EFFECTS OF CLIMATE CHANGE ON THE
BREEDING ECOLOGY AND TROPHIC INTERACTIONS
OF ARCTIC-BREEDING SHOREBIRDS

by

EUNBI KWON

B.S., Kongju National University, 2006
M.S., Ewha Womans University, 2009

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
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KANSAS STATE UNIVERSITY
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# Abstract

Impacts of climate change on biological systems include shifts in seasonal phenology. How do migratory animals adjust reproductive decisions as they shift timing of breeding? I investigated patterns of climate change at a network of Arctic sites in Alaska and Canada, and examined the impacts of climate change on the breeding phenology, reproductive performance, and trophic interactions of Arctic-breeding shorebirds. First, I compared the breeding performance of three species, Western Sandpiper, Semipalmated Sandpiper, and Red-necked Phalaropes, at Nome, Alaska, across a 14-year interval. I found that shorebirds responded to a decreasing temperature during laying by delaying timing of breeding. Delayed breeding shortened the incubation duration for two biparental species but extended incubation for a uniparental species. Despite a short Arctic summer, the breeding windows of three sympatric species were temporally distinct. The three species often nested within several meters from each other, but bred under different temperature regimes and adjusted their reproductive output to different sets of environmental factors. Shifts in breeding phenology can disrupt trophic interactions, especially the phenological match between peak prey availability and hatching of shorebirds. Comparing the extent of phenological mismatch between six shorebirds and their invertebrate prey at ten Arctic sites, peak demand of shorebird broods occurred on average 3.8 days ($\pm$ 13.8) later than local food peaks, and population demand curves overlapped with food curves by 47% ($\pm$ 14%). Latitudinal and longitudinal gradients in the extent of trophic mismatch were mediated through geographic variation in the seasonal phenology of invertebrates and shorebirds. For individual nests, both more northerly and easterly sites showed greater phenological mismatch with annual food peaks. Delayed emergence of food peaks at more northerly and easterly sites alleviated the extent of phenological mismatch. My multi-site study

provides the first evidence that large-scale geographic processes can determine the extent of phenological mismatch in a bitrophic system. Trends of climate change are sensitive to breeding stages and also vary along a longitudinal gradient. Variability in climatic trends in the Arctic, combined with species-dependent responses to local climate change, indicate that it will be challenging to predict the impacts of future climate change.

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# Acknowledgments

Every day of the past five and a half years has been my dream come true. It all could happen because of my advisor, Brett Sandercock, who did not doubt that I could undertake such a big project. I thank him from my heart for teaching me how to build a population demography model and to build a campfire. David Lank at Simon Fraser University has been another pillar for this project, and this study would not have been possible without him. I thank my committee members, Anthony Joern, David Haukos, Gregory Zolnerowich, and John Harrington, Jr., for their bottomless support and encouragement throughout my PhD program. The research project was funded by the Alaska Department of Fish and Game, and the Office of Polar Programs of the National Science Foundation. I thank the Sitnasuak Native Corporation for allowing access to the study plot, and I thank the National Park Service and Bering Straits Native Corporation for logistical support on site.

It was daunting at times for me to set up a field camp with new faces each summer. Whenever I felt weak, however, thinking of meeting the familiar faces in Nome let me get on the Alaska-bound plane with a smile and excitement. Nome became another hometown for me and thanks to my dearest friends there, Pearl Johnson, Dawyn Sawyer, Margaret Thomas, Connor Thomas, Jim Menard, Peter Bente, Tony Parsons, and many others. They greeted me and my field crew with the warmest hug every summer, and did not hesitate for a second to help us to study shorebirds in a little town in Alaska. Everything I studied for my PhD taught me about shorebirds, but my friends in Alaska gave me a life lesson on how to be sincere friends.

Four summers in Alaska were a success and a good memory all because of the people that I was fortunate to work with. Samantha Franks provided my confidence for conducting field research in Alaska. We were genuinely happy discussing shorebirds on the tundra and I owe her

To my parents, Kwon Oh-young and Kim Sub-hee,

and my brother, Yang-baek:


6,671 miles apart, you were still with me through the valleys.

# Chapter 1 - Introduction

Optimal timing of important life history events such as migration or reproduction are often determined by temporal distribution of resources (McNamara et al. 2011). A strong association between the timing of hatching in temperate song birds and peak abundance of their main prey, such as caterpillars, is a classic example (Stenseth and Mysterud 2002). As birds prepare for spring migration, a combination of the internal circannual rhythm, and both photoperiodic and non-photoperiodic environmental cues affect the timing of departure from the wintering grounds (Coppack and Pulido 2004; Dawson 2008; Bradshaw and Holzapfel 2010). Upon arrival at a breeding location, birds have to replenish physiological resources from a long flight, set up territories, find a mate, and build a nest, all before it becomes too late to lay an egg. Timing of egg laying is fine-tuned with both climatic conditions and food availability at the nesting site (Visser et al. 2012). Strong selective pressure on the timing of breeding is manifested with reduced fitness when hatching is mistimed with the food peak (Marvelde et al. 2011; Reed et al. 2013; Plard et al. 2014). Therefore, the timing of breeding is dependent on environmental cues early in the breeding season, whereas the selective pressure does not act until much later in the season. In seasonal habitats, a high pulse of resource abundance may present a single optimal window of breeding to the breeding population. However, inherent traits such as individual body quality and experience also come into play, and often drive earlier onset of breeding in high-quality breeders (Ratcliffe et al. 1998; Kokko 1999; Verhulst and Nilsson 2008). A common pattern is within-season declines in reproductive output, which have been widely detected in nature (Verhulst et al. 1995).

Anthropogenically-induced contemporary climate change is accumulating its footprint on biological systems across different taxonomic groups (Hughes 2000; Walther et al. 2002; Karl and Trenberth 2003; Rosenzweig et al. 2008). For example, Parmesan and Yohe (2003) described the phenological shifts of 484 species (including plants, butterflies, amphibians, and birds), 87% of which showed advances in timing of life history events or poleward changes in distributions. Numerous examples show significant advancement of egg-laying in birds (Crick et al. 1997; Brown et al. 1999; Dunn and Winkler 1999; Slater 1999; McCarty 2001; Both et al. 2004). However, most studies are from north temperate ecosystems, but few studies addressed Arctic or tropical environments (but see Post et al. 2010; Gilg et al. 2012).

Almost all bird species breeding in the Arctic are migratory. Costs of long-distance migration are compensated with a high pulse of invertebrate prey during the short Arctic summer (Alerstam et al. 2003). Arctic weather in the summer is capricious and often harsh with snow storms, which restrain birds from arriving too early (Martin and Wiebe 2004). However, late arrival or egg-laying can pose a risk of missing the food peak during a short Arctic summer (Smith et al. 2010). Therefore, optimal timing of breeding is especially important for breeding success and survival of Arctic-breeding birds (Meltofte et al. 2007).

In my dissertation research, I describe the patterns of climate change in the Arctic region of Alaska and Canada, and tested both long- and short-term climatic impacts on the breeding ecology as well as phenological synchrony between the Arctic invertebrates and six calidridine shorebirds. Three big questions follow when trying to understand the biological responses to contemporary climate change: Are changes in organismal responses genetic or plastic? Are changes adaptive or non-adaptive? And how do we know which specific environmental factor is

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causing a particular phenotypic or genetic change? It is difficult to conclusively distinguish whether a phenotypic change is genetically based or the result of phenotypic plasticity. Although few studies have demonstrated that seasonal phenology in birds is heritable, most studies point to the important role of phenotypic plasticity for organisms to track fast-paced climate change (Nussey et al. 2005; reviewed in Charmantier and Gienapp 2014). Whether the phenotypic change is adaptive and actually caused by the climate change is often at best inferred (Merilä and Hendry 2014). I tried to make robust inferences on climatic impacts of reproductive traits by showing trait-environment associations across multiple breeding populations of different species.

There are two ways of testing the biological impacts of climate change. Allochronic field studies compare the same population sampled at different points in time, whereas synchronic studies compare different populations sampled at approximately the same time (Hendry and Kinnison 1999; Merilä and Hendry 2014). The synchronic approach is particularly interesting because it promotes understanding of the impacts of climate change on a study system where long-term monitoring data are not available or possible to collect.

In Chapters 2 and 3, I took an allochronic approach, focusing on two time periods at a single location. In Chapter 2, I examine the relationship between the timing of breeding and reproductive performance of three sympatric shorebirds at Nome, Alaska. Comparing the relationships observed in the 1990s and 2010s, I test for decadal changes in multiple components of reproductive efforts and attribute trait shifts to the observed changes in the local climatic condition and subsequent changes in the timing of breeding. In Chapter 3, I test the effects of short-term weather conditions during different breeding stages on the determination of reproductive output for three shorebird species. In both chapters, I present strong evidence for

time-dependent climatic trends and significant ecological impacts of an unexpected cooling climate at an Arctic site.

In Chapter 4, I used a synchronic approach and compared the extent of phenological match between the timing of peak invertebrate abundance and timing of hatching in six shorebird species at ten Arctic sites during 2010-2012. Ten sites provided differing trends of climate change and daily weather conditions through summer. By substituting the space for time, I tested the climatic impact on the extent of phenological match. At the same time, I examined a broad geographic trend in the extent of phenological match and explain a potential mechanism that may drive such geographic pattern.

Concluding my dissertation research in the Arctic, I discuss the implications of my findings from evolutionary and ecological perspectives in Chapter 5.

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# Chapter 2 - Climate cooling presents the same cues but different energetic constraints to Arctic-breeding shorebirds

## Abstract

Biological impacts of climate change are exemplified by shifts in seasonal phenology. However, it is not well known how climate-induced shifts in breeding phenology affect the relationships between timing of breeding and different components of reproductive effort and breeding success. We monitored 1,335 nests of three shorebird species, Western Sandpipers, Semipalmated Sandpipers, and Red-necked Phalaropes, at a subarctic site during 1993-1996 and 2010-2014. We examined seasonal trends in reproductive traits as well as changes in the relationship between breeding timing and performance between the two study periods. We found both long-term (42-year window) and short-term cooling trends during prelaying and laying stages of three shorebird species. As a result of cooling temperatures during the egg-laying stage, three species of sympatric shorebirds delayed egg-laying by five days in the 2010s relative to the 1990s. Clutch size and daily nest survival showed strong seasonal declines; patterns of seasonal trends differed between the two study periods. Egg volume also showed strong seasonal declines with Western Sandpipers, but showed strong seasonal increases with Red-necked Phalaropes. However, population means of clutch size, egg volume, and daily nest survival did not change between the study periods. Unexpectedly, incubation duration changed between the two periods for all species: in two sandpipers with biparental incubation, the incubation duration decreased

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by two days, whereas incubation duration increased by two days in a phalarope with uniparental incubation. We suggest that different energetic costs of incubation can cause opposite responses to climate variability among biparental and uniparental shorebird species.

## Introduction

Evidence of climate change is found across all biomes as biological systems shift their seasonal phenology and geographic distributions in response to global warming (Parmesan and Yohe 2003). Advancement in the timing of breeding in avian study systems has been one of the clearest indicators of organismal responses (Crick et al. 1997; Brown et al. 1999; Dunn and Winkler 1999; Slater 1999; McCarty 2001; Both et al. 2004). Shifts in breeding phenology signify the phenotypic plasticity that provides breeders with an adaptive buffer under a changing climate (Charmantier et al. 2008). If birds time their breeding to increase either their chance of survival or their fitness (Perrins 1970; Marvelde et al. 2011), any phenological shift may impact reproductive performance.

Avian reproduction has multiple components that can vary with environmental conditions. For example, birds can vary their timing of nest initiation, egg volume or yolk content, egg-laying interval, clutch size, nest attentiveness, or duration of the incubation period. These reproductive traits often show seasonal trends due to either direct effects of the timing of breeding or differences in the quality of breeders (Verhulst and Nilsson 2008). For example, seasonal declines are commonly found with clutch size (Crick et al. 1993; Stenseth and Mysterud 2002), egg size (Birkhead and Nettleship 1982; Hipfner et al. 2005), and the number or quality of fledglings (Lepage 2000; Grant et al. 2005; García Borboroglu et al. 2008). As the timing of

breeding advances due to warming climate, one might expect to see changes in the seasonal relationships between the laying date and subsequent reproductive traits or potential long-term changes in the reproductive traits themselves (Figure 2-1). Winkler et al. (2002) hypothesized that the climate-induced long-term advancement in egg-laying will increase the mean clutch size of Tree Swallows (*Tachycineta bicolor*), given that the clutch size is strongly related to lay dates. However, the authors did not detect the expected increase in clutch size, and suggested that the warmer temperatures may help only the late breeders to increase their clutch size to the population mean, and thus, the maximum clutch size of the early breeders is constrained by factors other than the lay date (Winkler et al. 2002). Few studies have tested the impact of long-term changes in the climatic condition on the reproductive traits beyond the timing of egg laying (Skagen and Adams 2012). However, available studies are mostly on north temperate species of birds with reproductive traits that are flexible, such as variable clutch size or multiple breeding attempts per season (but see Skinner et al. 1998). Our study is the first test of the hypothesis of climate-induced long-term changes in reproductive traits with shorebirds.

Shorebirds breeding in the Arctic are long-distance migrants, with a short breeding season, an invariant clutch size, and fixed duration of incubation (Meltofte 2007; Colwell 2010). Their breeding habitats at high latitudes, however, have exhibited a higher rate of climate change than anywhere else on the globe over recent decades (IPCC 2014). Alternative climate change scenarios predict increased air temperature, especially during winter and spring, increased amount of snow and rainfall, rapid thawing of permafrost, and reduced cover of snow and ice in the Arctic region (AMAP 2012). Warming temperatures and earlier snow melt have already been observed at polar latitudes, and Arctic breeders from small-bodied *Calidris* sandpipers to large-

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bodied geese have advanced their timing of first egg laying accordingly (Pearce-Higgins et al. 2005; Hoye et al. 2007; Liebezeit et al. 2014). Changes in seasonal timing leave a question of how warming trends and consequent advances in the timing of breeding will affect other reproductive traits.

Three species of small-bodied shorebirds, Western Sandpipers *Calidris mauri*, Semipalmated Sandpipers *C. pusilla*, and Red-necked Phalaropes *Phalaropus lobatus*, breed sympatrically at Nome, Alaska, where their breeding ecology has been studied with standardized protocols for two 4-5-year periods over a decade apart (Sandercock 1997a, b, 1998; English 2014). After arrival at the breeding site, migratory shorebirds in Nome are faced with a short Arctic summer, which only lasts about two months from mid-May to mid-July. Reproductive traits of the population, including clutch size, egg volume, and hatching success, exhibit seasonal declines over the course of the season (Sandercock 1998; Sandercock et al. 1999), suggesting that within-season timing of breeding is key to reproductive success.

In 2010-2014, we monitored shorebird populations during the breeding season and constructed a dataset directly comparable to a historic dataset collected during 1993-1996. Based on the warming trend in the Arctic region, we hypothesized that spring temperatures should warm between study periods and timing of shorebird nest initiation should advance. We expected to find long-term changes in the population mean of reproductive traits of shorebirds under two conditions: 1) if reproductive traits of shorebirds show seasonal variation, and 2) if climatic change at Nome shifted the population mean date of clutch initiation between the two study periods. Given the previously documented seasonality in clutch size, egg volume, and hatching success with this population in 1993-1996 (Sandercock 1998; Sandercock et al. 1999), we

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predicted that earlier egg-laying in response to warmer temperatures would be coupled with increased mean clutch size, egg volume, and nesting success. In addition, we tested whether the relationships between the laying date and subsequent reproductive traits changed between the two study periods. Our study provides a valuable opportunity to quantify long-term changes in breeding performance of multiple species in a subarctic region that is experiencing rapid climate change.

## Methods

### (a) Study site

A 4-km$^2$ study plot was set up in 1993 near Cape Nome, 21 km east of Nome (64°20'N, 164°56'W) on the Seward Peninsula of western Alaska (Figure 2-2). The study plot was lowland tundra consisting of shallow ridges and tussocks. Interspersed ponds contained both fresh and brackish water inflowing through the channel connected to Bering Sea. Dominant vegetation was mainly ericaceous shrubs including *Empetrum nigrum, Carex lyngbyei, Salix herbacea*, *Betula nana*, mixed with moss and lichen. Located just below the Arctic Circle, our study site experiences a subarctic climate. River ice break up has been historically around May 26 followed by a short summer of median daily temperatures around 10-15℃. Monitoring breeding ecology of shorebirds was conducted for a 4-year period during 1993-1996 (hereafter, "early period"), and repeated for a second 5-year period 14 years later during 2010-2014 (hereafter, "late period").

## (b) Study species

We studied three species of migratory shorebirds, Western Sandpipers, Semipalmated Sandpipers, and Red-necked Phalaropes. The three species of shorebirds share a modal clutch size of four eggs and precocial young capable of self-feeding after hatching (Sandercock 1997b, 1998). The two sandpiper species are socially monogamous and both male and female share the incubation and brooding duties (Sandercock 1997a, 1998). Red-necked Phalaropes have a polyandrous mating system where only the male incubates the eggs and provides parental care post-hatching (Sandercock 1997b; Schamel 2000; English et al. 2014). Habitat preferences also vary, as Western Sandpipers tend to nest in upland habitats, Semipalmated Sandpipers nest in moderate to dry habitats, and Red-necked Phalaropes nest mostly in wet habitats. All three species of shorebirds have declining population trends based on monitoring data from the International Shorebird Survey (Thomas et al. 2006).

## (c) Field data collection

Migratory shorebirds typically arrived at Nome in mid-May, and the courtship displays associated with pair formation began immediately (Lanctot et al. 2000). Field crews located nests by walking through potential nesting habitats and observing incubating birds that flushed from the nest and gave distraction displays. For shorebird nests found during the egg-laying period, we estimated clutch initiation dates assuming that one egg was laid each day without skipping a day until a clutch was complete (Sandercock 1998). For nests found with four eggs or for which clutch size remained unchanged for three days, we floated eggs in warm water, measured the float angle, and estimated the date of clutch initiation by substituting the float angle in regression equations for each species (Sandercock et al. 1998a; Liebezeit et al. 2007). We calculated the

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length of the incubation period for each study period from the subset of nests that we found during egg-laying and monitored until successful hatching. For all other nests, we predicted the hatch date by adding the mean incubation duration per species for each study period to the date when the last egg was laid.

For every nest we found, egg length (L) and breadth (B) were measured to 0.1 mm with dial calipers, and egg volume was calculated using $V = kLB^2$, where $k = 0.47$ for pyriform eggs of shorebirds (Sandercock 1998). Nests were visited every five days until four days prior to the expected hatch date, when we started checking the nests daily to determine the fate of the nests. We considered nests to have *hatched* if chicks were located around the nest with attending parents. We considered nests to have *failed* when the nests did not hatch any young due to the following causes: predation, abandonment, weather, trampling, observer, or unknown. We assumed eggs were depredated if they disappeared from the nest cup prior to four days before expected hatch date, or if there were signs of predation such as scent of fox urine, a damaged nest scrape, or remains of eggs or birds. If nests were found empty within four days of the expected hatch date without apparent signs of predation, we classified the nest fate as unknown.

## (d) Data analysis

*Defining breeding stages.* We defined the egg-laying stage as the time window between the first and last clutch initiation date across all species and years pooled. The prelaying stage was defined as the two-week time window prior to the laying stage.

*Climatic changes at Nome.* To quantify climatic conditions at our study site, we used weather data from a 42-year period (1973-2014). Daily weather data including mean temperature, total amount of precipitation, and snow depth were collected from a meteorological station located ~8

km west of the study plot (Nome airport, station id: PAOM, 70200, 64°31'N, 165°26'W). We focused on daily weather conditions during two breeding stages, prelaying and laying. First, to show general climatic trends over a 42-year span at Nome, we fit linear mixed-effects models (LMMs) to the daily mean temperature and daily total precipitation for each of the two stages, with year as a fixed effect and date as a random effect. We extracted the maximum amount of snow accumulation during winter prior to May each year, and tested for year trends by using the Kendall's rank test. Next, to compare the weather conditions between the early and late period, we fit LMMs to the daily mean temperature and daily total precipitation with the period as a fixed effect, and year and date as random effects. We used function *lmer* in package lme4 (Bates et al. 2014) to fit the LMMs and function *cor.test* for the Kendall's rank test in program R (version 3.2.1, R Core Team, 2015).

*Effects of climate on timing of breeding.* We tested whether the date of clutch initiation depended on the environmental conditions within each period. Specifically, we tested a set of abiotic covariates including daily mean temperature and daily total precipitation averaged over the prelaying and laying stages for each year, and maximum snow accumulation during the prior winter. We fit a LMM with abiotic covariates and study period as fixed effects and year as the random effect. Covariates with variance inflation factors (VIF) greater than 5 were dropped from the model to reduce multicollinearity. We standardized explanatory variables using the function *standardize* in package arm (Gelman and Su 2015) and compared all possible sub-models using the function *dredge* in package MuMIn (Barton 2014). Competing models were compared based on Akaike Information Criteria (AIC; Burnham and Anderson 2002). Models with delta-AICc less than 2 were considered as candidates for the top model set (Burnham and Anderson 2002),

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and were model averaged to estimate coefficients of covariate effects using the function *model.avg* in package MuMIn. We took the sum of the Akaike weights of the top models in which the covariate appeared divided by the sum of all top model weights as an index of the relative importance (RI) of a given covariate (Burnham and Anderson 2002). We considered covariates with the relative importance value greater than 0.8 as an important predictor for the date of clutch initiation.

*Decadal changes in breeding parameters.* To test for decadal changes in the breeding performance of shorebirds, we tested for an effect of study period on timing of clutch initiation, clutch size, mean egg volume per clutch, and observed incubation duration, including a random effect of year. Three percent of the total nests were known to be renesting attempts and were excluded from all analyses. Additionally, when testing changes in the clutch size and egg volume, we excluded three nests that were depredated during laying and four nests that contained 5-7 eggs as the result of joint egg-laying by multiple females. We tested for the effect of study period for each species separately. As 80% of total nests had 4-egg clutches, we treated clutch size as a binomial variable with two outcomes, 2-3 eggs or 4 eggs in a clutch. We fit a generalized linear mixed model (GLMM) with binomial distribution (logit link) to clutch size for each species, using function *glmer* in package lme4. Distributions of other response variables were normal, so we used LMMs for analyses of those reproductive traits.

For each species, we estimated daily nest survival rates (DSR) using R package RMark as an interface to program MARK (White and Burnham 1999; Laake 2013). We excluded known renests as well as a subset of 249 nests that were subjected to experimental manipulations that could have affected nest survival (Sandercock 1997a,b; English 2014). We compared DSR of

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each species between two study periods by constructing a model with the period as only explanatory variable. Average nest success over a breeding season was calculated as the product of estimated DSR across egg laying (4 d) plus the observed incubation duration per period for each species (18-23 d). Estimates of variance and standard error for extrapolated estimates of nest survival were calculated using the delta method (Powell 2007). We used program CONTRAST to test for a significant difference in DSR between the two periods (Hines and Sauer 1989).

*Decadal changes in the seasonality of breeding parameters.* We used an analysis of covariance (ANCOVA) to test if the breeding parameters showed seasonality and patterns of seasonal trends changed between the two study periods. Prior to analyses, we subtracted the annual mean of date of clutch initiation from the first lay date of every nest to center the dates to the population mean for each species. Centering the dates to the annual mean eliminated the correlation between study period and date of clutch initiation, and allowed both factors to be included as fixed effects in our model, which allowed us to examine the individual-level effects of seasonal variation. We fit LMMs to the mean egg volume per clutch and incubation duration, and a GLMM to clutch size, with three fixed effects: study period, centered date of clutch initiation, and an interaction between period and date of clutch initiation. We included a random effect of year on both the intercept and effect of the date of clutch initiation. For inference, we examined the coefficients of all three fixed effects rather than selecting the best-fitting model for each breeding parameter. We concluded that the breeding parameter showed seasonality if the effect of clutch initiation date was significant ($p < 0.05$), and concluded that the pattern of seasonality changed between the two periods if the coefficient for the interaction between clutch initiation date and period was

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significant. For DSR, the same three fixed effects were tested using RMark as an interface to program MARK, which did not allow testing for a random effect of year.

## Results

### (a) Climate cooling

Patterns of long-term climate trend in Nome differed between the prelaying and laying stages. The prelaying stage of the three shorebird species pooled (April 29-May 12) cooled during the 42-year period between 1973 and 2014, but the trend was not statistically significant ($-0.2°C$ decade$^{-1}$, p = 0.157; Figure 2-3), with high annual variation. Our two study periods showed an even greater difference than expected based on the long-term trend, with the late period averaging 3.62°C cooler than the early period (t = $-3.04$, p = 0.014; Figure 2-3). In contrast, the laying stage (May 13-Jun 27) warmed over time ($+0.2°C$ decade$^{-1}$, p = 0.003; Figure 2-3), though temperature during the laying stage did not significantly differ between our two study periods (t = $-0.98$, p = 0.352).

### (b) Nest monitoring

A total of 483 shorebird nests were monitored during the early period in 1993-1996 and a total of 852 nests were monitored during the late period in 2010-2014. Western Sandpipers laid their first egg on May 26 ($\pm$ 6.4 days), and Semipalmated Sandpipers and Red-necked Phalaropes laid their first egg on average 4 and 10 days later than Western Sandpipers. Eggs of Western Sandpipers were on average 7.13 ml ($\pm$ 0.49) and on average 11% larger than eggs of Semipalmated Sandpipers and 17.9% larger than eggs of Red-necked Phalaropes. Mean mass of a 4-egg clutch corresponded to 100% adult female body mass for Western Sandpipers, 96% for

Semipalmated Sandpipers, and 60% for Red-necked Phalaropes. We were able to determine nest fate for 94% of 400 nests for the early period and 86% of 753 nests for the late period. Predation was the main cause of nest failure and was responsible for 88% of total nest failures.

## (c) Timing of laying

Daily mean temperature during the laying stage was an important determinant for the timing of clutch initiation for all three species (RI = 1.00) with no effects of precipitation or snow depth on any species (Table 2-1). A one degree decrease in the average daily mean temperature during the laying stage delayed the timing of clutch initiation by 0.8 days for Western Sandpipers, 0.9 days for Semipalmated Sandpipers, and 0.6 days for Red-necked Phalaropes (Table 2-1; Figure 2-4). The three species delayed the timing of clutch initiation by 4.3 to 4.8 days, between the two study periods (Table 2-2; Figure 2-5).

## (d) Seasonality in breeding performance

A modal clutch size of four eggs was observed in 81% of 1,376 nests. However, the probability of having less than four eggs was greater with clutches initiated later in the season for the two sandpiper species (Table 2-3; Figure 2-6a). Egg volume showed a strong seasonal decline in Western Sandpipers, no trend in Semipalmated Sandpipers, and marginal seasonal increase in Red-necked Phalaropes (Table 2-3; Figure 2-6b). There was no seasonality in the incubation duration for any species (Figure 2-6c), but strong seasonal declines in the daily nest survival rates of both sandpipers (Table 2-3; Figure 2-6d).

## (e) Decadal changes in breeding performance

Between the two study periods, mean clutch size of Western Sandpipers decreased by 0.06 eggs (Table 2-2 and 2-3). Egg volume did not differ between early and late study periods for any

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species (Table 2-3). The mean incubation duration decreased for Western Sandpiper and Semipalmated Sandpiper by $-2.2$ and $-1.9$ days, respectively, but increased by $+1.9$ days for Red-necked Phalaropes between the early and late periods (Table 2-2; Figure 2-6).

Daily nest survival rates (DSR) did not differ between the two study periods for any species, and ranged between 0.937 and 0.972 (Table 2-2; Figure 2-6). The expected probability of a nest surviving to hatch, based on DSR and mean length of the laying and incubation period, ranged between 0.34 and 0.46 for two sandpipers and between 0.18 and 0.33 for Red-necked Phalaropes (Table 2-2). The expected probability of nests surviving to hatch tended to be greater in the late period than the early period for Semipalmated Sandpipers ($+0.10$, $\chi^2 = 3.13$, d.f. $= 1$, p $= 0.077$), did not differ between periods for Western Sandpipers ($-0.05$, $\chi^2 = 0.74$, d.f. $= 1$, p $= 0.391$), but tended to be lower in the late period for Red-necked Phalaropes ($-0.15$, $\chi^2 = 3.08$, d.f. $= 1$, p $= 0.079$; Table 2-2).

### (f) Decadal changes in the seasonal trend

We did not detect significant changes in the seasonal trends in breeding performance between the two study periods for most breeding parameters. However, the negative seasonal trend of clutch size became stronger with a steeper slope for Western Sandpipers in the late period (Table 2-3; Figure 2-6a). On the other hand, the effects of clutch initiation date on the clutch size of Red-necked Phalaropes were positive during the early study period and mostly negative during the late period (Figure 2-6c). In Semipalmated Sandpipers, DSR was greater for nests initiated early in the season during the early period, but greater for nests initiated later in the season during the late period (Figure 2-6d).

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## Discussion

Our long-term study of climate variability and breeding performance of Arctic-breeding shorebirds resulted in three major findings. First, despite evidence for warming in other areas of the Arctic, we found a long-term cooling trend during the prelaying stage of shorebirds at Nome, Alaska. The mean temperature during laying as well as the prelaying stage were cooler in the 2010s compared to the 1990s. Second, responding to cooler temperatures during laying, all three species of shorebirds delayed egg laying by about five days during the late period. Last, despite changes in breeding phenology, the seasonal variation in egg volume and the daily nest survival did not lead to long-term changes in those traits. Instead, the relatively fixed traits of clutch size and incubation duration have changed across the two study periods.

### *Stage-sensitive climatic trends and delayed laying*

Temperature trends in Nome varied by breeding stages and periods of the 42-year time series. When the daily temperature data was fit with linear models over the 42-year window, the prelaying stage showed a cooling trend whereas the laying stage showed a warming trend. The difference in temperature trend between breeding stages, cooling trend for the prelaying stage and the warming trend for the laying stage, implies that a single annual metric may not be a good representation of a climatic trend. It is well established that the rate of climate change can vary among seasons of the year (Doran et al. 2002; AMAP 2012). However, cooling and warming trends at Nome were both observed within a 59-day period. Despite the short length of the Arctic summer, we need to be cautious when choosing a representative time window to test for trends of climate change.

Our results showed that the timing of clutch initiation in shorebirds was strongly related to cooling trends in temperature during the laying stage for all three species. The variation in temperature during the laying stage explained 40-71% of variation we observed in the timing of laying in Nome. Other factors that affect the timing of laying in Arctic-breeding shorebirds include timing of snow melt and food availability (Meltofte et al. 2007; Leibezeit et al. 2014). The long-term cooling trend of the prelaying stage in Nome, if it persists, will likely delay the timing of snow melt and emergence of invertebrates. The warming trend during the rest of the breeding stages, however, will keep the optimal timing for hatching and peaks in invertebrate abundance either constant or advanced (Tulp and Schekkerman 2008). A potential dissociation between the temperature conditions during the prelaying and laying stages may cause 'phenological mismatch' between the shorebird hatching and the peak emergence of invertebrate prey.

### *Seasonal trends and periodic changes of breeding parameters*

Seasonal declines in clutch size coupled with a significant delay in the date of clutch initiation resulted in a significant decrease in the mean clutch size of Western Sandpipers between the two study periods. The changes between the two periods, however, were relatively small despite statistical significance. Within-season variation in the clutch size, egg volume, incubation duration, and nesting success, whether statistically significant or not, conformed to trends previously reported for shorebirds. We found seasonal declines in the clutch size of both sandpiper species, egg volume of the Western Sandpipers, and the daily nest survival rate of all three species (Nol et al. 1997; Meltofte et al. 2007). Seasonal increases observed in the egg volume of the Red-necked Phalaropes were consistent with previous observations for the same

species at Cape Espenberg, Alaska (Meltofte et al. 2007). Seasonality in the incubation duration is rarely reported in shorebirds. Seasonal declines in incubation duration of Red-necked Phalaropes have been previously reported (Reynolds 1987: Schamel 2000). However, we did not find clear seasonality in the incubation duration with any species. Identifying the potential cause of seasonal trends in each of the reproductive traits will require mechanistic studies in the future. Here, we predict why observed seasonal trends combined with delayed laying did not lead to changes in the clutch size (except for Western Sandpipers), egg volume, and the daily nest survival between the two study periods.

Multiple factors could have prevented the long-term changes in the population mean of egg volume and daily nest survival in shorebirds. Unlike an invariant clutch size, egg volume and daily nest survival of three shorebird species showed considerable variation, which did not vary between the two study periods. For the egg volume, however, it is possible that the seasonal trend was not strong enough to shift the population mean of egg volume. It is notable that in all three species, the range of lay dates remained almost the same between the two periods. The population mean of lay dates has delayed about 5 days in the late period, but the first and last date of clutch initiation for each species were similar between periods. When the overall time window is not moving, the population mean can shift only when the slope of seasonality is great enough. Also notable is the amount of annual variation seen with the seasonal trend in the daily nest survival rates. In our study, we focused on comparing traits between the two periods, and treated year as a random factor. By averaging seasonal trends among years within each study period, our analytical approach likely masked potential relationship between annual mean lay date and the population mean of the trait. Unusual cooling trends and the consequent delay in

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egg-laying of our population raises the question whether we should expect different results for a cooling environment as opposed to a warming environment. However, the fact that both positive and negative seasonal trends with the egg volume, of Western Sandpiper and Red-necked Phalarope respectively, did not produce periodic shift in the population mean shows that the lack of mean shift is not due to a cooling trend alone.

### *Cost of incubation under climate cooling*

Clutch size and duration of incubation are thought to be invariant in shorebirds. Unexpectedly, we found that incubation duration increased by two days for the sandpipers but decreased by two days for the phalaropes over two decades at Nome. The rate of embryonic development of a species evolves to balance the trade-off between mortality of the incubating adult and time-dependent mortality risk on the eggs (Martin 2002). Incubation duration is also adjusted by the nest attentiveness, microclimate condition in the nest, and foraging condition for the incubating adults (Boersma 1982). Both sandpiper species provide biparental incubation and attend their clutch almost around the clock (Bulla et al. 2014), and at our site, the air temperature during the incubation stage remained similar between the two periods (E. Kwon, unpublished data). Therefore, the observed shortening in the incubation duration of sandpipers was likely due to trade-offs in reducing the mortality of both adults and their offspring, and not from a thermal relief. The mechanisms of how parents shorten the incubation period are unknown, but likely provide a clear advantage to the survival of eggs and potentially the survival of hatchlings. In Nome, both sandpiper species attained a 3% increase in their probability of a nest surviving until hatch by shortening the exposure days of the eggs to potential predation risks. Increased predation risk and chance of severe rain events towards the end of the breeding season likely

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increase the benefit of a shortened incubation period. Delayed egg-laying in Nome also could have forced shortening of incubation so that breeders meet optimal timing of south-bound migration. In both sandpiper species, females leave the breeding ground before males (Butler et al. 1987). However, with Western Sandpipers, the difference in departure timing of male and female breeders is less among late nests (Ydenberg et al. 2005). Shortening the stop-over duration to avoid high predation risk at a stop-over site also indicates that there may be a temporal threshold for successful migration for these sandpipers (Ydenberg et al. 2004).

If delayed egg-laying is inducing shorter incubation for sandpipers, why do we see the opposite trend for the phalaropes? The breeding windows of the three species almost completely overlap and the three species often nest within several meters from each other at Nome, Alaska. However, the energetic cost of incubation may be twice as high for uniparental incubation in phalaropes than for biparental incubation in sandpipers. Prolonged incubation at the early stages of a breeding season suggest that incubation can be energetically demanding for Red-necked Phalaropes (Schamel 2000). English (2014) observed that nest attentiveness of phalaropes was lower with cold weather conditions, high incubation loading, and poor body condition of incubating males. Consequently, incubation duration was longer during cold weather conditions and especially with early nests. Small eggs of socially polyandrous shorebird species compared to other shorebirds are explained by male incubation limitation (Lislevand and Thomas 2006). Our results on the seasonal increase in the egg volume of phalaropes, as opposed to the seasonal decrease seen in sandpipers, may suggest that colder temperatures during early season might limit the parental investment by male phalaropes. As Stevenson and Bryant (2000) argued, temperature is not just an environmental cue for timing of breeding but also a constraint on

various aspects of breeding. Organismal responses to temperature maybe consistent for sympatric species regardless of their life-history traits (Crick and Sparks 1999). However, in the Arctic, different energetic costs of species induced by differences in their mating strategy may affect how birds adjust to the climate change and subsequent changes in the optimal timing of breeding.

## *Conclusion*

Our study suggests that season-specific climate changes at a local scale may show the opposite sign from what is expected with long-term trends in global warming at a broader spatial scale. Sympatric species of shorebirds at Nome, Alaska used temperature as the same environmental cue to time their breeding and responded to cooling trends at the same rate. However, species with different systems of parental care responded in the opposite direction for different components of their reproductive effort. Changes in the climatic condition did not affect how the date of clutch initiation, relative to the population mean, affects shorebirds' reproductive performance. If the stage-specific climatic trends persist in the future, these shorebirds will face a disassociation of environmental cues on the breeding ground, the impact of which we do not yet fully understand.

# Acknowledgments

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Table 2-1. Relative effect sizes of covariates on the timing of clutch initiation from the final averaged model for each species of shorebirds at Nome, Alaska, 1993-1996 and 2010-2014. RI = relative importance (sum of the Akaike weights of the top models in which the covariate appeared divided by the sum of all top model weights). Covariates were standardized by centering and dividing by 2 SD's. Top models are given in Table S2-1.

| | Estimate | SE | RI |
|---|---|---|---|
| Western Sandpiper | | | |
| Intercept | 146.52 | 0.32 | N/A |
| $Temp_{lay}$ | -3.70 | 0.81 | 1.00 |
| $Temp_{prelay}$ | -2.51 | 0.88 | 1.00 |
| $Rain_{prelay}$ | 0.52 | 0.79 | 0.18 |
| Snow | 0.68 | 0.62 | 0.25 |
| Period | 0.57 | 1.04 | 0.17 |
| Semipalmated Sandpiper | | | |
| Intercept | 150.45 | 0.27 | N/A |
| $Temp_{lay}$ | -4.50 | 0.69 | 1.00 |
| Period | 3.29 | 0.59 | 1.00 |
| Snow | -0.91 | 0.51 | 0.56 |
| $Rain_{lay}$ | -0.84 | 1.03 | 0.14 |
| $Rain_{prelay}$ | -0.49 | 0.55 | 0.20 |
| Red-necked Phalarope | | | |
| Intercept | 158.04 | 0.44 | N/A |
| Period | 3.37 | 1.23 | 1.00 |
| $Temp_{lay}$ | -2.63 | 0.99 | 1.00 |
| $Rain_{prelay}$ | -0.67 | 0.94 | 0.25 |
| Snow | 0.37 | 0.85 | 0.21 |

Table 2-2. Comparison of breeding parameters of three species of migratory shorebirds between early (1993-1996) and late periods (2010-2014) at Nome, Alaska. Breeding parameters are compared separately for each shorebird species. WESA: Western Sandpiper; SESA: Semipalmated Sandpiper; RNPH: Red-necked Phalarope. Significant differences between early and late periods are in bold.

| Response | Early period | | Late period | | Period diff. |
|---|---|---|---|---|---|
| | mean ± sd | n | mean ± sd | n | |
| **(a) Date of clutch initiation** | | | | | |
| **WESA** | **May 24 ± 6.0** | **225** | **May 28 ± 6.0** | **309** | **+4.3** |
| **SESA** | **May 28 ± 5.6** | **202** | **Jun 2 ± 5.8** | **250** | **+4.8** |
| **RNPH** | **Jun 3 ± 6.2** | **56** | **Jun 8 ± 7.1** | **293** | **+4.8** |
| (b) Clutch size (egg) | | | | | |
| **WESA** | **3.86 ± 0.38** | **224** | **3.80 ± 0.47** | **309** | **−0.06** |
| SESA | 3.78 ± 0.48 | 202 | 3.82 ± 0.46 | 249 | +0.04 |
| RNPH | 3.86 ± 0.40 | 56 | 3.73 ± 0.55 | 291 | −0.13 |
| (c) Egg volume (*ml*) | | | | | |
| WESA | 7.17 ± 0.44 | 158 | 7.11 ± 0.53 | 263 | −0.06 |
| SESA | 6.31 ± 0.40 | 175 | 6.37 ± 0.39 | 212 | +0.06 |
| RNPH | 5.92 ± 0.36 | 55 | 5.83 ± 0.39 | 209 | −0.09 |
| (d) Incubation duration (day) | | | | | |
| **WESA** | **22.9 ± 0.6** | **19** | **20.7 ± 1.0** | **47** | **−2.2** |
| **SESA** | **22.0 ± 1.2** | **10** | **20.1 ± 1.1** | **25** | **−1.9** |
| **RNPH** | **19.6 ± 1.3** | **5** | **21.5 ± 1.3** | **17** | **+1.9** |
| (e) Daily nest survival | | | | | |
| WESA | 0.972 ± 0.004 | 156 | 0.965 ± 0.003 | 272 | −0.007 |
| SESA | 0.959 ± 0.004 | 160 | 0.966 ± 0.004 | 198 | +0.007 |
| RNPH | 0.953 ± 0.010 | 45 | 0.937 ± 0.007 | 154 | −0.016 |
| (f) Annual nest survival | | | | | |
| WESA | 0.46 ± 0.05 | 156 | 0.41 ± 0.03 | 272 | −0.05 |
| SESA | 0.34 ± 0.04 | 160 | 0.44 ± 0.04 | 198 | +0.10 |
| RNPH | 0.33 ± 0.08 | 45 | 0.18 ± 0.03 | 154 | −0.15 |

Table 2-3. Effects of study period, date of clutch initiation, and its interaction on the breeding parameters of shorebirds at Nome, Alaska, 1993-1996 and 2010-2014. Coefficients were taken from models with a random effect of year on the intercept and on the fixed effect of lay date. Generalized linear mixed model was fit to the clutch size and the corresponding z-values are shown. For the egg volume and the incubation duration, linear mixed models were fit and the corresponding t-values are shown. For DSR, fixed effect only models were fit and the lower and upper confidence interval are shown. WESA: Western Sandpiper; SESA: Semipalmated Sandpiper; RNPH: Red-necked Phalarope. Significant effects are in bold.

| | | Intercept | Period | | | | Clutch initiation | | | | Period × initiation | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Est. | Est. | SE | z, t | p < | Est. | SE | z, t | p | Est. | SE | z, t | p < |
| Clutch size | WESA | 2.22 | **-0.99** | **0.48** | **-2.05** | **0.040** | **-2.25** | **0.31** | **-7.29** | **0.001** | **1.48** | **0.65** | **2.27** | **0.024** |
| | SESA | 1.95 | -0.01 | 0.47 | -0.01 | ns | **-1.94** | **0.28** | **-6.84** | **0.001** | 0.90 | 0.57 | 1.57 | ns |
| | RNPH | 1.41 | -0.97 | 0.52 | -1.85 | ns | 0.03 | 0.29 | 0.12 | ns | **-2.22** | **1.08** | **-2.07** | **0.039** |
| Egg volume | WESA | 7.17 | -0.07 | 0.08 | -0.92 | ns | **-0.03** | **0.01** | **-2.52** | **0.034** | 0.00 | 0.01 | 0.28 | ns |
| | SESA | 6.31 | 0.06 | 0.08 | 0.76 | ns | 0.00 | 0.01 | -0.27 | ns | 0.00 | 0.01 | 0.35 | ns |
| | RNPH | 5.92 | -0.08 | 0.09 | -0.86 | ns | **0.02** | **0.01** | **1.94** | **0.058** | -0.01 | 0.01 | -1.09 | ns |
| Incubation duration | WESA | 22.89 | **-2.23** | **0.28** | **-7.86** | **0.001** | -0.01 | 0.03 | -0.45 | ns | -0.02 | 0.04 | -0.43 | ns |
| | SESA | 21.99 | **-1.93** | **0.41** | **-4.71** | **0.001** | -0.03 | 0.06 | -0.58 | ns | -0.02 | 0.08 | -0.30 | ns |
| | RNPH | 19.58 | **1.96** | **0.60** | **3.24** | **0.009** | 0.09 | 0.07 | 1.22 | ns | -0.03 | 0.09 | -0.37 | ns |
| | | Beta | Beta | SE | lci | uci | Beta | SE | lci | uci | Beta | SE | lci | uci |
| Daily nest survival rate (DSR) | WESA | 3.560 | -0.249 | 0.161 | -0.563 | 0.066 | **-0.046** | **0.022** | **-0.089** | **-0.004** | 0.036 | 0.028 | -0.019 | 0.092 |
| | SESA | 3.171 | 0.200 | 0.168 | -0.130 | 0.529 | **-0.039** | **0.020** | **-0.077** | **-0.000** | **0.082** | **0.033** | **0.018** | **0.146** |
| | RNPH | 3.014 | -0.310 | 0.249 | -0.798 | 0.178 | -0.033 | 0.030 | -0.091 | 0.026 | -0.015 | 0.035 | -0.084 | 0.053 |
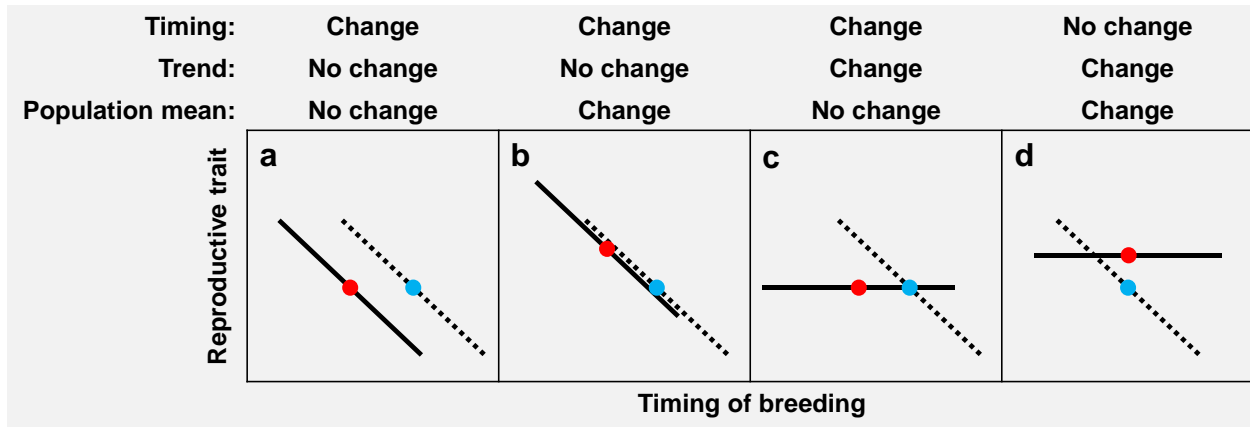
Figure 2-1. Hypothesized relationships between the timing of breeding and a reproductive trait under four different scenarios with changes in the timing of breeding and the seasonal trend and population mean of a reproductive trait. a: Population mean of a trait (point) did not change after the timing of breeding advanced. b: Population mean increased as the timing of breeding advanced keeping the seasonal trend consistent. c: Both the timing and seasonal trend changed without any difference in the population mean. d: Timing of breeding did not change, however, the population mean increased as the seasonal trend disappeared. The last scenario may occur if a favorable condition of warmed climate eliminates seasonal constraints and hence the seasonal trend. Note that these simplified graphs show a hypothetical trait which is negatively correlated with the timing of breeding, and possible advancement in the timing of breeding. After Winkler et al. (2002).
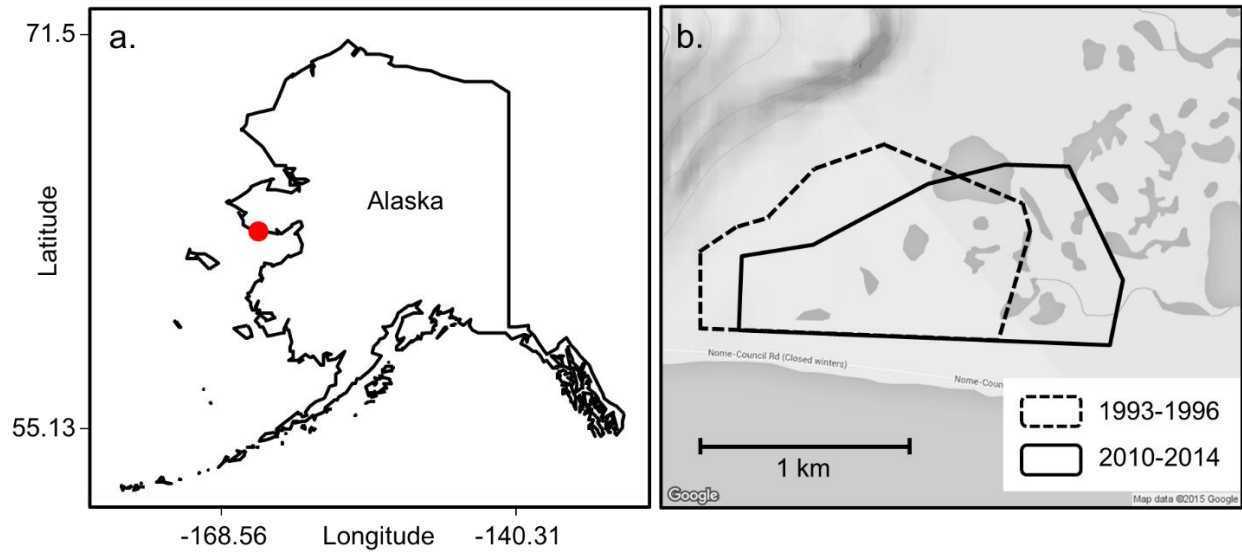
Figure 2-2. Map of study site at Nome, Alaska (a) and boundaries of study plots from two study periods (b). Darker shades in (b) indicate both fresh and marine water bodies.
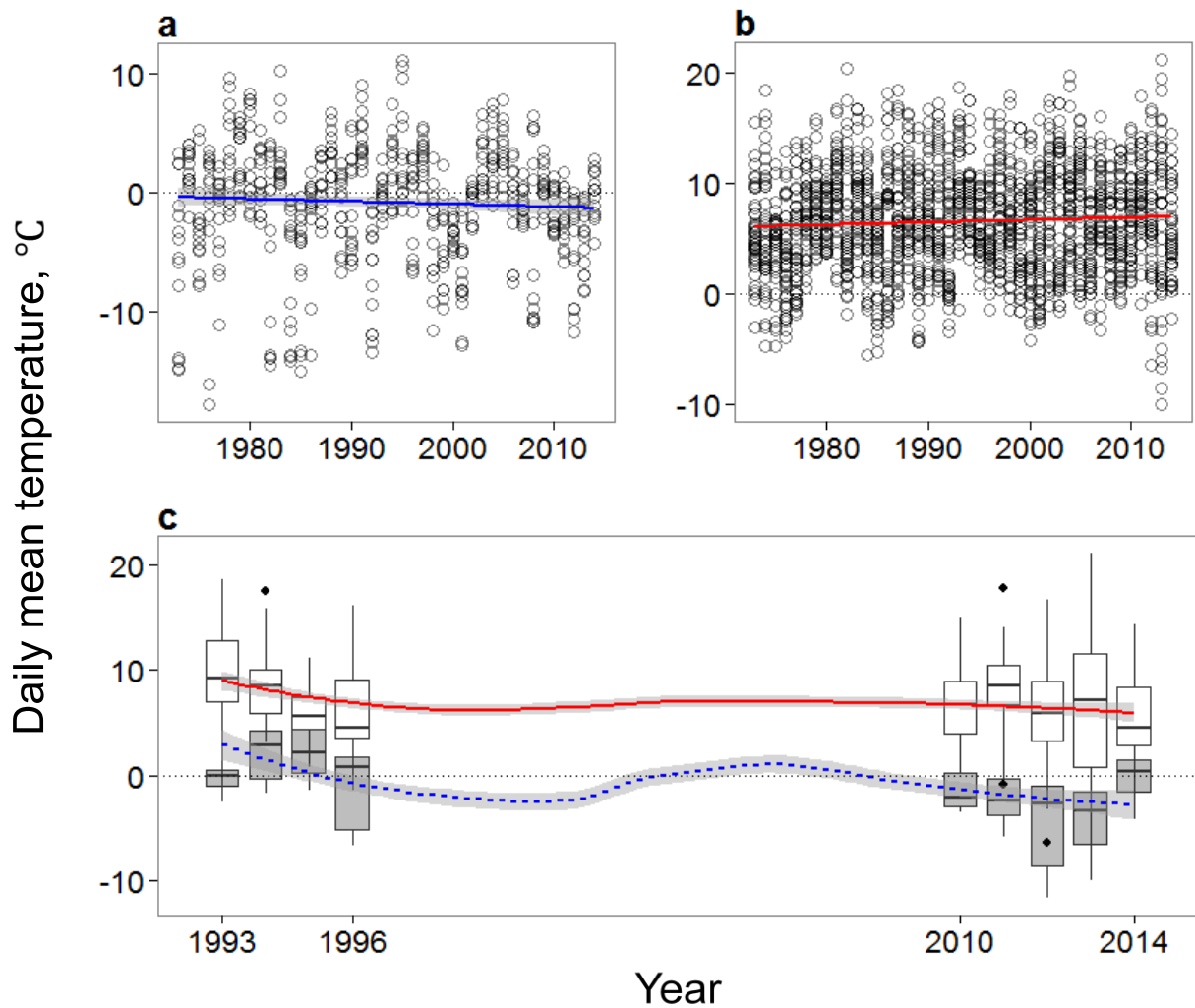
Figure 2-3. Long-term trends in climate over the 42-year period of 1973-2014 at Nome, Alaska. (a) Daily mean temperature during prelaying stage (April 29-May 12), beta estimate = −0.02, n.s. (b) Daily mean temperature during laying stage (May 13-June 27), beta estimate = +0.02, p = 0.01. (c) Box plots show distribution of the daily mean temperature during prelaying (grey) and laying stage (blank) for the study periods, 1993-1996 and 2010-2014. Loess spline curves were fitted to the daily mean temperatures for each stages for 1993-2014 to show the trend.
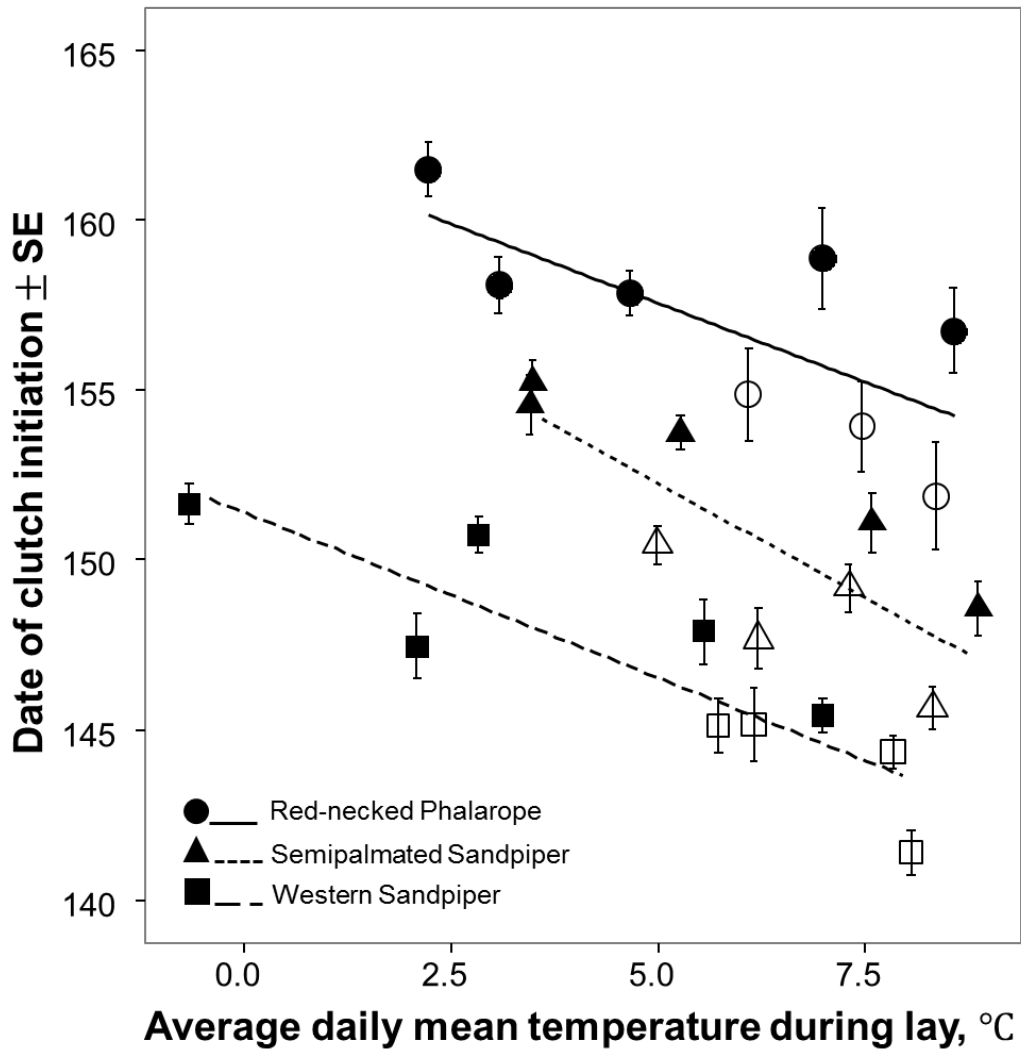
Figure 2-4. Influence of average daily mean temperature during laying stage on the mean date of clutch initiation per species per year. Open points = early period; closed points = late period. Lines are from linear regression models. In a nonleap year, calendar day 140 = May 20 and 165 = Jun 14. Western Sandpiper: $r^2 = 0.71$, n = 9 years, p = 0.003, Semipalmated Sandpiper: $r^2 = 0.56$, n = 9, p = 0.012, Red-necked Phalarope: $r^2 = 0.40$, n = 8, p = 0.056.
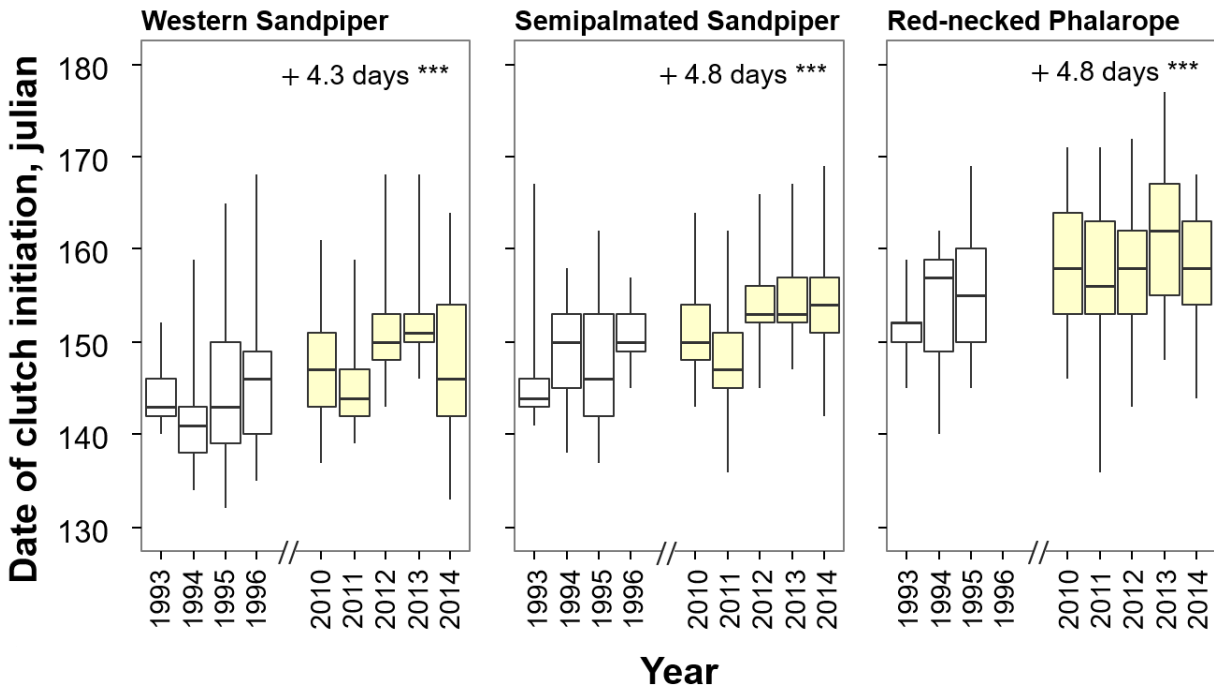
Figure 2-5. Dates of clutch initiation of three shorebird species at Nome, Alaska during 1993-1996 and 2010-2014. Differences in the population means between the early and late periods are shown with significance levels (***: p < 0.001). In a nonleap year, calendar day 140 = May 10 and 165 = Jun 29.
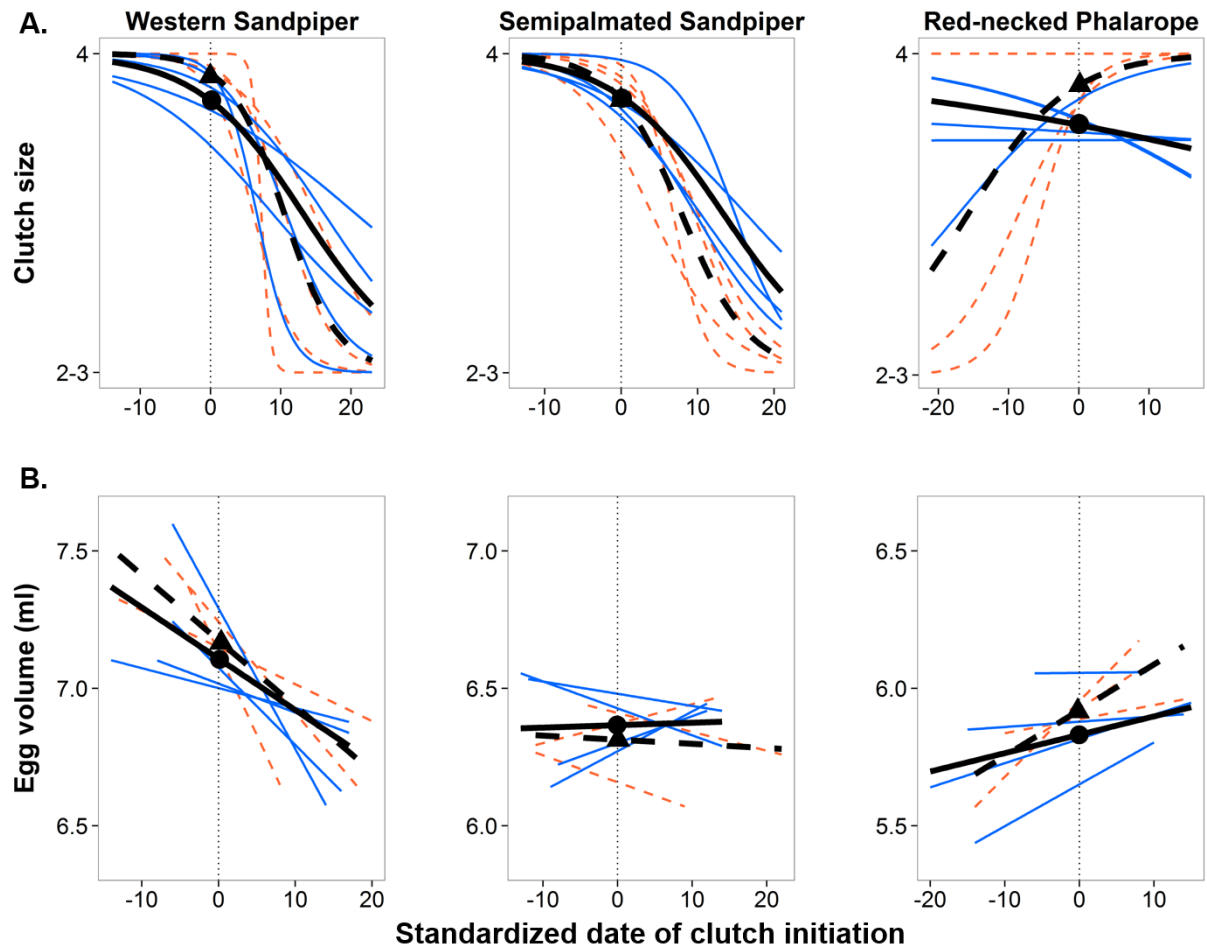
Figure 2-6. Seasonal trends in the clutch size, egg volume, incubation duration, and daily nest survival of shorebirds at Nome, Alaska. Each line represents year (red dotted: early period; blue solid: late period) and two bold lines represent the period mean (dotted: early period; solid: late period). The annual mean of lay date was subtracted from the lay date of each nest to center the dates on x-axis. Thus, negative value indicates lay dates earlier than the population mean of a species in a year. Points on the bold lines indicate population means of the breeding parameter for early (triangle) and late period (circle).
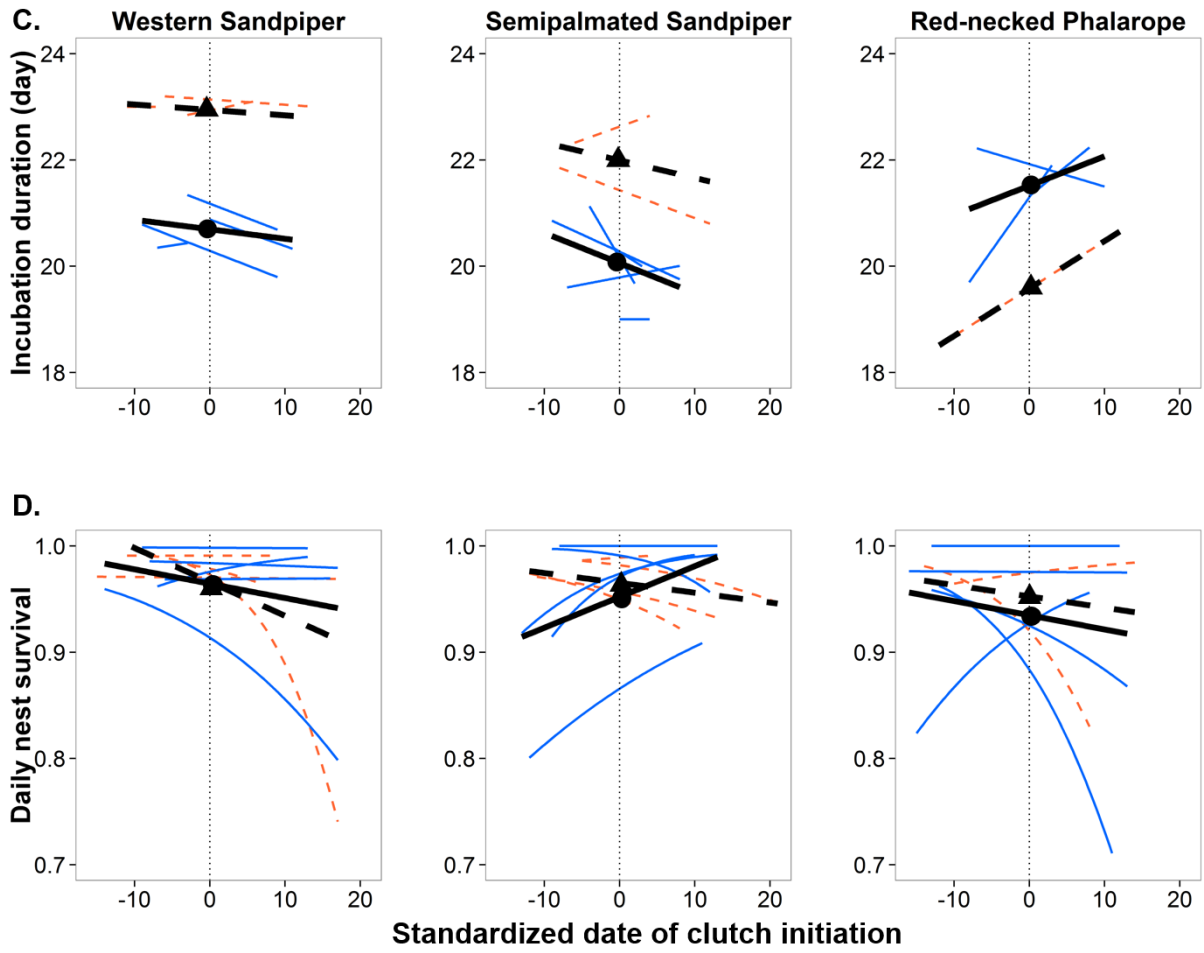
Figure 2-6. Continued.

Supplementary Table 2-1. Top model set of the effects of climatic covariates on timing of clutch initiation at Nome, Alaska, 1993-1996 and 2010-2014. Variables marked '-' are dropped from the global model to preclude collinearity among covariates. Variables marked 'V' are included in the given model. Blank indicates a variable that was tested in the global model but not present in the given submodel.

| | Model terms | | | | | Model rank | K | Deviance | AICc | ΔAIC | $w_i$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Period | $Temp_{prelay}$ | $Temp_{lay}$ | $Rain_{prelay}$ | $Rain_{lay}$ | Snow | | | | | | |
| Western Sandpiper | | | | | | | | | | | |
| | V | V | | - | | 1 | 5 | 3377.32 | 3387.43 | 0.00 | 0.40 |
| | V | V | | - | V | 2 | 6 | 3376.20 | 3388.36 | 0.93 | 0.25 |
| | V | V | V | - | | 3 | 6 | 3376.88 | 3389.04 | 1.61 | 0.18 |
| V | V | V | | - | | 4 | 6 | 3377.02 | 3389.17 | 1.75 | 0.17 |
| Semipalmated Sandpiper | | | | | | | | | | | |
| V | - | V | | | V | 1 | 6 | 2791.34 | 2803.52 | 0.00 | 0.37 |
| V | - | V | | | | 2 | 5 | 2793.84 | 2803.98 | 0.46 | 0.29 |
| V | - | V | V | | V | 3 | 7 | 2790.52 | 2804.78 | 1.26 | 0.20 |
| V | - | V | | V | | 4 | 6 | 2793.22 | 2805.41 | 1.89 | 0.14 |
| Red-necked Phalarope | | | | | | | | | | | |
| V | - | V | | - | | 1 | 5 | 2331.46 | 2341.64 | 0.00 | 0.54 |
| V | - | V | V | - | | 2 | 6 | 2330.94 | 2343.19 | 1.56 | 0.25 |
| V | - | V | | - | V | 3 | 6 | 2331.28 | 2343.52 | 1.88 | 0.21 |

# Chapter 3 - Effects of climatic conditions on the breeding parameters of Arctic-breeding shorebirds

## Abstract

Impacts of climate change are ubiquitous throughout the annual cycle of migratory organisms. Understanding climatic impacts on reproductive performance beyond the timing of arrival or breeding can be achieved by investigating relationships between weather variables and variable components of reproductive effort. We monitored the reproductive ecology of three species of shorebirds breeding sympatrically at a subarctic site for nine years, and examined the effects of temperature and precipitation on their reproductive output. We found that the three species of shorebirds initiated their clutches during partially distinct time windows, which caused each species to breed under different temperature and precipitation regimes. Reproductive effort of the three species were measured as clutch size, egg volume, incubation duration, and daily nest survival, and varied with different sets of environmental drivers. Overall, clutch initiation was earlier under warmer conditions for all three species. Temperature was positively correlated with egg volume and daily nest survival rates for two species. Two of three species invested more in their egg production with increased precipitation during the early part of the breeding season. Our study provides evidence for relationships between weather conditions on the breeding ground and various components of reproductive effort originally considered to be invariant among Arctic-breeding shorebirds.

## Introduction

Global warming trends and adaptive shifts in the timing of seasonal events have been well documented in a variety of organisms (Visser and Both 2005; Parmesan 2006; Carey 2009). Long-term data provide strong evidence on the role of temperature or thermal conditions as an environmental cue for the optimal timing of breeding in birds (Crick et al. 1997; Brown et al. 1999; Dunn and Winkler 1999; Devictor et al. 2008; Visser et al. 2009). However, long-term data collected beyond arrival at the breeding ground or the initiation of a nest are relatively rare. Naturally, our understanding of impacts of climate change on the reproductive performance is often skewed towards well-studied organisms (Winkler et al. 2002; Both and Visser 2005; Dunn et al. 2010; Reed et al. 2013).

Understanding the climatic impacts on reproductive performance is important because shifts in seasonal phenology coupled with climatic change alone does not mean that a population will not be viable (Moss et al. 2001; Dickey et al. 2008). Reproductive parameters such as clutch size, hatching success, the number of offspring, and brood survival are closely tied to climatic variables (Lesser Snow Geese *Chen caerulescens*: Skinner et al. 1998; Capercaillie *Tetrao urogallus*: Moss et al. 2001). When there are no long-term data available on the reproduction, short-term response to weather variables can be useful to predict organismal response to future climate change (Skagen and Adams 2012). Observed and predicted climate change entails substantial warming in both maximum and minimum temperatures, an increase in the frequency of extreme events, changes in precipitation and cloud cover, as well as interactions between temperature and precipitation (IPCC 2014). Relationships among temperature or precipitation

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and biological processes will help to predict the impact of extreme weather events, which are difficult to test given the stochastic nature of rare events (Jentsch et al. 2007).

Predicting future changes in precipitation and cloud cover is more complex than predicting future trends of surface temperature (Adler et al. 2008; Zhou et al. 2009). However, potential ecological consequences of changing precipitation regimes are not any different than the observed impacts from changing temperature (Knapp et al. 2008). Cloud cover is expected to increase more at higher latitudes than other regions, and predicted to advance the timing of snow melt in the Arctic (Zhang et al. 1996). Advanced spring phenology coupled with early snow melt or warming trends have been reported in the Arctic region. Ecological changes present a great threat to ~280 species of migratory birds that inhabit the Arctic during their breeding period (Callaghan et al. 2004; Høye et al. 2007; Post et al. 2009; Liebezeit et al. 2014).

In this study, we monitored three species of migratory shorebirds breeding sympatrically at a subarctic site for nine years. We tested the effects of mean temperature and total precipitation on clutch size, egg volume, incubation duration, and daily nest survival rate. Clutch size and incubation duration are often considered as fixed traits in shorebirds with limited inter-annual variation reported during extreme weather conditions (Meltofte et al. 2007; Colwell 2010). Here, we provide evidence of strong effects of weather on the variable and fixed reproductive traits of arctic-breeding shorebirds.

## Methods

### (a) Study site

A 4-km$^2$ study plot was established in 1993 near Cape Nome, 21 km east of Nome (64°20'N, 164°56'W) on the Seward Peninsula of western Alaska (see Figure 2-2). Monitoring the breeding

ecology of shorebirds was conducted for a 4-year period during 1993-1996 (hereafter, "early period"), and repeated for a second 5-year period 14 years later during 2010-2014 (hereafter, "late period").

## (b) Study species

We studied three species of migratory shorebirds: Western Sandpipers *Calidris mauri*, Semipalmated Sandpipers *C. pusilla*, and Red-necked Phalaropes *Phalaropus lobatus*. The three species of shorebirds share a modal clutch size of four eggs and precocial young capable of self-feeding after hatching (Sandercock 1997a, 1998). The two sandpiper species are socially monogamous and both male and female share the incubation and brooding duties (Sandercock 1997b, 1998). Red-necked Phalaropes have a polyandrous mating system where only the male incubates the eggs and provides parental care post-hatching (Sandercock 1997a; Schamel 2000; English et al. 2014). Species-specific climatic niche and life-history traits such as diet, habitat, migration distance, number of broods, molting strategy can affect seasonal phenology (Jiguet et al. 2007, 2010; Végvári et al. 2010). Our study system provided a unique opportunity to compare the reproductive performance of three shorebird species that have distinctive life-history traits.

## (c) Field data collection

We followed the same field protocol for data collection described in Chapter 2 (Field Data Collection).

## (d) Data analysis

*Defining breeding stages.* Based on nine years of population data on shorebird breeding ecology (Chapter 2), we defined laying stage as the time window between the dates when the first egg was laid in the first and last nest with species and years pooled, and the prelaying stage as the

two-week time window prior to the laying stage. Here, we additionally defined the incubation stage as the time window between the dates when the incubation started at the first nest and when the incubation was terminated at the last nest with species and years pooled. Hatch stage was then defined as the time window between dates when the earliest and the latest hatching occurred with species and years pooled. We used Julian dates for all calculations and analyses, but present the corresponding calendar dates in non-leap years to aid interpretation. Based on our definitions, the prelaying stage at Nome was April 29-May 12, the laying stage was May 13-Jun 27, the incubation stage was May 17-Jul 23, and the hatch stage was Jun 5-Jul 20.

*Climatic changes at Nome.* In Chapter 2, we described the long-term (1973-2014) climatic conditions at Nome, Alaska, during the prelaying and the laying stages of breeding shorebirds. In addition to the first two stages, we describe the climatic conditions during the incubation and the hatch stages using the same analytical methods. Daily weather data included mean temperature, total amount of precipitation and snow depth compiled from a meteorological station located ~8 km to west of the study plot (Nome airport, station id: PAOM, 70200, 64°31'N, 165°26'W). We extracted daily weather data by the four stages for each of the 42 years. First, to show general climatic trend over 42-year span in Nome, we fit linear mixed-effects models (LMMs) to the daily mean temperature and daily total precipitation for each of the four stages, with year as a fixed effect and date as a random effect. We obtained the maximum amount of snow accumulation during winter prior to May each year, and tested year trends using the Kendall's rank test. Next, to compare the climatic conditions between the early (1993-1996) and late study period (2010-2014), we fit LMMs to the daily mean temperature and daily total precipitation with the period as a fixed effect, and year and date as random effects. We used a *t*-test to test if

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the maximum amount of snow accumulation differ between the two periods because we had only

one measure per year. We used function *lmer* in package lme4 (Bates et al. 2014) to fit the

LMMs and function *cor.test* for the Kendall's rank test in program R (version 3.2.1, R Core

Team, 2015).

*Species effect on the breeding window.* To test for a species-effect on timing of clutch initiation,

we fit a LMM to the dates of clutch initiation with species as a fixed effect and climatic variables

and year as random effects (Table 3-1). Daily mean temperature and daily total precipitation

were averaged over each of the four predefined breeding stages. See below *Model selection and*

*model averaging* section for detailed procedure on model selection. We compared the effect size

of species to the effect size of other covariates in the top model set.

*Species effect on the weather condition during breeding.* To test for a species-effect on average

daily mean temperature and sum of daily total precipitation during breeding stages, we redefined

three breeding stages, prelaying, laying, and incubation stage, specific to each nest. For each

nest, we identified the prelaying stage as a week prior to the observed or estimated lay date.

Nest-specific laying stage was identified as the time window between the dates when the first

and the last egg of the clutch was laid. Nest-specific incubation stage was then identified as the

date when the last egg was laid + n days, where n was the mean number of days in the known

incubation duration for each species. We fit a LMM to average daily mean temperature and sum

of daily total precipitation separately with species as a fixed effect and year as a random effect

for each breeding stage.

*Environmental drivers for the reproductive traits.* To identify environmental drivers for the

reproductive traits, we tested a set of both climatic and ecological covariates on each of the traits

for each shorebird species (Table 3-1). We included date of clutch initiation as an ecological covariate for clutch size, egg volume, and incubation duration. For egg volume and incubation duration, we included clutch size as an additional covariate. We fit LMMs to the egg volume and incubation duration, and GLMM to the clutch size with binomial distribution (logit link). See the *Model selection and model averaging* section below for detailed procedures on model selection. We took the sum of the Akaike weights of the top models in which the covariate appeared divided by the sum of all top model weights as an index of the relative importance (RI) of a given covariate (Burnham and Anderson 2002). We considered covariates with the relative importance value greater than 0.8 as important predictor for the response variable.

*Environmental drivers of daily nest survival*. We tested a similar set of covariates on the daily nest survival rates (DSR) separately for each shorebird species (Table 3-1). We used an R package RMark as an interface to program MARK (White and Burnham 1999; Laake 2013). Both daily mean temperature and daily total precipitation were included in models as occasion-specific covariates (Cooch and White 2015). We developed a set of candidate models in which the covariates were allowed to have either additive or interactive effects with study period. See the *Model selection and model averaging* section below for detailed procedures on model selection.

*Model selection and model averaging*. Covariates with variance inflation factors (VIF) greater than 5 were dropped from a model. We standardized explanatory variables using the function *standardize* in package arm (Gelman and Su 2015) and compared all possible sub-models using the function *dredge* in package MuMIn (Barton 2014). Models with ΔAICc < 2 were considered

as candidates for the best fitting model and averaged to estimate coefficients of covariate effects

using the function *model.avg* in package MuMIn.

## Results

### (a) Long-term climate change at Nome

In Chapter 2, we showed that the prelaying stage cooled over time by $-0.2$℃ decade$^{-1}$

whereas the laying stage warmed $+0.2$℃ decade$^{-1}$ (see Chapter 2). Both the incubation and the

hatch stages warmed over time by $+0.2$℃ decade$^{-1}$ ($p < 0.05$; Table 3-2, Figure 3-1a). Despite

the warming trends, however, the daily mean temperature during the two stages did not differ

between the two study periods (Table 3-2). The number of days with rain and daily total

precipitation did not show significant year trends between 1973 and 2014 for any of the breeding

stages (Figure 3-1b). However, the daily total precipitation during the incubation and hatch

stages was greater in the late period than in the early period (Table 3-2). Despite significant long-

term increases in the maximum snow depth between 1973 and 2014 (Figure 3-1c), the average

maximum snow depth did not differ between the early and late periods (Table 3-2).

### (b) Species-specific laying window and weather condition during breeding

A total of 1,335 shorebird nests were monitored during the early (1993-1996) and late study

periods (2010-2014). The timing of clutch initiation of all species was delayed in the late period

and delayed with cooled temperature during laying stage (Chapter 2). However, differences

among species were 2-4 times greater than the effect of study period or mean temperature (Table

3-3; Figure 3-2). The order of breeding among three species remained consistent during nine

years of monitoring, but the amount of overlap in the timing of breeding among three species

varied annually (Figure 3-3). Average daily mean temperature was different among three species at all three breeding stages, and Western Sandpipers bred under cooler temperatures than Semipalmated Sandpipers or Red-necked Phalaropes (Table 3-4; Figure 3-4). The sum of daily total precipitation differed among three species during incubation stage, and Red-necked Phalarope nests were exposed to more rain than the other two species (Table 3-4; Figure 3-4).

## (c) Clutch size and egg volume

The sum of daily total precipitation during laying stages was an important determinant for clutch size of Western Sandpipers and showed a positive correlation with the probability of laying a four-egg clutch (RI = 1; Table 3-5). We did not find any effect of temperature or precipitation on the clutch size of the other two species. The mean egg volume of a clutch responded to different factors by species (Figure 3-5). Similar to results of Chapter 2 where we did not control for environmental factors, the egg volume of Western Sandpipers decreased by 0.3% with a one-day delay in clutch initiation, but did not vary with mean temperature or precipitation (Table 3-6). The egg volume of Semipalmated Sandpipers, on the other hand, increased 0.1% with a 1 mm increase in daily total precipitation during the prelaying stage (Table 3-6). For Red-necked Phalaropes, the egg volume increased by 0.3% per 1℃ increase in the average daily mean temperature during the laying stage (Table 3-6).

## (d) Incubation duration

Environmental covariates did not explain more variation in incubation duration than the effect of study period. However, we still found a varying set of environmental covariates that affected incubation duration of each species. For Western Sandpipers, the incubation duration shortened with greater amount of daily total precipitation during the prelaying stage (Table 3-7;

Figure 3-6). For Semipalmated Sandpipers, the incubation duration did not vary with climatic variables, but was shorter for late clutches and nests with more eggs (Table 3-7). From a single best fit model, the incubation duration of Red-necked Phalaropes was shorter with greater mean temperature during the prelaying stage (−1 day per 4℃ increase) or greater daily total precipitation during the incubation stage (−1 day per 20mm; Figure 3-6). For phalaropes, the incubation duration was also shorter with more eggs in the clutch, or longer for late clutches in a season (Table 3-7).

## (e) Daily nest survival

Different factors affected the daily survival rate of nests of all three species. For Western Sandpipers, the top model included interactive effects of rain×period, and the second best model with interactive effects of temperature×period collectively carried 86% of the model weight (Table 3-8). Study period was therefore the most important factor for Western Sandpiper daily nest survival rate, which was lower in the late period (Table 3-9). Reduced daily nest survival rate of Western Sandpipers during the late period was partly due to the negative relationship with daily precipitation (Figure 3-7), which increased between the two study periods (Chapter 2). For Semipalmated Sandpipers, the daily mean temperature and the additive effects of temperature+period collectively carried 88 % of the model weight (Table 3-8). Daily nest survival rate of Semipalmated Sandpipers showed a positive relationship with daily mean temperature for both periods (Table 3-9; Figure 3-7). For Red-necked Phalaropes, the date of clutch initiation and additive and interactive effects with period collectively carried 79% of the model weight (Table 3-8). Thus, daily nest survival rate of Red-necked Phalarope decreased on average 4.7% per day through a breeding season (Table 3-9).

## Discussion

Temperature during most stages of the breeding season and the amount of snow accumulation have increased for the past four decades at Nome, Alaska. Our observations of long-term climatic conditions matched general climatic trends of the Arctic region (AMAP 2012). First, we found that the three sympatric species of shorebirds initiated their clutch during partially distinct time windows. Second, differences among breeding windows caused each species to lay and incubate eggs under different temperature and precipitation regimes. Third, reproductive components of the three species, including clutch size, egg volume, incubation duration, and daily nest survival, varied with different sets of environmental drivers.

### *Species-defined breeding window and temperature effects*

Three shorebird species nested at Nome during distinctive breeding windows. The range of dates of clutch initiation overlapped among the three species, but the mean date of clutch initiation was 4-10 days earlier for Western Sandpipers then for Semipalmated Sandpiper and Red-necked Phalaropes. Species-dependent breeding timing among sympatric species can arise due to species differences in mating system or migration distance (Myers 1981). A polyandrous mating system coupled with uniparental care may limit phalaropes from laying eggs early in the season, when food resources are limited (Whitfield and Tomcovich 1996).

Red-necked Phalaropes initiated their clutch 10 days later than Western Sandpipers at Nome. As a result, phalaropes experienced on average ~1℃ warmer temperatures during the prelaying and laying stages than the other two species. What is the biological significance of a 1℃ increase in air temperature? In our subarctic system, a 1℃ increase in the average daily mean temperature during the laying stage advanced the clutch initiation by one day for all three species, and

increased the egg volume of Red-necked Phalaropes by 0.3% (see Table 3-3 and 3-6). A 1℃ increase also improved the daily nest survival of Semipalmated Sandpipers by 75% (see Table 3-9). Our results indicate that arctic-breeding shorebirds are sensitive to temperature changes as little as ± 1℃.

Intraspecific variation in the clutch size and egg volume of shorebirds has been rarely attributed to the weather conditions. Extreme cold weather during summer decreased clutch size of Semipalmated Plovers, *Charadrius semipalmatus*, but did not affect egg volume (Nol et al. 1997). The opposite trend was observed for Killdeer, *Charadrius vociferus*, where warmer springs led to smaller clutches across their breeding range (Torti and Dunn 2005). It is not surprising that temperature has relatively little effect on the clutch size or egg volume of shorebirds. It is partly because shorebirds lay an invariant clutch size of four eggs, but also because the energetic costs of heating the eggs are low relative to the costs of staying active in a cold environment (Piersma et al. 2003; Cresswell at al. 2004; Meltofte 2007). However, the benefit of increasing temperature influenced daily nest survival of Semipalmated Sandpipers and similarly has been shown with improved chick survival in Dunlin (McKinnon et al. 2013).

### *Effects of precipitation on breeding performance*

Precipitation co-varies with surface temperature in a complex manner. In coastal environments at high latitudes, more precipitation accompanies warm conditions in winter and cool conditions in summer (Trenberth and Shea 2005). At Nome, during the nest-specific prelaying stages, more precipitation occurred with cooler conditions, whereas more precipitation occurred with warmer conditions during the nest-specific laying and incubation stages (see Figure S3-1 and S3-2).

Our results showed that Western Sandpipers were more likely to lay a 4-egg clutch when the nest-specific laying stage was wetter. Semipalmated Sandpipers laid 1% bigger eggs per every 1 mm increase in the total precipitation during the nest-specific prelaying stage. Thus, both sandpipers invested more in the egg production under wetter conditions. We suggest two potential mechanisms to explain this observation. First, the pattern may result from greater availability of resources that can be invested in eggs. Wet conditions during the early part of the breeding season may advance the emergence or increase abundance of invertebrates later in the season. Major prey items of these shorebirds include an array of dipteran flies and midges, and springtails, most of which have an aquatic origin (Holmes and Pitelka 1968; Holmes 1972; Baker 1977). Early season precipitation and increased cloud cover can greatly advance the timing of snow melt in the Arctic, and in turn, the emergence of invertebrate prey (Zhang et al. 1996). Increased amounts of precipitation and higher soil moisture levels can also improve the survival of soft-bodied, soil-dwelling invertebrates such as Collembola, which are susceptible to desiccation (Dollery et al. 2006). Second, both sandpipers may invest more in their eggs when environmental conditions are unfavorable for chick survival to increase the survival and reproductive gain. Positive correlations between egg size, and the body condition and survival of offspring, have been well documented in birds (Galbraith 1988; reviewed in Williams 1994). Intraspecific variation in egg size is often strongly correlated with female body size or condition (Nol et al. 1997; Hargitai et al. 2005; Lislevand et al. 2005). Therefore, the proximate or adaptive mechanisms we suggest here should be further tested by controlling the effects of female quality on both clutch size and egg size.

In shorebirds, intraspecific variation in incubation duration often covaries with date of clutch initiation (Colwell 2010). We found strong effects of precipitation on incubation duration after controlling for the effect of date of clutch initiation. We observed that Western Sandpipers shortened incubation duration when the prelaying stage was wetter, whereas Red-necked Phalaropes shortened incubation duration when the incubation stage was wetter. Monitoring the incubation behavior of phalaropes at Nome, English (2014) reported that male phalaropes spent less time off the nest when relative humidity at the nest increased. Birds can adjust the rate of embryonic development partly through modifying their incubation behavior (Deeming and Reynolds 2015). Phalarope males likely sped up embryonic development by spending more time sitting on a clutch when it was raining during the incubation stage. On the other hand, a shortened incubation duration of Western Sandpipers was correlated with precipitation during prelaying stage. If early-season precipitation increases food availability later in the season as we suggested, perhaps improved foraging efficiency can reduce the time spent off-nest and shorten the duration of incubation for Western Sandpipers.

Last, we found negative effects of daily total precipitation on daily nest survival rate of Western Sandpipers during the late study period. Probability of a nest to survive the given day was coupled with daily total precipitation for the same day. Thus, our results suggest instantaneous negative effects of rain on nest survival. We proposed that early-season precipitation may forecast higher prey abundance later in the season. However, precipitation during incubation can greatly reduce the amount of arthropod activity and consequently decrease the foraging efficiency of shorebirds (Tulp and Schekkerman 2001, 2008). Coupled with reduced

foraging efficiency, potential negative impacts of rain on the thermoregulation of incubating parent may explain the decreased daily nest survival rate of Western Sandpipers.

### *Breeding under future climate*

In this study, we tested the effects of temperature and precipitation on the reproductive performance of three species of arctic-breeding shorebirds. An organism's immediate response to a short-term weather pattern is not necessarily the same as a response to long-term climatic trend. Thus, the effects of weather and climate should be tested simultaneously to parse out the relative importance of short-term versus long-term drivers for the observed changes in biological systems (Knape and Valpine 2011). However, simultaneous testing of weather and climatic variables requires long-term ecological monitoring. When such data are lacking, known correlations between weather variables and reproductive parameters can be useful as seed data to model the potential response of organisms to predicted future climate change (Rehfisch et al. 2004; Skagen and Adams 2012). After all, study of climate response must start from an understanding of how organisms respond to the surrounding weather.

The determinate clutch size of four eggs will likely remain invariant for the projected warm and wet summer. The egg volume of both Semipalmated Sandpiper and Red-necked Phalarope increased with wetter prelaying stage and warmer laying stage, respectively. Based on climatic scenarios for the region as well as local trends, egg volume of Semipalmated Sandpiper and Red-necked Phalarope will likely increase in the future with increasing temperature and rain until the energetic cost of producing an egg becomes greater than the adaptive benefits of a larger egg. Since larger egg volume is associated with greater hatching success and chick survival (Galbraith 1988; reviewed in Williams 1994), therefore, we expect that continuing climate change could

improve reproductive success of these two species. Reproductive success of Semipalmated Sandpipers may be further improved by higher nest survival with the warming trend in the Arctic summer.

## *Conclusion*

We showed that seasonal trends in the Arctic environment present different temperature-precipitation regimes to three sympatric shorebirds that initiate their clutches at slightly different times in the season. Our study provides evidence for relationships among weather conditions and various aspects of reproductive output originally considered relatively fixed for Arctic-breeding shorebirds. Our findings suggest that nesting success may be improved for two out of three study species as climate change continues. Future studies should focus on how the weather-dependent variation in the reproductive traits we observed in this study affects hatching success as well as post-hatch offspring survival until independence.

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Table 3-1. Environmental and ecological factors modeled for potential effects on the reproductive traits of shorebirds. '+' indicates a set of covariates tested for the response variable. As climatic variables, daily mean temperature (Temp) and daily total precipitation (Rain) were extracted for three breeding stages (prelay: prelaying, lay: laying, inc: incubation) either predefined for the population (Pop.) or for each nest (Nest).

| Type | Covariate | Date of clutch initiation | Clutch size | Egg volume | Incubation duration | Daily nest survival[1] |
|---|---|---|---|---|---|---|
| Random | Year | + | + | + | + | |
| Grouping | Period | + | + | + | + | Period |
| | Species | + | | | | |
| Climatic | $Temp_{prelay}$ | Pop. | Nest | Nest | Nest | Daily mean temperature |
| | $Temp_{lay}$ | Pop. | Nest | Nest | Nest | Daily total precipitation |
| | $Temp_{inc}$ | | | | Nest | |
| | $Rain_{prelay}$ | Pop. | Nest | Nest | Nest | |
| | $Rain_{lay}$ | Pop. | Nest | Nest | Nest | |
| | $Rain_{inc}$ | | | | Nest | |
| | Snow | + | | + | + | |
| Ecological | Lay date | | + | + | + | Lay date |
| | Clutch size | | | + | + | Nest age |
| | Egg volume | | | | + | Time trend |

[1] Daily nest survival rate (DSR) was examined using RMark as an interface to Progam Mark, hence we tested only the fixed effects.

Table 3-2. Long-term trends (1973-2014) and differences between periods in daily weather variables at Nome, Alaska. The early period included 1993-1996 and the late period included 2010-2014. Daily mean temperature and daily total precipitation were examined for four breeding stages, prelaying: Apr 29-May 12, laying: May 13-Jun 27, incubation: May 17-Jul 23, hatch: Jun 5-Jul 20. The maximum depth of snow recorded during the previous winter was extracted for each year. Slope for 42-year trend is reported per decade. Significance level (sig) as ns: p > 0.05, *: p ≤ 0.05, **: p ≤ 0.01, *** P ≤ 0.001

| Climatic variables | | 42-year trend | | Early period | | Late period | | Period diff. | Sig |
|---|---|---|---|---|---|---|---|---|---|
| | | slope | sig | mean ± sd | n | mean ± sd | n | | |
| Mean temperature (°C) | Prelaying | −0.2 | ns | 1.64 ± 3.94 | 56 | −2.40 ± 3.26 | 70 | −4.03 | ** |
| | Laying | +0.2 | ** | 7.65 ± 3.74 | 184 | 6.90 ± 4.97 | 230 | −0.77 | ns |
| | Incubation | +0.2 | ** | 8.91 ± 4.11 | 268 | 8.57 ± 4.25 | 335 | −0.34 | ns |
| | Hatch | +0.2 | *** | 9.52 ± 3.99 | 184 | 9.74 ± 3.73 | 230 | +0.22 | ns |
| Total precipitation (mm) | Prelaying | −0.02 | ns | 0.70 ± 1.70 | 55 | 0.39 ± 0.79 | 60 | −0.31 | ns |
| | Laying | −0.04 | ns | 0.58 ± 2.05 | 183 | 1.05 ± 2.97 | 196 | +0.49 | ns |
| | Incubation | +0.05 | ns | 0.68 ± 2.11 | 267 | 1.64 ± 3.46 | 303 | +0.96 | * |
| | Hatch | +0.05 | ns | 0.69 ± 1.71 | 183 | 1.85 ± 3.49 | 208 | +1.16 | ** |
| Maximum Snow depth (mm) | | +2.7 | ** | 881.4 ± 452.6 | 4 | 766.1 ± 277.6 | 5 | −115.3 | ns |

Table 3-3. Effect sizes of explanatory variables on date of clutch initiation from the final averaged model. Top model sets are given in Table S3-1. RI = relative importance. Early period was the baseline for the study period; Red-necked Phalarope was the baseline for the three species, Semipalmated Sandpiper (sesa) and Western Sandpiper (wesa). Covariates were standardized by centering and dividing by 2 SD's.

|  | RI | Estimate | SE |
| --- | --- | --- | --- |
| Intercept | N/A | 156.95 | 0.36 |
| Period | 1.00 | 2.46 | 0.72 |
| Species: sesa | 1.00 | −5.68 | 0.45 |
| Species: wesa | 1.00 | −10.42 | 0.49 |
| $Temp_{lay}$ | 1.00 | −2.75 | 0.76 |
| $Rain_{lay}$ | 0.83 | 1.38 | 0.70 |
| $Temp_{prelay}$ | 0.35 | −1.07 | 0.78 |
| $Rain_{prelay}$ | 0.18 | 0.42 | 0.42 |
| Snow | 0.17 | −0.42 | 0.46 |

Table 3-4. Effect sizes of species on daily mean temperature and sum of daily total precipitation during three breeding stages at each shorebird nest. Red-necked Phalarope was the baseline for the three species, Semipalmated Sandpiper (sesa) and Western Sandpiper (wesa). Random effect: year. Degree of freedom was 1,323 and was constant for all analyses.

| | Daily mean temperature | | | | Total precipitation | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | SE | t | p≤ | Estimate | SE | t | p≤ |
| **Prelaying stage** | | | | | | | | |
| Intercept | 7.55 | 0.47 | 16.188 | 0.001 | 5.92 | 1.37 | 4.333 | 0.001 |
| Species:sesa | −0.75 | 0.13 | −5.979 | 0.001 | −0.47 | 0.49 | −0.962 | 0.336 |
| Species:wesa | −1.25 | 0.12 | −10.134 | 0.001 | −1.39 | 0.48 | −2.884 | 0.004 |
| **Laying stage** | | | | | | | | |
| Intercept | 8.27 | 0.60 | 13.883 | 0.001 | 3.14 | 1.12 | 2.796 | 0.005 |
| Species:sesa | −0.95 | 0.22 | −4.225 | 0.001 | 0.13 | 0.38 | 0.337 | 0.736 |
| Species:wesa | −1.14 | 0.22 | −5.208 | 0.001 | −0.52 | 0.37 | −1.412 | 0.158 |
| **Incubation stage** | | | | | | | | |
| Intercept | 8.93 | 0.56 | 15.901 | 0.001 | 23.53 | 4.75 | 4.956 | 0.001 |
| Species:sesa | −0.51 | 0.07 | −7.616 | 0.001 | −8.03 | 0.66 | −12.095 | 0.001 |
| Species:wesa | −0.90 | 0.07 | −13.760 | 0.001 | −6.82 | 0.65 | −10.518 | 0.001 |

Table 3-5. Effect sizes of covariates on clutch size from the final averaged model. Top model sets are given in Table S3-2. RI = relative importance. Early period was the baseline for the study period. '-' indicates a covariate tested but not present in the final model. Important covariates (RI > 0.80) are in bold. Covariates were standardized by centering and dividing by 2 SD's.

| | Western Sandpiper | | | Semipalmated Sandpiper | | | Red-necked Phalarope | | |
|---|---|---|---|---|---|---|---|---|---|
| | RI | Est. | SE | RI | Est. | SE | RI | Est. | SE |
| Intercept | N/A | 2.20 | 0.21 | N/A | −0.20 | 0.05 | N/A | −0.23 | 0.06 |
| $Temp_{prelay}$ | 0.12 | −0.08 | 0.35 | 0.12 | 0.03 | 0.11 | 0.14 | 0.08 | 0.12 |
| $Temp_{lay}$ | 0.69 | 0.49 | 0.28 | 0.12 | 0.04 | 0.11 | 0.12 | 0.04 | 0.12 |
| $Rain_{prelay}$ | - | - | - | 0.13 | 0.05 | 0.10 | 0.16 | −0.10 | 0.13 |
| $Rain_{lay}$ | **1.00** | **1.42** | **0.64** | 0.19 | 0.10 | 0.10 | - | - | - |
| Date of clutch initiation | **1.00** | **−2.01** | **0.27** | **1.00** | **−0.35** | **0.11** | 0.12 | −0.03 | 0.12 |
| Period | 0.37 | −0.42 | 0.34 | 0.13 | 0.05 | 0.10 | 0.15 | −0.12 | 0.16 |

Table 3-6. Effect sizes of covariates on egg volume from the final averaged model. Top model sets are given in Table S3-3. RI = relative importance. Early period was the baseline for the study period. Important covariates (RI > 0.80) are in bold. Covariates were standardized by centering and dividing by 2 SD's.

| | Western Sandpiper | | | Semipalmated Sandpiper | | | Red-necked Phalarope | | |
|---|---|---|---|---|---|---|---|---|---|
| | RI | Est. | SE | RI | Est. | SE | RI | Est. | SE |
| Intercept | N/A | 7.12 | 0.03 | N/A | 6.34 | 0.03 | N/A | 5.86 | 0.04 |
| $Temp_{prelay}$ | 0.14 | 0.08 | 0.06 | 0.69 | 0.08 | 0.05 | 0.11 | 0.06 | 0.05 |
| $Temp_{lay}$ | 0.61 | 0.09 | 0.05 | 0.16 | 0.04 | 0.04 | **0.95** | **0.13** | **0.05** |
| $Rain_{prelay}$ | 0.05 | −0.03 | 0.05 | **0.94** | **0.09** | **0.05** | 0.11 | −0.05 | 0.06 |
| $Rain_{lay}$ | 0.19 | −0.05 | 0.05 | 0.34 | 0.05 | 0.04 | 0.16 | 0.05 | 0.05 |
| Snow | 0.19 | 0.07 | 0.06 | 0.16 | 0.05 | 0.06 | 0.10 | 0.05 | 0.06 |
| Date of clutch initiation | **1.00** | **−0.24** | **0.05** | 0.05 | −0.01 | 0.04 | 0.53 | 0.08 | 0.05 |
| Period | 0.12 | −0.06 | 0.07 | 0.10 | 0.04 | 0.06 | 0.26 | −0.10 | 0.07 |
| Clutch size | 0.13 | 0.05 | 0.05 | 0.10 | 0.03 | 0.04 | 0.12 | 0.04 | 0.05 |

Table 3-7. Effect sizes of covariates on incubation duration from the final averaged model. Top model sets are given in Table S3-4. RI = relative importance. Early period was the baseline for the study period. Blank indicates a covariate not tested; '-' indicates a covariate tested but not present in the final model. Important covariates (RI > 0.80) are in bold. Top model set included a single model for Red-necked Phalarope. Covariates were standardized by centering and dividing by 2 SD's.

| | Western Sandpiper | | | Semipalmated Sandpiper | | | Red-necked Phalarope | | |
|---|---|---|---|---|---|---|---|---|---|
| | RI | Est. | SE | RI | Est. | SE | RI | Est. | SE |
| Intercept | N/A | 21.20 | 0.11 | N/A | 20.67 | 0.17 | N/A | 21.05 | 0.14 |
| $Temp_{prelay}$ | 0.07 | −0.24 | 0.23 | - | - | - | **1.00** | **−1.58** | **0.39** |
| $Temp_{lay}$ | - | - | - | - | - | - | - | - | - |
| $Temp_{inc}$ | 0.13 | −0.25 | 0.26 | 0.29 | 0.51 | 0.39 | | | |
| $Rain_{prelay}$ | **0.94** | **−0.64** | **0.29** | - | - | - | - | - | - |
| $Rain_{lay}$ | - | - | - | - | - | - | - | - | - |
| $Rain_{inc}$ | 0.20 | −0.30 | 0.23 | - | - | - | **1.00** | **−2.40** | **0.45** |
| Snow | 0.57 | 0.51 | 0.30 | | | | | | |
| Date of clutch initiation | 0.19 | −0.30 | 0.23 | **1.00** | **−1.39** | **0.41** | **1.00** | **2.09** | **0.38** |
| Period | **1.00** | **−2.12** | **0.30** | **1.00** | **−1.60** | **0.41** | **1.00** | **2.50** | **0.41** |
| Clutch size | 0.06 | 0.21 | 0.22 | **1.00** | **−1.65** | **0.54** | **1.00** | **−1.77** | **0.43** |
| Egg volume | - | - | - | - | - | - | - | - | - |

Table 3-8. Top model sets for the daily nest survival rates of three shorebird species. Full model set is given in Table S3-5. Lay date is the date of clutch initiation for each nest.

| model | K | Deviance | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|---|
| Western Sandpiper | | | | | |
| rain × period | 4 | 1208.11 | 1216.12 | 0.00 | 0.521 |
| temp × period | 4 | 1208.99 | 1217.00 | 0.88 | 0.336 |
| Semipalmated Sandpiper | | | | | |
| temp | 2 | 968.48 | 972.48 | 0.00 | 0.570 |
| temp + period | 3 | 967.68 | 973.69 | 1.21 | 0.312 |
| Red-necked Phalarope | | | | | |
| lay date | 2 | 528.11 | 532.12 | 0.00 | 0.345 |
| lay date + period | 3 | 526.25 | 532.26 | 0.14 | 0.321 |
| lay date × period | 4 | 525.95 | 533.97 | 1.85 | 0.137 |

Table 3-9. Effect sizes of covariates on the daily nest survival rate from the final averaged model. RI = relative importance. Early period was the baseline for the study period. Important covariates (RI > 0.80) are in bold. Covariates were standardized by centering and dividing by 2 SD's.

|  | RI | Estimate | SE |
|---|---|---|---|
| Western Sandpiper | | | |
| Intercept | N/A | 4.91 | 1.48 |
| Rain | 0.61 | 14.08 | 7.28 |
| **Period** | **1.00** | **−1.57** | **1.51** |
| Period × rain | 0.61 | −14.36 | 7.29 |
| Temperature | 0.39 | 0.05 | 0.29 |
| Temperature × period | 0.39 | 0.81 | 0.37 |
| Semipalmated Sandpiper | | | |
| Intercept | N/A | 3.34 | 0.11 |
| **Temperature** | **1.00** | **1.01** | **0.20** |
| Period | 0.35 | 0.15 | 0.17 |
| Red-necked Phalarope | | | |
| Intercept | N/A | 2.92 | 0.22 |
| **Lay date** | **1.00** | **−0.61** | **0.27** |
| Period | 0.57 | −0.32 | 0.25 |
| Lay date × period | 0.17 | −0.27 | 0.49 |
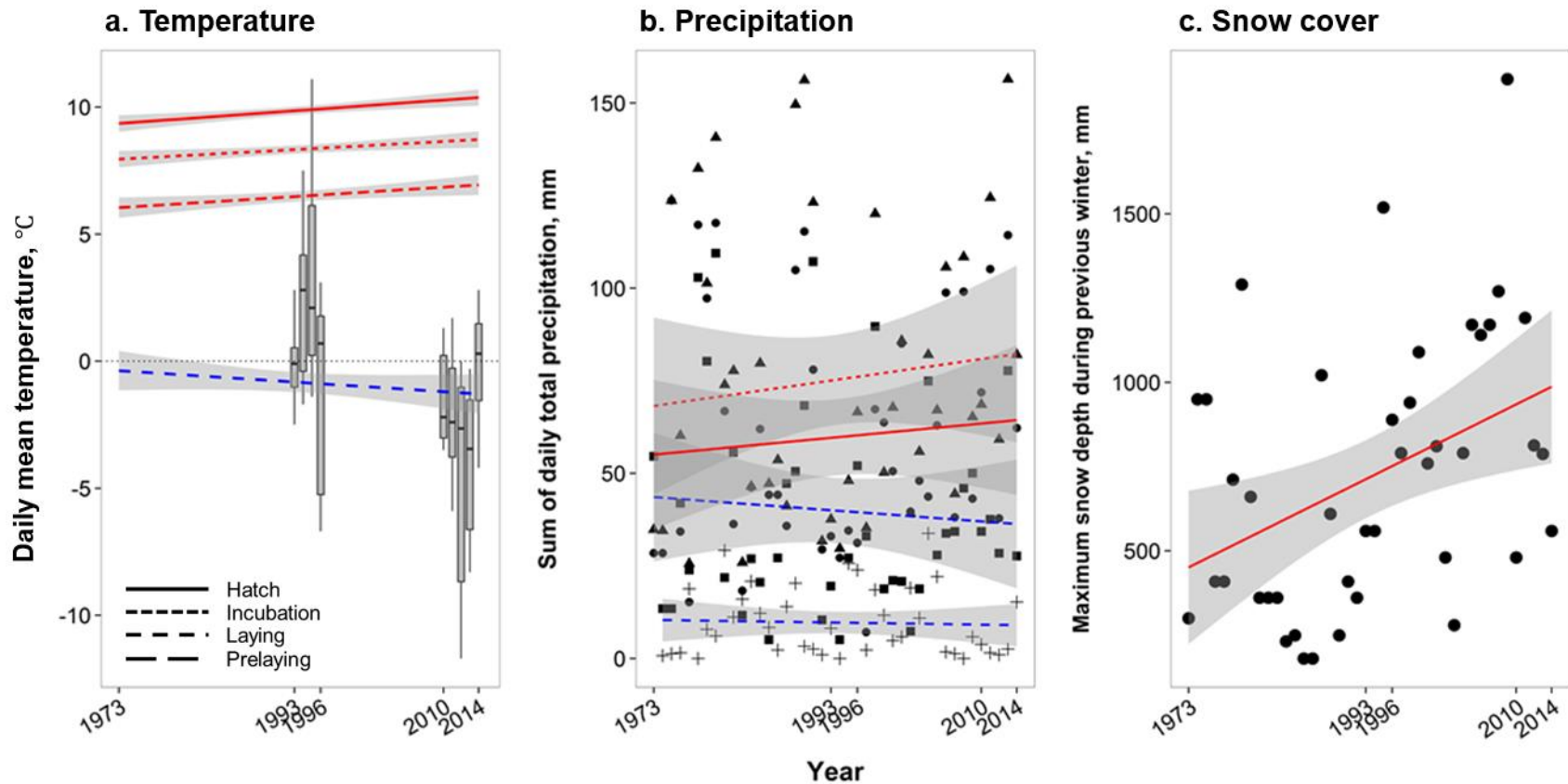
Figure 3-1. Long-term climatic trends in Nome, Alaska between 1973 and 2014. a: Linear trends of the daily mean temperature for four breeding stages. Prelaying stage is cooling but other three stages are warming. Box plots indicate the distribution of daily mean temperature for prelaying stage of each year during study period (1993-1996 and 2010-2014). b: Linear trends of the sum of daily total precipitation for four breeding stages. Amount of precipitation is increasing in the incubation and hatch stages. c: Linear trend of maximum snow depth during previous winter ($r^2 = 0.140$, n = 42 years, p = 0.008). Increasing trends are shown in red, and decreasing trends are shown in blue.

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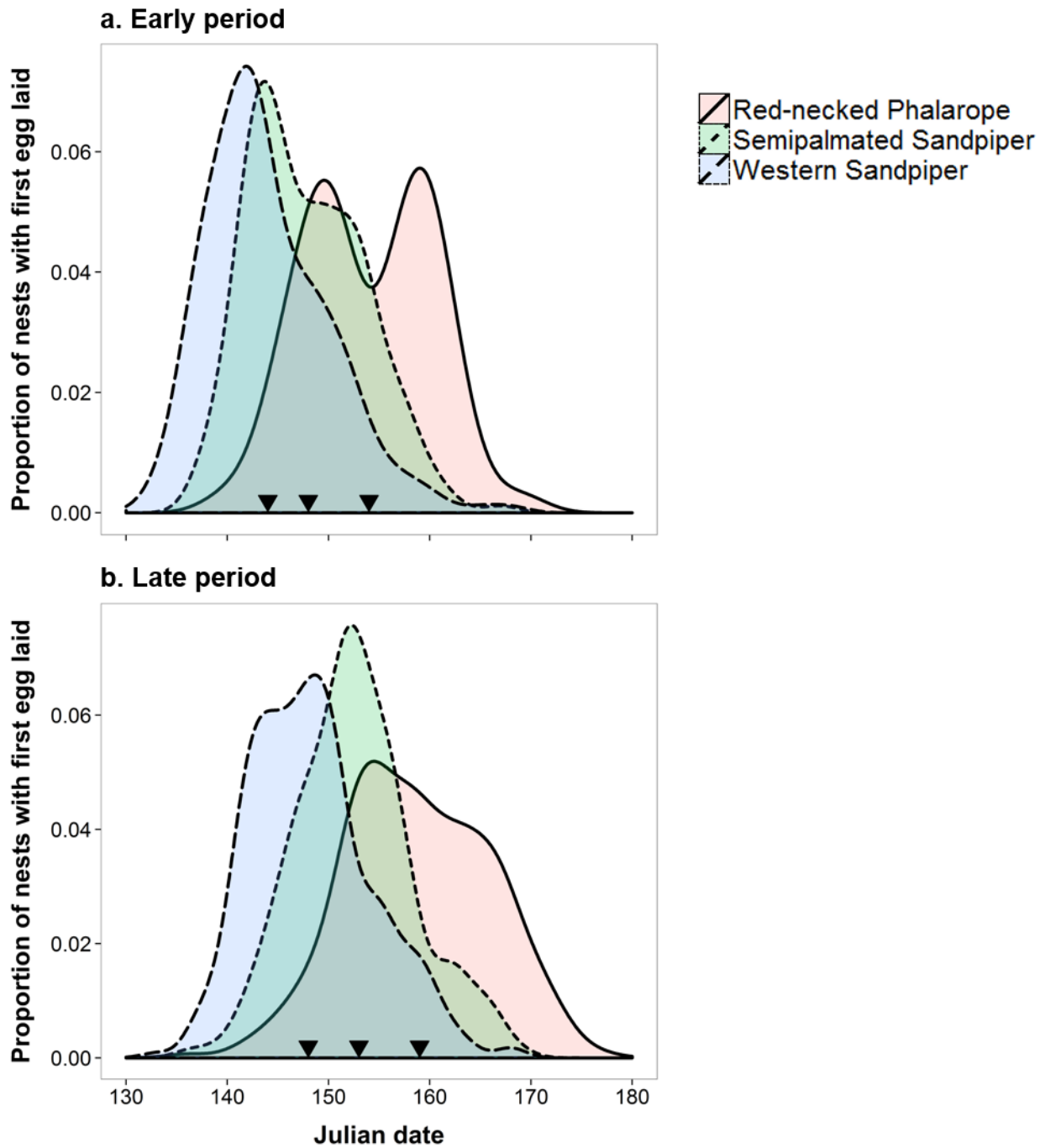
Figure 3-2. Distribution of the date of clutch initiation of three shorebird species by study periods. Early period: 1993-1996, late period: 2010-2014. Julian date of 130 is May 10 for non-leap years. Points indicate mean date of clutch initiation for each species.

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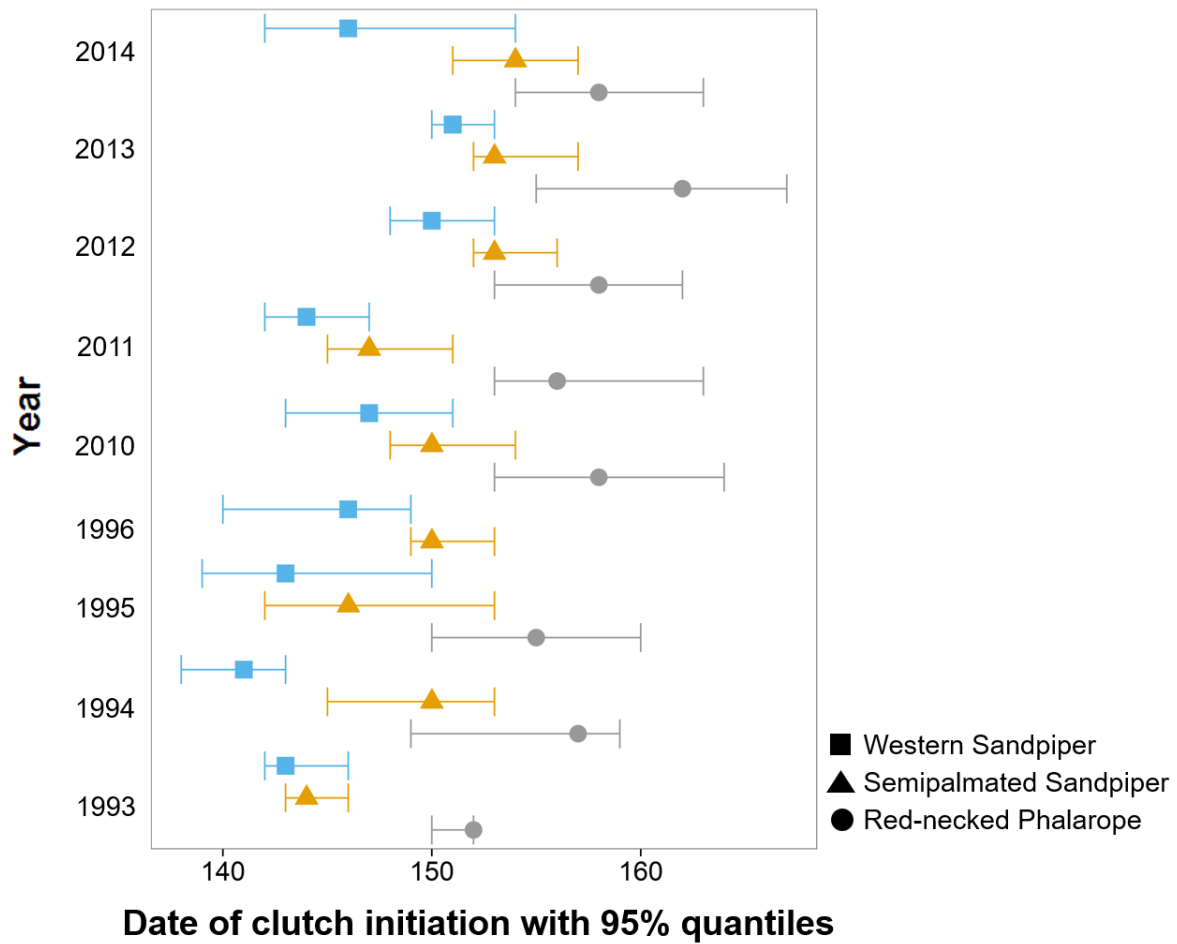
Figure 3-3. Species-defined distributions of clutch initiation dates with 95% quantiles. Julian date of 140 is May 20 for non-leap years.
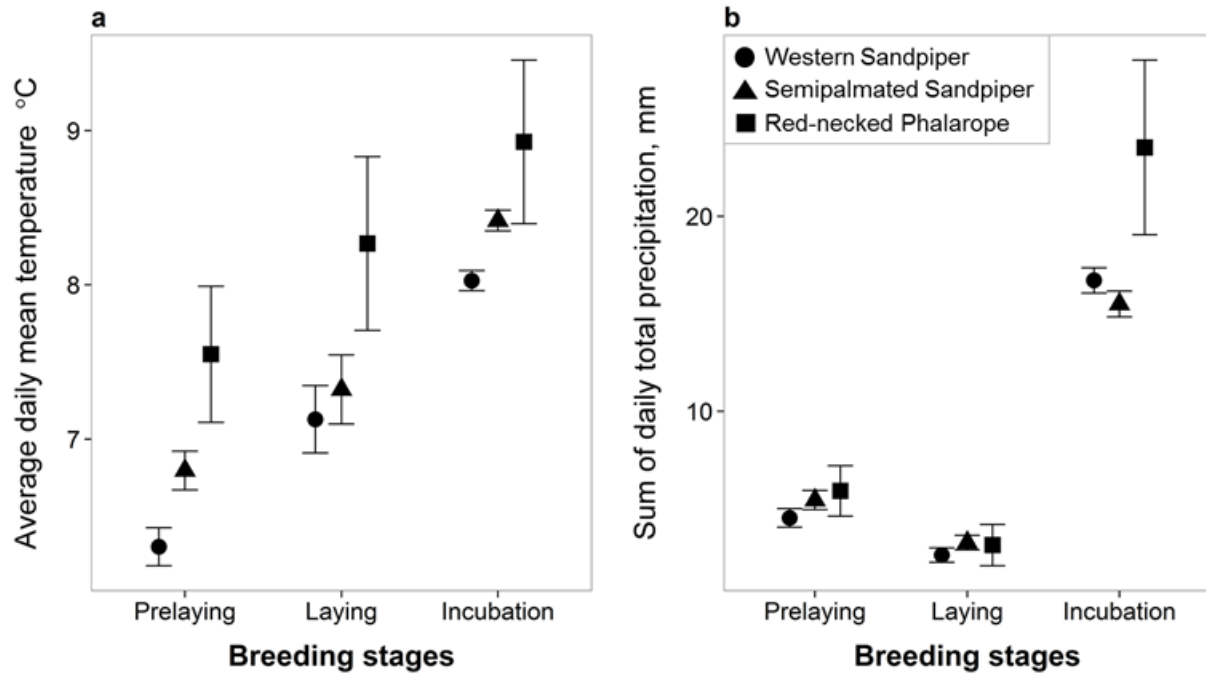
Figure 3-4. Stage-defined weather conditions at individual nests for three sympatric species of shorebirds breeding at Nome, Alaska during 1993-1996 and 2010-2014.
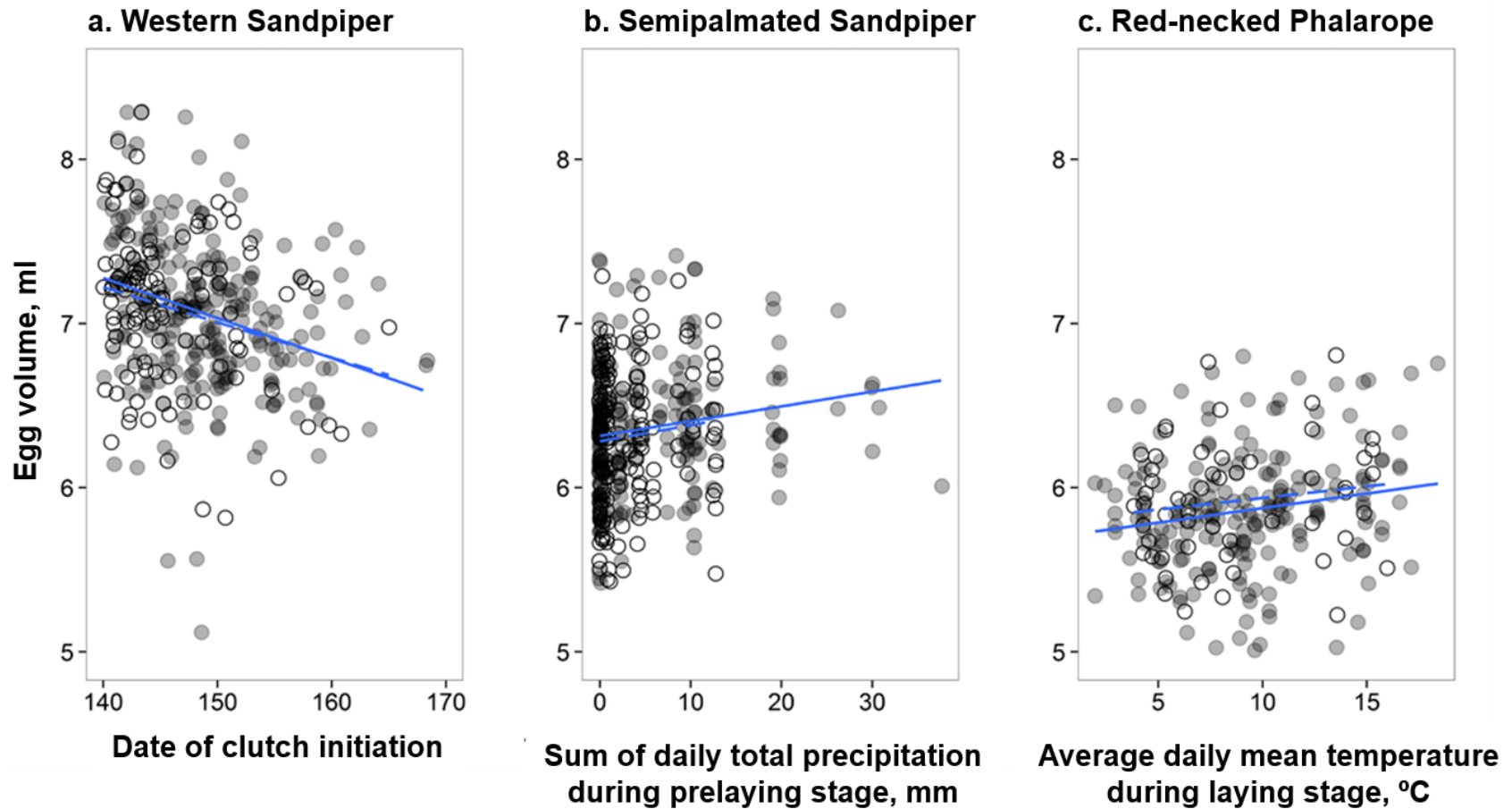
Figure 3-5. Mean egg volume per clutch and its relation to ecological and environmental covariates. Early period: blank circle and dashed line; late period: filled circle and solid line. Points are jittered for 40% resolution for clarity. Julian date of 140 is May 20 for non-leap years.
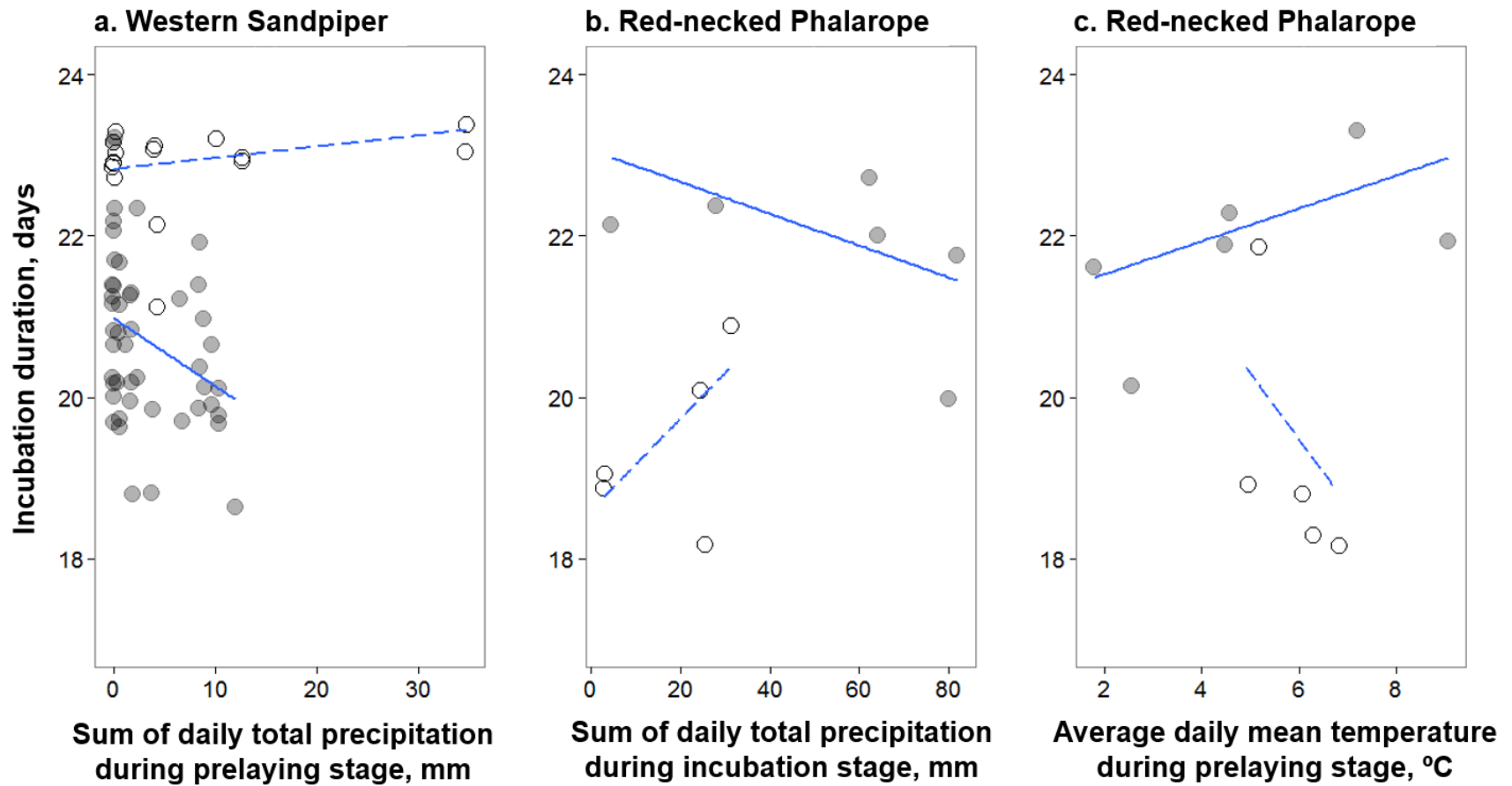
Figure 3-6. Incubation duration of shorebirds and its relation to environmental covariates. Early period: blank circle and dashed line; late period: filled circle and solid line. Points are jittered for 40% resolution for clarity.
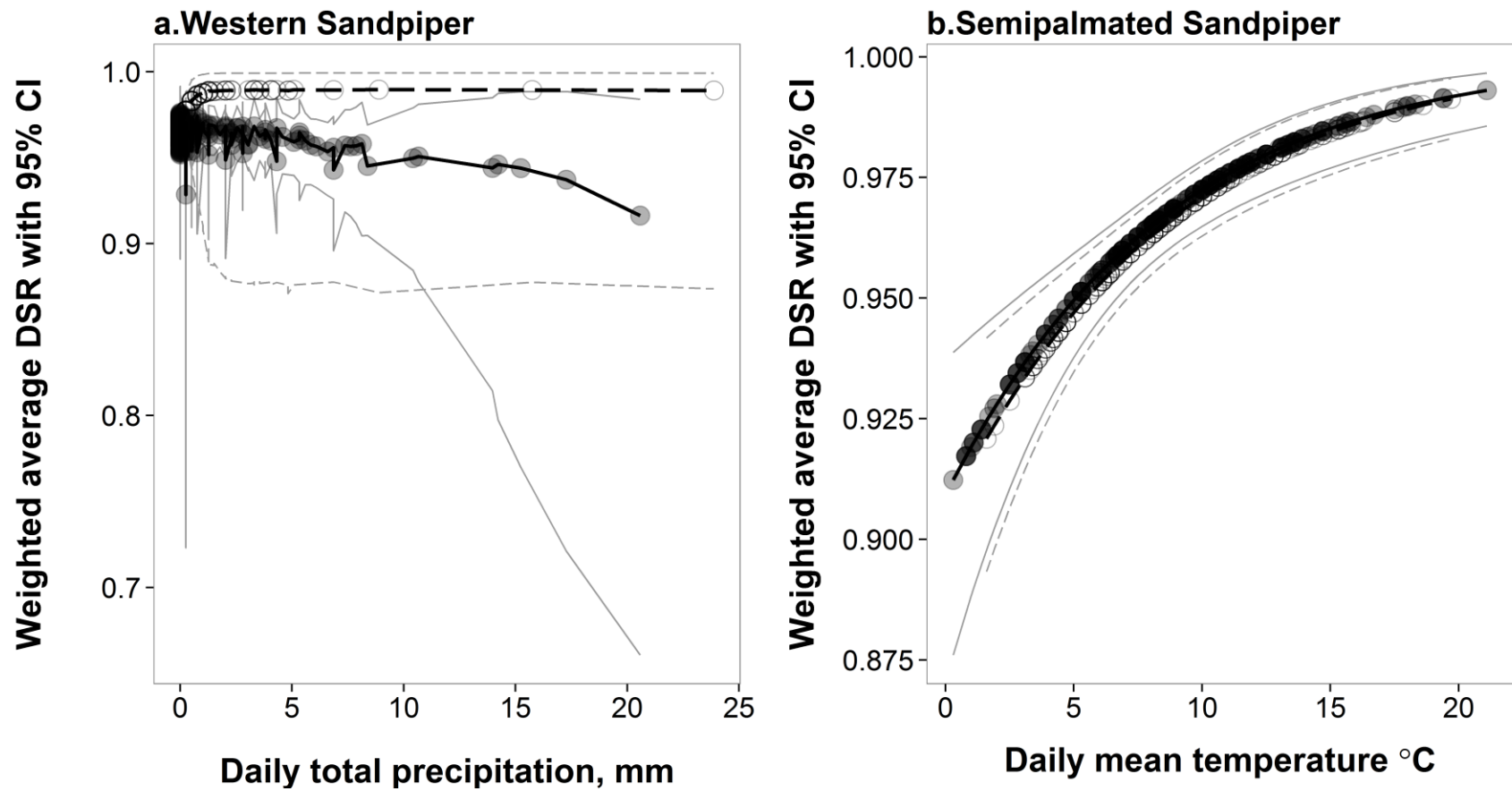
Figure 3-7. Averaged daily nest survival estimates of two sandpiper species from the top model set. Early period: blank circle and dashed line; late period: filled circle and solid line. Estimates are accompanied with 95% confidence interval.

Supplementary Table 3-1. Top model set for the effects of ecological and environmental covariates on the date of clutch initiation at Nome, Alaska during 1993-1996 and 2010-2014. Variables marked 'V' are included in the given model.

| Model terms | | | | | | | Model rank | K | Deviance | AICc | ΔAIC | $w_i$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $Temp_{prelay}$ | $Temp_{lay}$ | $Rain_{prelay}$ | $Rain_{lay}$ | Snow | Period | Species | | | | | | |
| | V | | V | | V | V | 1 | 8 | 8545.94 | 8562.05 | 0.00 | 0.30 |
| V | V | | V | | V | V | 2 | 9 | 8544.96 | 8563.09 | 1.04 | 0.18 |
| | V | V | V | | V | V | 3 | 9 | 8544.96 | 8563.10 | 1.04 | 0.18 |
| V | V | | | | V | V | 4 | 8 | 8547.14 | 8563.25 | 1.19 | 0.17 |
| | V | | V | V | V | V | 5 | 9 | 8545.14 | 8563.27 | 1.21 | 0.17 |

Supplementary Table 3-2. Top model set for the effects of ecological and environmental covariates on clutch size at Nome, Alaska during 1993-1996 and 2010-2014. Models were selected for each shorebird species separately. Variables marked 'V' are included in the given model.

| Temp$_{prelay}$ | Temp$_{lay}$ | Rain$_{prelay}$ | Rain$_{lay}$ | Period | Lay date | Model rank | K | Deviance | AICc | ΔAIC | w$_i$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Western Sandpiper** | | | | | | | | | | | |
|  | V |  | V |  | V | 1 | 5 | 369.46 | 379.57 | 0.00 | 0.33 |
|  | V |  | V | V | V | 2 | 6 | 368.02 | 380.19 | 0.62 | 0.24 |
|  |  |  | V |  | V | 3 | 4 | 372.64 | 380.73 | 1.16 | 0.18 |
|  |  |  | V | V | V | 4 | 5 | 371.32 | 381.43 | 1.86 | 0.13 |
| V | V |  | V |  | V | 5 | 6 | 369.40 | 381.56 | 1.99 | 0.12 |
| **Semipalmated Sandpiper** | | | | | | | | | | | |
|  |  |  |  |  | V | 1 | 3 | 877.80 | 883.86 | 0.00 | 0.32 |
|  |  | V |  |  | V | 2 | 4 | 876.84 | 884.93 | 1.07 | 0.19 |
|  |  |  | V |  | V | 3 | 4 | 877.58 | 885.67 | 1.81 | 0.13 |
|  |  |  |  | V | V | 4 | 4 | 877.60 | 885.69 | 1.83 | 0.13 |
|  | V |  |  |  | V | 5 | 4 | 877.64 | 885.74 | 1.88 | 0.12 |
| V |  |  |  |  | V | 6 | 4 | 877.70 | 885.80 | 1.94 | 0.12 |
| **Red-necked Phalarope** | | | | | | | | | | | |
| (null model) | | | | | | 1 | 2 | 677.90 | 681.94 | 0.00 | 0.31 |
|  | V |  |  |  |  | 2 | 3 | 677.22 | 683.29 | 1.35 | 0.16 |
|  |  |  | V |  |  | 3 | 3 | 677.34 | 683.42 | 1.48 | 0.15 |
| V |  |  |  |  |  | 4 | 3 | 677.48 | 683.55 | 1.61 | 0.14 |
|  |  | V |  |  |  | 5 | 3 | 677.78 | 683.84 | 1.90 | 0.12 |
|  |  |  |  |  | V | 6 | 3 | 677.84 | 683.91 | 1.97 | 0.12 |

Supplementary Table 3-3. Top model set for the effects of ecological and environmental covariates on egg volume at Nome, Alaska during 1993-1996 and 2010-2014. Models were selected for each shorebird species separately. Variables marked 'V' are included in the given model.

| Model terms | | | | | | | | Model Rank | K | Deviance | AICc | ΔAIC | $w_i$ |
| $Temp_{prelay}$ | $Temp_{lay}$ | $Rain_{prelay}$ | $Rain_{lay}$ | Snow | Period | Lay date | Clutch | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Western Sandpiper** | | | | | | | | | | | | | |
| | V | | | | | V | | 1 | 5 | 568.96 | 579.11 | 0 | 0.13 |
| | | | | | | V | | 2 | 4 | 571.68 | 579.78 | 0.67 | 0.09 |
| | V | | V | | | V | | 3 | 6 | 567.84 | 580.05 | 0.94 | 0.08 |
| | V | V | | | | V | | 4 | 6 | 568.02 | 580.22 | 1.12 | 0.08 |
| V | V | | | | | V | | 5 | 6 | 568.12 | 580.33 | 1.22 | 0.07 |
| | V | | | | V | V | | 6 | 6 | 568.12 | 580.33 | 1.22 | 0.07 |
| | V | | | | | V | V | 7 | 6 | 568.14 | 580.34 | 1.24 | 0.07 |
| V | | | | | | V | | 8 | 5 | 570.22 | 580.37 | 1.27 | 0.07 |
| | | V | | | | V | | 9 | 5 | 570.32 | 580.45 | 1.35 | 0.07 |
| | | | | | | V | V | 10 | 5 | 570.62 | 580.76 | 1.66 | 0.06 |
| | | | V | | | V | | 11 | 5 | 570.72 | 580.86 | 1.76 | 0.05 |
| V | V | | | | | V | | 12 | 6 | 568.68 | 580.88 | 1.78 | 0.05 |
| | | | | | V | V | | 13 | 5 | 570.82 | 580.96 | 1.86 | 0.05 |
| | V | V | V | | | V | | 14 | 7 | 566.74 | 581.02 | 1.91 | 0.05 |

Supplementary Table 3-3. Continued.

| | | Model terms | | | | | | Model rank | K | Deviance | AICc | ΔAIC | $w_i$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $Temp_{prelay}$ | $Temp_{lay}$ | $Rain_{prelay}$ | $Rain_{lay}$ | Snow | Period | Lay date | Clutch | | | | | | |
| Semipalmated Sandpiper | | | | | | | | | | | | | |
| V | | V | | | | | | 1 | 5 | 365.20 | 375.36 | 0.00 | 0.12 |
| V | | V | V | | | | | 2 | 6 | 363.46 | 375.68 | 0.32 | 0.10 |
| | | V | | | | | | 3 | 4 | 367.76 | 375.86 | 0.50 | 0.09 |
| | | | | | | | | 4 | 3 | 370.66 | 376.73 | 1.37 | 0.06 |
| V | | V | | V | | | | 5 | 6 | 364.56 | 376.79 | 1.43 | 0.06 |
| V | | V | | | | | V | 6 | 6 | 364.62 | 376.83 | 1.48 | 0.06 |
| V | V | V | | | | | | 7 | 6 | 364.64 | 376.85 | 1.50 | 0.06 |
| V | | V | | | V | | | 8 | 6 | 364.64 | 376.86 | 1.50 | 0.06 |
| | V | V | | | | | | 9 | 5 | 366.76 | 376.92 | 1.57 | 0.06 |
| | | V | V | | | | | 10 | 5 | 366.92 | 377.08 | 1.72 | 0.05 |
| | | V | | V | | | | 11 | 5 | 367.02 | 377.18 | 1.82 | 0.05 |
| V | | V | V | | V | | | 12 | 7 | 362.94 | 377.24 | 1.88 | 0.05 |
| V | | V | V | V | | | | 13 | 7 | 362.96 | 377.25 | 1.89 | 0.05 |
| V | | V | V | | | | V | 14 | 7 | 363.00 | 377.30 | 1.94 | 0.05 |
| V | V | V | V | | | | | 15 | 7 | 363.04 | 377.34 | 1.98 | 0.05 |
| V | | V | | | | V | | 16 | 6 | 365.12 | 377.34 | 1.99 | 0.05 |

| Model terms | | | | | | | | Model rank | K | Deviance | AICc | ΔAIC | $w_i$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $\text{Temp}_{prelay}$ | $\text{Temp}_{lay}$ | $\text{Rain}_{prelay}$ | $\text{Rain}_{lay}$ | Snow | Period | Lay date | Clutch | | | | | | |
| Red-necked Phalarope | | | | | | | | | | | | | |
| | V | | | | | V | | 1 | 5 | 229.88 | 240.11 | 0.00 | 0.12 |
| | V | | | | | | | 2 | 4 | 232.50 | 240.65 | 0.54 | 0.09 |
| | V | | | | V | V | | 3 | 6 | 228.52 | 240.85 | 0.74 | 0.08 |
| | V | | | | V | | | 4 | 5 | 230.92 | 241.16 | 1.05 | 0.07 |
| | V | | | | | V | V | 5 | 6 | 228.96 | 241.29 | 1.18 | 0.07 |
| | V | | V | | | V | | 6 | 6 | 229.02 | 241.34 | 1.23 | 0.06 |
| | V | V | | | | | | 7 | 5 | 231.20 | 241.42 | 1.31 | 0.06 |
| V | V | | | | | | | 8 | 5 | 231.30 | 241.54 | 1.43 | 0.06 |
| | V | | V | | V | V | | 9 | 7 | 227.16 | 241.61 | 1.50 | 0.06 |
| | V | | | V | | V | | 10 | 6 | 229.44 | 241.77 | 1.66 | 0.05 |
| V | V | | | | V | | | 11 | 6 | 229.46 | 241.79 | 1.68 | 0.05 |
| | V | | | | | | V | 12 | 5 | 231.60 | 241.82 | 1.72 | 0.05 |
| | V | V | | | | V | | 13 | 6 | 229.50 | 241.83 | 1.72 | 0.05 |
| | | | | | | V | | 14 | 4 | 233.84 | 242.00 | 1.89 | 0.05 |
| | | V | | V | | | | 15 | 5 | 231.82 | 242.06 | 1.95 | 0.04 |
| | | V | V | | | | | 16 | 5 | 231.84 | 242.07 | 1.96 | 0.04 |

Supplementary Table 3-4. Top model set for the effects of ecological and environmental covariates on incubation duration at Nome, Alaska during 1993-1996 and 2010-2014. Models were selected for each shorebird species separately. Variables marked 'V' are included in the given model. We did not include snow in the global model for Semipalmated Sandpipers in order to avoid multicollinearity among variables.

| $Temp_{prelay}$ | $Temp_{lay}$ | $Temp_{inc}$ | $Rain_{prelay}$ | $Rain_{lay}$ | $Rain_{inc}$ | Snow | Period | Lay date | Clutch | Vol | Model rank | K | Deviance | AICc | ΔAIC | $w_i$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Western Sandpiper | | | | | | | | | | | | | | | | |
| | | V | | | | V | V | | | | 1 | 6 | 146.08 | 159.69 | 0.00 | 0.15 |
| | | V | | | | | V | | | | 2 | 5 | 148.80 | 159.92 | 0.23 | 0.13 |
| | | V | | | | V | V | V | | | 3 | 7 | 143.82 | 160.01 | 0.32 | 0.13 |
| | | V | | | V | V | V | | | | 4 | 7 | 144.30 | 160.50 | 0.81 | 0.10 |
| | | V | | | V | | V | | | | 5 | 6 | 147.02 | 160.64 | 0.94 | 0.09 |
| | V | V | | | | | V | | | | 6 | 6 | 147.56 | 161.19 | 1.49 | 0.07 |
| V | | V | | | | V | V | | | | 7 | 7 | 145.00 | 161.20 | 1.51 | 0.07 |
| | | V | | | | V | V | | V | | 8 | 7 | 145.22 | 161.41 | 1.72 | 0.06 |
| | | | | | | | V | | | | 9 | 4 | 152.68 | 161.42 | 1.73 | 0.06 |
| | | V | | | | | V | V | | | 10 | 6 | 147.86 | 161.47 | 1.77 | 0.06 |
| | V | V | | | | V | V | | | | 11 | 7 | 145.48 | 161.68 | 1.99 | 0.06 |
| Semipalmated Sandpiper | | | | | | | | | | | | | | | | |
| | | | | | | - | V | V | V | | 1 | 6 | 80.34 | 95.98 | 0.00 | 0.71 |
| | | V | | | | - | V | V | V | | 2 | 7 | 78.68 | 97.77 | 1.79 | 0.29 |

Supplementary Table 3-5. Full model set for the daily nest survival rates of shorebirds breeding at Nome, Alaska during 1993-1996 and 2010-2014. Models with ΔAICc less than 2 are in bold.

| Model | K | Deviance | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|---|
| **Western Sandpiper** | | | | | |
| **rain × period** | 4 | 1208.11 | 1216.12 | 0.00 | 0.521 |
| **temp × period** | 4 | 1208.99 | 1217.00 | 0.88 | 0.336 |
| temp + period | 3 | 1213.48 | 1219.48 | 3.36 | 0.097 |
| temp | 2 | 1217.33 | 1221.33 | 5.21 | 0.038 |
| lay date × period | 4 | 1220.03 | 1228.04 | 11.92 | 0.001 |
| lay date + period | 3 | 1222.73 | 1228.73 | 12.61 | 0.001 |
| lay date | 2 | 1224.82 | 1228.82 | 12.70 | 0.001 |
| period | 2 | 1224.95 | 1228.95 | 12.83 | 0.001 |
| null | 1 | 1227.04 | 1229.04 | 12.92 | 0.001 |
| rain + period | 3 | 1224.12 | 1230.13 | 14.01 | 0.000 |
| rain | 2 | 1226.37 | 1230.37 | 14.25 | 0.000 |
| time | 2 | 1226.67 | 1230.67 | 14.55 | 0.000 |
| time + period | 3 | 1224.69 | 1230.69 | 14.57 | 0.000 |
| nest age + period | 3 | 1224.92 | 1230.93 | 14.81 | 0.000 |
| time × period | 4 | 1222.98 | 1230.99 | 14.87 | 0.000 |
| nest age | 2 | 1227.02 | 1231.02 | 14.90 | 0.000 |
| nest age × period | 4 | 1224.90 | 1232.90 | 16.78 | 0.000 |
| **Semipalmated Sandpiper** | | | | | |
| **temp** | 2 | 968.48 | 972.48 | 0.00 | 0.570 |
| **temp + period** | 3 | 967.68 | 973.69 | 1.21 | 0.312 |
| temp × period | 4 | 967.63 | 975.64 | 3.16 | 0.118 |
| time × period | 4 | 978.23 | 986.24 | 13.76 | 0.001 |
| nest age × period | 4 | 986.64 | 994.65 | 22.17 | 0.000 |
| lay date × period | 4 | 990.37 | 998.38 | 25.90 | 0.000 |
| null | 1 | 996.46 | 998.46 | 25.98 | 0.000 |
| rain × period | 4 | 991.01 | 999.02 | 26.54 | 0.000 |
| period | 2 | 995.02 | 999.02 | 26.54 | 0.000 |
| nest age | 2 | 996.31 | 1000.32 | 27.84 | 0.000 |
| lay date | 2 | 996.33 | 1000.33 | 27.85 | 0.000 |
| time | 2 | 996.43 | 1000.44 | 27.96 | 0.000 |
| rain | 2 | 996.45 | 1000.45 | 27.97 | 0.000 |
| nest age + period | 3 | 994.71 | 1000.72 | 28.24 | 0.000 |
| time + period | 3 | 994.87 | 1000.88 | 28.40 | 0.000 |
| lay date + period | 3 | 994.88 | 1000.88 | 28.40 | 0.000 |
| rain + period | 3 | 994.91 | 1000.91 | 28.43 | 0.000 |

Supplementary Table 3-5. Continued for Red-necked Phalarope.

| Model | K | Deviance | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|---|
| **Red-necked Phalarope** | | | | | |
| **lay date** | 2 | 528.11 | 532.12 | 0.00 | 0.345 |
| **lay date + period** | 3 | 526.25 | 532.26 | 0.14 | 0.321 |
| **lay date × period** | 4 | 525.95 | 533.97 | 1.85 | 0.137 |
| nest age + period | 3 | 530.09 | 536.11 | 3.98 | 0.047 |
| nest age | 2 | 532.36 | 536.37 | 4.25 | 0.041 |
| nest age × period | 4 | 528.93 | 536.96 | 4.84 | 0.031 |
| null | 1 | 536.66 | 538.66 | 6.54 | 0.013 |
| Rain | 2 | 534.94 | 538.94 | 6.82 | 0.011 |
| period | 2 | 534.99 | 539.00 | 6.88 | 0.011 |
| rain × period | 4 | 531.21 | 539.24 | 7.12 | 0.010 |
| rain + period | 3 | 533.85 | 539.87 | 7.75 | 0.007 |
| time | 2 | 536.29 | 540.30 | 8.18 | 0.006 |
| temp | 2 | 536.65 | 540.66 | 8.53 | 0.005 |
| temp + period | 3 | 534.68 | 540.69 | 8.57 | 0.005 |
| time + period | 3 | 534.95 | 540.97 | 8.84 | 0.004 |
| temp × period | 4 | 532.95 | 540.97 | 8.85 | 0.004 |
| time × period | 4 | 534.26 | 542.29 | 10.16 | 0.002 |
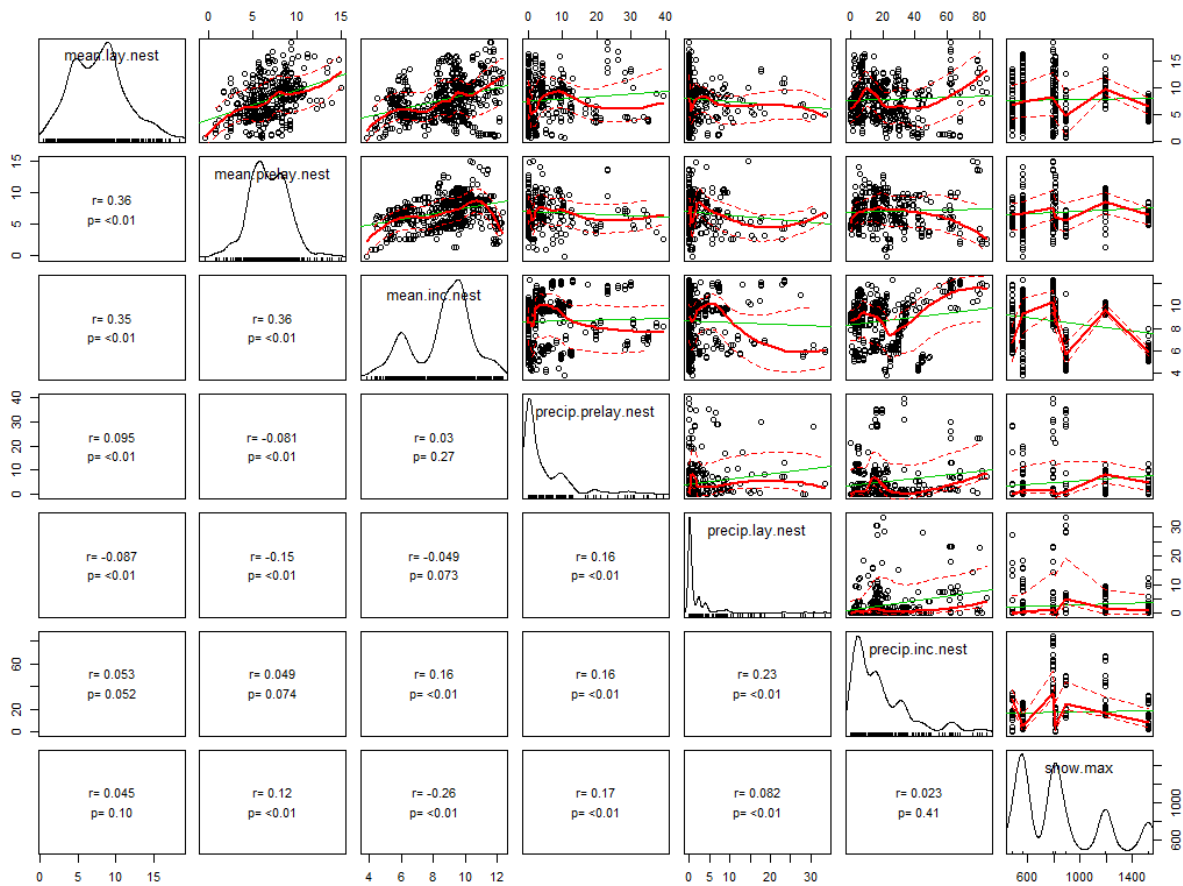
Supplementary Figure 3-1. Matrix of scatterplots to show the covariance among environmental variables. Average daily mean temperature was calculated for each nest during its prelaying, laying, incubation stages and shown here as mean.prelay.nest, mean.lay.nest, mean.inc.nest. Sum of daily total precipitation was calculated the same way and shown here as precip.prelay.nest, precip.lay.nest, precip.inc.nest. Maximum accumulation of snow from the previous winter was extracted from each year and shown here as snow.max. We pooled weather conditions from three species here.
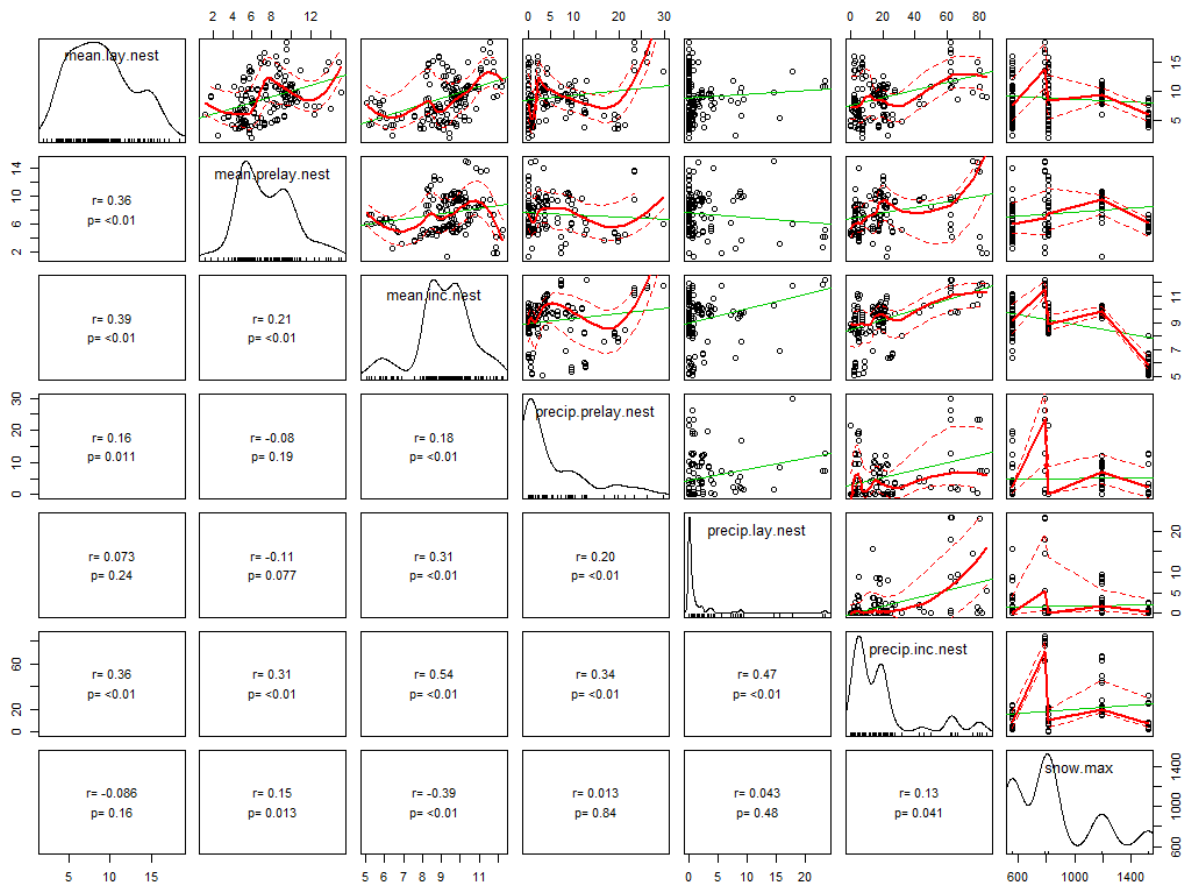
Supplementary Figure 3-2. Matrix of scatterplots to show the covariance among environmental variables for nests of Red-necked Phalaropes.

# Chapter 4 - Geographic variation in the intensity of phenological mismatch between Arctic-breeding shorebirds and their invertebrate prey

## Abstract

Responses to climate change can vary across functional groups and trophic levels, causing a temporal decoupling of trophic interactions or a 'phenological mismatch'. Despite a growing number of examples, single-species studies at local study sites cannot explain why we observe variation in the intensity of phenological mismatches among different bitrophic interactions. We tested for geographic patterns in phenological mismatch between six Arctic-breeding shorebird species and their invertebrate prey at ten coastal Arctic sites across ~13 degrees of latitude and ~84 degrees of longitude in North America. We estimated the extent of phenological mismatch between invertebrates and shorebirds at: 1) an individual nest level as the difference in days for the peak demand at each nest vs. the food peak and 2) a population level as the overlapped area under fitted curves for total daily biomass of invertebrates and hatching of shorebird chicks. For both measures of phenological mismatch, we used Structural Equation Modeling to test causal relationships among: 1) environmental factors including geographic location, current climate conditions, and long-term trends in climate change, 2) phenology of invertebrates and shorebirds, and 3) phenological mismatch between the two trophic levels. We found latitudinal and longitudinal gradients in the extent of phenological mismatch which were

mediated through geographic variation in the phenology of invertebrates and shorebirds. For individual shorebird nests, both more northerly and easterly sites showed greater phenological mismatch with annual food peaks. However, we also found that the delayed emergence of food peak at more northerly and easterly sites alleviated the extent of phenological mismatch. Our multi-site study provides the first evidence that large-scale geographic processes can determine the extent of phenological mismatch in a bitrophic system.

## Introduction

Phenology is the seasonal timing of a biological process or behavior, which is generally assumed to be optimized for the fitness of an organism in relation to its physical and biological environment. Changes in phenology are one of the most common signals of biological responses to modern climate change (Parmesan and Yohe 2003; Rosenzweig et al. 2008). Ecological responses to climate change have been shown to vary across functional groups and trophic levels (Parmesan 2007). Uneven shifts in the phenology of organisms can lead to decoupling of biological interactions, especially predator-prey interactions, resulting in "phenological mismatch" (Visser et al. 1998; Durant et al. 2007).

Phenological mismatches are widespread in terrestrial, freshwater, and marine ecosystems (reviewed by Parmesan 2006, Thackeray et al. 2010). Despite the ubiquity of phenological mismatches due to climate change, identifying general patterns has been challenging. Case studies have shown that life-history strategies of an organism can play a role in determining the impact of phenological mismatch on fitness (Saino et al. 2009; Kerby and Post 2013). However, phenological mismatch is also likely affected by environmental cues, geographic variation in

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large-scale drivers such as climate change, and the choice of phenological metric. In particular, the rate of climate change is not constant across biomes and latitudes (Loarie et al. 2009; Burrows et al. 2011). Consequently, geographic gradients are often found in the extent of ecological responses to climate change. Some studies have found stronger responses at higher latitudes, where a faster rate of climate change has been reported (Parmesan 2007). However, the direction of the correlation between ecological responses and geographic gradients is often unclear or even opposite to predicted patterns (Dunn and Winkler 1999; Rubolini et al. 2007).

Spatial variation in single-trophic level responses leads us to expect geographic variation in the response of multi-trophic level interactions. However, directly comparable replicates of ecological communities monitored for geographic variation of phenological mismatch are rare. Thus far, phenological mismatches have been estimated at more than one location for only a few species. For Great Tits (*Parus major*), a breeding population in the UK has matched an earlier peak emergence of caterpillars by advancing timing of egg laying by 14 days over 47 years (Charmantier et al. 2008). In contrast, a Dutch breeding population departed from perfect match with peak caterpillar numbers to being 7.6 days late over 20 years (Both et al. 2009). Studies of multiple species across a geographic gradient of sites are needed to characterize variation in the extent of phenological mismatch, elucidate patterns, and formulate testable hypotheses on the mechanisms of phenological mismatches.

The Arctic biome provides a highly seasonal environment with a relatively simple food web (Gauthier et al. 2004; Liebezeit et al. 2014). The Arctic is a good system for studying phenological mismatch because climate change models predict that the greatest degree of climate change will occur at high latitudes (IPCC 2014). Hindcasting arthropod abundance by

correlations with weather conditions, Tulp and Schekkerman (2008) reported that the estimated timing of peak arthropod abundance has already advanced 7 days over 30 years at the Taimyr Peninsula of northern Russia. Shifts in prey abundance are expected to drive the advancement of the optimal breeding date for Arctic breeding birds (Meltofte et al. 2007a). Long-distance migration imposes high energetic requirements on Arctic breeding birds, and requires that birds migrate through diverse landscapes where climate change may be occurring at different rates (Senner 2012). Timing of long-distance movements is also constrained by other events in their annual life cycle such as nesting, growth, and feather molt (Lourenço and Piersma 2015). Little to no variation in the timing of pre-breeding stages may indicate that the timing of breeding is under strong selective pressure (Conklin et al. 2013), suggesting optimal timing with conditions on the breeding grounds would be particularly challenging to achieve for these birds. Migratory shorebirds are usually income breeders that rely on exogenous food intake upon arrival on the breeding grounds to produce eggs (Klaassen et al. 2001; Yohannes et al. 2010), and phenological asynchrony with the local food peak corresponding with lower nest survival in shorebirds (Senner 2013). Thus, there should be strong selective pressure for Arctic-breeding shorebirds to achieve a phenological match with their invertebrate prey at the breeding grounds. Failure to match changes in prey phenology could indicate inherent limitations in the ability of shorebirds to adapt to climate change, and would have implications for the conservation status of these species.

Understanding geographic patterns of phenological mismatch may also provide insights for region-specific trends in shorebird population numbers. Data from long-term survey programs indicate steep declines among populations in Atlantic Canada and the northeastern United States,

but stable populations in the Midwest (Bart et al. 2007). Eastern population declines include the Semipalmated Sandpiper (*Calidris pusilla*), which was once the most abundant migrant and breeder along eastern coast of North America (Gratto-Trevor and Cooke 1987; Morrison et al. 2000). This species has shown widespread declines at both breeding sites and stopover sites in eastern Canada (Andres et al. 2012; Smith et al. 2012). Similarly, Red-necked Phalaropes (*Phalaropus lobatus*) have virtually disappeared from a major stopover site in the Bay of Fundy between 1970 and 1990, with unknown impacts on breeding populations (Brown et al. 2010; Nisbet and Veit 2015). Several studies pointed to negative effects of phenological mismatch on rates of offspring survival and recruitment of other avian and mammalian systems, both of which are important determinants for population size (Reed et al. 2013b; Plard et al. 2014). However, no link has been made between phenological mismatch and population trends of shorebirds in North America due to a lack of information on the extent of phenological mismatch in remote Arctic habitats.

We examined patterns of phenological mismatches among six shorebird species and their invertebrate prey at ten Arctic sites through a distributed research collaborative network: the Arctic Shorebird Demographics Network (ASDN, Brown et al. 2014). We used a mechanistic approach to test for effects of exogenous factors on the phenological mismatch between two trophic levels as mediated through the single-trophic level responses (Figure 4-1). Based on previous studies, we hypothesized that the effect of climate change would be stronger at higher latitudes, which would in turn creates greater mismatch at more northerly sites. We also hypothesized that the degree of mismatch would be greater at higher longitude (more easterly sites), corresponding to the geographic trend in population declines. For both latitudinal and

longitudinal gradients, we tested for ecological links among invertebrate phenology, invertebrate abundance, and shorebird phenology on the degree of mismatch between the peak timing of invertebrate emergence and hatching of shorebird nests.

## Methods

### (a) Study species

We tested the phenological mismatch on a bitrophic system including six Arctic-breeding shorebird species and their invertebrate prey. The six study species were small to medium-sized shorebirds (Scolopacidae) with average body masses ranging from 25 g to 75 g: Dunlin (*Calidris alpina*), Pectoral Sandpiper (*C. melanotos*), Semipalmated Sandpiper (*C. pusilla*), Western Sandpiper (*C. mauri*), Red Phalarope (*Phalaropus fulicarius*), and Red-necked Phalarope (*P. lobatus*). The six species share similar breeding ecology with an invariant clutch size of four eggs, an 18-23 day incubation period, and precocial young that are capable of self-feeding after hatching (Poole 2005). The six species differ in mating systems, breeding range, and migratory routes (Table S4-1). Five of six species exhibit ongoing population declines in parts of their range in North America, while Pectoral Sandpipers appear to have stable populations (Thomas et al. 2006).

After migratory shorebirds arrive at the breeding grounds in the Arctic, they forage on proteinaceous food sources such as larvae of semiaquatic invertebrates. Studies of adult diet have reported midges (Chironomidae) and crane flies (Tipulidae) as the main food sources for all six species, with additional consumption of other small flies (Diptera), beetles (Coleoptera: Carabidae), and spiders (Arachnidae, Holmes and Pitelka 1968; Holmes 1972; Baker 1977; Jehl 1986). Little is known about the diet of shorebird chicks, but broods are often observed feeding

with their parents in dwarf shrub-graminoid habitat after hatching, presumably consuming a diet similar to adults (Safriel 1975).

## (b) Study sites

The Arctic Shorebird Demographics Network is a distributed research network comprised of 16 sites along the Arctic coast of Alaska, Canada, and Russia with the shared objective of understanding the drivers of population demography and recent population declines among Arctic-breeding shorebirds (Brown et al. 2014). A coordinated monitoring effort with standardized methodology provided us with a rare opportunity to examine phenological mismatches at a broad geographic scale. Field data for our study were collected at ten network sites during the 3-year period of 2010-2012 (Figure 4-2). The ten sites spanned ~13 degrees of latitude (58 to 71° N) and ~84 degrees of longitude (−164 to −81° W), with the two most distant sites separated by 3,850 km. Sites in western Alaska and eastern Canada were mosaics of dry or mesic tundra with interspersed lakes and ponds. Northern Alaska and a northwestern Canada sites had tundra polygons interspersed with dry and mesic tundra. The community of shorebird species varied among sites, but showed broad overlap in species composition. We monitored between ~25 to 300 shorebird nests per year at each of the ten study sites (Table S4-2).

## (c) Field data collection

### Climatic variables

Annual phenology of terrestrial invertebrates and shorebirds of the Arctic tundra biome is mainly determined by the timing of snow melt and ambient temperature (Høye and Forchhammer 2008; Liebezeit et al. 2014). Across ten sites, timing of snow melt was correlated with the daily mean temperature of the egg-laying period of shorebirds (ASDN, unpublished

data). Therefore, we used site-specific mean daily temperature as a proxy for spring conditions. Mean daily temperature for each of ten sites was collected from the nearest available meteorological station (Figure 4-2; Table S4-3). The earliest year that we had daily weather data available for all ten sites was 1990, and we examined a recent 25-year period for long-term climatic conditions (1990-2014).

We focused on temperature conditions during the egg-laying period of shorebirds, which varied by species, site, and year. The egg-laying period was defined as the time window between the dates of clutch initiation for the first to last nest. We used median dates of our three study years to define this period for each species at each site. We used information from every shorebird nest monitored. Renesting may be common in some species (Gates et al. 2013), but known renests were rare and <5% of our sample of nests (ASDN, unpublished data).

Shorebirds typically need a minimum of 5-8 days after arrival at their breeding grounds before they lay the first eggs as income breeders (Klaasen et al. 2001; Meltofte et al. 2007b). Because environmental conditions during this time can directly affect timing of egg laying, we also examined climatic conditions prior to the egg-laying period. The pre-laying period was defined as the two-week time window prior to the start date of the egg-laying period per species at each site. For each site, we calculated the *climatic trend of temperature* as the change in the mean daily temperatures during the egg-laying period over the 25-year period. First, we assessed mean daily temperature for each day of the year. To quantify how the mean daily temperature changed for each date during 1990 to 2014, we fitted a linear model to the mean daily temperature of each day of the year as the response and the year as the predictor using R package 'stats' (R Core Team 2015). We used the slope of the model as an index of long-term

temperature change for each Julian date at each site. We averaged the slopes across all days in the egg-laying period to obtain an estimate of the overall temperature change during the laying period over the past 25 years at each site. The climatic trend outside of the egg-laying period was also examined for variance across study sites. For each site, we parameterized *long-term trend of climatic variance* as the long-term change in year-to-year variation in mean temperature of a set date during spring. The overall mean date of clutch initiation for all shorebirds at our ten sites during 2010-2012 was Jun 4 (ASDN, unpublished data). Here, we calculated the difference in the daily mean temperature for Jun 1 between each pair of consecutive years from 1990 to 2014. We fit a linear model to the interannual differences and used the slope of the model as an index of long-term change in temperature variance at each site. We also described the *current climate* at each site by calculating the mean daily temperature of the pre-laying period and the egg-laying period for each of the three study years 2010-2012.

**Invertebrate biomass**

To determine the seasonal phenology and abundance of terrestrial food resources, we sampled terrestrial invertebrates from the onset of snow melt to the completion of shorebird hatching. Two line transects were deployed at random in dry and mesic habitats of the study site where nests of breeding shorebirds were monitored. Each line consisted of five modified Malaise pitfall traps set up 15 m apart on each of the transects. For the modified traps, we set a 36 cm × 36 cm frame fitted with 2-mm mesh perpendicular to the ground on top of a 38 cm × 8 cm × 5 cm container filled with trap solution. The trap solution contained 20-30% propylene glycol and 70-80% water with a drop of commercial-grade surfactant. Trap stations were visited every three days and accumulated samples were stored in 50 mL Whirl-Pak® with 70-100% isopropanol. In

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the laboratory units, invertebrate samples were sorted, identified to order or family, and measured for body length. We estimated biomass from body length using taxon-specific conversion coefficients (Benke et al. 1999). Total daily biomass was then calculated as the sum of biomass of all invertebrate taxa collected on each sampling occasion divided by 3 days.

## Shorebird nesting

Arctic-breeding shorebirds usually lay one egg every 1-2 days (Sandercock 1998; Colwell 2006). For nests found during laying, we estimated the date of first egg-laying by subtracting the number of eggs found from the date the nest was found. The scheduled hatch date was then calculated by adding the number of days in the species-specific incubation period to the date when last egg was laid (Brown et al. 2014). For nests found during incubation, we floated eggs in a small cup of warm water and estimated the float angle. We predicted hatch date from the float angle and a species-specific regression equation (Liebezeit et al. 2007). McKinnon et al. (2013) showed that growth rate of Dunlin chicks is determined by arthropod biomass and daily temperature after the age of five days. Therefore, we set the date of expected peak food demand for the shorebird chicks from each nest as the date five days after the predicted hatch date. We could not predict hatch date if a nest was depredated before we measured the float angle of eggs. Every shorebird nest with a predicted hatch date was included in the analyses. Use of predicted hatch dates instead of actual hatch dates allowed us to include failed nests in our analyses of phenology.

## (d) Parameterization of phenological mismatch

We calculated the date of peak invertebrate biomass as the date with the greatest total daily invertebrate biomass for each year at each site. The extent of *phenological mismatch for*

*individual nests* ($M_{ind}$) was calculated as the number of days for the difference between the date of peak food demand for shorebird chicks (five days after predicted hatch) versus the date of peak invertebrate biomass (Figure 4-3). To estimate the extent of *phenological mismatch at a population level* ($M_{pop}$), we identified seasonal distributions for invertebrate biomass and hatching of shorebirds. We quantified invertebrate phenology as the *available food distribution* of daily total biomass over the season, and the *shorebird demand distribution* of each species as the predicted temporal distribution of 5-day-old broods based on timing of laying of both successful and unsuccessful nests. Daily values of total invertebrate biomass and the number of 5-day-old broods were converted into percentiles of the season total value, to standardize scales for direct comparison between the two distributions. At most sites, unimodal peaks were identified for both invertebrates and shorebirds. When there was more than one peak with similar heights, we used the median date between peaks as an alternative date of the peak. At nine of ten sites, sampling of invertebrates was discontinued 3 to 21 days before the last estimated hatch date of a shorebird nest. The latest initiated nests failed to survive until the estimated hatch date, and invertebrate sampling was discontinued when no active nests were remaining. To interpolate invertebrate biomass during the period after sampling ceased, we fitted a natural cubic spline to each food distribution and substituted missing values with interpolated values. A smoothing curve was then fit to each of the available food distribution and shorebird demand distribution against date of season using the '*gam*' and '*predict*' functions in the 'mgcv' package of Program R (version 3.1.3, Wood 2000; R Core Team 2015). We developed a smoothed demand curve for each shorebird species at each site and year, and overlaid it with the available food curve. The extent of phenological mismatch at the population level ($M_{pop}$) was then calculated as the area of

overlap between the food curve and demand curve with the '*integrate.xy*' function in R package

'sfsmisc' (Maechler 2015) (Figure 4-3). We then estimated an overlap coefficient for each

shorebird species for each site and year, by the following function:

$$\text{Overlap coefficient}_{i,j,k} = \frac{2 \times \text{overlap area under two curves}}{\text{total area under food curve}_{i,j} + \text{total area under demand curve}_{i,j,k}}$$

where $i$ was the site, $j$ was the year and $k$ was the shorebird species. The estimated overlap

coefficient described how much of the food curve was being utilized by shorebirds as well as

how much of the demand curve was met by the food curve. Complete phenological match, where

the overlap coefficient is 1, occurs when both curves match exactly, but not necessarily when

one curve is nested under the other curve. Values of our metric for individual mismatch ($M_{ind}$)

increased as shorebird nests hatched further away from the food peak, and the individual

mismatch increases. Values of our metric for population mismatch ($M_{pop}$), on the other hand,

decrease as the population mismatch increases. The idea of estimating the overlap area rather

than pinpointing peak dates has been suggested in theory (Durant et al. 2007; Miller-Rushing et

al. 2010), but our study is the first empirical application of the approach.

Development of a metric of phenological mismatch that is easily applicable and directly

comparable is key to making comparisons among sites or species. Previous studies have

measured an interval between the date of resource peak and date of peak demand, compared rates

of temporal shifts at different trophic levels, or developed a metric to evaluate fitness

consequences in relation to the timing of breeding (Visser et al. 1998; Both and Visser 2001;

Sanz et al. 2003; Pearce-Higgins et al. 2005; Nielsen and Møller 2006; Charmantier et al. 2008; Both et al. 2009; Gaston et al. 2009; Saino et al. 2009; Bauer et al. 2010). Recently, Reed et al. (2013b) used separate metrics to define mismatch at both individual and population-level. Our individual-level metric was identical to methods of Reed et al. (2013b). Our population-level metric improves on past methods because it incorporates different shapes of the phenology curves at both trophic levels instead of averaging the mismatch measures at an individual level.

## (e) Data analysis

All statistical analyses were conducted with packages in Program R (version 3.1.3, R Core Team 2015). The degree of phenological mismatch at individual nest level ($M_{ind}$) and at population level ($M_{pop}$) were our two *bitrophic level* response variables. Three *single-trophic level* response variables included ecological timing, variance in timing, and food availability. The three *exogenous factors* were geographic gradients, current climate, and climatic change. We predicted that both the current weather and climate change would vary with geography, which in turn, would correlate with single trophic level responses that determine phenological mismatch (Figure 4-1). We first tested for latitudinal and longitudinal variance in the current weather and climatic change using Spearman's rank correlation test in R package 'stats' (R core team 2015). Next, we used current weather as well as the geographic gradients as explanatory variables to assess potential geographic patterns in ecological timing and food abundance. We tested the significance of latitude and longitude on the variation in timing of the food peak and mean biomass using mixed effects models with year as a random effect in R package 'lme4' (Bates et al. 2014). When testing latitudinal and longitudinal variance in the timing of egg laying,

we treated shorebird species and year as random effects. Within each site and year, we restricted our analyses to shorebird species for which we had >20 nests with predicted hatch dates.

Our hypothesis of geographic trends in phenological mismatch was based on the assumption that the variation in the extent of mismatch is derived from the hypothesized exogenous factors, and not from differences in the composition of local invertebrate community. We tested if the number of invertebrate taxa detected differed among years or sites using mixed effects models with sampling date as a random effect in R package 'lme4' (Bates et al. 2014). We also tested latitudinal and longitudinal variance in the number of detected taxa with year and sampling date as random effects. We then used Canonical Correspondence Analysis (CCA) in R package 'vegan' to test for similarities in invertebrate community composition among the ten Arctic sites (Oksanen et al. 2015). We excluded any invertebrate taxa that were detected in <10 samples across sites and years. Invertebrate community abundance data were natural log transformed. We used stepwise variable selection in both directions with site and year variable in R package 'stats' (R core team 2015). Variables were not added unless addition decreased the AIC value (Hastie and Pregibon 1992). Models with ΔAICc < 2 were considered as parsimonious to the top ranked model. The variance inflation factors (VIF) for the variables were all less than 10, suggesting that there was no redundancy in a model (O'Brien 2007). With the best fitting model, we conducted a permutation test to assess significance of constraints on community composition using R package 'car' (Fox and Weisberg 2011). Terms were added in the model, 'site' first and then 'year', and permuted 1,000 times.

**Structural equation modeling**

In analyses of phenological mismatch and other higher-order ecological responses, more than one variable may be responsible for explaining the observed variance. Consequently, underlying mechanisms are better understood when multiple explanatory variables are tested simultaneously. We used Structural Equation Modeling (SEM) to identify exogenous and endogenous drivers for the bitrophic level responses of which the explanatory variables show multicollinearity. SEM provides a means to examine networks of causal relationships, and allows factors of interest to be both explanatory and response variables in the model (Grace 2006). Traditional SEM produces a variance-covariance matrix among all variables given the specified model. Goodness-of-fit of the model is then defined by the discrepancy between the modeled matrix and the observed matrix. However, the approach assumes multinormality among variables, and models with large sample sizes can show statistically significant deviations among matrices even when absolute deviations are small (Grace 2006). Our dataset did not satisfy the assumption of multinormality, even after the Bollen-Stine chi-square bootstrapping (Bollen and Stine 1992), nor did our large sample size allow the discrepancy between matrices to be rejected. Thus, we used an alternative approach called piecewise SEM. Piecewise SEM estimates a separate variance-covariance matrix for each piecewise model, and then pieces together the path estimates to construct a causal model (Shipley 2009).

Our two response variables for piecewise SEM were the degree of phenological mismatch at individual level and the degree of phenological mismatch at population level (Figure 4-1). We included three exogenous factors as our explanatory variables; each was measured with two subordinate variables. *Geographic gradients* included latitude and longitude, and *climate change* included the change in mean daily temperatures and annual variance over a 25-year period.

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*Current climate* included the mean daily temperature during pre-laying and laying periods for each of the years field monitoring was conducted. Both geographic gradients and climate change were site-specific factors, whereas current weather was specific to each site and year. We had three factors that we hypothesized as mediating the effects of the three exogenous factors. *Ecological timing* included two subordinate variables, the date of food peak and the date of first egg-laying. *Variance of timing* included the variance measures for the available food curve and the shorebird demand curve. *Food availability* was mean invertebrate biomass for each year at each site. Values of the three mediating factors were specific to each site and year, except for date of nest initiation, which was specific to each shorebird nest. All variables were standardized with $\log_e$ transformations prior to analyses so that we can directly compare the strengths of different causal relationships (Grace 2006). Describing the model structures, we refer to factors instead of specific subordinate variables for simplicity. However, each subordinate variable under a specific factor forms a node for alternative pathways.

Path models were determined *a priori* for which we set exogenous factors and response variables in hierarchical order as follows. We conducted the analyses in two steps. First, we constructed two candidate models to test the hierarchy among exogenous factors (Figure 4-4). The two versions of the full model differed only in that one model had the geographic gradient affecting the current weather and climate change, whereas the other model placed the three exogenous factors at the same level. We used Shipley's test of directional separation (d-sep test) to evaluate overall model fit (Shipley 2013). We then compared two models using AICc and the '*get.sem.fit*' function in the open-source R package 'piecewiseSEM' (version 0.9). We retained the candidate model with smaller AICc value as our full model for the next step of model

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selection. In the second step, the full model included all three hypothesized exogenous factors (structured as per results of the first step) as well as all three mediating factors. We tested the full model against all possible submodels. Each path model was a linear mixed-effects regression with year and shorebird species as random factors, and was fitted with R package 'lme4' (Bates et al. 2014). We evaluated the fit of each model using the Shipley's d-sep test, and compared models using AICc as described above. We repeated the same modeling procedure separately for individual-level response and population-level response. Standardized regression coefficients ($\beta$) were derived from the best supported model(s) with $\Delta$AIC less than 2, and reported for each segment of the path. The direct effects were the beta coefficients between latitude or longitude and phenological mismatch. We then calculated indirect effects as the product of all beta coefficients in a given path (Mitchell 2001). The total indirect effects of latitude or longitude on the phenological mismatch was calculated as the sum of indirect effects of all the possible paths from latitude or longitude to the phenological mismatch. The indirect effects and the total indirect effects were not accompanied with a significance level, but were used to compare the relative strength of different paths in our model.

## Results

### (a) Cooling and warming

At all ten sites, the greatest amount of warming occurred during the cooler parts of the year over the past 25 years (1990-2014, Figure 4-5). Our two easternmost sites, Churchill and East Bay, experienced warming year-round. However, at eight other sites, some periods of the year showed a cooling trend while others showed warming trends (Figure 4-5). Global warming was not uniform and temperatures during the laying period of shorebirds have actually been

decreasing over the past 25 years at three western sites (Nome, Cape Krusenstern, and Colville River Delta). Despite opposing climatic trends at the western and eastern edges of our gradient, neither longitude nor latitude explained the long-term changes in daily mean temperatures during the laying period (latitude: $r_s = -0.17$, longitude: $r_s = 0.2$). Interannual variation in temperature increased over 25 years at nine of ten sites (excluding Cape Krusenstern where the slope was near zero), but the change did not vary with latitude or longitude. The mean daily temperatures on Jun 1 during the study years (2010 to 2012) were the lowest at the most northern site (Barrow), but were not linearly related to latitude because two southernmost sites showed similar low temperatures.

### (b) Invertebrate food resources

*Invertebrate community structure.* A total of 3,860 invertebrate samples were collected in all sites and years combined. Collected samples included 77 taxa, 40 of which were selected for analyses based on an adequate number of occurrences, set as detected in more than 10 samples pooling all the sites and years. Spiders (Araneae) alone made up 36% of the gross invertebrate biomass of all samples, and 90% of the biomass was comprised of Araneae plus eight other taxa in descending order of occurrence: beetles (Coleoptera: Carabidae), higher flies (Brachycera), parasitoid wasps (Hymenoptera), nonbiting midges (Chironomidae), crane flies (Tipulidae), bees (Hymenoptera), fungus gnats (Mycetophilidae), and other miscellaneous hymenopterans. The number of invertebrate taxa detected did not vary among years, but varied among sites because fewer taxa were detected at northerly or more eastern sites (latitude: $t = -6.12$, d.f. $= 376.2$, $p < 0.001$; longitude: $t = -4.75$, d.f. $= 342.9$, $p < 0.001$). Taxon diversity increased as the breeding season progressed ($t = 12.53$, $p < 0.001$). Our Canonical Correspondence Analysis indicated that

the invertebrate community composition differed by site ($F_{9,374} = 19.67$, p = 0.001) and by year ($F_{2,374} = 7.85$, p = 0.001). Relatively uncommon invertebrate taxa such as jumping plant lice (Psyllidae) and black flies (Simuliidae) separated invertebrate communities at Colville and Churchill from the other eight sites (Figure S4-1). Significant differences in the invertebrate community composition remained among eight sites after removing Colville and Churchill ($F_{7, 263} = 13.88$, p = 0.001), but visual inspection of the biplot indicated considerable overlap in the community composition (Figure S4-1). Thus, we assumed the invertebrate communities were similar enough for the purposes of our analysis.

*Timing and magnitude of food peaks.* Dates of invertebrate food peaks were earlier in 2011 than in other years, but did not differ between 2010 and 2012 (2010 vs. 2011: d.f. = 11, t = −2.64, p = 0.02; 2010 vs. 2012: d.f. = 11, t = −0.73, p = 0.48). Dates of the food peak also varied among sites. The earliest peak at the most northern site was 31.7 days before the latest peak at the secondmost western site (d.f. = 11, t = −3.63, p = 0.004). However, timing of food peaks did not vary with latitude or longitude (latitude: d.f. = 19, t = 1.37, p = 0.19, longitude: d.f. = 19, t = 0.40, p = 0.70). The average amount of food available to shorebirds (*mean biomass per sample*) and height of the food pulse (*maximum biomass*) varied among sites but not across years within each site. Mean biomass of invertebrates was lower at higher latitudes (t = −2.12, p = 0.047), but maximum biomass did not show any geographical patterns.

*Variance of food peaks*. Width of the food curve was not significantly different among years at nine of ten sites, but the widest curve (Canning River) was 2.7 times wider than the average of the other sites. The food curve was also significantly wider at higher latitudes and food resources

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for shorebird chicks would be available for a longer seasonal period (d.f. = 19, t = 2.51, p = 0.02).

## (c) Timing of laying in Arctic shorebirds

We monitored 3,164 shorebird nests with estimable hatch dates. After controlling for daily mean temperature on Jun 1, the mean date of clutch initiation was delayed by 0.4 days with each one-degree increase in latitude (d.f. = 3159.6, t = 7.12, p < 0.001), or 0.06 days for each one-degree increase in longitude (d.f. = 3158, t = 7.09, p < 0.001, Figure S4-2). With species and year pooled for each site, the mean date of clutch initiation ranged from Jun 8 (SD = 0.6, n = 85) at our southernmost site to Jun 14 (SD = 0.2, n = 859) at our northernmost site, and from Jun 1 (SD = 0.3, n = 529) at our westernmost site to Jun 28 (SD = 1.5, n = 22) at our easternmost site. Timing of clutch initiation also varied among species: Dunlin were the first species to lay eggs across sites and years, followed by Western Sandpipers and Semipalmated Sandpipers, but with only a ~0.1 day difference from Dunlin. Pectoral Sandpipers, Red Phalaropes, and Red-necked Phalaropes initiated their nests later than Dunlin by 1.8, 3.2, and 7.8 days, respectively (p < 0.001 for all three species).

## (d) Extent of phenological mismatch

Interannual phenological variation was ~ 3× greater for peak invertebrate biomass ($\bar{x}$ = 12.2 days) than for hatching and peak demand of shorebird chicks ($\bar{x}$ = 4.4 days, t-test: d.f. = 14.74, t = −3.32, p = 0.005, Figure S4-3). At the level of individual nests, phenological mismatch was greater at higher latitudes (d.f. = 2481.7, t = 5.77, p < 0.001), but did not vary with longitude. Thus, individual nests were estimated to hatch less synchronously with the food peak at northern than southern sites. Individual nests were predicted to hatch as early as 28 days prior to the food

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peak (Semipalmated Sandpiper at Barrow in 2012) or as late as 43 days after the food peak (Pectoral Sandpiper at Canning River Delta in 2011). Pectoral Sandpipers were most closely matched with the food peak, followed by Semipalmated Sandpipers, Red Phalaropes, Western Sandpipers, Dunlin, and Red-necked Phalaropes (Table S4-4). At a population level, the shorebird demand curve overlapped with the food availability curve by as little as 2% (Semipalmated Sandpipers at Prudhoe Bay in 2010) or as much as 77% (Pectoral Sandpipers at Barrow in 2012, Figure S4-4). Nevertheless, the extent of overlap between the curves did not vary among years or species or with latitude or longitude. Site explained three times more variability than shorebird species for population responses ($\Delta R^2_{site}$ / $\Delta R^2_{pop}$ = 2.72), and seven times more for individual responses ($\Delta R^2_{site}$ / $\Delta R^2_{ind}$ = 7.26).

## (e) Geographic variation in phenological mismatch

We found different patterns of climate change across the longitudinal gradient, but our alternative full model structured with three exogenous factors at the same level fit the data better than a model with exogenous factors at two levels, where latitude and longitude affected mismatch via climate change and current climate (Table 4-1; Figure 4-4b). Thus, direct effects of both latitudinal and longitudinal location of the sites on the single-trophic level responses were stronger than the indirect effects mediated through climatic conditions. We therefore retained the alternative model as our global model for a second set of model selection. A model where latitude and longitude affected phenological mismatch via invertebrate phenology and shorebird phenology was a best fit to the data, with strong support for a direct path from geographic gradient to the bitrophic level response as well as the effects mediated by phenology of invertebrates and shorebirds (Table 4-2). Neither current climate nor long-term patterns of

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climate change improved the model fit. Therefore, the extent of phenological mismatch between shorebirds and their invertebrate prey was most affected by the phenology of each taxon, which was in turn most affected by the geographic location of each site. The best-fitting causal pathways were consistent between individual-level and population-level measures of phenological mismatch (Table 4-2).

Path coefficients from the best fit model suggested that both the food peak and the date of egg laying were later at higher latitudes and higher longitudes (Figure 4-6). At an *individual nest level*, a delayed food peak decreased mismatch ($\beta = -5.010$, $p < 0.001$), whereas delayed clutch initiation of shorebird nests increased the individual mismatch ($\beta = 0.718$, $p = 0.016$). Thus, higher latitudes significantly delayed both timing of food peak and egg-laying by shorebirds, which significantly affected individual mismatch in opposite directions. Latitude decreased individual mismatch through delayed food peaks ($\beta_{sum} = -2.425$), more than it increased the mismatch with delayed egg-laying by shorebirds ($\beta_{sum} = 0.155$, Table 4-3). Direct effects of latitude tended to increase mismatch at individual nests, but were not statistically significant ($\beta = 2.921$, $p = 0.101$). Therefore, latitude had an overall positive effect on individual match, with better individual match at more northerly sites resulting from later food peaks. Direct effects of longitude tended to increase individual mismatch, but were not significant. Individual match was improved at more easterly sites by delayed food peak and shorebird hatch ($\beta_{sum} = -0.113$). In contrast, at a *population level*, a delayed food peak increased the extent of phenological mismatch ($\beta_{sum} = -0.013$, $p < 0.001$), but timing of egg laying did not have a significant effect on mismatch ($\beta = 0.0$, $p = 0.085$). Increase in latitude and longitude both increased the extent of mismatch at population level, but only the latitudinal effect was significant ($\beta = -0.079$, $p <$

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0.001). The indirect effects of latitude and longitude mediated through the phenology of invertebrates and shorebirds were less important than direct effects at a population level (Table 4-3).

## Discussion

We detected broad geographic processes through which both latitude and longitude had an impact on the extent of phenological mismatch between shorebirds and their invertebrate prey. Our study is the first to compare the intensity of phenological mismatch among different sites, and test for common mechanisms underlying patterns of phenological mismatch. At least three previous studies have collected data on multiple trophic levels at multiple sites, but geographic variation was not a focus and comparisons among sites were not reported (Pearce-Higgins et al. 2005; Saino et al. 2009; Bauer et al. 2010).

Phenology of terrestrial organisms is a phenotypically plastic trait and can vary with annual environmental conditions (Visser et al. 2009; Charmantier and Gienapp 2014; Franks et al. 2014). In our three-year study period, invertebrate phenology varied on average about three times more than shorebirds breeding at the same Arctic sites. Patterns of variation in phenology observed at two trophic levels agree with previous reports that consumers at higher trophic levels shift their phenology to a lesser extent than plants or consumers at lower trophic levels, creating a phenological mismatch (Parmesan 2006; Hoye et al. 2007; Thackeray et al. 2010; Gienapp et al. 2014). However, the observed changes in phenology of both invertebrates and shorebirds were not always in the direction expected from temperature change among years. We interpret the variation found in the timing of invertebrates and shorebirds at a given site as an example of phenological plasticity, which can be either adaptive or non-adaptive (Ghalambor et al. 2007;

Charmantier and Gienapp 2013). Our relatively short 3-year study period provided us with a brief snapshot of trophic interactions. However, our aim was to substitute a temporal gradient with a spatial gradient and thereby, examine the causes of variation in the extent of phenological mismatch.

### *Geographic gradients in phenological mismatch*

We found significant geographic variation in the extent of phenological mismatch at both the individual nest level and population level. Interspecific differences in the extent of mismatch were found at a given site, but site was still a better predictor than shorebird species for the observed extent of phenological mismatch at a continental scale. We identified significant geographic gradients where phenological mismatch varied with both latitude and longitude. At the level of individual nests, unexpected positive effects of delayed food peak and egg laying offset, and even overrode, the direct negative effects of increasing latitude and longitude. On the other hand, at the population level, an increase in latitude directly increased phenological mismatch. Due to the geography of the Arctic biome of North America, longitude and latitude of our study sites were collinear. However, using SEM, we estimated the partial regression coefficients for latitude and longitude separately while holding the other variable constant. Both short-term and long-term environmental factors as well as ecological factors were associated with latitude and longitude.

Atmospheric temperature has been cooling during the first half of the breeding season at 8 of 10 study sites over the past 25 years. Periodic cooling and consequent temporal sign switching in ecosystem response is not an unusual phenomenon (see review in Parmesan and Yohe 2003). Our comparison between the hypothesized path model and the alternative path model, however,

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showed that both the long-term pattern of climate change and the current temperature condition during laying period did not mediate the effects of latitude and longitude, suggesting that some environmental variable that we did not test may underlie broad geographical patterns in the phenology of Arctic invertebrates and shorebirds. We used the seasonal changes in daily mean temperature as a proxy for spring conditions at our sites. However, it is possible that other environmental variables, such as snow accumulation from the previous winter, early summer precipitation, and vegetation cover may show geographic gradients that could help to explain our observations of geographic variation in phenological mismatch.

Ecological factors such as life-history traits of a given shorebird species could also affect the extent of phenological mismatch by constraining timing of breeding. Timing of egg laying in long-distance migrants is often strongly dependent on the timing of arrival on their breeding ground, as well as their wintering location and migration strategy such as migration distance and use of different flyways (Myers 1981; Both and Visser 2001; Both et al. 2006; Gienapp and Bregnballe 2012). Breeding latitude is thought to affect migration distance (but see Henningsson and Alerstam 2005), especially for species with low migratory connectivity where breeding populations mix on wintering grounds (Western Sandpiper: Franks et al. 2012; Dunlin: Gill et al. 2013). In addition, longitude of a breeding location often corresponds to the flyway that a shorebird population uses for spring migration. However, adjacent flyways also overlap considerably, especially around breeding grounds in the Arctic region (Piersma and Lindström 2004), which makes it difficult to uniquely link each breeding population to a certain flyway. The fact that a suite of traits related to timing are specific to different populations in species with differential migration precludes a strong overall species effect on the extent of phenological

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mismatch, and also implies that we need population-based estimates, instead of species-based estimates, to identify potential geographic gradients in ecological factors.

### *Mismatch at individual vs. population levels*

Our final path model showed that a delayed food peak alleviated phenological mismatch at individual nests, but increased phenological mismatch at a population level. The population mismatch can be increased with a delayed food peak if the food peak is greater when delayed. We observed that higher food peaks were often less matched with the shorebird demand curve and resulted in a greater extent of population mismatch. Life-history strategies of Arctic invertebrates assure rapid development during the short summer (Danks 2004). Delayed onset of warming at the beginning of the season likely constricts the time window available for invertebrate development, and consequently can make the food peak narrower and taller. Given the cooling trends found during the early part of the breeding season, shorebirds at our Arctic sites may encounter later and taller food peaks in future years, which we predict will cause opposite effects on individual and population-level mismatch.

We found one other disparity between individual and population-level mismatch, in that early breeders were expected to hatch eggs closer to the local food peak whereas the timing of egg-laying did not affect population-level mismatch. The population-level metric is more robust to outliers and variation in individual responses. Additionally, our measure of mismatch at a population level varied as a function of seasonal changes in both food abundance and brood density of shorebirds. Hence, individual mismatch did not directly translate into population mismatch. We suggest that both metrics can be used depending on available data and goals of a field study. Defining phenological mismatch at an individual level may serve to test underlying

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evolutionary mechanisms, whereas a population-level assessment could assist with management efforts for species of conservation concern.

Our final path model showed that at the individual level, early breeders were expected to hatch eggs closer to the local food peak. Effects of breeding timing on fitness are often impossible to disentangle from the effects of breeder's quality on fitness (Verhulst and Nilsson 2007), but a causal link has been shown in some cases (Brinkhof and Cavé 1997; Siikamäki 1998). In the Arctic, where food availability quickly declines after the food peak, phenological mismatch with the food peak may strengthen directional selection for early breeding. For example, delayed timing of snow melt has been reported to increase the number of goslings per female in Black Brant, *Branta bernicla nigricans*, possibly by slowing advances in food peaks (Clausen and Clausen 2013). Our final path model also showed that a delayed food peak can improve phenological match at individual nests.

### *Are shorebirds mistimed?*

Concerning conservation of a species or an ecosystem, studies on phenological mismatch face an inevitable question: what levels of phenological mismatch are sufficient to reduce fitness? The original 'Match-Mismatch Hypothesis' predicted that the population growth rate of a consumer increases as its reproductive phenology becomes closer to the abundance phenology of its resources (Cusing 1990). Rigorous monitoring of well-studied systems over the long term has reported negative impacts of phenological mismatch on individual's fitness, and in some cases on population growth (Clausen and Clausen 2013; Reed et al. 2013b; Plard et al. 2014; but see Reed et al. 2013a). Short-term studies may be unable to measure demographic responses to phenological mismatch, but, as we have done, can identify general patterns underlying variation

in phenological mismatch. Here, we showed that the degree of phenological mismatch follows geographic gradients, providing new evidence regarding the mechanisms that underlie phenological mismatch. Given that simultaneous monitoring on multiple trophic levels is challenging, use of 'space-for-time substitutions' can broaden our understanding on ecosystem responses to climate change (Blois et al. 2013).

## *Conclusions*

In conclusion, we show that widely distributed Arctic sites showed three different patterns of climate change during the laying period of shorebirds over the past 25 years. Phenology of invertebrates showed greater variation than shorebirds in our system, and the extent of phenological mismatch varied significantly among sites and species at individual and population levels. We identified both latitudinal and longitudinal gradients in the extent of phenological mismatch. However, geographic patterns were not mediated by climatic conditions as we expected, but through latitude- or longitude-dependent variation in phenology. Individual shorebird nests at more northerly or easterly sites were less well matched with the annual food peak. However, the delayed food peak at northerly or easterly sites partially offset the negative direct effects of latitude and longitude. Our results suggest that large-scale geographic processes determine the intensity of phenological mismatch between Arctic-breeding shorebirds and their invertebrate prey. The opposite signs of direct and indirect effects corroborate the importance of understanding phenological mismatch as a complex process involving both environmental and ecological mediating factors as well as broad geographic drivers.

# Acknowledgments

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Table 4-1. Comparison of two global models with the hypothesized structure and an alternative structure for the individual- and population-level phenological mismatch. The hypothesized model had a geographic gradient affecting current weather and climate change, whereas the alternative model had the three exogenous factors at the same level. Fisher's C statistic, the number of pairs in the basis set (k), null probability (p), AIC corrected for small sample size (AICc), delta-AICc, and the number of parameters (K) for each model is shown.

| Response | Model Description | Fisher.C | k | $p \leq$ | AICc | $\Delta$ AICc | K |
|---|---|---|---|---|---|---|---|
| Individual-level mismatch | Alternative model | 364.367 | 10 | 0 | 497.3 | 0 | 65 |
| | Hypothesized model | 1070.808 | 26 | 0 | 1195.3 | 698.1 | 61 |
| Population-level mismatch | Alternative model | 364.367 | 10 | 0 | 497.3 | 0 | 65 |
| | Hypothesized model | 1406.782 | 26 | 0 | 1531.3 | 1034.1 | 61 |

Table 4-2. Comparison of eight competing models showing different causal relationships among exogenous factors, single-trophic level responses, and bi-trophic level responses. Model descriptions show the combination of exogenous factor(s) and single-trophic level response(s) that were unique to each model. Each model included path(s) from single-trophic level response(s) to a bi-trophic level response and also a direct path from exogenous factor(s) to a bi-trophic level response. P-values greater than 0.05 indicate that the model represents the data well and no significant paths are missing from the current model. Only models with a probability greater than 0.001 are shown. See Table 1 for definitions of parameters shown. The model set and estimated parameters were identical for the individual-level response and population-level response because they both contained the same paths.

| Model Description | Fisher.C | k | $p \leq$ | AICc | $\Delta$ AICc | K |
|---|---|---|---|---|---|---|
| Geography $\rightarrow$ Timing | 1.521 | 1 | 0.467 | 35.7 | 0.0 | 17 |
| Temperature $\rightarrow$ Timing | 1.960 | 1 | 0.375 | 42.2 | 6.5 | 20 |
| Climate $\rightarrow$ Timing | 6.911 | 1 | 0.032 | 43.1 | 7.4 | 18 |
| Climate $\rightarrow$ Variance | 8.784 | 1 | 0.012 | 45.0 | 9.3 | 18 |
| Geography & Temperature $\rightarrow$ Timing | 2.493 | 1 | 0.287 | 48.9 | 13.1 | 23 |
| Geography & Temperature $\rightarrow$ Variance | 4.612 | 1 | 0.100 | 51.0 | 15.3 | 23 |
| Geography & Temperature & Climate $\rightarrow$ Timing | 1.518 | 1 | 0.468 | 66.2 | 30.5 | 32 |
| Geography & Temperature & Climate $\rightarrow$ Variance | 4.434 | 1 | 0.109 | 69.1 | 33.4 | 32 |

Table 4-3. Path coefficients and relative sizes for the direct and indirect effects of latitude and longitude on the phenological mismatch at an individual and population level. Path coefficients were estimated from the best fit model. Total indirect effect estimates are the sum of an indirect effect through food and indirect effect through laying. The relative size of each path coefficient for an indirect effect of latitude or longitude is compared to the corresponding direct path coefficient.

|  |  | Path coefficient | | Relative size of path coefficient (/direct effect) | |
| --- | --- | --- | --- | --- | --- |
|  |  | Latitude | Longitude | Latitude | Longitude |
| Individual-level | direct effect | 2.921 | 0.003 | **1** | 1 |
|  | total indirect effect | -2.270 | -0.113 | 0.78 | **37.67** |
|  | indirect effect through food | -2.425 | -0.120 |  |  |
|  | indirect effect through laying | 0.155 | 0.007 |  |  |
| Population-level | direct effect | -0.079 | -0.010 | **1** | **1** |
|  | total indirect effect | -0.006 | -0.0003 | 0.08 | 0.03 |
|  | indirect effect through food | -0.006 | -0.0003 |  |  |
|  | indirect effect through laying | 0.000 | 0.000 |  |  |
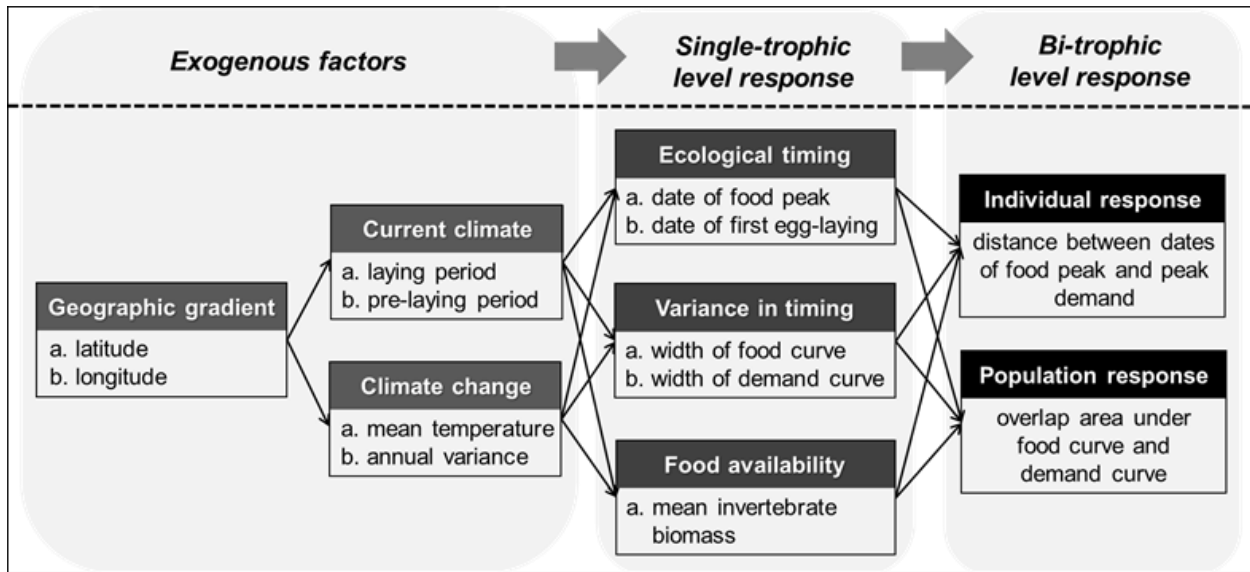
Figure 4-1. Hypothesized causal relationships among geographic gradients, climatic conditions, single-trophic level responses, and bi-trophic level responses.
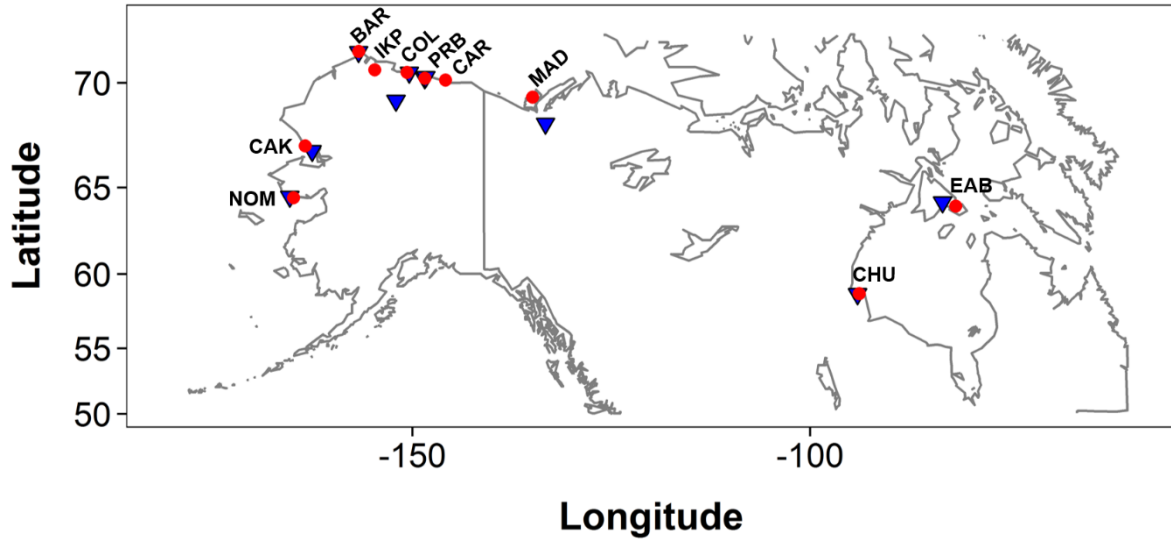
Figure 4-2. Locations of study sites and weather stations where daily temperature data were collected during 1990-2014. Red circle: study site, blue triangle: weather station. Study sites in the Arctic Shorebird Demographic Network (ASDN) are indicated with three-letter abbreviation; from west to east, Nome (NOM), Cape Krusenstern (CAK), Barrow (BAR), Ikpikpuk River (IKP), Colville River (COL), Prudhoe Bay (PRB), Canning River (CAR), Mackenzie Delta (MAD), Churchill (CHU), and East Bay (EAB).
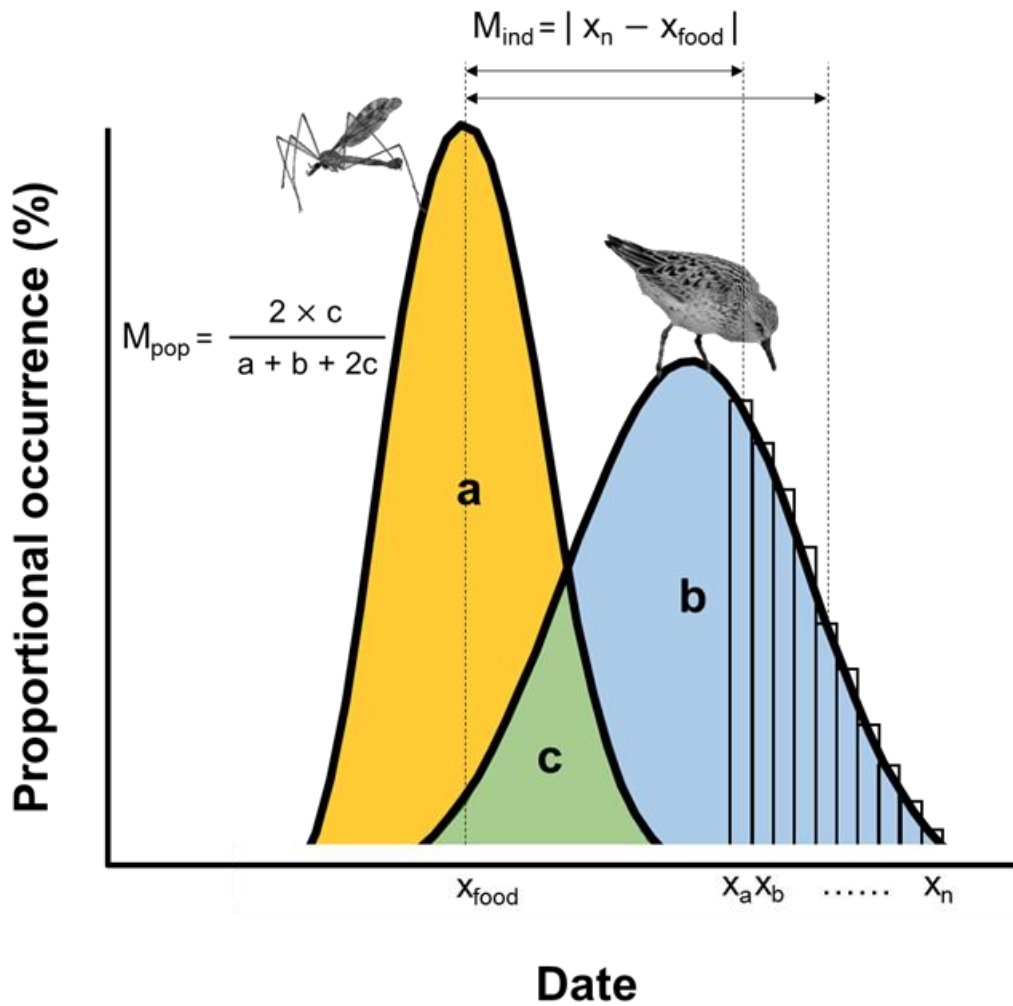
Figure 4-3. Parameterization of phenological mismatch at an individual nest level ($M_{ind}$) and at a population level ($M_{pop}$). $M_{ind}$ is calculated as the number of days between the date of food peak ($X_{food}$) and the date of estimated peak demand for each nest ($X_n$). $M_{pop}$ is calculated as the overlapped area (c, green) under curves of available food (a, yellow) and peak shorebird demand (b, blue) multiplied by two and divided by the sum of areas under the two curves.
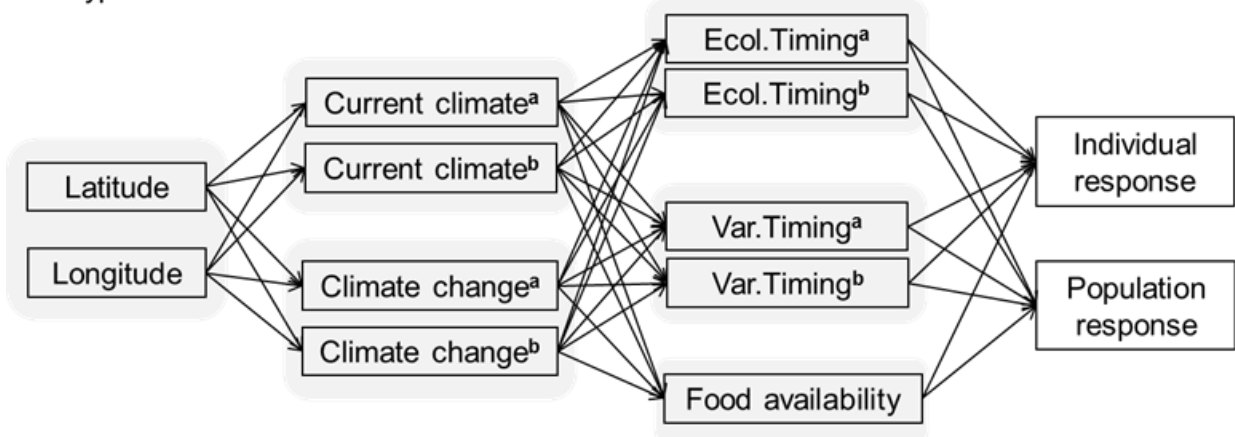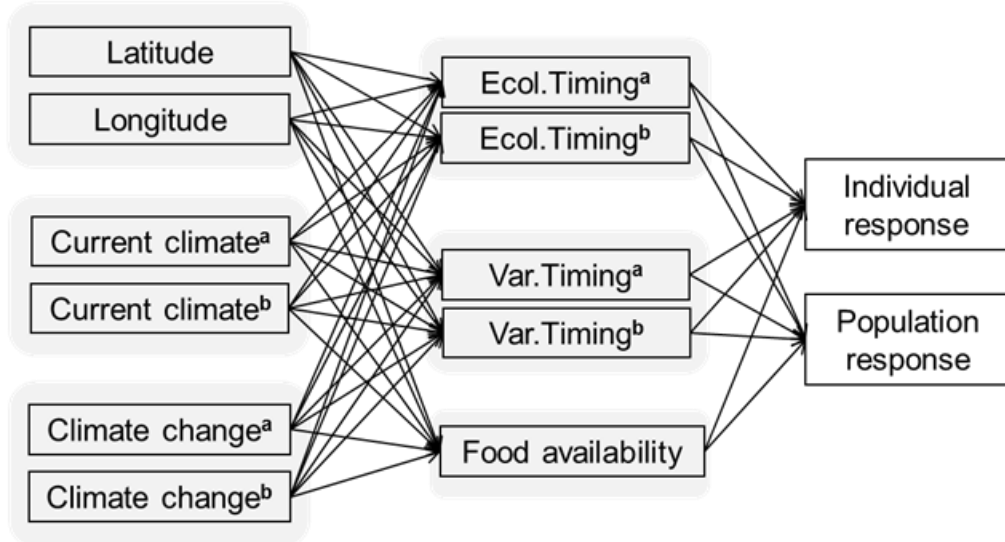
Figure 4-4. First set of model selection testing the hierarchical relationships among the factors geographic gradient, current climate, and climate change variables. a: Model hypothesized in this study; b: alternative model with geographic gradient having direct effects on ecological timing, ecological variance, and food availability instead of having indirect effects through the current climate and climate change. Superscripts a and b denote subordinate variables and corresponds to the variables in Figure 4-1.
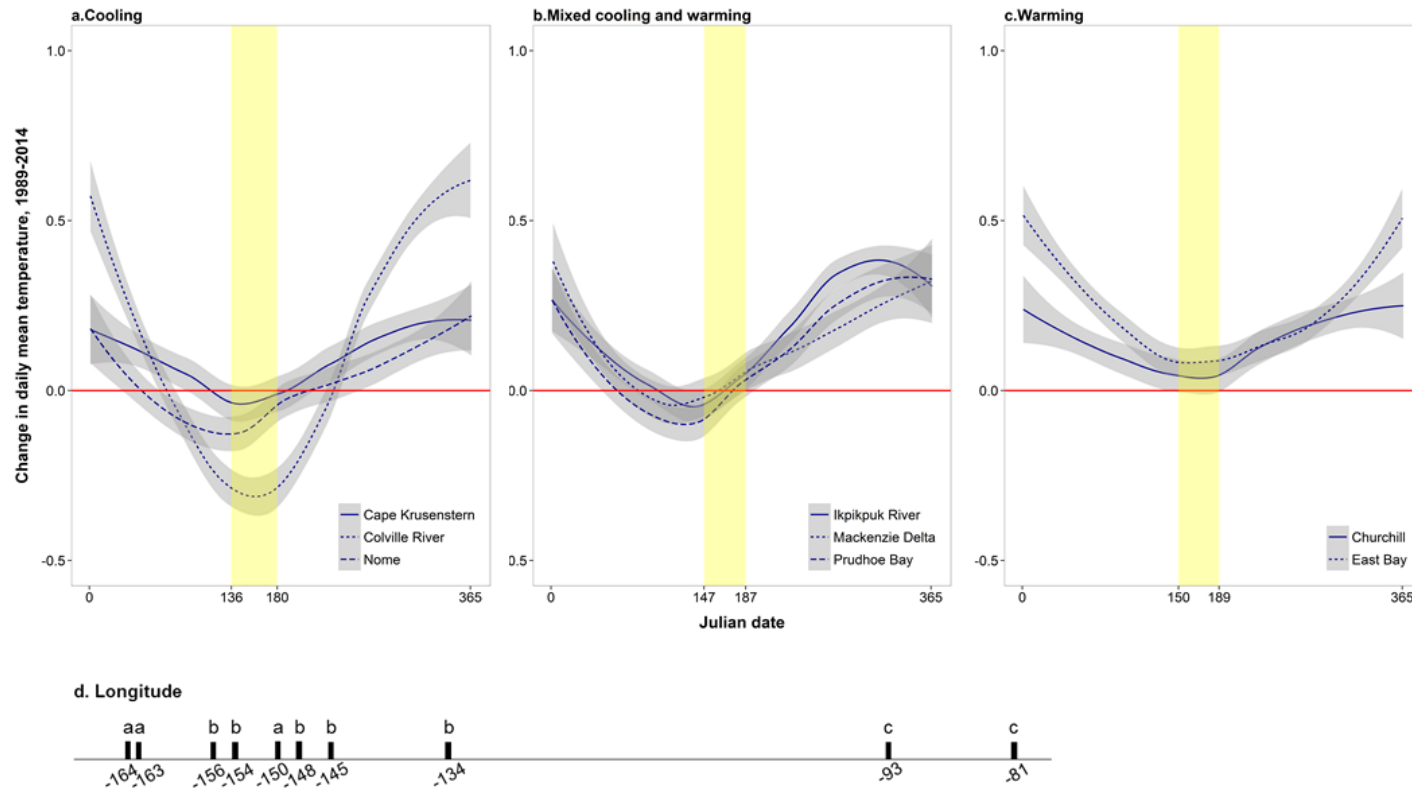
Figure 4-5. Change in daily mean temperature at ten Arctic sites during a 25-year period (1989-2014). (a): cooling trend over the laying period. (b): mixed trend over the laying period. (c): warming trend over the year. (d): longitudinal location of ten sites labeled with corresponding climatic pattern. Horizontal (red, solid) line is at y = 0, indicating 'no change' in daily mean temperature. Vertical (yellow) bar indicates the time window which spans between the date of first egg laying of a first nest and a last nest monitored during 2010-2012 at sites of the same pattern combined. Standard errors are shown as gray bars around the mean slope.

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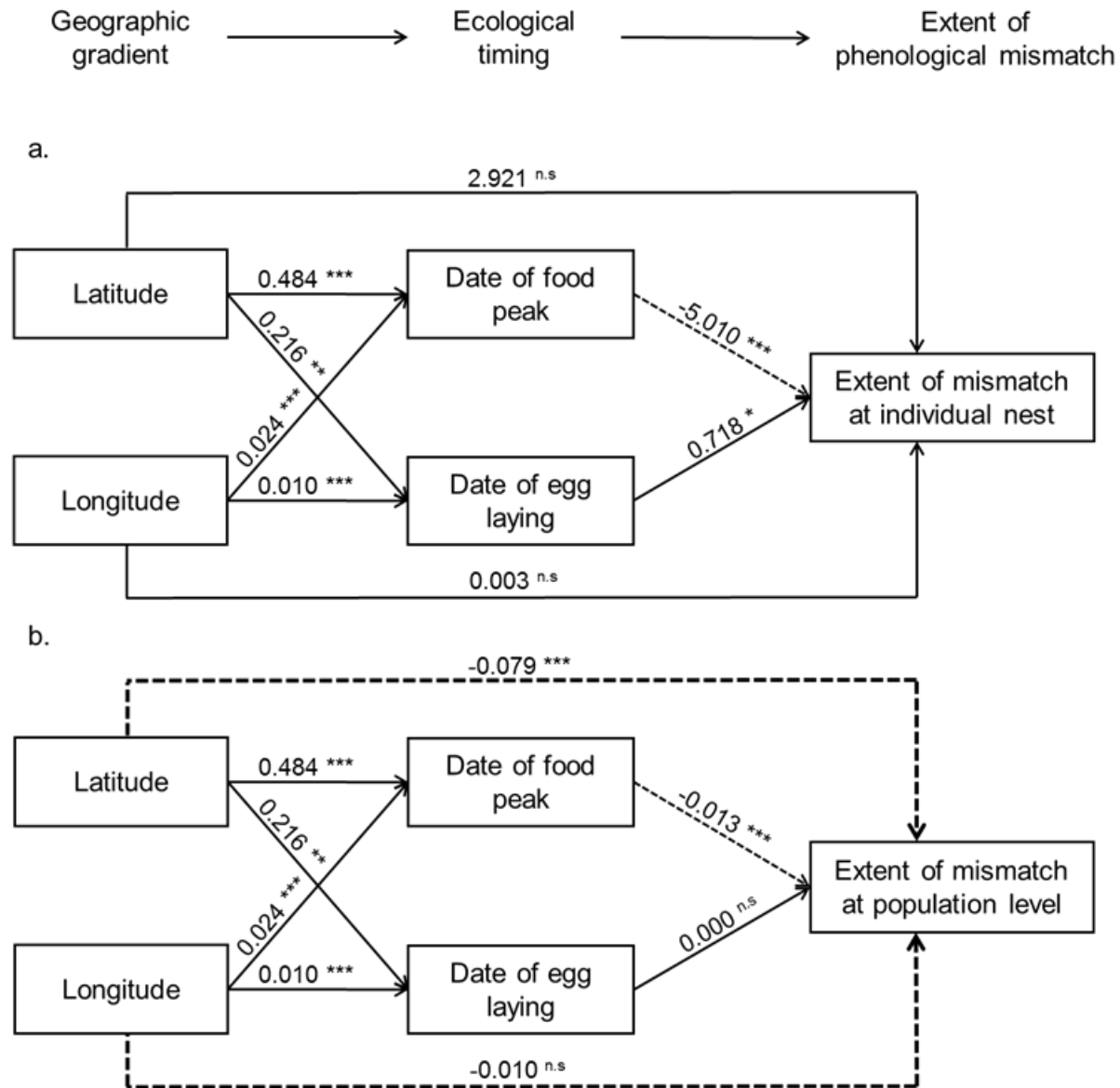
Figure 4-6. Final path models showing the relationships among geographic gradient, ecological timing, and the degree of phenological mismatch at the individual nest level (a) and at the population level (b). Partial regression coefficients are directly comparable and shown for each path. Dashed arrows indicate a negative effect; solid indicates a positive effect. Asterisks denote significance of each path: ***< 0.001; **<0.01; *<0.05; n.s = not significant.

Supplementary Table 4-1. Ecological characteristics of six shorebird species.

| Species | Incubation period | Incubating parent | Mating System | Nesting habitat | Population trend |
|---|---|---|---|---|---|
| Dunlin | 21-22 | Both | Monogamous | Moderate | Apparent decline |
| Pectoral Sandpiper | 21-23 | Female | Polygynous | Wet | Stable |
| Red Phalarope | 18-20 | Male | Polyandrous | Wet | Significant decline |
| Red-necked Phalarope | 19-21 | Male | Polyandrous | Wet | Apparent decline |
| Semipalmated Sandpiper | 20-22 | Both | Monogamous | Moderate to dry | Significant decline |
| Western Sandpiper | 20-22 | Both | Monogamous | Moderate to wet | Significant decline |

Sources: Thomas et al. 2006 (and references therein); Brown et al. 2014 (and references therein); Poole 2005.

Supplementary Table 4-2. Sample size of nests monitored for six shorebird species at ten sites during 2010-2012. Sites are listed from westernmost site to easternmost site. Only species with >20 nests monitored per year at a site were included in the analyses.

| Year | Site | Dunlin | Pectoral Sandpiper | Red Phalarope | Red-necked Phalarope | Semipalmated Sandpiper | Western Sandpiper |
|---|---|---|---|---|---|---|---|
| 2010 | Nome | | | | 24 | 30 | 44 |
| | Cape Krusenstern | 21 | | | | | |
| | Barrow | 32 | 35 | 71 | | 39 | |
| | Ikpikpuk | 30 | 34 | 26 | | 118 | |
| | Prudhoe Bay | | 21 | | | 35 | |
| | Canning River | | 46 | | 29 | 70 | |
| | Churchill | 26 | | | | | |
| | East Bay | | | 22 | | | |
| 2011 | Nome | | | | 49 | 68 | 90 |
| | Cape Krusenstern | | | | | 36 | |
| | Barrow | 31 | 107 | 158 | | 42 | |
| | Ikpikpuk | 30 | 24 | 21 | 21 | 117 | |
| | Colville | | | | | 73 | |
| | Prudhoe Bay | | 25 | | | 40 | |
| | Canning River | | 78 | 26 | 34 | 80 | |
| | Mackenzie River Delta | | | | 17 | | |
| | Churchill | 33 | | | | | |
| 2012 | Nome | | | | 94 | 58 | 72 |
| | Cape Krusenstern | 22 | | | | 55 | 35 |
| | Barrow | 36 | 90 | 143 | 24 | 51 | |
| | Ikpikpuk | 26 | | 22 | 26 | 79 | |
| | Colville | | | | 20 | 101 | |
| | Prudhoe Bay | | | | | 39 | |
| | Canning River | | | | 52 | 136 | |
| | Mackenzie River Delta | | | | 4 | | |
| | Churchill | 26 | | | | | |

(Note: West → East direction indicated for sites.)

Supplementary Table 4-3. Geographic locations of the ten study sites in the Arctic Shorebird Demographics Network and locations of the nearest weather stations.

| Site | | | | Weather station | | | | |
|------|----------|-----------|-----|----------|-----------|---------------|------------|----------|
| | Latitude | Longitude | | Latitude | Longitude | Elevation (m) | Start date | End date |
| Nome | 64.44457 | -164.96137 | MUNICIPAL AIRPORT | 64.51110 | -165.44000 | 1.2 | 1/1/1973 | 10/30/2014 |
| Cape Krusenstern | 67.11423 | -163.49556 | KOTZEBUE RALPH WEIN AP | 66.86670 | -162.63330 | 9.5 | 9/12/1897 | 9/18/2014 |
| Colville River | 70.43698 | -150.67647 | UMIAT AP | 69.22000 | -152.08000 | 85.0 | 1/1/1990 | 12/31/1996 |
| | | | COLVILLE VILLAGE | 70.43220 | -150.40940 | 1.5 | 1/1/1997 | 12/31/2014 |
| Prudhoe Bay | 70.19777 | -148.44996 | DEADHORSE AP | 70.19170 | -148.47720 | 18.6 | 6/1/1999 | 9/18/2014 |
| | | | PRUDHOE BAY | 70.25000 | -148.33330 | 22.9 | 4/1/1986 | 6/13/1999 |
| Canning River | 70.11795 | -145.85062 | DEADHORSE AP | 70.19170 | -148.47720 | 18.6 | 6/1/1999 | 9/18/2014 |
| | | | PRUDHOE BAY | 70.25000 | -148.33330 | 22.9 | 4/1/1986 | 6/13/1999 |
| Ikpikpuk River | 70.55254 | -154.73091 | BARROW POST ROGERS AP | 71.28330 | -156.78140 | 9.5 | 1/1/1901 | 5/6/2014 |
| Barrow | 71.30153 | -156.76003 | BARROW POST ROGERS AP | 71.28330 | -156.78140 | 9.5 | 1/1/1901 | 5/6/2014 |
| Mackenzie Delta | 69.37102 | -134.88782 | INUVIK AIRPORT | 68.18000 | 133.29000 | 68.0 | 11/13/1958 | 2/6/2014 |
| Churchill | 58.73759 | -93.81954 | CLIMATE | 58.71700 | -94.06700 | 29.0 | 2/1/2006 | 2/6/2014 |
| | | | UA | 58.73300 | -94.06700 | 28.0 | 1/1/1943 | 12/31/2010 |
| East Bay | 63.98703 | -81.69661 | HARBOUR | 64.20000 | -83.36700 | 64.0 | 3/1/1943 | 2/6/2014 |

Supplementary Table 4-4. Test results of fixed effects of site and shorebird species on the individual and population level metrics of phenological mismatch. Asterisks denote significance level: \*\*\*< 0.001; \*\*<0.01; \*<0.05.

| | Individual-level mismatch | | | | | Population-level mismatch | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Coef.β | SE(β) | t | p≤ | | Coef.β | SE(β) | t | p≤ | |
| Fixed effect: Site (Barrow was the baseline site) | | | | | | | | | | |
| Random effect: Year, Species | | | | | | | | | | |
| (Intercept) | 11.10 | 2.22 | 5.00 | 0.007 | \*\* | 0.50 | 0.03 | 15.87 | 0.001 | \*\*\* |
| Ikpikpuk | 2.28 | 0.43 | 5.34 | 0.001 | \*\*\* | -0.15 | 0.04 | -3.63 | 0.001 | \*\*\* |
| Colville | -0.40 | 0.64 | -0.63 | 0.528 | | -0.01 | 0.07 | -0.21 | 0.837 | |
| Prudhoe Bay | -0.57 | 1.03 | -0.55 | 0.581 | | -0.49 | 0.08 | -5.87 | 0.001 | \*\*\* |
| Canning River | 2.37 | 0.44 | 5.33 | 0.001 | \*\*\* | -0.03 | 0.05 | -0.74 | 0.465 | |
| Mackenzie | -13.00 | 1.64 | -7.92 | 0.001 | \*\*\* | 0.09 | 0.08 | 1.04 | 0.303 | |
| Cape Krusenstern | 3.12 | 0.70 | 4.46 | 0.001 | \*\*\* | 0.01 | 0.06 | 0.14 | 0.889 | |
| Nome | -2.47 | 0.55 | -4.51 | 0.001 | \*\*\* | 0.06 | 0.05 | 1.27 | 0.208 | |
| East Bay | 0.45 | 1.57 | 0.29 | 0.773 | | 0.20 | 0.11 | 1.74 | 0.087 | |
| Churchill | -1.07 | 0.93 | -1.15 | 0.252 | | -0.11 | 0.07 | -1.64 | 0.107 | |
| | | | | | | | | | | |
| Fixed effect: Species (Dunlin was the baseline species) | | | | | | | | | | |
| Random effect: Year, Site | | | | | | | | | | |
| (Intercept) | 11.01 | 2.53 | 4.36 | 0.005 | \*\* | 0.43 | 0.05 | 9.00 | 0.001 | \*\*\* |
| Pectoral Sandpiper | -3.24 | 0.62 | -5.26 | 0.001 | \*\*\* | 0.10 | 0.06 | 1.67 | 0.100 | |
| Semipalmated Sandpiper | -1.54 | 0.56 | -2.74 | 0.006 | \*\* | 0.05 | 0.05 | 1.09 | 0.281 | |
| Western Sandpiper | -0.81 | 0.80 | -1.02 | 0.310 | | 0.06 | 0.08 | 0.77 | 0.445 | |
| Red Phalarope | -1.51 | 0.61 | -2.50 | 0.013 | \* | 0.05 | 0.06 | 0.80 | 0.426 | |
| Red-necked Phalarope | 2.76 | 0.68 | 4.07 | 0.001 | \*\*\* | 0.10 | 0.06 | 1.80 | 0.078 | |
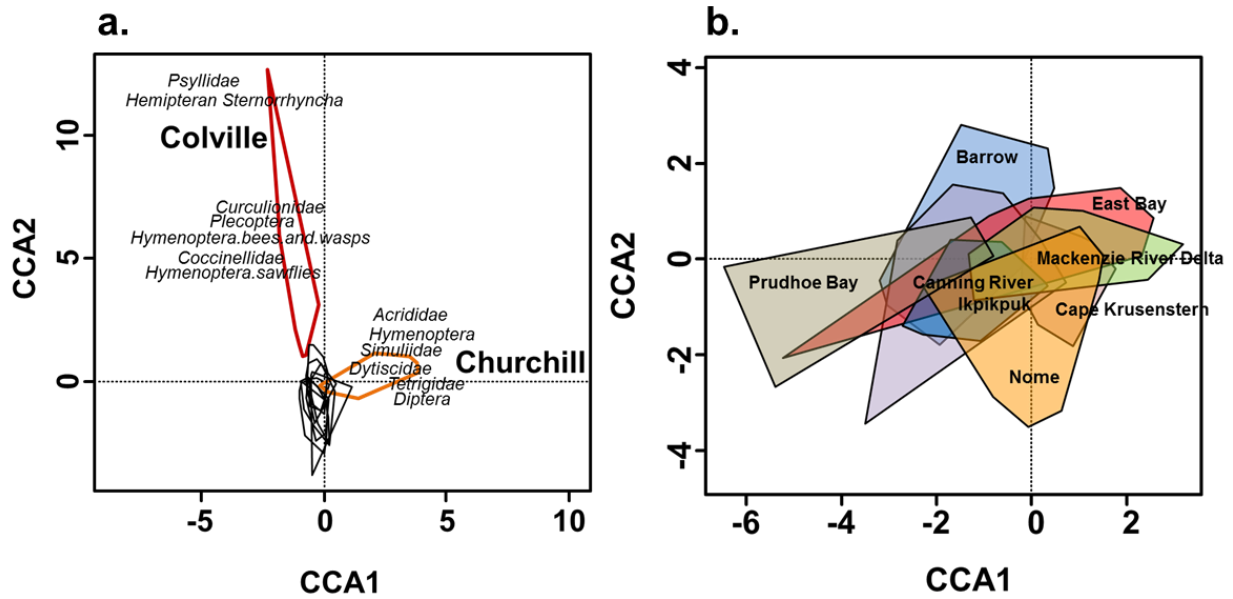
Supplementary Figure 4-1. Biplot of Canonical Correspondence Analysis showing similarities among invertebrate community composition at ten Arctic sites monitored during 2010-2012. Convex hulls were added to encircle sample points by site. Significant overlap among polygons indicates that sites share similar invertebrate community composition. (a): CCA biplot including all ten sites. Colville River and Churchill sites are separated by the invertebrate taxa that are shown on two axes. (b): CCA biplot for the remaining eight sites after excluding Colville River and Churchill sites.
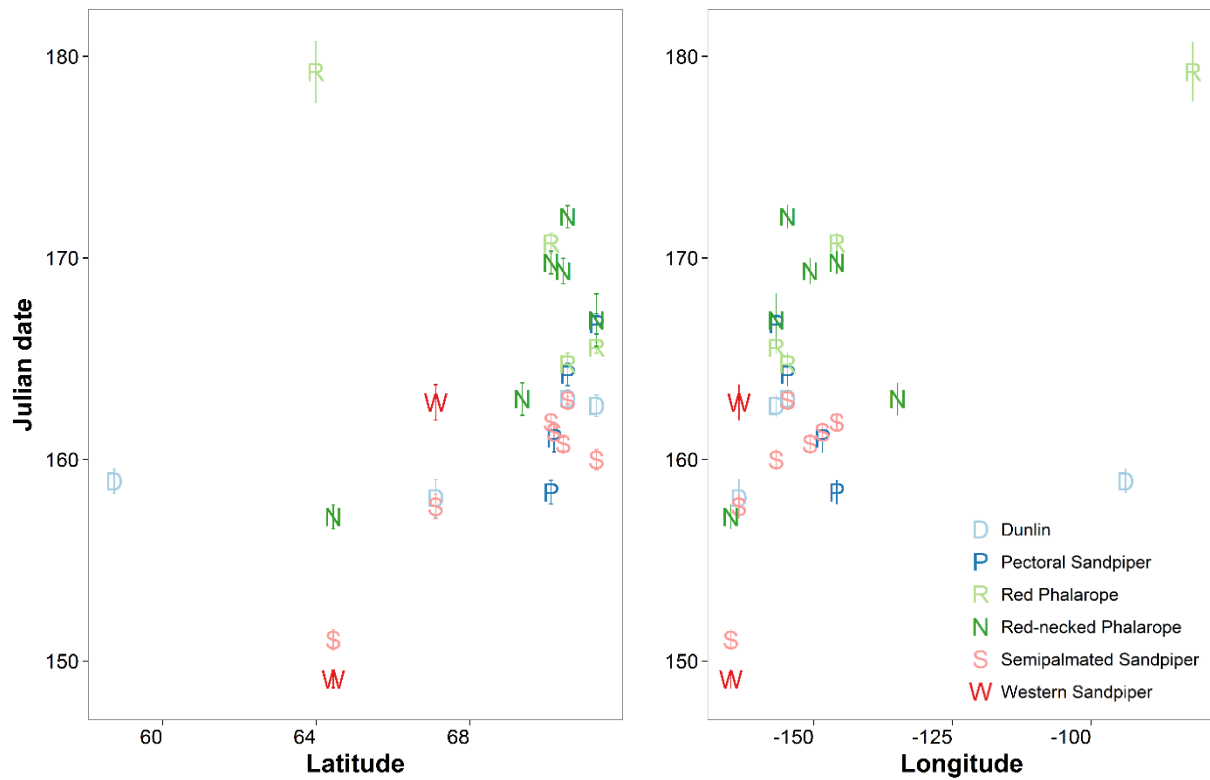
Supplementary Figure 4-2. Dates of first egg-laying for six shorebird species across latitudes and longitudes. Species are coded by letters. Error bars indicate standard errors.
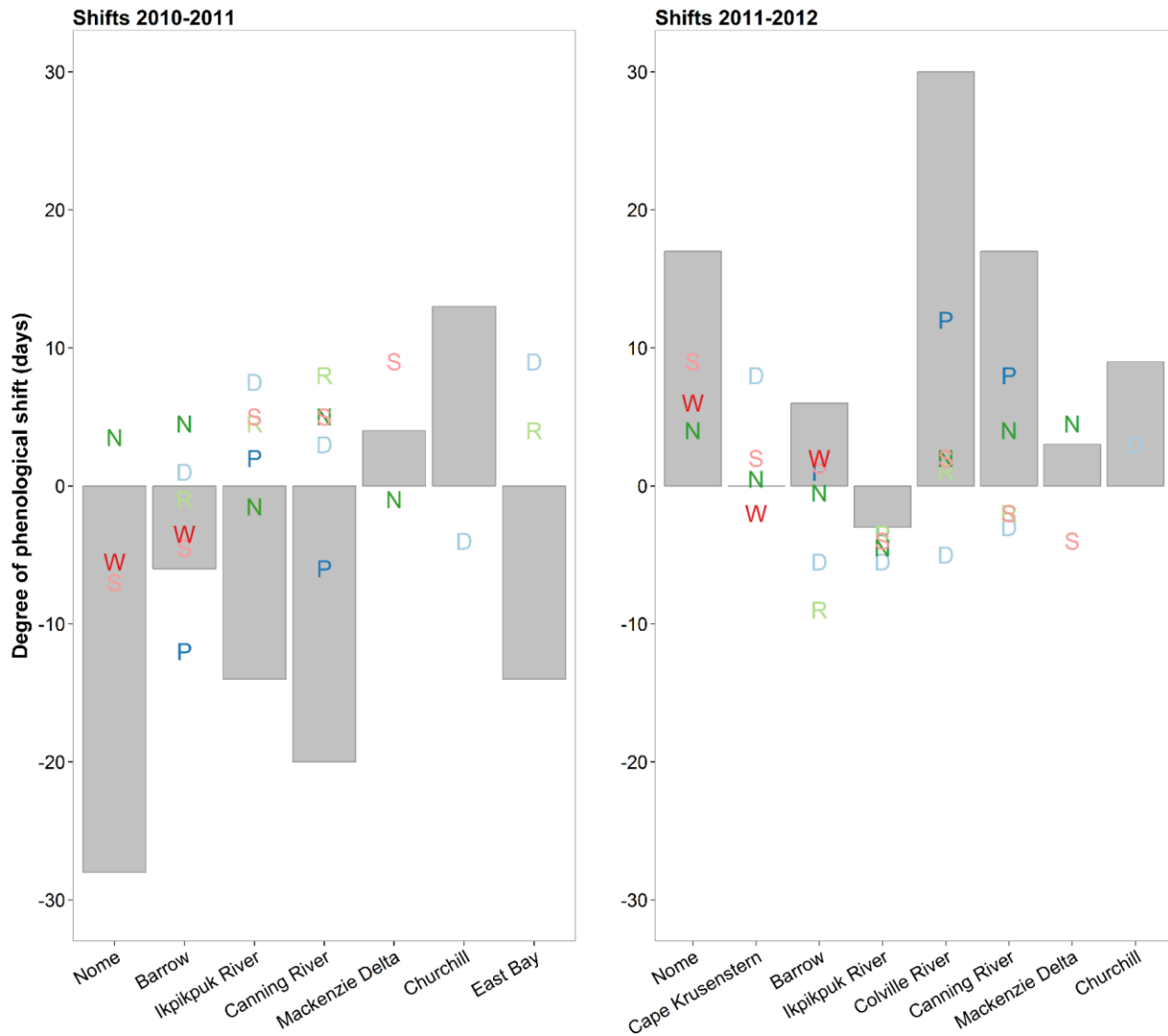
Supplementary Figure 4-3. Extent of phenological shifts for six shorebird species and invertebrates between 2010-2011 and 2011-2012. Degree of shifts are presented as the differences in Julian dates of the mean date of estimated hatch for shorebirds (letter) and of the date of peak biomass for invertebrates (gray bar) between the years. Availability of data varied among years, so some sites are not shown for each pair of years.

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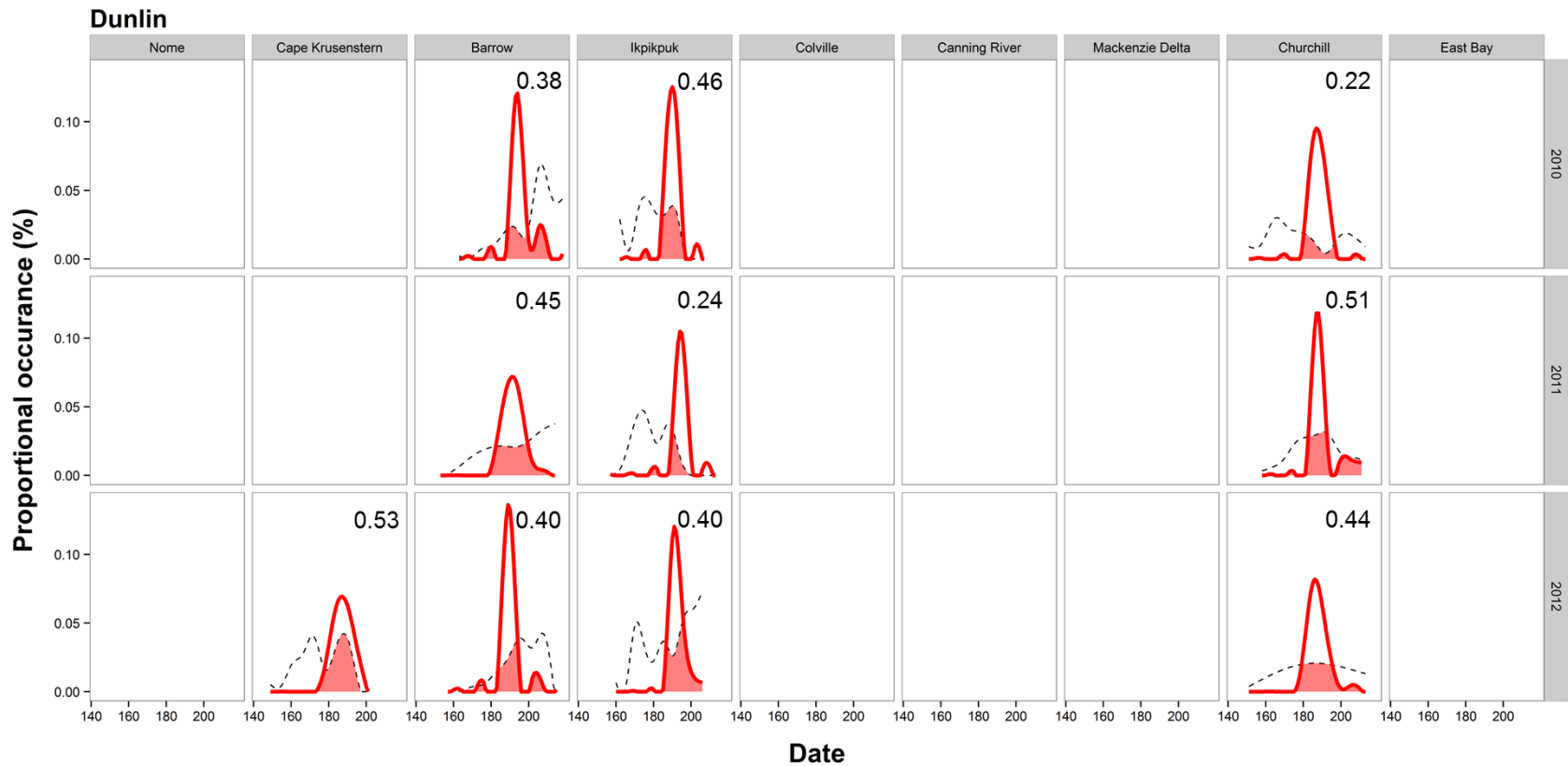
Supplementary Figure 4-4. Seasonal distribution of shorebird nests at peak food demand (red, solid line) and daily total biomass of invertebrate prey (black, dotted line) for each combination of shorebird species, site, and year. Shaded area indicates the overlap area under the two curves. The overlap coefficient is shown in the upper right corner of each plot where available. Blank panels indicate gaps in the dataset for years when invertebrates were not monitored or sites where a shorebird species did not occur.

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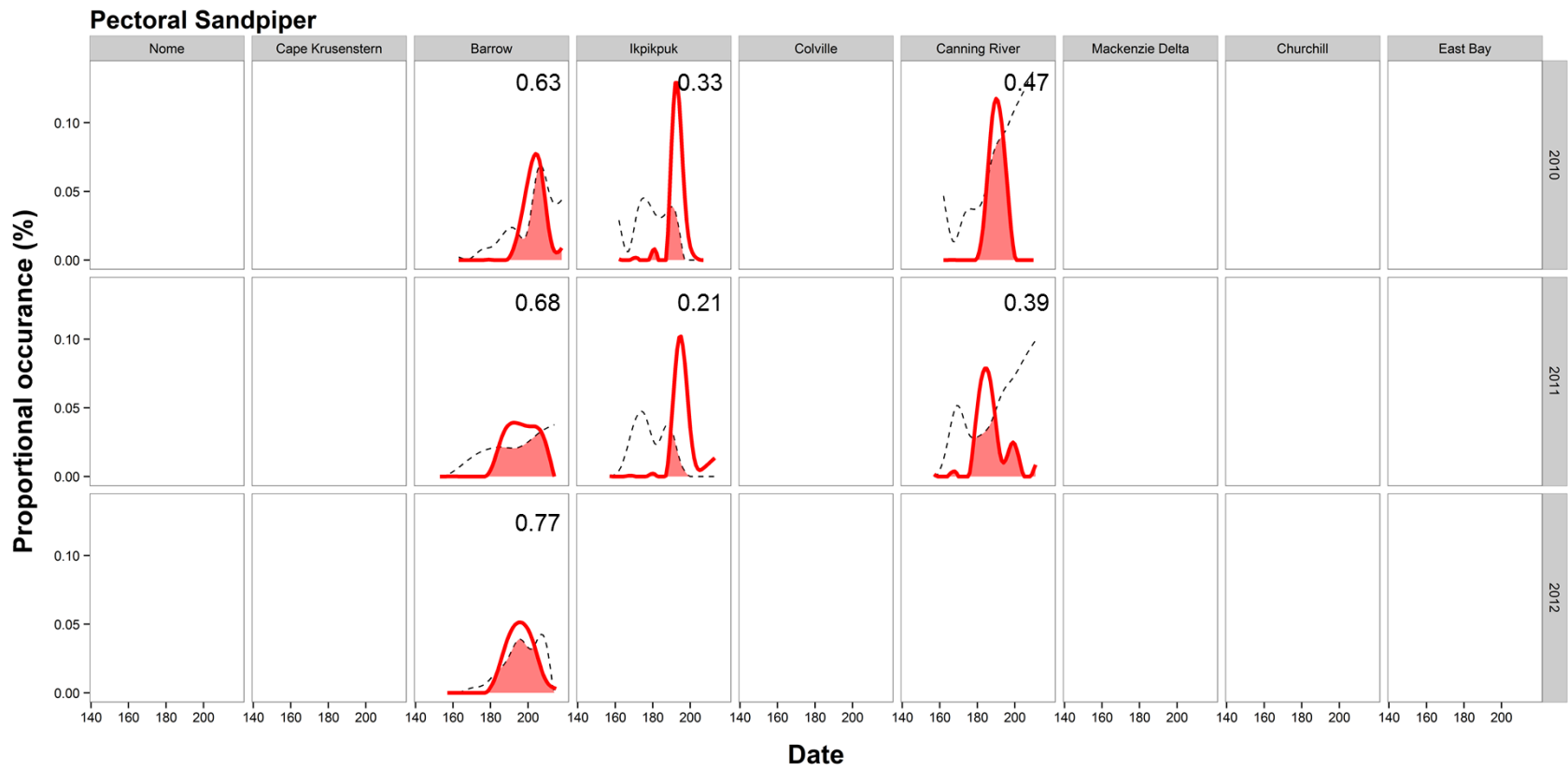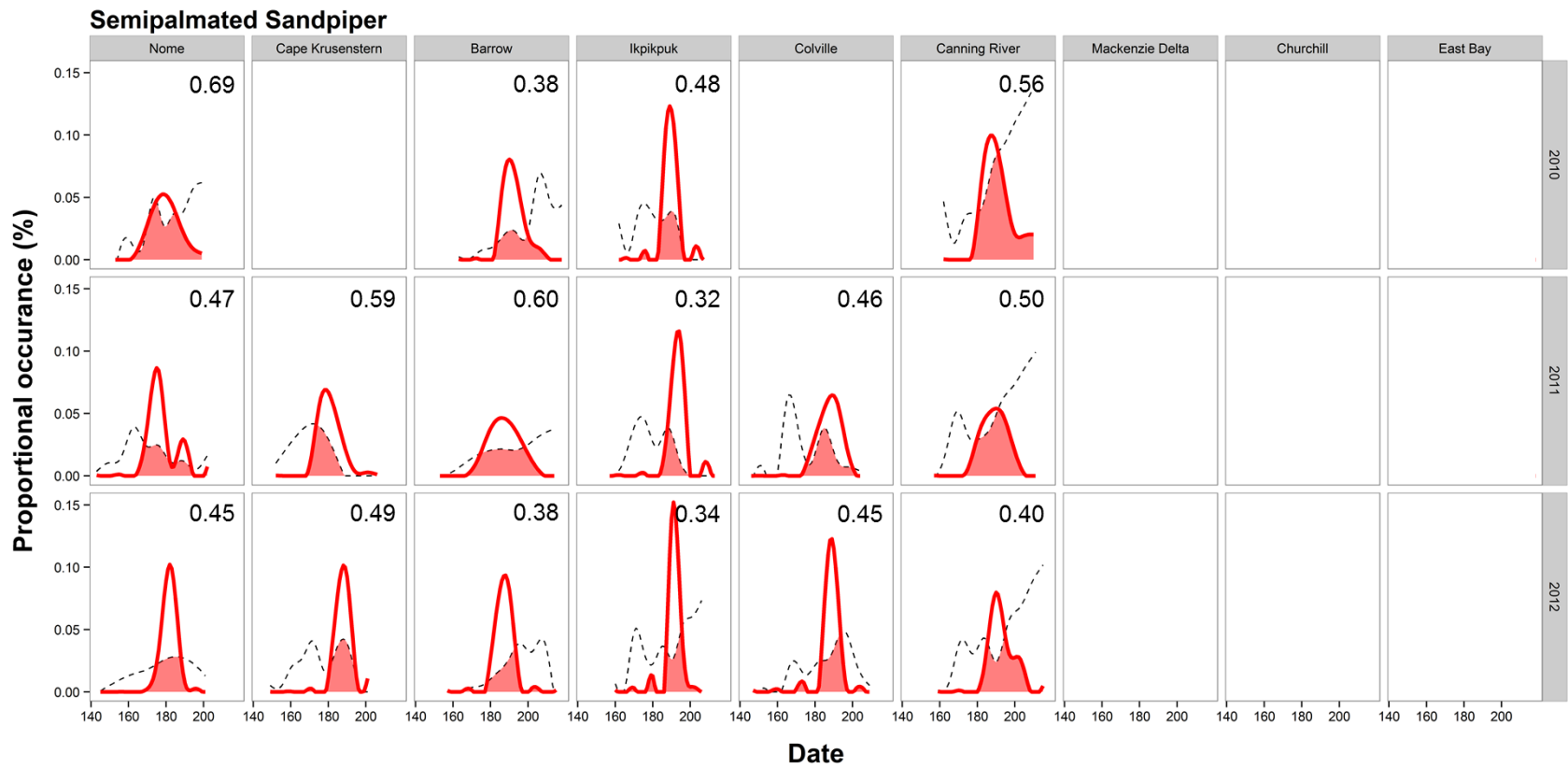
Supplementary Figure 4-4. Continued for Pectoral Sandpiper.
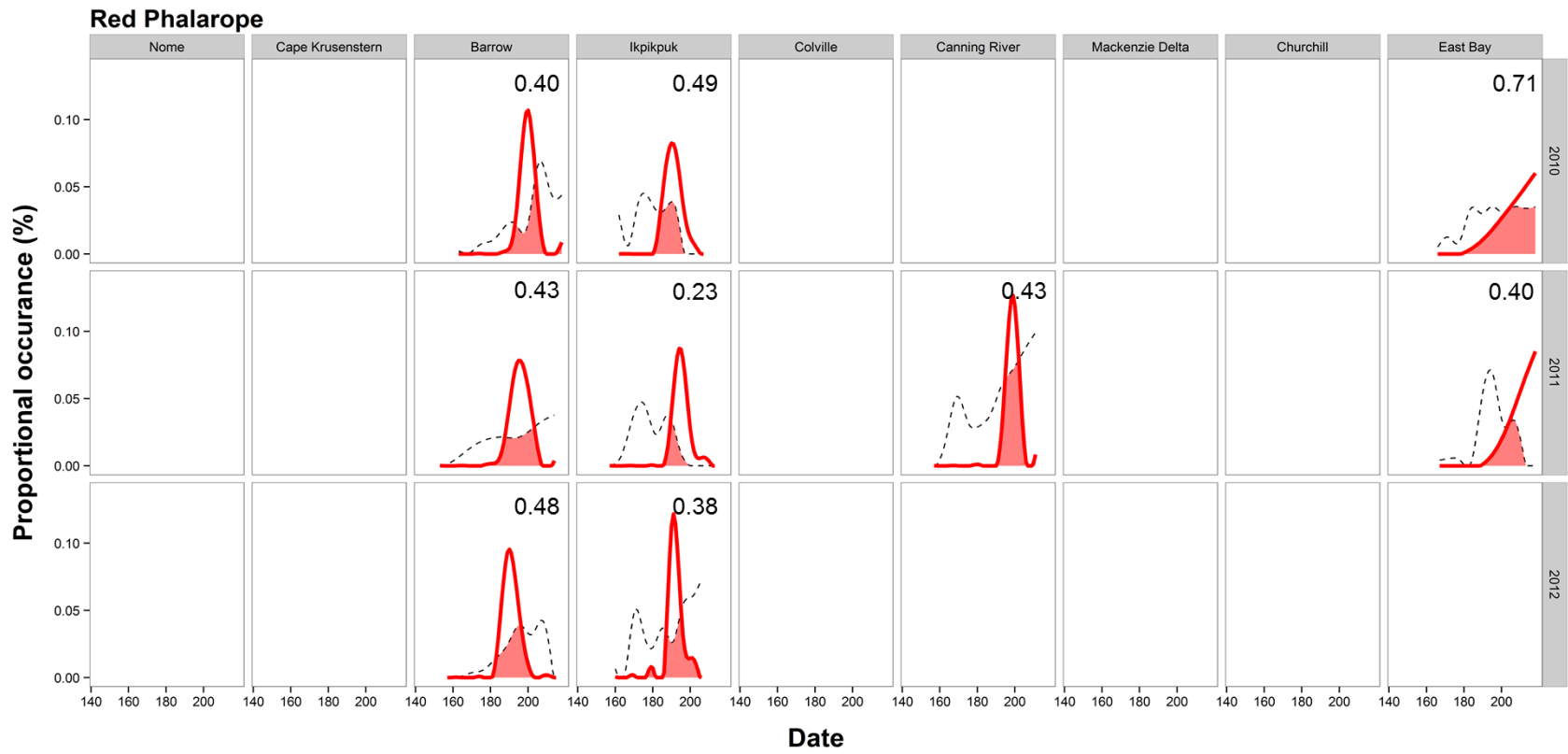
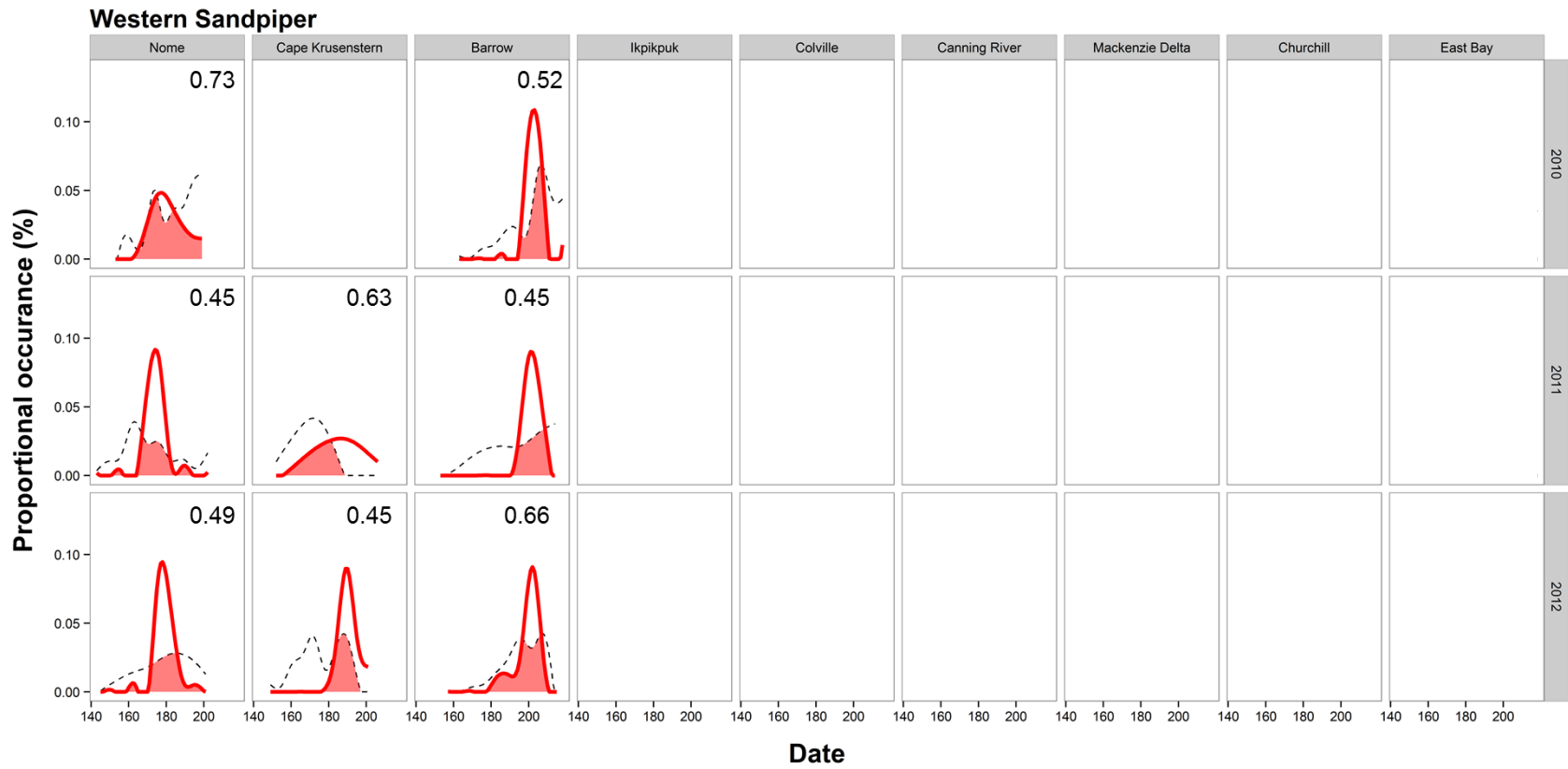Supplementary Figure 4-4. Continued for Red Phalarope.
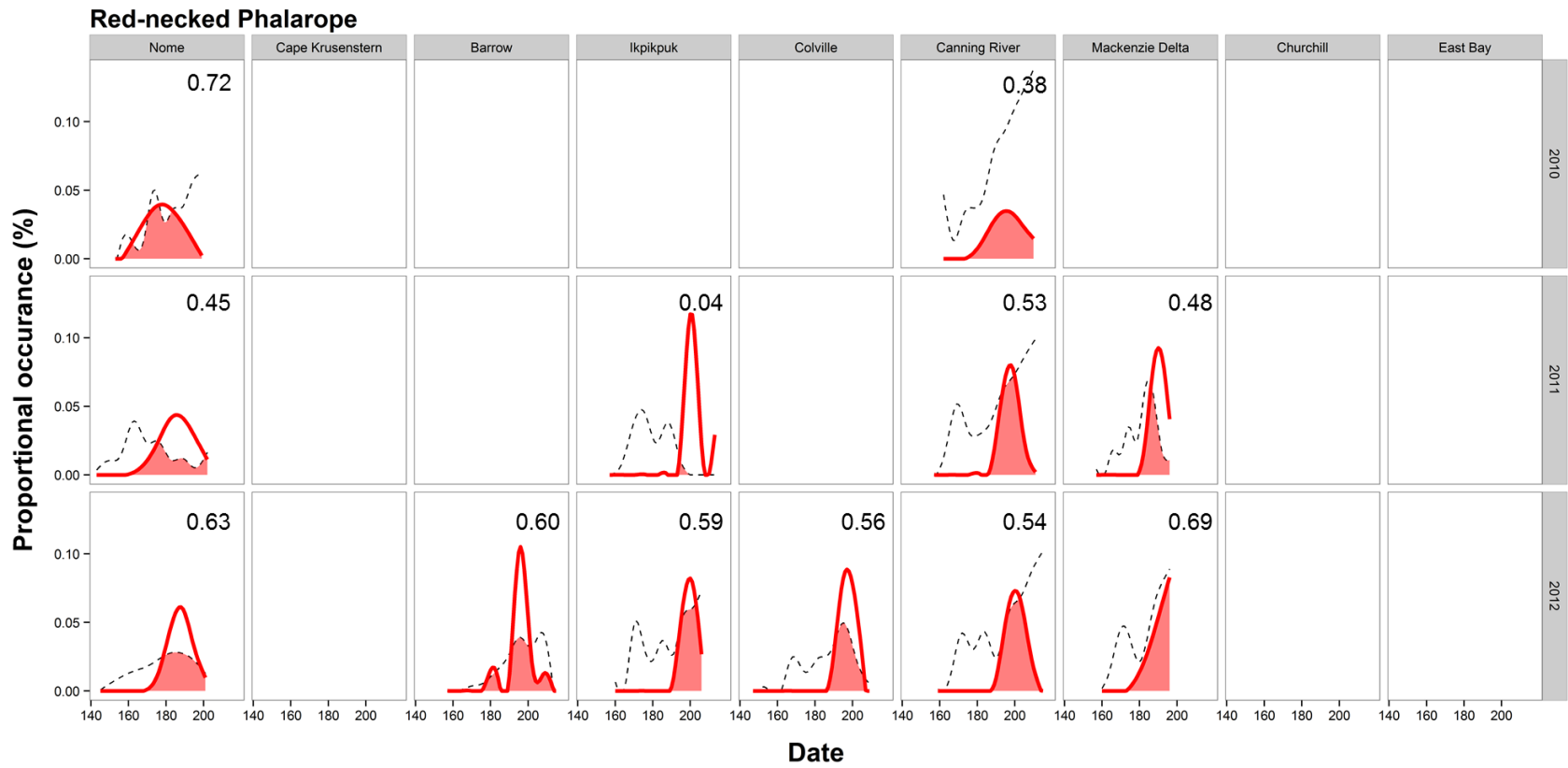
**Red-necked Phalarope**

Supplementary Figure 4-4. Continued for Red-necked Phalarope.

Supplementary Figure 4-4. Continued for Semipalmated Sandpiper.

Supplementary Figure 4-4. Continued for Western Sandpiper.

# Chapter 5 - Conclusion

The Arctic Monitoring and Assessment Programme (AMAP 2012) reported that 1) temperatures have increased sharply in recent decades over most of the Arctic region, especially in winter, and winter temperature in Alaska and western Canada has increased by ~3-4 °C over the past half century, 2) the Arctic snow-cover extent in May and June shrunk by 18% between 1966 and 2008, and 3) Arctic precipitation (rain and snow) has increased by about 8% on average over the past century. Average Arctic autumn-winter temperatures are projected to increase by ~ 3 to 6 °C by 2080, even using scenarios in which greenhouse gas emissions are projected to be lower than they have been for the first decade of 21st century (AMAP 2012). Greater increases of precipitation are also projected for the next 100 years.

At ten Arctic sites across western Alaska to eastern Canada, I found that the warming trend of winter temperature was significant and consistent across ten sites. However, a longitudinal gradient of warming trend was found for summer during 1990-2014. Sites in western Alaska showed a long-term cooling trend for the breeding window of shorebirds, sites on the northern slope of Alaska and Canada showed mixed cooling and warming trends, and sites in eastern Canada showed year-round warming trends (Chapter 4). A closer look at the long-term climate change at Nome, Alaska, during 1974-2014, forewarns that trends of climate change are not only sensitive to seasons but also variable among breeding stages (Chapter 3). Long-distance movements coupled with spatial heterogeneity in the rate of climate change have made migratory shorebirds a group of taxa of special concern under climate change (Fontaine et al. 2009; Senner

2012). My dissertation study suggests that temporal heterogeneity in the rate of climate change on the breeding ground may pose additional threats to summer residents in this region.

The overall goal of my study was to gauge impacts of climate change on the breeding phenology and reproductive performance of Arctic shorebirds. I found evidence that sympatric species of shorebirds are closely tracking temperature change at their breeding ground and timing their breeding accordingly (Chapter 2). Three focal species at Nome present vastly different geographic distributions and use different flyways for migration (Poole 2005). My finding that the three species are responding to the local temperature change at the same rate supports the idea that the environmental drivers on the breeding grounds are more important factor than carry-over effects from wintering or stop-over sites (Ockendon et al. 2013). Differences in parental care systems and subsequent energetic demands for the three species, however, led them to adjust their breeding performances in opposite directions (Chapter 2). My dissertation research has led to two important findings: first, climate change and subsequent shifts in breeding phenology can cause variation in the reproductive investments and output. Second, population projection under climate change needs to be species-specific rather than region- or site-specific.

Importance of species-specific studies becomes more obvious knowing that even slight changes in the timing of breeding puts sympatric breeders into different temperature-precipitation regimes (Chapter 3). Arctic-breeding shorebirds are physiologically adapted for breeding at high latitudes (Piersma 2002; Martin and Wiebe 2004), but I found that shorebirds are still sensitive to small changes in the daily temperature or precipitation (Chapter 3). Merilä and Hendry (2014) point out how most climate change studies, instead of directly testing, infer

climate change as the specific causal agent for the observed phenotypic change. However, even such inference is not possible without first knowing how organisms respond to their natural thermal environment. Understanding short-term responses of reproductive traits to temperature or precipitation is a prerequisite for understanding the mechanisms of how climate change at a broad-scale might affect reproduction of an organism.

To further specify the climate change as a causal driver for phenotypic changes, we need experimental selection methods (Merilä and Hendry 2014). Artificial warming of the environment in a natural, or semi-natural, setting can incorporate the traditional treatment-control comparison into climate change research, and provide strong evidence on the ecological impacts of climate change (Visser et al. 2009; Liu et al. 2011). Manipulation studies can also untangle the impacts of temperature and precipitation, which are difficult to separate with observational studies on a natural population (Legault and Cusa 2015). When tested beyond a range of thermal or moist conditions that an organism experiences in nature, experimental manipulations can identify the thermal optima or physiological ceiling of an organism and help to predict how one might respond to extreme climatic conditions (Piersma and van Gils 2010).

Evolutionary selective pressure on the optimal timing of breeding takes action when the precocial young of shorebirds feed on their own after hatching (McKinnon et al. 2012; Senner and Sandercock, unpubl.ms.). Whether a pair of breeding birds or a breeding population is mistimed for the food peak or not can be determined only by proving the diminished fitness return coupled with temporal asynchrony with the food peak (Visser et al. 2012). My dissertation study focused on identifying broad-scale mechanisms, which determine the extent of phenological mismatches by comparing pseudo-replicates over a large space at a single point in

time (Chapter 4). I found striking geographic and temporal variation in the extent of phenological mismatch between the hatching of shorebirds and the food peak, and showed that individual shorebird nests hatched their young as early as $-28$ days before or as late as $+43$ days after the food peak. Such individual variation led breeding populations to overlap with the food peak by 2-77% depending on the species, year, and site. In Chapters 2 and 3, I highlighted the species-specific variation in the phenotypic responses owing to differences in their life-history traits. However, at a continental-scale, site-specific drivers likely overrode the species differences.

An interesting finding from Chapter 4 is the latitudinal and longitudinal gradients in the extent of phenological mismatch in Arctic waders. My results suggest that large-scale geographic processes determine the intensity of phenological mismatch between shorebirds and their invertebrate prey. However, the observed geographic patterns were not mediated by climatic conditions as I predicted, but through latitude- or longitude-dependent variation in spring phenology at both trophic levels (Chapter 4). Despite the alleviating effects of delayed food peak at northerly or easterly sites, individual shorebird nests were less well matched with the annual food peak at those sites. A lower degree of phenological match at easterly sites coincides with pronounced population declines of the same group of species (Brown et al. 2010; Andres et al. 2012; Smith et al. 2012). So, are phenological mismatches causing shorebird populations to decline? Demographic costs of phenological mismatch have been reported for other taxa (Clausen and Clausen 2013; Reed et al. 2013b; Plard et al. 2014; but see Reed et al. 2013a). The fact that growth and survival of precocial young of shorebirds was reduced when mistimed with food peaks in other studies suggests a potential demographic cost for shorebirds (McKinnon et

al. 2012; Senner and Sandercock, unpubl.ms.). However, the causal link between the phenological mismatch and population trends should be tested with prolonged monitoring of post-hatch survival and recruitment of the chicks.

Changes in the cryosphere are causing fundamental changes to the characteristics of Arctic ecosystems (AMAP 2012). With thawing of permafrost, land will either dry out or becomes waterlogged and low lying coastal areas could collapse altogether. At the same time, warming climate and enhanced vegetation cover will amplify each other in a feedback loop, and result in expansion of woody plants in tundra habitats (Zhang et al. 2013). Contemporary climate change will ultimately lead to habitat changes for Arctic waders.

The six study species of my dissertation research are representative of a group with widespread population declines, and conservation concerns are relevant because the species have been determined to be vulnerable if exposed to modern climate change (Fernández et al. 2010). Given that population declines are a continent-wide trend with migratory shorebirds (Morrison et al., 2000, 2006), long-term monitoring on Arctic shorebirds with a synthesizing view on the Arctic ecosystem as a whole is more required than ever (Post and Høye 2013). The success of the Arctic Shorebird Demographics Network as a distributed research network provides a useful model for a synchronic approach to understand ecological impacts of climate change and address broad-scale questions.

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