



# Shorebird Reproductive Response to Exceptionally Early and Late Springs Varies Across Sites in Arctic Alaska

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While increases in overall temperatures are widely reported in the Arctic, large inter-annual variation in spring weather, with extreme early and late conditions, is also occurring. Using data collected from three sites in Arctic Alaska, we explored how shorebird breeding density, nest initiation, nest synchrony, nest survival, and phenological mismatch varied between two exceptionally early (2015 and 2016) and late (2017 and 2018) springs. We assessed these differences in the context of long-term data from each site and whether species exhibited conservative or opportunistic reproductive strategies. Conservative shorebirds typically display nest-site fidelity and territoriality, consistent population densities, relatively even individual spacing, and monogamous mating systems with bi-parental incubation. In contrast, opportunistic shorebirds display the opposite traits, and a polygamous mating system with uniparental incubation. In this study, we evaluated 2,239 nests from 13 shorebird species, 2015–2018, and found that shorebirds of both strategies bred earlier and in higher numbers in early, warm springs relative to historic levels (based on 3,789 nests, 2005–2014); opposite trends were observed in late springs. In early springs, nests were initiated less synchronously than in late springs. Nest survival was unrelated to spring type, but was greater in earlier laid nests overall. Invertebrate food resources emerged earlier in early springs, resulting in a greater temporal asynchrony between invertebrate emergence and chick hatching in early than late springs. However, invertebrate abundance was quite variable among sites and years regardless of spring type. Overall, our results were generally consistent with predicted relationships between spring conditions and reproductive parameters. However, we detected differences among sites that could not be explained by other ecological factors (e.g., predators or alternative prey). Differences in shorebird community composition and other subtler methodological/ecological differences among sites highlight the difficulty of understanding the complex nature of these ecological systems and the importance of evaluating questions at multiple sites across multiple years. Our study demonstrates that shorebirds exhibit a high degree of behavioral flexibility in response to variable Arctic conditions, but whether this flexibility is enough to allow them to optimally track changing environmental conditions or if evolutionary adjustments will be necessary is unknown.

**Keywords:** Arctic, environmental variation, nest density, nest initiation, nest survival, nest synchrony, trophic mismatch, wader

## INTRODUCTION

The timing of reproduction is a central topic in avian biology (Perrins, 1970; Drent and Daan, 1980). The general consensus is that species generally time breeding efforts to coincide with periods of high food availability (Lack, 1968). For migratory birds, the timing of such efforts relies on the successful integration of circannual and environmental cues (Gwinner, 1996). In response to recent climate warming, many migratory bird species have adjusted the timing of arrival and breeding efforts to coincide with earlier spring conditions (Crick et al., 1997; Forchhammer et al., 1998; Stenseth et al., 2002; Walther et al., 2002; Parmesan and Yohe, 2003). Other studies indicate that species that are unable to advance their arrival dates may experience negative population consequences (Møller et al., 2008; Kwon et al., 2019); arrival dates may be further constrained by migratory life history, diet, or breeding habitat (Both and Visser, 2001; Jonzén et al., 2006; Both et al., 2010). Disentangling the factors that affect the timing of avian reproductive efforts is especially complex in an era of climate warming (Miller-Rushing et al., 2010; Mortensen et al., 2016).

The ability of individuals to adjust their reproductive phenology may be especially challenging for migratory birds that breed in the Arctic. Because temperatures in the Arctic are increasing more rapidly than in other regions of the earth (Serreze and Francis, 2006; Hodgkins, 2014), environmental cues that migratory animals use to order their annual cycles may now be less reliable due to a spatial decoupling of broad-scale environmental conditions (Robinson et al., 2009; Both et al., 2010). Although long-distance migrations enable individuals to take advantage of abundant food resources, lower predation pressure, reduced competition, and lower pathogen loads found in the Arctic (Gilg and Yoccoz, 2010), Arctic-breeding birds must contend with very short breeding seasons, harsh climatic conditions, and now, rapidly changing, variable, and unpredictable environmental conditions caused by climate change (Meltofte et al., 2007a; Schmidt et al., 2019). The rapid rate of warming at northern latitudes has led to earlier, warmer, and longer summers in these regions (Richter-Menge et al., 2019). In addition, summer rainfall has increased significantly (Kattsov and Källén, 2005) and winter snowfall is predicted to increase at high latitudes (Räisänen, 2007), with as much as a 21% increase in northern Alaska by the end of the century (Littell et al., 2018). Increased snowpack may counter warming temperatures and decrease the rate of snowmelt, but it is unclear how this will alter large-scale hydrological patterns (Musselman et al., 2017). Along with a general warming pattern, both spring and summer weather has also exhibited extreme annual variation (Richter-Menge et al., 2019). As such, these new changes to annual weather conditions have the potential to greatly impact the reproductive demographics of birds in Arctic environments (Schmidt et al., 2019).

Shorebirds are one of the most diverse and abundant avian taxonomic groups of the Arctic environment, with 41 species (117 subspecies or populations) migrating to the Arctic to breed (Smith et al., 2020). Three potential demographic metrics that may be influenced by annual weather conditions are nest

density, nest initiation, and nest synchrony. Shorebirds time their arrival in the Arctic after long migrations to coincide with appropriate spring environmental conditions (Meltofte et al., 2007a; Ward et al., 2016; Ely et al., 2018). Beyond the need for open habitats in which to nest, shorebirds are insectivorous, and the availability of invertebrates is critical to these species, which exploit them to sustain bodily functions, develop eggs, and for young to grow (Klaassen et al., 2001; Piersma et al., 2003; Saalfeld et al., 2019). Temperature and the timing of snowmelt affect the availability of invertebrates in Arctic ecosystems (Høye and Forchhammer, 2008; Tulp and Schekkerman, 2008; Bolduc et al., 2013; Saalfeld et al., 2019), with later snowmelt and colder temperatures equating to later activity (as terrestrial invertebrates break diapause) and emergence (adult eclosion from juvenile stages) of invertebrates due to the direct link between development and sediment temperatures (Custer and Pitelka, 1978; Butler, 1980). However, the timing of shorebird arrival in the Arctic is largely driven by environmental conditions that affect departure time from wintering sites (Rowan, 1925; Gwinner and Helm, 2003; Battley, 2006). Evidence suggests some shorebirds can delay, or even back-track, while on migration if they encounter inclement weather as they near the breeding grounds (Senner et al., 2015; Ely et al., 2018), but shorebirds are likely unable to meaningfully speed up migration if spring conditions in the Arctic are much earlier than average (Saalfeld and Lanctot, 2017). In years of severe weather and late arrival of spring, shorebirds are thought to forego breeding altogether or depart to other areas to breed (Meltofte et al., 2007a and references therein), which could alter local densities of shorebirds (Saalfeld and Lanctot, 2015, but see Robinson et al., 2014).

In years of early snowmelt, shorebirds have been shown to lay eggs shortly after arrival on the breeding grounds (Klaassen et al., 2001; Meltofte et al., 2007b), while breeding is delayed in years with later snowmelt (Smith et al., 2010; Liebezeit et al., 2014). The time between arrival and egg-laying may be determined by food availability during the pre-laying period (Meltofte et al., 2007b), as well as the availability of snow-free sites to nest (Mayfield, 1978; Smith et al., 2010). Recent studies have shown that species have advanced nest initiation dates over several decades as spring temperatures have increased (McKinnon et al., 2012; Liebezeit et al., 2014; Saalfeld and Lanctot, 2017, but see Reneerkens et al., 2016), although in most cases not sufficiently fast to keep up with earlier snowmelt. Further, nest synchrony is likely to increase if time constraints imposed by late, cold springs limit when appropriate conditions to breed are available (Nol et al., 1997; Meltofte et al., 2007b; Smith et al., 2010). Additionally, the ability to nest early may also enable species to re-nest should their first clutch fail, which would result in more asynchronous nesting. Thus, the breeding density and patterns of nest initiation of Arctic-breeding shorebirds are sensitive to spring conditions, but not always in predictable ways.

Spring weather conditions may also impact egg and chick survival through changes in predation rates and timing of invertebrate availability. In years with a deeper snowpack and late snowmelt, the survival of alternative prey—a term used to denote food resources, such as arvicoline rodents (lemmings and voles),

that predators of shorebirds and their nests may alternatively consume—often increases, yielding higher abundances during spring and summer (Korslund and Steen, 2006; Kausrud et al., 2008). The presence of higher numbers of alternative prey may promote increased numbers of breeding shorebirds (Blomqvist et al., 2002; Robinson et al., 2014) and mitigate the risk of predation on their nests (Béty et al., 2002; Smith et al., 2007; McKinnon et al., 2012, but see Weiser et al., 2018a). Persistent spring snow cover may also directly increase the predation of shorebird nests, as late-melting snow limits the area available for nesting, allowing predators to concentrate their search effort (Byrkjedal, 1980; Meltofte et al., 1981; Machín et al., 2019), and the growth of vegetative cover is phenologically delayed making nests more obvious (Laidlaw et al., 2020). However, late-melting snow may also lead to synchronous nesting that could dilute the risk of predation to any one nest (Smith et al., 2010). Because Arctic-breeding shorebirds are primarily income breeders (Klaassen et al., 2001; Piersma et al., 2003, but see Hobson and Jehl, 2010), changes in the timing and abundance of invertebrates may in turn affect shorebird nest attendance due to adult food limitations (Tulp and Schekkerman, 2006; Reneerkens et al., 2011). Adults leaving nests unattended or making more trips away from the nest may increase the likelihood of predation by reducing crypsis of the eggs (adults are better camouflaged than eggs themselves) or drawing attention to the nest (activity near a nest can reveal its location, Smith et al., 2007, 2012; Reneerkens et al., 2011; Bulla et al., 2016; Meyer et al., 2020). But evidence linking warm springs with increased nesting success is equivocal; Weiser et al. (2018a) found limited evidence for such a relationship, with only two of 14 species investigated across a broad geographic region of the Arctic having higher nest survival in warm springs. The availability of invertebrates also directly affects the ability of young to forage and survive, with mismatches between invertebrate availability and chick hatching predicted to be especially decoupled in early springs when shorebirds do not arrive early enough to time their breeding efforts with invertebrate availability (McKinnon et al., 2012; Machín et al., 2018; Kwon et al., 2019; Saalfeld et al., 2019).

Seasonal weather patterns are unlikely to affect reproductive responses of all shorebird species in the same way (Smith et al., 2010; Robinson et al., 2014; Taylor et al., 2018; Machín et al., 2019). One overarching ecological factor that might explain the ability of shorebirds to adapt to changing climatic conditions on Arctic breeding grounds is their reproductive strategy. Arctic-breeding shorebirds have previously been broadly grouped into two reproductive strategies termed ‘conservative’ and ‘opportunistic’ depending on a number of characteristics (Holmes, 1966, 1971; Pitelka et al., 1974). Conservative shorebirds typically display strong nest-site fidelity and territoriality, monogamous mating systems with bi-parental incubation and chick care, and are generally evenly spaced across appropriate habitats. On the other hand, opportunistic shorebirds typically display low nest-site fidelity, a polygamous mating system with uniparental incubation and chick care, and occur patchily and in variable numbers from year-to-year across appropriate habitats. Pitelka et al. (1974) hypothesized that by returning to the same breeding locations each year, conservative

species would have an increased knowledge of local resources, allowing at least a moderate number of offspring to be produced annually, regardless of local conditions. In contrast, opportunistic shorebirds would theoretically have a greater opportunity for more offspring to be produced in some years or locations by forgoing site fidelity and instead selecting the most favorable annual breeding locations. Only two studies on shorebirds have evaluated whether being conservative or opportunistic affected breeding response to seasonal variation in environmental conditions (Saalfeld and Lanctot, 2015, 2017). They found that conservative species tended to have low variability in annual nest densities, and that there were some phenotypically flexible adjustments in most species to snowmelt, although opportunistic species appeared to adjust better than conservative species.

Clearly, the large number of factors that affect shorebird breeding parameters interact and their effects are difficult to disentangle, especially with the influence of regional and local climate change operating directly and indirectly in the background (Juhász et al., 2020). In this study, we took advantage of two exceptionally early and late springs to evaluate how shorebirds were affected by weather conditions at three sites on the Arctic Coastal Plain of Alaska. Response to variable local conditions can provide insight to how shorebirds may adapt to future climatic conditions, allowing winners and losers of climate change and seasonal variability to be identified. We analyzed how nest density, nest initiation dates, nest synchrony, nest survival, and phenological mismatch differed between early and late springs (relative to long-term data collected over many years) within three shorebird communities as a function of their reproductive strategies. To better understand the influence of other confounding factors, we also summarized the occurrence of potential alternative prey (arvicoline rodents) and shorebird nest predators (avian and mammalian). Our goal was to identify life-history traits that may help shorebirds moderate the effects of environmental stochasticity.

We summarized our predictions of how spring weather conditions and other important interacting factors may affect Arctic-breeding shorebirds in **Table 1**. First, we predicted that opportunistic species would nest in higher densities during early springs and in lower densities in late springs, as low site-fidelity affords these species the opportunity to select the most favorable annual breeding locations. This prediction assumes opportunistic species have the ability to assess conditions over large geographic areas and use the timing and rate of snowmelt to make settlement decisions (Pitelka et al., 1974; Lanctot and Weatherhead, 1997; Kempenaers and Valcu, 2017). In contrast, due to their site-fidelity, we predicted that conservative species would nest at consistently similar densities to their historic levels in early springs, but in lower densities during late springs, as late springs may inhibit individuals from acquiring the necessary exogenous reserves for egg laying (Nol et al., 1997; Meltofte et al., 2007b; Smith et al., 2010). Second, we predicted earlier nest initiation dates in early springs and later initiation dates in late springs for all species. However, we predicted a greater response in these dates for opportunistic species given their greater ability to track annual spring conditions as compared to conservative species. Third, we predicted that all

**TABLE 1** | Predictions of how shorebirds would respond to early and late spring conditions by opportunistic and conservative reproductive strategies and the outcomes at Utqiagvik, Colville River, and Prudhoe Bay, 2015–2018.

Factor	Predictions for conservative species	Predictions for opportunistic species	Outcome Utqiagvik	Outcome Colville River	Outcome Prudhoe Bay
Nest density	No change in nest densities in early springs but lower densities in late springs	Higher nest densities in early springs, lower densities in late springs	Yes	Equivocal; both conservative and opportunistic species had higher nest densities in early springs	Equivocal; opportunistic species had slightly higher nest densities in early springs
Nest initiation	Marginally earlier nest initiation dates in early springs; marginally later nest initiation dates in late springs	Earlier nest initiation dates in early springs; later nest initiation in late springs; greater response than conservative species	Yes	Equivocal; both conservative and opportunistic species had earlier nest initiation dates in early springs but at similar rates	Equivocal; both conservative and opportunistic species had earlier nest initiation dates in early springs but at similar rates
Nest synchrony	Less synchrony in early springs; greater synchrony in late springs	Less synchrony in early springs; greater synchrony in late springs; greater response than conservative species	Yes	Yes; but conservative and opportunistic species had similar nest synchrony	Equivocal; conservative species did not show consistent results between early and late springs
Nest survival	Higher survival in early springs; lower survival in late springs	Higher survival in early springs; lower survival in late springs	Yes; but variable rates across late springs for opportunistic species	No	No
Phenological mismatch	Greater mismatch in early springs	Greater mismatch in early springs; lower response than conservative species	Equivocal; only one early spring showed evidence of mismatch	Equivocal; only one early spring showed evidence of mismatch	-No data-

species would exhibit greater nest synchrony in late springs due to time constraints limiting when appropriate conditions are available. During early springs, however, we predicted reduced nest synchrony for all species, as being able to lay earlier affords individuals more time to lay both initial and replacement nests. However, as opportunistic species may be better able to respond to earlier conditions (see above), we predicted even less synchrony in opportunistic species. Fourth, we predicted lower nest survival for all species in late springs, as birds may be forced to breed in snow-free patches that are more easily searched by predators (Machin et al., 2019, notwithstanding the potential benefits of nesting synchronously) and because vegetative cover is delayed. We predicted an opposite pattern in early springs, with all species having higher nest survival. Finally, we predicted that early springs would lead to a phenological mismatch between invertebrate availability and nest hatching dates for all species, although opportunistic species might be more resilient to potential mismatches due to their greater ability to adjust to local conditions.

## MATERIALS AND METHODS

We monitored seasonal weather conditions and shorebirds at three field sites in northern Alaska: Utqiagvik (71° 17' N, 156° 47' W), Colville River (70° 26' N, 150° 40' W), and Prudhoe Bay (70° 19' N, 148° 42' W) from 2015 to 2018. Long-term data, dating back as far as 2005, were obtained from each site to

compare to these 4 years. All three sites are located on the Arctic Coastal Plain, with the maximum distance between sites about 325 km. All sites consist of a mosaic of low, wet marsh habitats and higher, well-drained upland habitats (Kessel and Cade, 1958; Brown et al., 1980). Utqiagvik is located at the northern most portion of Alaska (Point Barrow), and as such, has a colder, later summer on average (Taylor et al., 2018). Utqiagvik (Taylor et al., 2018) and Prudhoe Bay (Liebezeit et al., 2009) were in areas of human development, but study plots were placed >300 m from roads and buildings to minimize any potential influence of human activity (see, e.g., Liebezeit et al., 2009). The Colville River site is located on the outer delta of the river (Hupp et al., 2017). All sites followed a common set of field protocols and data formats developed for the Arctic Shorebird Demographics Network (see brief descriptions below, Brown et al., 2014). Plot size varied by site, with six study plots at Utqiagvik (each 600 × 600 m, 216 ha total), one large plot at the Colville River that was initially 323 ha in size (2011–2016), but reduced to 262 ha in 2017, and 12 plots at Prudhoe Bay (each 100 × 1000 m, 120 ha total).

## Weather

To assess seasonal differences in weather among years (i.e., 2015–2018), we obtained daily temperature data from the nearest meteorological station (National Climate Data Center, 2020) located at Utqiagvik (Wiley Post-Will Rogers Memorial Airport ~10 km away from our study plots), Colville River (Colville Village located ~10 km away), and Prudhoe Bay

(Deadhorse Airport 2–21 km away). From these data, we calculated cumulative daily temperatures in June for each year by summing average daily temperatures (average of the minimum and maximum temperature for a given day) for each day in June. Using the same technique, we also generated long-term temperature averages for the 10 years prior to the study (i.e., 2005–2014).

We determined the loss of snow at our sites in each year by estimating the percent daily snow cover on plots every 2–5 days between late May and the end of June or until 10% snow cover remained. Using these data, we averaged snow cover estimates across all survey locations at each site for each survey day and extrapolated estimates to dates between survey days to generate the percentage of snow cover for each day in June. When average snow cover was < 10% before the end of June, we assumed no snow remained 2 days after the last survey. Additionally, when snow surveys started after 1 June, we removed days in early June when data were not available. Using the same approach, we also generated long-term averages of snow cover for each day in June that had data for all years (i.e., Utqiagvik and Prudhoe Bay: 2005–2014, Colville River: 2011–2014).

## Alternative Prey and Predator Abundance

The number of arvicoline rodents (alternative prey) and avian and mammalian predators were determined at each site and year using incidental observations each day by field staff conducting other field activities. Using these counts, we estimated the number of arvicoline rodents [voles (*Microtus* sp.) and lemmings (*Dicrostonyx* sp.)], foxes [arctic (*Vulpes lagopus*) and red (*V. vulpes*)], and avian predators [Glaucous Gull (*Larus hyperboreus*), Pomarine Jaeger (*Stercorarius pomarinus*), Parasitic Jaeger (*S. parasiticus*), Long-tailed Jaeger (*S. longicaudus*), Common Raven (*Corvus corax*), Sandhill Crane (*Antigone canadensis*), Snowy Owl (*Bubo scandiacus*), Short-eared Owl (*Asio flammeus*), Golden Eagle (*Aquila chrysaetos*), Peregrine Falcon (*Falco peregrinus*), Gyrfalcon (*F. rusticolus*), Northern Harrier (*Circus hudsonius*), Ruddy Turnstone (*Arenaria interpres*), and Rough-legged Hawk (*Buteo lagopus*)] observed per person per day by dividing the total number of individuals within each category observed in June by the average number of people in the field per day and the total number of days in June that observations occurred. For comparison, we also generated long-term (i.e., Utqiagvik: 2005–2014, Colville River: 2011–2014, Prudhoe Bay: 2010–2014) estimates of these abundances for June using the same techniques. Incidental counts of alternative prey such as these correlate strongly with exhaustive mark-recapture techniques used to estimate abundance (Fauteux et al., 2018). While this may not be true for some predators (e.g., counts of fox, Liebezeit and Zack, 2008), our goal was to broadly generalize the abundance of alternative prey and predators in our two early and two late springs relative to long-term counts. Doing so allowed us to better eliminate potentially confounding factors impacting our analysis of the inter-annual variation in shorebird responses.

## Invertebrate Availability

To estimate invertebrate biomass at Utqiagvik and Colville River (no invertebrate data were collected at Prudhoe Bay), we used 10–16 modified “Malaise” pitfall traps equally distributed among mesic and xeric tundra habitats to capture available invertebrates throughout the nesting season. These traps consisted of a 38 cm × 5 cm × 7 cm plastic container placed at ground level that captured non-flying invertebrates, and a 36 cm × 36 cm mesh screen placed perpendicular above the container to capture aerial invertebrates that hit the screen and fell into the trap (Brown et al., 2014). These traps act passively to measure both abundance and activity levels of invertebrates, and as such, have previously been used as a proxy for invertebrate availability for insectivorous birds in the Arctic (Schekkerman et al., 1998, 2003; Bolduc et al., 2013; Saalfeld et al., 2019). We typically sampled traps every 3 days between early June and late July. Individual prey items were identified to family or order and length was measured to the nearest 0.25 mm for individuals < 2 mm and to the nearest 0.5 mm for individuals > 2 mm. We calculated mass for each individual using published length-mass regression equations based on taxon (Rogers et al., 1977; Schoener, 1980; Sage, 1982; Gowing and Recher, 1984; Wrubleski and Rosenberg, 1990; Sample et al., 1993; Hóðar, 1996; Ganihar, 1997; Hawkins et al., 1997; Lang et al., 1997; Sabo et al., 2002). We estimated total biomass per trap day (assuming equal biomass for all days within a sampling period) for all invertebrates except large-bodied bees and wasps within the order Hymenoptera. The latter are likely too large for most shorebirds to consume (Pearce-Higgins and Yalden, 2002; Schekkerman and Boele, 2009).

## Shorebird Reproduction Metrics

We located shorebird nests by conducting area searches or dragging ropes across the tundra to flush adults from nests and by following birds exhibiting behaviors indicative of nesting back to their nests (Brown et al., 2014). Search effort varied between sites. At Utqiagvik, one rope drag was conducted toward the end of June and daily searches were conducted 6 days per week throughout June on each plot (4 h per day, Saalfeld and Lanctot, 2015). At the Colville River, 2–3 observers searched the study plot for 6–8 h each day during June. At Prudhoe Bay, study plots were searched for nests using alternating rope and single-person area searches (two each) between early and late June (Bentzen et al., 2017).

We estimated nest initiation date (date first egg laid) based on the number of eggs if nests were found during egg-laying (assuming 1 egg laid per day for all taxa, although plovers may take 1.5 days, Colwell, 2006), or by back-calculating from known hatch date using standard incubation duration. If these two methods could not be used, we employed an egg-floatation technique to estimate nest initiation (Sandercock, 1998; Liebezeit et al., 2007; Brown et al., 2014). This technique relies on the fact that eggs lose mass as the embryos inside develop, causing them to sink initially and later float in water. Nests were revisited generally every 5 days during incubation. We recorded a nest as hatched if at least one chick was observed in the nest, or if eggshell fragments indicative of hatching, or an egg tooth, were found in

the nest within 4 days of the expected hatch date (Mabee, 1997; Brown et al., 2014). We recorded the hatch date as (1) the day that downy chick(s) were first found in the nest, (2) the day after eggs were observed with pipped holes in the shells, or (3) 2 days after eggs were observed with star-cracks in the shells (Brown et al., 2014). We classified nests as unsuccessful or failed if we found broken eggshells indicative of predation in the nest, if the clutch disappeared more than 4 days before the predicted hatch date, or if the eggs remained unattended by parents for  $\geq 3$  days. We recorded nest fate as unknown if there was unclear or conflicting evidence at the nest site (Brown et al., 2014). If fate was unknown ( $n = 108$ ), nests were considered successful until the last day they were known to be active (a metric important for the nest survival analysis). We did not include nests found at hatch for nest survival analyses.

## Statistical Analyses

Based on air temperature and snow conditions, we classified each year as having a spring that was either “early” or “late” (hereafter ‘spring’). We also grouped species into either a conservative or opportunistic reproductive strategy (hereafter ‘strategy’) based on Saalfeld and Lanctot (2015) (Table 2). In the case of the Long-billed Dowitcher, which exhibits traits of both strategies, we considered it an opportunistic breeder because of its low to non-existent site fidelity and territoriality, which likely has the most effect on the reproductive predictions tested here (Saalfeld and Lanctot, 2015; Takekawa and Warnock, 2020).

We used general linear models (PROC MIXED, SAS Institute, Inc., Cary, NC, United States) with each nest treated as an independent data point to evaluate the categorical effects of site, year, spring, and strategy on nest initiation date. Here, we used an *a priori* model set consisting of all single variable models, as well as all additive and multiplicative combinations of the above

variables (25 models). We used all possible model combinations in our analysis because all variables and their interactions were thought to be biologically meaningful. However, we restricted models so that year and spring did not enter the same model. We also did not include information on alternative prey, predators, and invertebrates because there was no meaningful variation (alternative prey and predators) or data was not available for all sites (invertebrates at Prudhoe Bay). Similarly, we used the same *a priori* model set (with the inclusion of nest initiation date as a continuous effect) and data structure to investigate variation in daily nest survival using Program MARK (White and Burnham, 1999; Dinsmore et al., 2002). For all multi-model comparisons, we used Akaike’s Information Criterion corrected for small sample sizes ( $AIC_c$ ), in which we considered the model with the lowest  $AIC_c$  value to be the best-supported, and models with a  $\Delta AIC_c < 2$  to be plausible (Burnham and Anderson, 2002).

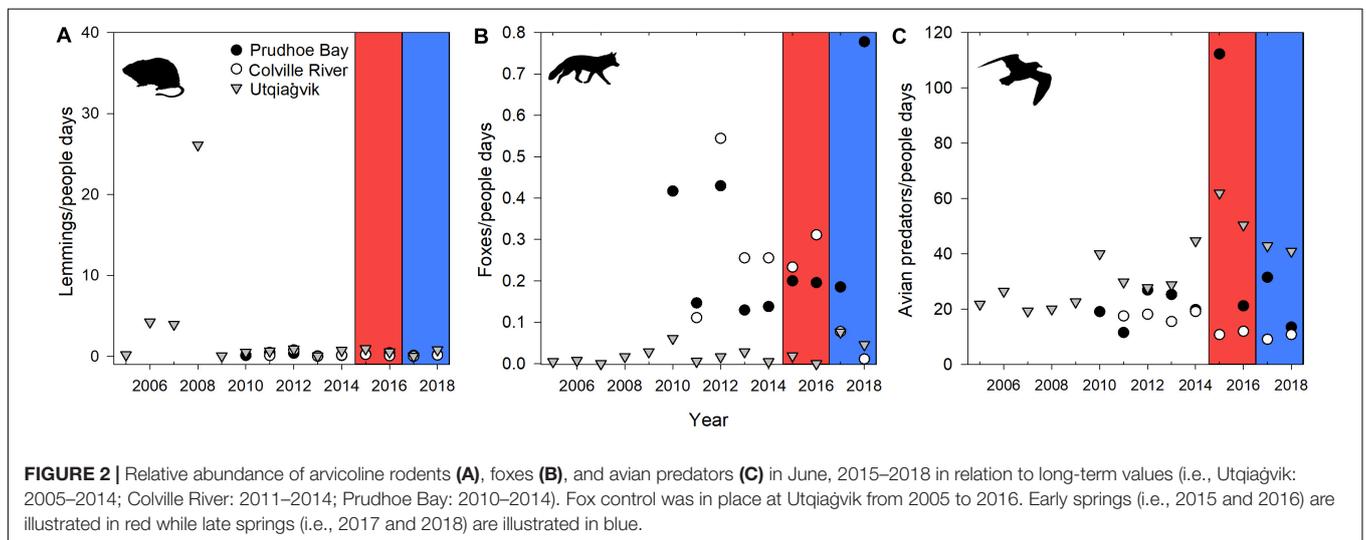
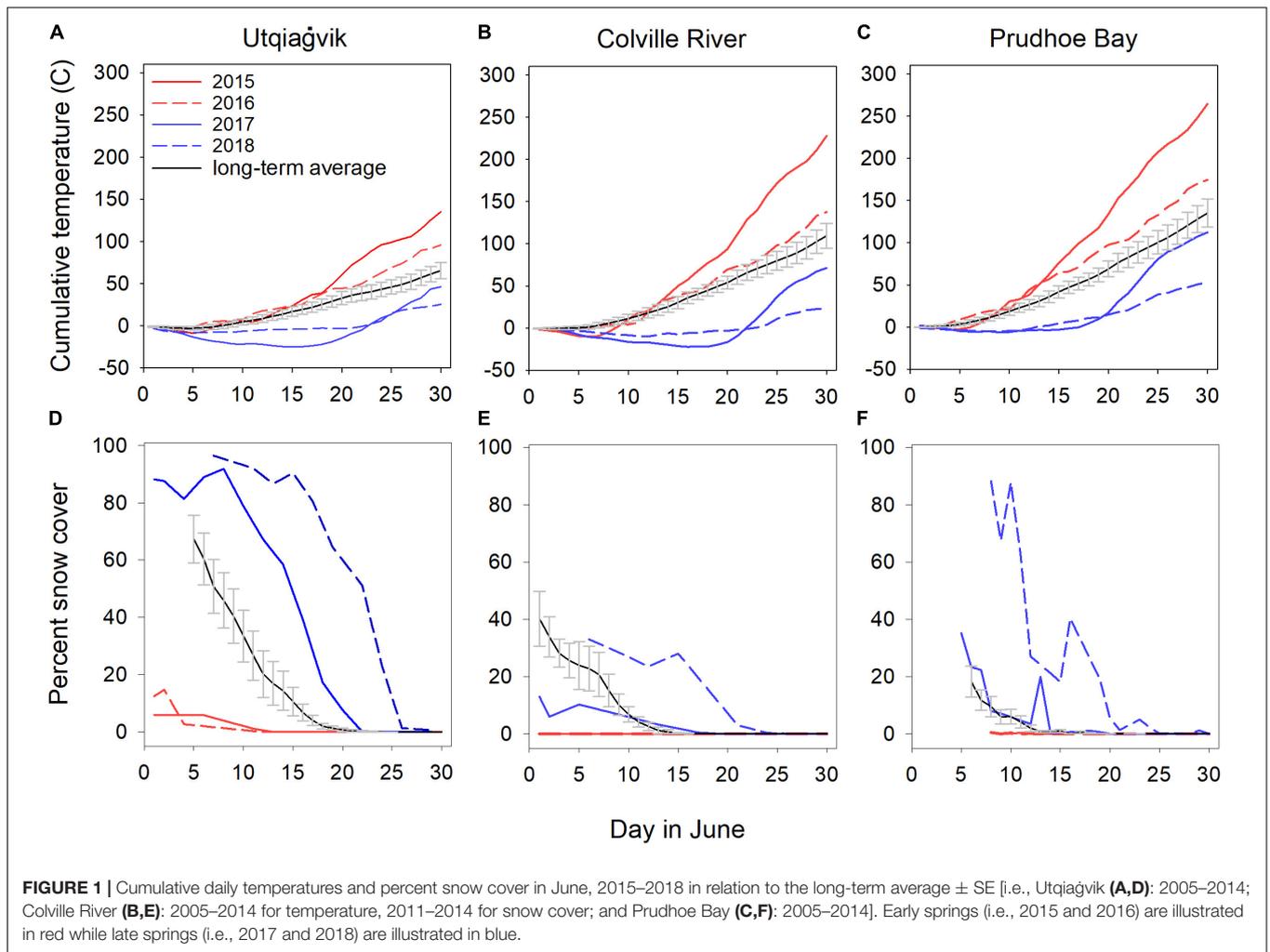
For each site, year, and reproductive strategy, we also calculated estimates for nest density (i.e., cumulative number of nests found throughout study plot(s) divided by the total area of the plot(s) in ha) and nest synchrony (i.e., standard deviation of nest initiation dates of the cumulative number of nests throughout study plot(s); Nol et al., 1997). When calculating nest densities, we restricted nests to those found in the smaller study plot at the Colville River across all years.

For comparison to the early and late springs that were the focus of this study, we also generated long-term estimates of nest density, nest initiation, nest synchrony, and nest survival for all years (i.e., Utqiagvik and Prudhoe Bay: 2005–2014, Colville River: 2011–2014 [small plot for nest density, and large plot for other parameters]). Here, we compared values from the early and late springs to the long-term median values to determine whether an effect was present (i.e., value was above or below the median value as predicted).

**TABLE 2** | Number of shorebird nests by species located at Utqiagvik, Colville River, and Prudhoe Bay, 2015–2018.

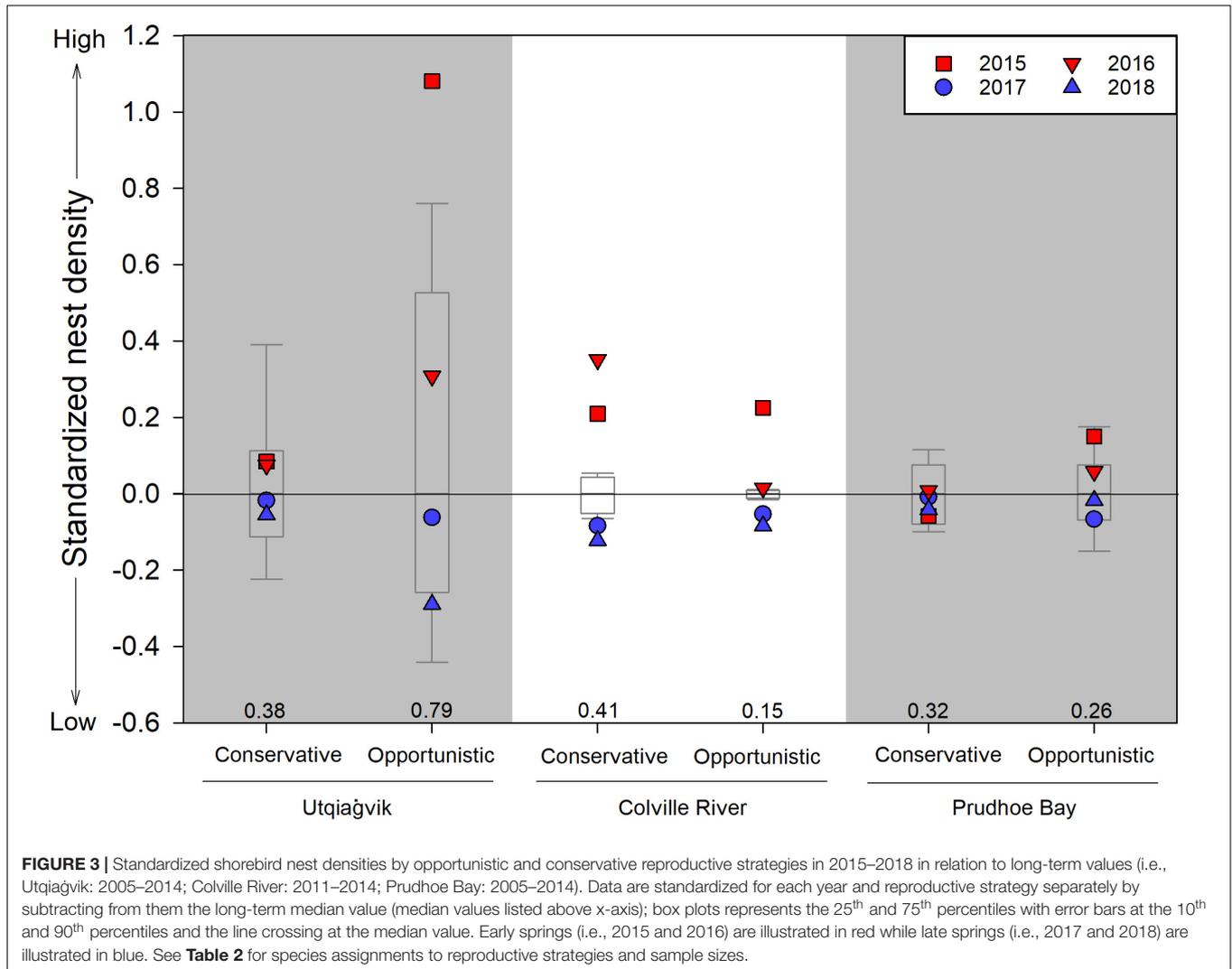
	Utqiagvik	Colville River <sup>a</sup>	Prudhoe Bay	Reproductive strategy <sup>b</sup>
Black-bellied Plover, <i>Pluvialis squatarola</i>	0 (0)	25 (18)	1 (3)	Cons
American Golden-Plover, <i>Pluvialis dominica</i>	40 (100)	0 (1)	4 (10)	Cons
Semipalmated Plover, <i>Charadrius semipalmatus</i>	0 (0)	0 (1)	0 (0)	Cons
Bar-tailed Godwit, <i>Limosa lapponica</i>	0 (0)	5 (1)	0 (0)	Cons
Ruddy Turnstone, <i>Arenaria interpres</i>	0 (1)	16 (26)	0 (1)	Cons
Stilt Sandpiper, <i>Calidris himantopus</i>	0 (0)	1 (0)	18 (41)	Cons
Dunlin, <i>Calidris alpina</i>	136 (336)	56 (55)	12 (24)	Cons
White-rumped Sandpiper, <i>Calidris fuscicollis</i>	0 (6)	0 (0)	0 (0)	Oppor
Buff-breasted Sandpiper, <i>Calidris subruficollis</i>	0 (15)	0 (0)	2 (6)	Oppor
Pectoral Sandpiper, <i>Calidris melanotos</i>	255 (552)	53 (18)	62 (167)	Oppor
Semipalmated Sandpiper, <i>Calidris pusilla</i>	110 (259)	417 (323)	105 (302)	Cons
Western Sandpiper, <i>Calidris mauri</i>	64 (91)	1 (0)	0 (0)	Cons
Long-billed Dowitcher, <i>Limnodromus scolopaceus</i>	65 (197)	0 (2)	15 (20)	Oppor
Red-necked Phalarope, <i>Phalaropus lobatus</i>	46 (71)	51 (62)	47 (82)	Oppor
Red Phalarope, <i>Phalaropus fulicarius</i>	544 (883)	75 (69)	13 (46)	Oppor
Total	1,260 (2,511)	700 (576)	279 (702)	

Number of nests from past years at each site is listed parenthetically: Utqiagvik (2005–2014), Colville River (2011–2014), and Prudhoe Bay (2005–2014). <sup>a</sup>An additional 63 nests were located outside the smaller plot boundary in 2015–2018 (83 in 2011–2014) that were used for nest initiation, nest synchrony, and nest survival analyses. <sup>b</sup>See text for definition of conservative (Cons) and opportunistic (Oppor) reproductive strategies.



At Utqiaġvik and Colville River, we investigated phenological mismatch by graphing the area of overlap (a visual representation of the degree of phenological match) between daily invertebrate

biomass and the number of broods at their peak energetic demand. To do this, we first estimated predicted hatch date of all nests, regardless of eventual fate, by assuming a 4-egg clutch



with 1 egg laid per day and standard incubation periods. Next, we estimated the number of shorebird broods at their peak energetic demand (i.e., age when chick body mass was 25% of adult body mass after Kwon et al., 2019) for each day of the field season. As our data included several species not included in Kwon et al. (2019) and with little information on growth rates, we chose to use 6 days post-hatch (middle value between 3 and 9 days used by Kwon et al. (2019)) for all species as the date of peak energetic demand. We then graphed the area of overlap between daily invertebrate biomass and the number of broods at their peak energetic demand using the same scale in all cases. All values throughout the paper are reported as means  $\pm$  standard error.

## RESULTS

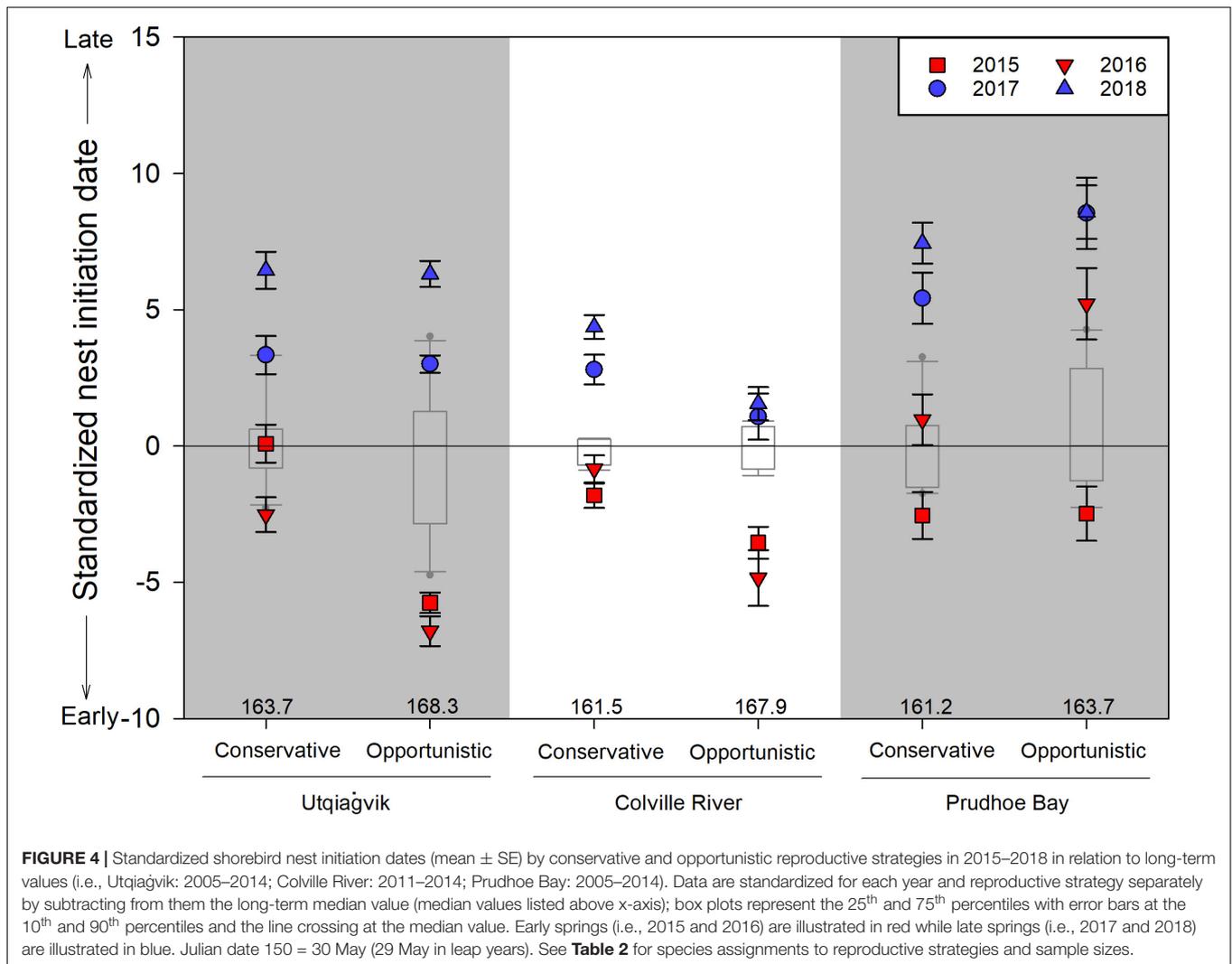
### Weather

The years 2015 and 2016 had considerably warmer temperatures and less snow cover as compared to 2017 and 2018 across all sites (i.e., mean cumulative temperature from 1 to 30 June across sites

was  $209 \pm 39^\circ\text{C}$  in 2015,  $136 \pm 23^\circ\text{C}$  in 2016,  $77 \pm 19^\circ\text{C}$  in 2017, and  $34 \pm 10^\circ\text{C}$  in 2018; mean % snow cover on 10 June across sites was  $0.7 \pm 0.7\%$  in 2015,  $0.3 \pm 0.2\%$  in 2016,  $30.2 \pm 24.3\%$  in 2017, and  $69.2 \pm 21.3\%$  in 2018; **Figure 1**). Additionally, 2015 and 2016 had consistently warmer temperatures and less snow cover than the long-term average, while 2017 and 2018 had consistently colder temperatures and more snow cover than the long-term average (**Figure 1**). Based on this, we considered 2015 and 2016 as exceptionally early springs and 2017 and 2018 as exceptionally late springs.

### Alternative Prey and Predator Abundance

At all sites, the abundance of alternative prey in June was consistently low during the 2015–2018 study period (**Figure 2**). Fox abundance, however, was higher in 2018 at Prudhoe Bay than the first 3 years of this study, while at the Colville River, fox abundance was slightly lower in 2017 and 2018 as compared to 2015 and 2016 (**Figure 2**). At Utqiaġvik, however, fox abundance



was fairly consistent and low from 2005 to 2018 despite the fact that an active fox-control program occurred between 2005 and 2016 to promote the reproduction of Steller's Eiders (*Polysticta stelleri*; Barto et al., 2016). Avian predators were generally consistent within sites in the 4 years of this study, except for higher abundances in 2015 at Prudhoe Bay (**Figure 2**). Utqiagvik generally had 2–3 times the number of avian predators compared to the other sites (except Prudhoe Bay in 2015), with the Colville River having consistently lower numbers.

## Nest Densities

Across all sites, we monitored 2,239 nests belonging to 13 species and six genera of shorebirds from 2015 to 2018, and an additional 3,789 nests belonging to 15 species and seven genera from 2005 to 2014 (**Table 2**). The *Calidris* and *Phalaropus* genera were the most common, followed by *Limnodromus*, *Pluvialis*, *Arenaria*, and *Limosa*. Nest densities were almost always higher in early springs (11 of 12 site/strategy cases had values above the long-term median value) and lower in late springs (12 of 12 cases) compared to long-term levels (**Figure 3**). The most dramatic

differences were seen in opportunistic species at Utqiagvik, which were found in much higher densities in early ( $1.49 \pm 0.39$  nests/ha) compared to late springs ( $0.62 \pm 0.11$ ). The Colville River site had the opposite pattern, where the most dramatic differences were seen in conservative species, which were found in much higher densities in early ( $0.69 \pm 0.07$ ) compared to late ( $0.31 \pm 0.02$ ) springs (**Figure 3**).

## Nest Initiation Dates

Nest initiation dates were always earlier in early springs compared to late springs, regardless of the reproductive strategy (**Figure 4**). Furthermore, initiation dates were earlier in 9 of 12 site/strategy cases during earlier springs compared to long-term values. In contrast, initiation dates were always later in late springs (12 of 12 cases) compared to long-term values. The best-supported model mirrored these general patterns, with variation in nest initiation date best explained by the interaction between site, year, and strategy (**Tables 3, 4**;  $R^2 = 0.295$ ). Within-year comparisons showed opportunistic species nested later than conservative species in 11 of 12 cases.

**TABLE 3** | Top-ranked models (plus intercept-only model) explaining variation in initiation dates of shorebird nests at Utqiagvik, Colville River, and Prudhoe Bay, 2015–2018.

Model	K <sup>a</sup>	AIC <sub>c</sub> <sup>b</sup>	ΔAIC <sub>c</sub> <sup>c</sup>	w <sub>i</sub> <sup>d</sup>
Site × year × strategy	24	14790.6	0.0	1.0
Site × year + strategy	13	14878.5	87.9	0.0
Site × spring × strategy	12	14892.1	101.5	0.0
Year × strategy + site	10	14925.5	134.9	0.0
Year × strategy	8	14939.4	148.8	0.0
Intercept	1	15613.2	822.6	0.0

Variables include site, year, spring (early or late), and reproductive strategy (conservative or opportunistic). We restricted models so that year and spring did not enter the same model. <sup>a</sup>No. of parameters in the model. <sup>b</sup>Akaike's information criterion corrected for small sample size. <sup>c</sup>Difference between model AIC<sub>c</sub> and AIC<sub>c</sub> value of the best model. <sup>d</sup>AIC<sub>c</sub> relative weight attributed to model.

## Nest Synchrony

In 11 of 12 strategy/site cases, shorebirds nested less synchronously during early springs compared to long-term values, and in 8 of 12 cases, nested more synchronously during late springs compared to long-term values (**Figure 5**). During late springs, opportunistic species nested more synchronously than conservative species at Utqiagvik and the Colville River, but not at Prudhoe Bay. In contrast, during early springs, opportunistic species nested less synchronously than conservative species at Utqiagvik and Prudhoe Bay, but not at the Colville River.

## Nest Survival

Relative to long-term values, daily nest survival during late springs was lower than the long-term median values in 8 of 12 cases, while daily nest survival was greater than the long-term median values in early springs in just 3 of 12 cases (**Figure 6**). Similarly, our analyses found that variation in daily nest survival was best explained by a model that included site, year, initiation date, and reproductive strategy (**Tables 5, 6**). Based on this model, both conservative and opportunistic species had greater nest survival in early springs compared to late springs at Utqiagvik, while opposite trends or no differences between early and late springs were found at the other two sites (**Figure 6**). We also found that daily nest survival declined with initiation date across sites, years, and reproductive strategies ( $\beta_{\text{initiation}} = -0.04 \pm 0.01$ , 95% CI  $-0.05, -0.03$ ).

## Hatch Dates and Invertebrate Abundance

Invertebrate availability was later in late springs than early springs, although there was large variation in the absolute abundance and phenology among years and sites (**Figures 7, 8**). In early springs, timing of peak food demand for the majority of both conservative and opportunistic broods occurred after peak invertebrate emergence, with less overlap between the two curves (**Figures 7, 8**, red area). This was especially apparent in 2015 at both Utqiagvik and the Colville River. In contrast, in late springs, the timing of peak food demand for the majority of broods occurred when invertebrate biomass was more available, with greater overlap between the two curves (**Figures 7, 8**, blue area).

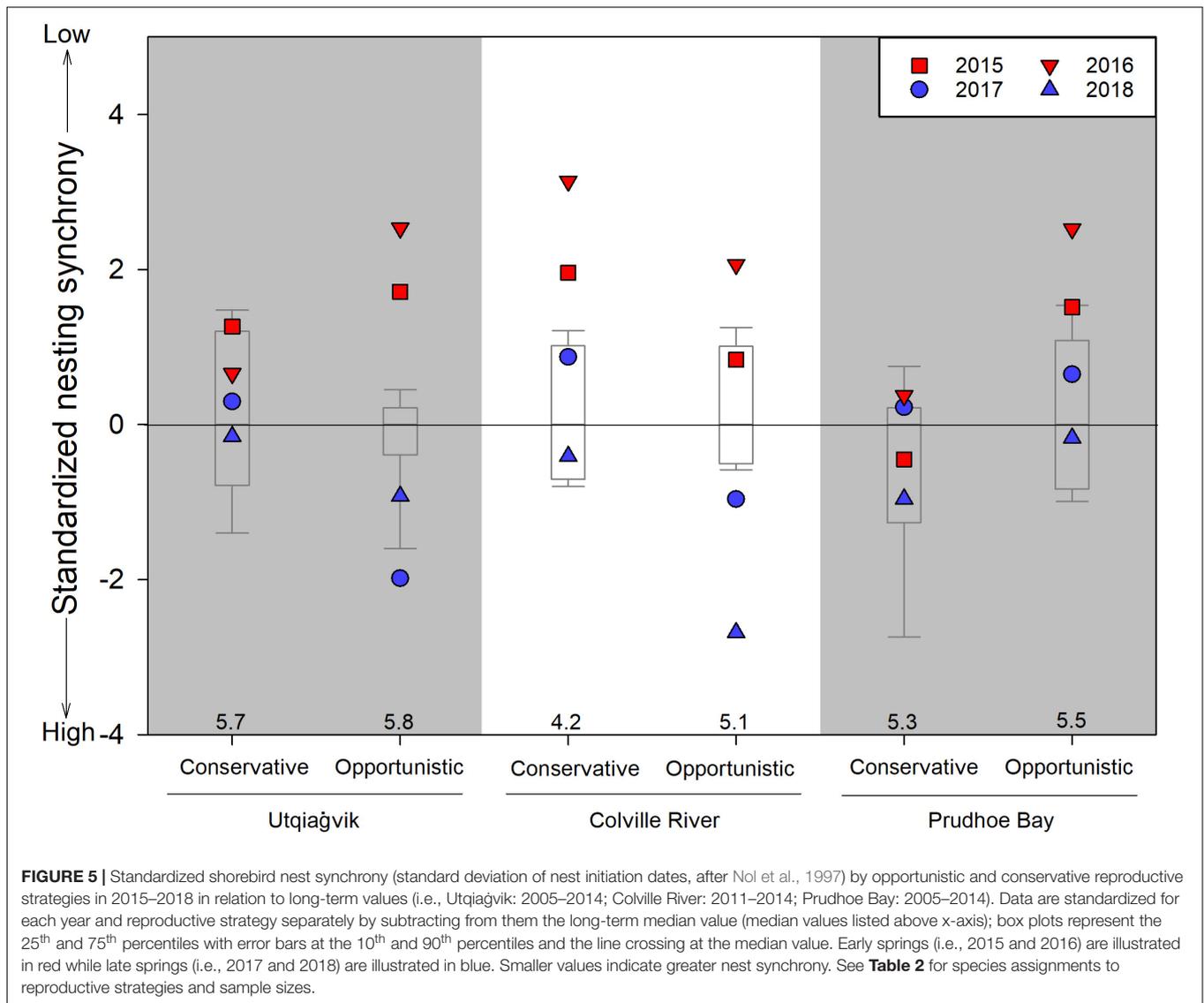
**TABLE 4** | Parameter estimates from top-ranked model (site\*year\*strategy) explaining variation in initiation dates of shorebird nests at Utqiagvik, Colville River, and Prudhoe Bay, 2015–2018.

Parameter	Estimate	SE
Intercept <sup>a</sup>	172.31	1.21
Site (Utqiagvik)	2.31	1.37
Site (Colville River)	-2.87	2.03
Year (2015)	-11.07	1.53
Year (2016)	-3.36	1.62
Year (2017)	-0.04	1.85
Strategy (conservative)	-3.64	1.66
Site*year (Utqiagvik*2015)	-1.00	1.69
Site*year (Colville River*2015)	5.97	2.33
Site*year (Utqiagvik*2016)	-9.74	1.79
Site*year (Colville River*2016)	-3.03	2.48
Site*year (Utqiagvik*2017)	-3.27	2.02
Site*year (Colville River*2017)	-0.44	2.80
Site*strategy (Utqiagvik*conservative)	-0.83	1.95
Site*strategy (Colville River*conservative)	0.13	2.45
Year*strategy (2015*conservative)	1.08	2.24
Year*strategy (2016*conservative)	-3.11	2.25
Year*strategy (2017*conservative)	-1.98	2.44
Site*year*strategy (Utqiagvik*2015*conservative)	4.63	2.56
Site*year*strategy (Colville River*2015*conservative)	-2.17	2.98
Site*year*strategy (Utqiagvik*2016*conservative)	7.25	2.59
Site*year*strategy (Colville River*2016*conservative)	4.30	3.06
Site*year*strategy (Utqiagvik*2017*conservative)	2.18	2.80
Site*year*strategy (Colville River*2017*conservative)	0.89	3.38

Variables include site, year, and reproductive strategy (conservative or opportunistic). <sup>a</sup>Intercept represents estimates for nests at Prudhoe Bay in 2018 with an opportunistic reproductive strategy.

## DISCUSSION

In our multi-species assessment of the demographic response of Arctic-breeding shorebirds to variable spring conditions across three sites in Alaska, many results clearly fit our predictions and involved birds making adjustments that are perceived as adaptive responses to prevailing environmental conditions (**Table 1**). Such results were not wholly surprising, because our predictions were based on a wealth of prior studies investigating these relationships (see introduction). The most interesting results of this study, then, concern those that did not fit our predictions. For example, we observed strong differences among sites in the magnitude (e.g., nest density; **Figure 3**) and direction (e.g., nest initiation and nest synchrony responses among conservative and opportunistic species; **Figures 4, 5**) of certain demographic responses. Given the close proximity and similarity of habitats across our three study sites, this was unexpected. It is possible that some variation in our response variables was present due to the potential effects of fox control at Utqiagvik, human infrastructure at Prudhoe Bay and Utqiagvik, or subtle differences in other ecological variables that we did not measure (e.g., hydrology, geomorphology). Notably, inter-site variation in the abundance of alternative prey or avian and mammalian nest predators seems unlikely to have driven these patterns, because the abundance of

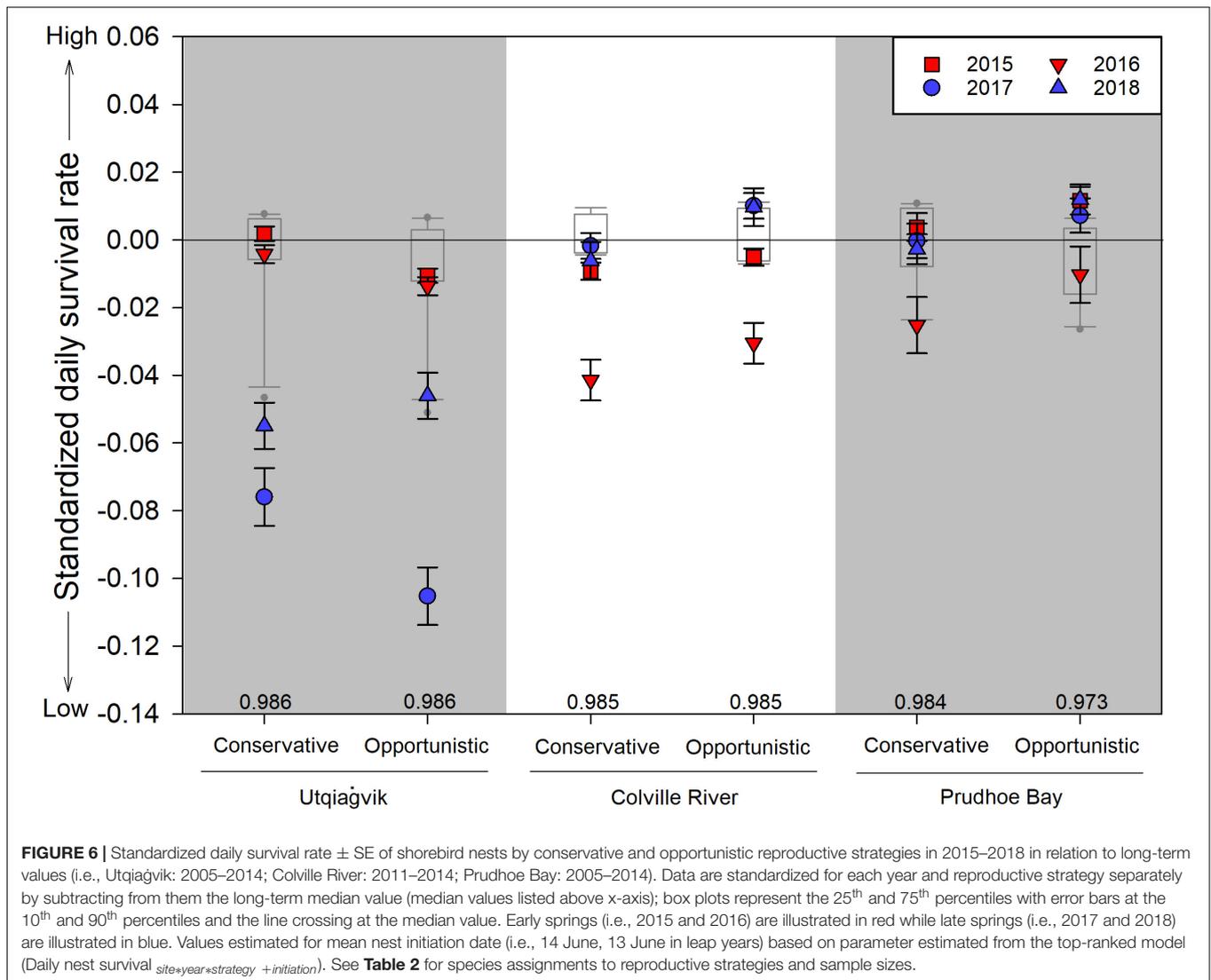


alternative prey was low at all sites in all years, and the relatively high numbers of mammalian and avian predators at some sites and years were not associated with nest survival in a consistent and predictable way (**Table 1**).

There were small methodological differences among the sites that might have contributed to different results among study sites. Our sites had different numbers and sizes of plots (e.g., many small linear plots versus six square plots versus one large plot), plots were searched for nests at different frequencies and with different approaches (timing, order and use of area search versus rope-drag techniques), and each site had different numbers of long-term years with which to compare the early and late spring information. These differences may influence the likelihood of finding nests (e.g., see McCaffery and Ruthrauff, 2004; Smith et al., 2009) and potentially affect perceptions of how reproductive parameters may change in early and late springs. Given the sheer number of nesting efforts monitored across these sites during our studies, however, we

do not believe that these methodological differences account for magnitude of the demographic differences observed across sites. A more striking difference between the sites, however, was the difference in the shorebird community structure and the absolute numbers of particular species. For, example, opportunistic species (e.g., Red Phalarope and Pectoral Sandpiper) were dominant at Utqiagvik, while conservative species (e.g., Semipalmated Sandpiper, Dunlin) were dominant at the Colville River; the shorebird community at Prudhoe Bay was more balanced (**Table 2**). These differences in community composition might explain why Utqiagvik followed the predictions for opportunistic species more closely than the other sites (**Table 1**).

Our prediction that nest densities for conservative species would not change in early springs compared to the long-term median value was not supported at the Utqiagvik and Colville River sites (both sites increased between 0.08 and 0.35 nests/ha), but was supported at Prudhoe Bay (**Figure 3**). However, our prediction that opportunistic species would nest in higher



densities in early springs was met at all three study sites. This was especially notable at Utqiagvik, where nest densities of opportunistic species were 0.31 to 1.1 nests/ha greater in early springs compared to long-term levels. Some of the increase in nest density during early springs may be due to birds laying replacement nests, but this seems unlikely to account for the large increases in nest density for opportunistic species at Utqiagvik and conservative species at the Colville River. Following our prediction, both conservative and opportunistic species nested at lower densities during late springs, although the decline in nesting density was very small ( $<0.29$  nests/ha) compared to long-term levels. In fact, in several years and at multiple sites, nest density was not affected at all. Changes in nest density were generally absent at Prudhoe Bay, regardless of reproductive strategy and the type of spring. While it is difficult to know the extent of replacement nesting (detailed mark-resight or paternity investigations are needed), it is likely that social cues that either limit conspecific nesting (Cunningham et al., 2016) or enhance it are important (Kempnaers and Valcu, 2017).

Most of our results support past assertions that opportunistic species are able to adjust to spring conditions better than conservative species, presumably due to their ability to assess conditions over large portions of their breeding range (Lancot and Weatherhead, 1997; Kempnaers and Valcu, 2017). However, other assertions that birds are unable to breed during late springs due to the inability to acquire the necessary exogenous reserves (Nol et al., 1997; Meltofte et al., 2007b; Smith et al., 2010) seem less supported, as nest densities remained near long-term levels during these exceptionally late springs (except for at Utqiagvik). It is possible that the late spring conditions experienced in some of our study areas were not sufficiently poor to inhibit breeding efforts as has been reported at other sites (see, e.g., Schmidt et al., 2019).

Other studies have shown that Arctic-breeding shorebirds align the timing of nest initiation, although not always as fast as necessary, with the availability of snow-free habitats (Meltofte et al., 2007a; Smith et al., 2010; Grabowski et al., 2013; Liebezeit et al., 2014; Machín et al., 2019). Kwon et al. (2019) likewise found

**TABLE 5** | Top-ranked models (plus intercept-only model) explaining daily survival rates of shorebird nests at Utqiagvik, Colville River, and Prudhoe Bay, 2015–2018.

Model	$K^a$	$AIC_c^b$	$\Delta AIC_c^c$	$w_i^d$
Site × year × strategy + initiation	25	4887.1	0.0	0.6
Site × year × initiation	24	4889.6	2.6	0.2
Site × year + initiation	13	4889.9	2.8	0.1
Site × year + initiation + strategy	14	4890.2	3.1	0.1
Site × year + strategy	13	4927.5	40.4	0.0
Site × year × strategy	24	4928.0	40.9	0.0
Site × year	12	4933.3	46.2	0.0
Intercept	1	5381.5	494.4	0.0

Variables include site, year, spring (early or late), reproductive strategy (conservative or opportunistic), and nest initiation date. We restricted models so that year and spring did not enter the same model. <sup>a</sup>No. of parameters in the model. <sup>b</sup>Akaike's information criterion corrected for small sample size. <sup>c</sup>Difference between model  $AIC_c$  and  $AIC_c$  value of the best model. <sup>d</sup> $AIC_c$  relative weight attributed to model.

**TABLE 6** | Parameter estimates from top-ranked model (site\*year\*strategy + initiation) explaining variation in daily survival rates of shorebird nests at Utqiagvik, Colville River, and Prudhoe Bay, 2015–2018.

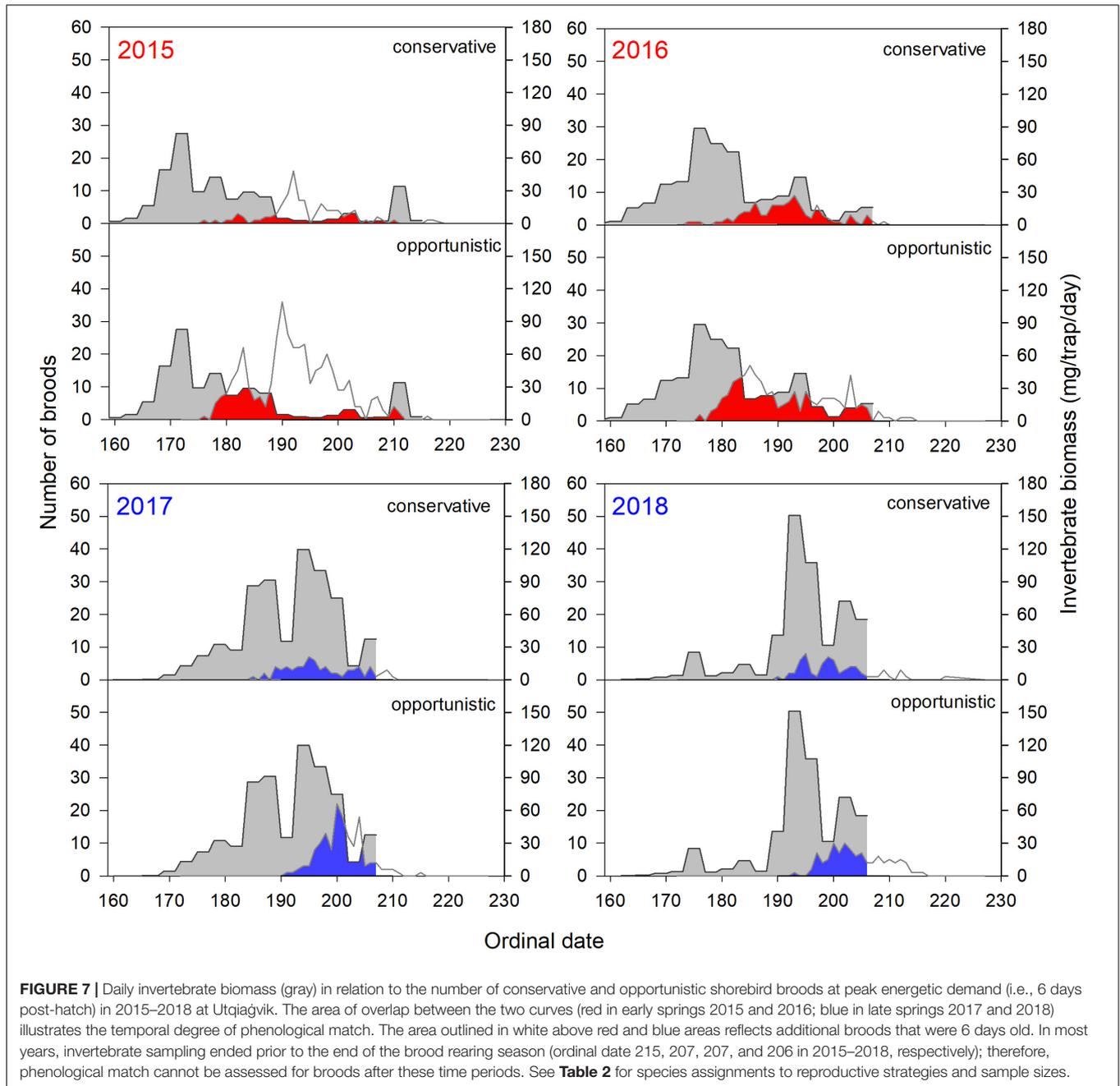
Parameter	Estimate	SE
Intercept (Utqiagvik*2015)	4.27	0.14
Intercept (Utqiagvik*2016)	4.15	0.15
Intercept (Utqiagvik*2017)	2.58	0.16
Intercept (Utqiagvik*2018)	3.33	0.19
Intercept (Colville River*2015)	4.46	0.21
Intercept (Colville River*2016)	3.62	0.23
Intercept (Colville River*2017)	5.86	0.72
Intercept (Colville River*2018)	5.79	1.01
Intercept (Prudhoe Bay*2015)	4.74	0.37
Intercept (Prudhoe Bay*2016)	3.83	0.28
Intercept (Prudhoe Bay*2017)	4.49	0.44
Intercept (Prudhoe Bay*2018)	4.77	0.38
Strategy (Utqiagvik*2015*conservative)	0.73	0.25
Strategy (Utqiagvik*2016*conservative)	0.44	0.24
Strategy (Utqiagvik*2017*conservative)	0.32	0.17
Strategy (Utqiagvik*2018*conservative)	-0.15	0.19
Strategy (Colville River*2015*conservative)	-0.20	0.23
Strategy (Colville River*2016*conservative)	-0.23	0.23
Strategy (Colville River*2017*conservative)	-1.23	0.75
Strategy (Colville River*2018*conservative)	-1.39	1.03
Strategy (Prudhoe Bay*2015*conservative)	0.19	0.62
Strategy (Prudhoe Bay*2016*conservative)	-0.12	0.39
Strategy (Prudhoe Bay*2017*conservative)	0.17	0.55
Strategy (Prudhoe Bay*2018*conservative)	-0.25	0.51
Initiation	-0.04	0.01

Variables include site, year, reproductive strategy (conservative or opportunistic), and nest initiation date.

that despite differences in ecological and physical environments outside the breeding grounds, shorebirds at 10 sites spread across the Arctic responded to the timing of snowmelt on the breeding grounds by adjusting the timing of breeding in similar ways. None of these studies, however, assessed how reproductive strategy influenced the timing of nesting. Our prediction that

birds would nest earlier in early springs and later in late springs was generally supported in this study. We found that shorebirds initiated egg laying earlier in early springs relative to long-term values in most cases (4 of 6 conservative/sites, 5 of 6 opportunistic/sites); the rest nested at the same time or later than long-term values (**Figure 4**). In contrast, in late springs, both conservative and opportunistic species always initiated nests later than long-term values. Within a year and site, opportunistic species nested later than conservative species in 11 of 12 cases. Thus, birds adjusted less reliably to early springs than late springs in this study, but opportunistic species always nested later than conservative species regardless of spring type. We suspect that the need to attract or compete for mates may delay nesting in opportunistic species whereas the site faithfulness of conservative species may allow them to relocate their old mate much faster (Lanctot et al., 2000). In addition, the uniparental incubation patterns present in opportunistic species may impose higher anticipatory energetic costs (Drent et al., 2006) that results in longer pre-breeding delays in nesting compared to conservative species. In contrast, conservative species that practice bi-parental incubation can anticipate more time to feed during incubation (i.e., they can lay eggs despite potentially being in worse body condition). In addition, opportunistic species may end up breeding later in late springs because their arrival is delayed due to their attempts to breed in other parts of the Arctic experiencing earlier spring conditions (Kempnaers and Valcu, 2017). The conservative species, in contrast, go to a single site and wait to initiate nests as soon as habitat opens.

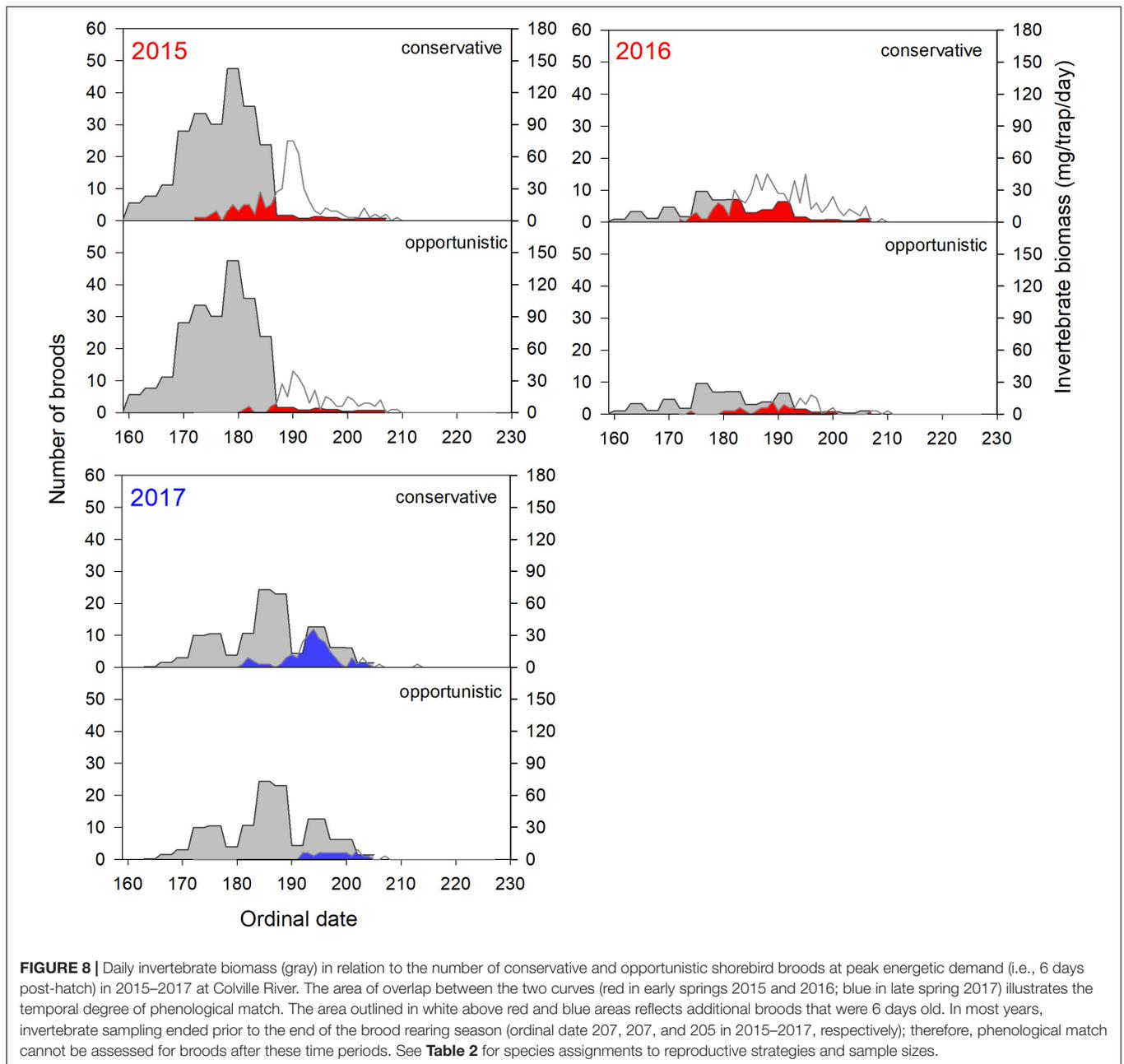
Like many Arctic-breeding birds (e.g., Custer and Pitelka, 1977; Findlay and Cooke, 1982), shorebirds tend to breed synchronously, perceived both as a response to help dilute the individual risk of nest predation (Smith et al., 2010), but also to time the hatching of their young to match future peaks in food resources (Holmes and Pitelka, 1968). However, the warmer and longer breeding seasons that are a byproduct of earlier springs may lengthen the nesting period as shorebirds not only nest earlier but also have more time to re-nest should their first nest fail. Such a situation effectively decreases the synchrony of nesting events in early springs. While we had little information to confirm the presence of re-nests, prior research from Utqiagvik indicates that virtually all shorebirds re-nest (Naves et al., 2008) and that for Dunlin in particular, re-nesting can occur at a high frequency (82–95 and 35–50% of nests whose clutches were experimentally removed during early and late incubation, respectively, subsequently re-nested; Gates et al., 2013). In contrast, later springs are thought to lead to more synchronous nesting, likely due to the shorter period of time in which birds have to nest (Nol et al., 1997; Meltofte et al., 2007b; Smith et al., 2010). These patterns, as outlined above and in our initial predictions, were mostly confirmed in our study, with nesting being less synchronous in early springs (11 of 12 strategy/year cases) and more synchronous in late springs (8 of 12 strategy/year cases) relative to historic levels (2005–2014; **Figure 5**). However, we did not find consistent patterns in nest synchrony between conservative and opportunistic species within years and sites. Collectively these results suggest that, at least across these three sites, the extent to which shorebirds nested



synchronously was based primarily on the type of spring and not the reproductive strategy of the species.

We predicted that shorebirds would have higher nesting success in early springs compared to late springs. Contrary to our predictions, we found only a few site/year cases where these predicted relationships were followed (Figure 6). For example, as predicted, nest survival was lower in the late springs of 2017 and 2018 at Utqiagvik compared with historic levels. However, these two springs occurred after fox control was stopped in 2016, and it seems possible that higher (i.e., natural) fox densities present in subsequent years might have lowered nest survival

(and not the late springs). Our consistently low counts of fox at Utqiagvik between 2005 and 2018 (Figure 2) do not support this idea, although it is possible that our opportunistic counts do not accurately reflect fox activity in the area (see Liebezeit and Zack, 2008). In most site/year cases, however, nest survival was not related to spring type in the ways that we predicted. This was particularly true for the Colville River and Prudhoe Bay sites in the early spring of 2016, when nest survival was lower than the historic levels despite having an early spring. The failure to document lower nest survival in late springs may be because the persistent snow cover not only reduced available



habitat for nesting (which could concentrate predation intensity) but also resulted in lower overall densities of breeding shorebirds, decreasing nest encounter rates by predators. If encounter rates are sufficiently low, foxes may choose to hunt elsewhere.

Regardless of the spring type, we found a consistent decline in daily nest survival with nest initiation date, suggesting some selective pressure exists to nest as early as possible. Failing to breed early may lead to smaller clutch sizes, less re-nesting, and ultimately lower adult survival (Weiser et al., 2018b), but breeding early may also be detrimental should predation intensity be greater early in the spring (Reynolds, 1987; Reneerkens et al., 2016). Interestingly, a seasonal decline in nest survival has been

found in some studies (Sandercock et al., 1999; Weiser et al., 2018b), but not others (e.g., Smith and Wilson, 2010; Reneerkens et al., 2016; Senner et al., 2017), and so selection pressures likely operate differently across years and sites. This is unsurprising, given that nest survival is primarily driven by both predators and the availability of alternative prey to shorebird predators (Blomqvist et al., 2002; Smith et al., 2007; Gilg and Yoccoz, 2010; McKinnon et al., 2014; Reneerkens et al., 2016), which can vary tremendously from site to site and year to year (Liebezeit et al., 2009; Saalfeld and Lanctot, 2015).

Early springs often resulted in more broods hatching after peak food availability (**Figures 7, 8**). Kwon et al. (2019) also found

that site-specific timing of snowmelt determined the extent of phenological mismatches at the population level for six species of shorebirds breeding across the North American Arctic. However, it remains unclear whether this increased temporal asynchrony is harmful to young. McKinnon et al. (2013) and Corkery et al. (2019) both reported chicks growing sufficiently well even under depressed food conditions caused by phenological mismatch, perhaps due to lower thermoregulatory needs during the warmer springs. In contrast, Saalfeld et al. (2019) found that shorebirds experienced increased phenological mismatch with earlier snowmelt, and that, in general, chicks that hatched from nests initiated earlier experienced greater food availability and grew at faster rates than chicks from nests that hatched later. Hill (2012) confirmed that insect biomass was a strong predictor of chick survival in Dunlin. Thus, it is still unclear whether hatching after peak invertebrate availability is disadvantageous, as it likely depends on overall food abundance and weather conditions during a given breeding season.

Overall, our study demonstrates that Arctic-breeding shorebirds exhibit a high degree of behavioral flexibility in response to variable Arctic conditions. Similar adaptability has been documented in a wide variety of organisms from terrestrial and marine ecosystems from around the globe (Parmesan and Yohe, 2003; Hickling et al., 2006; Chen et al., 2011; Poloczanska et al., 2013), but such adjustments have been recognized only relatively recently in shorebirds (e.g., Liebezeit et al., 2014; Kwon et al., 2019). It is necessary to determine whether existing behavioral flexibility in nesting is already sufficient to keep pace with advancing Arctic phenologies (Berteaux et al., 2004; Williams et al., 2008), or whether additional evolutionary adjustments (e.g., Hoffmann and Sgrò, 2011; Helm et al., 2019) will be required. It is important to understand these relationships given change is continuing to happen (Schmidt et al., 2019) and the potential impacts are large (see, e.g., Wauchope et al., 2016). Such information will better articulate life-history attributes that may buffer migratory birds against extreme environmental events (Williams et al., 2008).

## DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: “Data from the Colville

River used in this study are publicly available from the U.S. Geological Survey (<https://doi.org/10.5066/P9BJBRTO>). Data for Utqiagvik are available from the Arctic Data Center (<https://doi.org/10.18739/A23R0PT35>). The raw data from Prudhoe Bay will be made available by the authors upon request.”

## ETHICS STATEMENT

The animal study was reviewed and approved by Colville River Site: US Geological Survey/Alaska Science Center Institutional Care and Use Committee. Prudhoe Bay Site: Alaska Department of Fish and Game Institutional Care and Use Committee. Utqiagvik Site: US Fish and Wildlife Service Alaska Region Institutional Care and Use Committee.

## AUTHOR CONTRIBUTIONS

RM, RL, SS, and DR conceptualized the study. RM and SS analyzed the data. RM wrote the manuscript. RL, SS, and DR contributed significantly to data interpretation and writing. All authors approved the final manuscript and collected the data.

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