many situations (although see Meltofte et al. 2007b). In order to better understand arctic-breeding bird phenology across the Arctic, future studies should examine the interaction of snow melt timing and food abundance at a regional scale.

Timing of green-up (SOST) was the most important explanatory variable for pectoral sandpipers though comparatively weak and secondarily important (with respect to snow melt) for the remaining species examined. As might be expected, timing of green-up was highly correlated with snow melt ($r = 0.83$) yet snow melt was consistently more important as an explanatory variable with respect to breeding phenology. The difference in scale between green-up (site-based) versus snow melt (plot-based) may explain the stronger response to snow melt as species may be responding to cues at a more local scale. Pectoral sandpipers are known to have relatively low nest site fidelity and have highly variable nest densities at particular sites from year to year, which may be related to their polygynous mating system and that females do not establish distinct nesting territories (Farmer et al. 2013). Thus, this species may more readily select snow-free areas to nest regardless of prior nesting location as opposed to species that exhibit more rigid nest site fidelity and wait for snow

Fig. 4 Observed and model-predicted clutch initiation date values bound by 85 % confidence intervals for the five target species across all sites plotted against the most important explanatory variable affecting clutch initiation timing



to melt at traditional nest site locations. Phalaropes are also a nonterritorial species (Rubega et al. 2000; Tracy et al. 2002) yet they showed the tightest correlation between clutch initiation and snow melt among all the species examined (see Fig. 4). Both phalarope species, but particularly the red-necked phalarope, tend to select nest sites in wet to emergent tundra (Rodrigues 1994). Such sites are highly influenced by snow melt and were often some of the last areas to melt at the study sites (J. Liebezeit, pers. obs.). Consequently, phalaropes initiated nests later than the other species examined (see Table 2). This strong affinity for wet nesting sites helps explain the observed strong response to snow melt.

Our data were not consistent with predictions under the predator/re-nest hypothesis. Our results contrast that of Smith et al. (2010) who found support for this hypothesis, suggesting that birds may have selective pressure to nest earlier, which would enable more opportunities to nest in the future if initial nests are depredated. A competing hypothesis by Byrkjedal (1980) proposed that clutch initiation may be delayed until snow melt is almost complete as predators may be less successful at detecting nests once all

the snow is gone. We were unable to test this “predation/snow hypothesis” as nest searching often began after most snow had already melted. We included a curvilinear response in our analysis of CID by year at Prudhoe (see Fig. 3) because we expected there might be a cyclical predator–prey response (Gilg et al. 2009) that would lend additional support to the predator/re-nest hypothesis. Because of the lack of relationship between predator abundance and nest phenology, there appears to be an alternative explanation for the curvilinear relationship that we are unable to explain at this time.

In summary, our findings provide evidence that a range of bird species, with disparate wintering grounds and migration pathways, different mating strategies (e.g., monogamous vs. polyandrous), and different chick development (precocial vs. altricial) appear to be advancing breeding phenology in a similar manner. As these species migrate long distances, they must rely on endogenous cues to initiate migration (Piersma et al. 1999; Both and Visser 2001) unlike short-distance migrants that may be more reliant on climatic cues to time migration (Miller-Rushing et al. 2008; Lehikoinen and Sparks 2010; Doxa et al. 2012).

Therefore, clutch initiation phenology for the species we assessed appears to be governed by conditions on the breeding grounds and snow melt timing is a key explanatory variable. Our findings support growing evidence that overall changes in the cryosphere may dictate a variety of vertebrate responses to climate change at higher latitudes (Gilg et al. 2012).

This study documents that some arctic-breeding shorebird and passerine species are altering their breeding phenology to initiate nesting earlier, which supports previous findings in the Arctic (Melfo et al. 2007a; Høye et al. 2007; Grabowski et al. 2013) as well as for a number of temperate-breeding species (Crick et al. 1997; Winkler et al. 2002; Both et al. 2004). In the short term, this may enable these species to avoid the negative consequences of a trophic mismatch (e.g., lower reproductive success) as they appear to be exhibiting a flexible response to at least some environmental factors. In the long-term, the potential for a decoupling of trophic phenomena at any number of stages during the breeding season (e.g., at chick hatch; see Tulp and Schekkerman 2008) is increased as arctic conditions rapidly transform in a changing climate. At the same time, some evidence indicates increasing temperatures could offer physiological relief from trophic constraints for arctic-breeding shorebirds (McKinnon et al. 2013). In order to better understand the consequences of breeding phenology in the Arctic, future studies need to examine the phenological trajectories of both predator and prey with respect to climate-mediated changes in the cryosphere at a regional scale. Just as importantly, degree of phenotypic flexibility must be evaluated (e.g., climate sensitivity analyses) at the species level as this is likely the main response mechanism (see Gilg et al. 2012) for allowing species to cope with rapid climate changes in the Arctic.

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