Life-history attributes of Arctic-breeding birds drive uneven responses to environmental variability across different phases of the reproductive cycle

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Abstract

1. Animals exhibit varied life-history traits that reflect adaptive responses to their environments. For Arctic-breeding birds, traits like foraging guild, egg nutrient allocation, clutch size, and chick growth are predicted to be under increasing selection pressure due to rapid climate change and increasing environmental variability across high-latitude regions. 2. We compared four migratory birds (black brant [Branta bernicla nigricans], lesser snow geese [Chen caerulescens caerulescens], semipalmated sandpipers [Calidris pusilla], and Lapland longspurs [Calcarius lapponicus]) with varied life histories at an Arctic site in Alaska, USA, to understand how life-history traits help moderate environmental variability across different phases of the reproductive cycle. 3. We monitored aspects of reproductive performance related to the timing of breeding, reproductive investment, and chick growth from 2011–2018. 4. In response to early snow melt and warm temperatures, semipalmated sandpipers advanced their site arrival and bred in higher numbers, while brant and snow geese increased clutch sizes; all four species advanced their nest initiation dates. During chick rearing, longspur chicks were relatively resilient to environmental variation whereas warmer temperatures increased the growth rates of sandpiper chicks but reduced growth rates of snow goose goslings. These responses generally aligned with traits along the capital-income spectrum of nutrient acquisition and altricial-precocial modes of chick growth. Under a warming climate, the ability to mobilize endogenous reserves likely provides geese with relative flexibility to adjust the timing of breeding and the size of clutches. Warmer temperatures, however, may negatively affect the quality of herbaceous foods and slow gosling growth. 5. Species may possess traits that are beneficial during one phase of the reproductive cycle and others that may be detrimental at another phase, uneven responses that may be amplified with future climate warming. These results underscore the need to consider multiple phases of the reproductive cycle when assessing the effects of environmental variability on Arctic-breeding birds.

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3. We monitored aspects of reproductive performance related to the timing of breeding, reproductive investment, and chick growth from 2011–2018.

4. In response to early snow melt and warm temperatures, semipalmated sandpipers advanced their site arrival and bred in higher numbers, while brant and snow geese increased clutch sizes; all four species advanced their nest initiation dates. During chick rearing, longspur chicks were relatively resilient to environmental variation whereas warmer temperatures increased the growth rates of sandpiper chicks but reduced growth rates of snow goose goslings. These responses generally aligned with traits along the capital-income spectrum of nutrient acquisition and altricial-precocial modes of chick growth. Under a warming climate, the ability to mobilize endogenous reserves likely provides geese with relative flexibility to adjust the timing of breeding and the size of clutches. Warmer temperatures, however, may negatively affect the quality of herbaceous foods and slow gosling growth.

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KEYWORDS

INTRODUCTION

Compared to temperate and tropical ecosystems, the reproductive period of most animals in the Arctic is compressed due to the brief availability of food and short period of benign weather (MacLean & Pitelka, 1971; Wingfield & Hunt, 2002). Nevertheless, the sheer abundance of resources at these sites supports the reproduction of a diversity of animal groups that employ a variety of life-history strategies to exploit conditions in the Arctic. For migratory birds, these traits include reproductive strategies along the capital-income spectrum of resource allocation (Drent & Daan, 1980; Klaassen et al., 2001), the altricial-precocial spectrum of chick development (Starck & Ricklefs, 1998), and variable investments in clutch size (Jetz et al., 2008; Winkler & Walters, 1983). Life history theory predicts an optimization of such traits within a species (Roff, 2002; Stearns, 1992), and comparison of these traits among co-occurring species over multiple breeding occasions provides insight into factors that promote successful reproduction across varying environmental conditions.

Such comparisons are especially relevant in the Arctic considering the rapid pace of ecosystem change due to climate effects (Berteaux et al., 2004; Hoffmann & Sgrò, 2011). The effects of climate change are disproportionately expressed at high-latitude regions (Arctic Climate Impact Assessment, 2004; IPCC, 2013), where the rate of warming is rapid (Bekryaev et al., 2010; Serreze & Barry, 2011), the onset of spring is advancing (Høye et al., 2007; Parmesan & Yohe, 2003), and the growing season is lengthening (Piao et al., 2007; Tucker et al., 2001). In addition to these steady trends, the Arctic is also experiencing an increased frequency of punctuated, extreme climatic events (Landrum & Holland, 2020). Taken together, these rapidly changing

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conditions present new challenges to organisms already inhabiting extreme Arctic environments (Berteaux et al., 2004; Gilg et al., 2012).

We studied the breeding ecology of migratory birds at an Arctic site in Alaska to assess the response of the avian community to climate-related environmental variation. We focused our research efforts on the four most common species at the site: two geese (black brant [*Branta bernicla nigricans*] and lesser snow geese [*Chen caerulescens caerulescens*]), one shorebird (semipalmated sandpiper [*Calidris pusilla*]), and one passeriform landbird [Lapland longspur (*Calcarius lapponicus*]). These species encompass a range of life-history traits relating to reproductive effort (Table 1). Black brant (hereafter brant) and lesser snow geese (hereafter snow geese) are large-bodied, herbivorous waterfowl. Both species deposit endogenous nutrients into eggs (Schmutz et al., 2006; Sharp et al., 2013), but snow geese acquire relatively more exogenous nutrients from Arctic plants when foraging conditions prior to nesting are favorable (Hupp et al., 2018). In contrast, semipalmated sandpipers and Lapland longspurs (hereafter longspurs) are small-bodied birds that rely on exogenously derived nutrients (insects and seeds) for egg production (Hobson & Jehl, 2010; Klaassen et al., 2001; Meijer & Drent, 1999). Brant (2–6 eggs; Lewis et al., 2020), snow geese (2–6 eggs; Hamann et al., 1986), and longspurs (2–8 eggs; Custer & Pitelka, 1977) also regulate their reproductive investment by producing variable numbers of eggs, but the clutch size of semipalmated sandpipers is invariant (4 eggs; MacLean, 1972; Sandercock, 1997). Finally, brant (Lewis et al., 2020), snow geese (Mowbray et al., 2020), and semipalmated sandpipers (Holmes & Pitelka, 1968) produce precocial chicks that exit the nest shortly after hatch and are self-feeding, but longspur chicks are altricial and derive all their food resources from the provisioning efforts of adult longspurs (Custer & Pitelka, 1977).

TABLE 1 Life-history variation among reproductive traits for four species of Arctic-breeding bird, black brant (BLBR), lesser snow goose (LSGO), semipalmated sandpiper (SESA), and Lapland longspur (LALO)

	species	species	species	species
life-history trait	BLBR	LSGO	SESA	LALO
nutrient source	herbaceous	herbaceous	insect	insect, seed
resource allocation	endogenous	flexible	exogenous	exogenous
clutch investment	variable; 2–6 eggs	variable; 2–6 eggs	invariant; 4 eggs	variable; 2–8 eggs
chick growth	precocial	precocial	precocial	altricial

The intra-specific variation in life-history traits represents functional attributes (e.g., resource use and allocation, reproductive investment, modes of chick growth) that reflect selective forces acting under a rapidly changing climate (Berteaux et al., 2004; Gienapp et al., 2008). To this end, we monitored the annual arrival, pre-lay duration, nest initiation, clutch size, and nesting effort of brant, snow geese, semipalmated sandpipers, and longspurs, and measured relevant environmental variables across the breeding season. We predicted that geese would exhibit more flexibility to interannual variability in spring temperature and snowmelt compared to semipalmated sandpipers and longspurs by adjusting the timing of breeding and reproductive investment due to their comparatively greater endogenous reserves and relative flexibility along the capital-income spectrum.

Because species possess traits that may promote resilience during one phase of the reproductive cycle but other traits which may be detrimental at other phases, assessing the response of species to shared environmental conditions across different phases of the reproductive cycle (e.g., Nolet et al., 2020) provides more meaningful insights into reproductive outcomes than assessments focused on just one phase. As such, in addition to monitoring responses during the pre-breeding and nesting periods, we also monitored the growth of chicks of these four species in conjunction with climatic variables and measures of the seasonal availability of herbivorous and insectivorous food resources. Because numerous studies have demonstrated that rapid growth of avian young yields larger chicks (Larsson & Forslund, 1991; Ruthrauff & McCaffery, 2005) that survive at higher rates (Lindholm et al., 1994; Naef-Daenzer et al., 2001) and have a higher probability of recruitment (Cooch et al., 1993; Magrath, 1991; Sedinger et al., 1995) than smaller same-age

chicks, variation in chick growth reflects a meaningful demographic response to environmental variability. We predicted that the young of brant, snow geese, and semipalmated sandpipers would be more sensitive to variation in food abundance due to their precocial nature. We predicted that this would be reflected by relatively strong variation in body mass as a function of food abundance compared to chicks of longspurs, which are provisioned entirely by adults. Taken together, assessments of climatological (temperature, wind, and snow cover) and environmental (seasonal availability and absolute abundance of food resources) factors in relation to life-history traits across multiple phases of the reproductive cycle elucidate characteristics of Arctic-breeding birds that may mitigate negative effects of future climate change.

2. MATERIALS AND METHODS

We conducted our study on the Arctic Coastal Plain of Alaska at the Colville River Delta (70.44° N, 150.67° W). This site is ˜5 km from the Beaufort Sea, and is a lowland ecosystem of lakes, polygonal ponds, graminoid-dominated wetlands, dune ridges, and upland tundra communities (Kessel & Cade, 1958; Walker, 1983). Our study period was 2011–2018, but not all data were collected in all years because we integrated new aspects to the study over time. We typically arrived at the site in early spring (˜20 May) prior to the initiation of nests, and remained at the site through late July to monitor the fate of nests and measure chick growth. We conducted systematic searches for semipalmated sandpiper (2011–2018) and Lapland longspur (2015–2018) nests across a 2.6-km^2 plot adjacent to our camp, and we traveled by boat within 15 km of our camp to monitor goose nests at nearby nesting areas. To standardize search efforts across known-area plots for geese, from 2015–2018 we counted the number of brant and snow goose nests at 61 randomly selected circular plots (15-m or 25-m radius, depending on nest density) within these nesting areas.

2.1 Reproductive and environmental phenology

We maintained daily checklists to determine the first arrival date for each species at our study site. If a species was present at our site upon our arrival, we instead used the first-arrival information collected from a site 10 km from our camp (see Ward et al., 2016). Once nesting commenced, we determined the initiation date of each nest using standard techniques (see Supporting Information S1.1). Nests of longspurs were only monitored from 2015–2018, but we monitored nests of the other three species from 2011–2018.

We collected a suite of environmental variables at or near our study site. We recorded the percent cover of snow at 10 (2018) or 20 (2011–2017) 25-m radius plots that we monitored each year. We assessed snow cover upon arrival at the field site and every 2–6 days (typically 2 d) thereafter until snow cover averaged <5%. We averaged the daily values of snow cover across the plots and used the annual date when snow cover averaged 50% as an indicator of annual snowmelt. To characterize spring temperatures that preceded our arrival at the field site, we accessed weather observations at a site 10 km away (Colville Village, Alaska; National Oceanic and Atmospheric Administration, 2020), and determined values for accumulated thaw-degree days for each year. We also used an on-site weather station to record hourly temperature and wind speed, values which we summarized in running 3-day averages for use in chick-growth analyses.

2.2 Resource abundance

We monitored the seasonal abundance of the primary food resources available to juvenile birds at our site. We began monitoring both herbivorous and insectivorous food resources as early in the season as possible based on snow cover and ground thaw, and monitored these resources throughout the period of chick growth. For brant and snow geese, this involved estimating the biomass of the halophytic sedge *Carex subspathacea* (hereafter *subspathacea*; Gadallah & Jefferies, 1995; Hupp et al., 2017) by measuring the Normalized Difference Vegetation Index (NDVI). In brief, we estimated *subspathacea* biomass at a series of vegetation plots based on NDVI, and averaged these values across plots for each sample date across the season. We fit lognormal models to each year's sample averages to describe the non-linear seasonal trends in biomass,

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and used daily predictions from these year-specific estimates to determine the biomass of *subspathacea* that was available to goslings when they were 15 days old (see Supporting Information S1).

Chicks of semipalmated sandpipers (Holmes & Pitelka, 1968) and longspurs (Custer et al., 1986) are insectivores. To monitor the availability of these food resources we collected surface-active arthropods every three days from ten modified Malaise traps following protocols of the Arctic Shorebird Demographic Network (Brown et al., 2014; Saalfeld et al., 2019; see Supporting Information S1). We collected arthropod samples at our site from 2015–2017.

2.3 Chick growth

We measured growth rates of brant and snow goose goslings (2012–2017) and semipalmated sandpipers (2015–2017) based on juveniles that were marked at hatch, and recaptured and weighed at later dates (see Supporting Information S1.1). From 2015–2017, we visited longspur nests and weighed chicks as soon as possible after the first egg in each nest hatched, and weighed chicks at approximately 3-day intervals thereafter. We could not uniquely mark longspur chicks as they were too small to retain tags, and instead modeled the growth of longspur chicks using brood-averaged masses.

2.4 Analysis

We compared similar environmental metrics across groups in our analyses, modified as necessary due to inherent differences in relevant life-history traits. To assess factors that influenced the timing of breeding (Table 2a), we determined the length of the pre-lay period (the number of days between when a species was first detected at our study site and that species' mean date of nest initiation) and mean nest initiation date for each species each year. We monitored nests of semipalmated sandpipers and longspurs discovered on our core study plot, and brant and snow geese at nearby colonies. We calculated the average clutch size for each species for each year of study from these samples. To evaluate nesting effort relative to environmental variables from 2015–2018, we counted nests of shorebirds and longspurs in our core study plots, and goose nests in random plots.

TABLE 2 Predictor variables used to assess variation in (a) reproductive phenology and investment and (b) chick growth of black brant (BLBR), lesser snow goose (LSGO), semipalmated sandpiper (SESA), and Lapland longspur (LALO) breeding at the Colville River, Alaska, 2011–2018

	species	species
variable	BLBR	LSGO
(a) reproductive phenology and investment	(a) reproductive phenology and investment	(a) reproductive phenol
snow cover	annual date 50% snow cover	annual date 50% snow c
temperature	annual thaw-degree days (TDD) from 1 Jan–10 Jun	annual thaw-degree day
(b) chick growth	(b) chick growth	(b) chick growth
resource abundance	*Carex subspathacea* biomass (g m^{-2}) on day 15	*Carex subspathacea* bio
nest timing	incubation – date 50% snow	incubation – date 50% s
temperature	lifetime TDD (°C)	lifetime TDD (°C)
wind	3-day ave. (m s^{-1})	3-day ave. (m s^{-1})

To assess evidence for species-specific responses to snow cover (date of 50% snow cover each year) and temperature (accumulated thaw-degree days from 1 January–10 June each year), we estimated slope parameters of least-squares linear regression models. We first fit models with unique slopes for each species (i.e., models with full interaction between species and environmental variables), with arrival date, duration of the pre-lay period, date of nest initiation, clutch size, and nesting effort (the annual number of nests of each species enumerated on known-area plots) as response variables. If none of the species-specific slopes in these models differed from 0 (i.e., no evidence of a species-specific response to snow cover or temperature), we then fit

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more parsimonious models with a common slope among species to further assess support for a response to the two environmental variables. Next, we compared these four response variables among the four species using standard anova techniques and conducted Tukey's HSD tests for post-hoc examination of differences between species. For these assessments, we considered results to be biologically meaningful at $\alpha = 0.05$.

To assess factors that influenced the growth of brant and snow goose goslings, we fit linear models to estimate body mass as a function of gosling age and sex. Because we weighed goslings only once, we did not estimate a growth curve for the period from hatch until fledge, but instead modeled the growth of both goose species over the span of ages represented in our samples (see Hupp et al., 2017). Although the mass gain of goslings from both species is non-linear overall (Ankney et al., 1991), gosling growth rates are well approximated by a linear fit for the period shortly prior to fledging over which we recaptured goslings (Cooch et al., 1991). For semipalmated sandpiper and longspur chicks, we $\log_{10}$-transformed both mass and age to control for inherent patterns of unequal variance from hatch until fledging (NB: goslings were captured only during the linear phase of their growth cycle such that variances were equal across ages, making log transformation unnecessary). Because we uniquely marked goslings and semipalmated sandpiper chicks, we modeled the growth of individuals of these species, but used the average brood mass per nest visit as our response variable for longspurs. Finally, to focus on post-hatch factors affecting chick growth, we excluded mass measurements collected on the day of hatch for longspurs. For semipalmated sandpipers, we similarly censored values collected prior to two-days age because chicks of Arctic-breeding shorebirds rely primarily on internal yolk reserves to fuel growth after hatch (Norton, 1973; Schekkerman et al., 1998).

We compared similar environmental metrics across all four chick-growth model sets (Table 2b; see Supporting Information S1.2), and fit linear-mixed effects models using least-squares regression to each species independently using the package 'lme4' (Bates et al., 2015), and standardized all four environmental variables to minimize collinearity and facilitate model interpretation. We fit an intercept-only (null) model in all model sets, and otherwise included chick age (semipalmated sandpipers and longspurs) or chick age and sex (brant and snow geese) as unstandardized covariates in all models. We combined these covariates along with additive combinations of the aforementioned environmental variables to create an all-subsets model set of 17 models for each species. We fit mixed-effects models in order to control for multiple observations of individuals from the same nest (all species) and repeat measures of individuals across time (semipalmated sandpipers). We employed multimodel comparisons to rank the support of each model based on Akaike's information criterion adjusted for small sample size (AIC_c) and averaged model results for each species in proportion to Akaike weights w_i following the approaches of Burnham and Anderson (2002). We calculated the conditional and marginal R^2 of each model using the R package 'piecewiseSEM' (Lefcheck, 2016) to assess objective model performance (Nakagawa & Schielzeth, 2013), and performed multimodel comparisons and model averaging using the R package 'AICcmodavg' (Mazerolle, 2019). We considered predictor variables with 95% confidence intervals that did not overlap zero to be biologically meaningful, and generated model-averaged predictions for each species using contrasting values of these biologically meaningful predictor variables to visualize chick mass under varying conditions. Specifically, we generated predictions representing growth under what we term optimal (i.e., 75th-quartile values for predictor variables with positive parameter estimates, 25th-quartile values for predictor variables with negative parameter estimates) and sub-optimal (i.e., 25th-quartile values for positive parameters, 75th-quartile values for negative parameters) conditions. For environmental variables whose model-averaged parameter estimates overlapped zero (i.e., uninformative predictors), we set these predictor values at mean levels in the model-averaging process. All analyses were performed in R (R Core Team, 2021), and values represent mean ± SD unless otherwise noted.

3. RESULTS

Over the course of our study, we monitored 1,447 brant nests, 1,374 snow goose nests, 821 semipalmated sandpiper nests, and 142 longspur nests. We experienced highly variable environmental conditions during the study period. In spring, the date of 50% snow cover ranged over a nearly three-week period from 20

May (2016)–8 June (2013) and values for accumulated thaw-degree days 1 January–10 June ranged from 7.2 (2018)–56.1 (2015). Warmer springs had earlier dates of snowmelt (adjusted $R^2 = 0.53$, $P = 0.02$), but our study period also encompassed years with mixed patterns between the two variables (e.g., years with relatively early [2015] or late [2013] snowmelt as functions of spring temperature). We also recorded prolonged periods of high (e.g., average temperature 17.3°C from 13–16 July 2016) and near-freezing temperatures (e.g., average temperature 3.4°C from 7–13 July 2015) during periods of chick growth.

3.1 Variation in reproductive phenology and investment

Mean dates of arrival at the breeding site ($F_{3,28} = 11.2$, $P < 0.001$; Fig. 1a), duration of the pre-lay period ($F_{3,24} = 13.7$, $P < 0.001$; Fig. 1b), nest initiation ($F_{3,24} = 16.9$, $P < 0.001$; Fig. 1c), and clutch size ($F_{3,24} = 17.0$, $P < 0.001$; Fig. 1d) varied considerably among the four species (see Fig. 2 for statistically significant interspecific comparisons). Regardless of spring conditions, snow geese (15 May $\pm$ 4.0 days) and longspurs (14 May $\pm$ 2.4 days) arrived earliest each spring (Fig. 1a), followed approximately one week later by brant and semipalmated sandpipers (both 22 May $\pm$ 3.6 days and $\pm$ 4.2 days, respectively). Early arrival did not necessarily confer rapid nesting, however: the pre-lay period (Fig. 1b) was longest for longspurs (mean 27.8 $\pm$ 2.9 days), and shortest for brant (12.6 $\pm$ 4.7 days), followed by snow geese (13.8 $\pm$ 5.1 days) and semipalmated sandpipers (19.3 $\pm$ 3.2 days). Due to their early arrival and short pre-lay period, snow geese consistently initiated nests before the other three species (Fig. 1c). Mean nest initiation was 30 May ($\pm$ 4.6 days) for snow geese, 4 June ($\pm$ 5.2 days) for brant, 8 June for longspurs ($\pm$ 9.3 days), and 10 June ($\pm$ 5.4 days) for semipalmated sandpipers. Longspurs had the largest clutches (4.8 $\pm$ 1.1 eggs; Fig. 1d), followed by snow geese (4.0 $\pm$ 1.2 eggs), semipalmated sandpipers (3.8 $\pm$ 0.5 eggs), and brant (3.7 $\pm$ 1.0 eggs).

FIGURE 1 Variation in arrival date (a), pre-lay interval (b), date of nest initiation (c), and clutch size (d) and of black brant (BLBR), snow geese (LSGO), semipalmated sandpipers (SESA), and Lapland longspurs (LALO) at a site on the Colville River, Alaska, 2011–2018. Horizontal lines represent the median, diamonds the mean, black circles the actual annual values, boxes the 25th and 75th percentiles, and whiskers the range of values. All interspecific comparisons of these values were statistically significant ($P < 0.05$) based on post-hoc Tukey HSD comparisons, except for comparisons linked by horizontal bars at bottom of each plot (e.g., mean arrival dates of black brant and semipalmated sandpipers do not statistically differ; Fig. 2a). For (a) and (c), ordinal date 140 is 20 May

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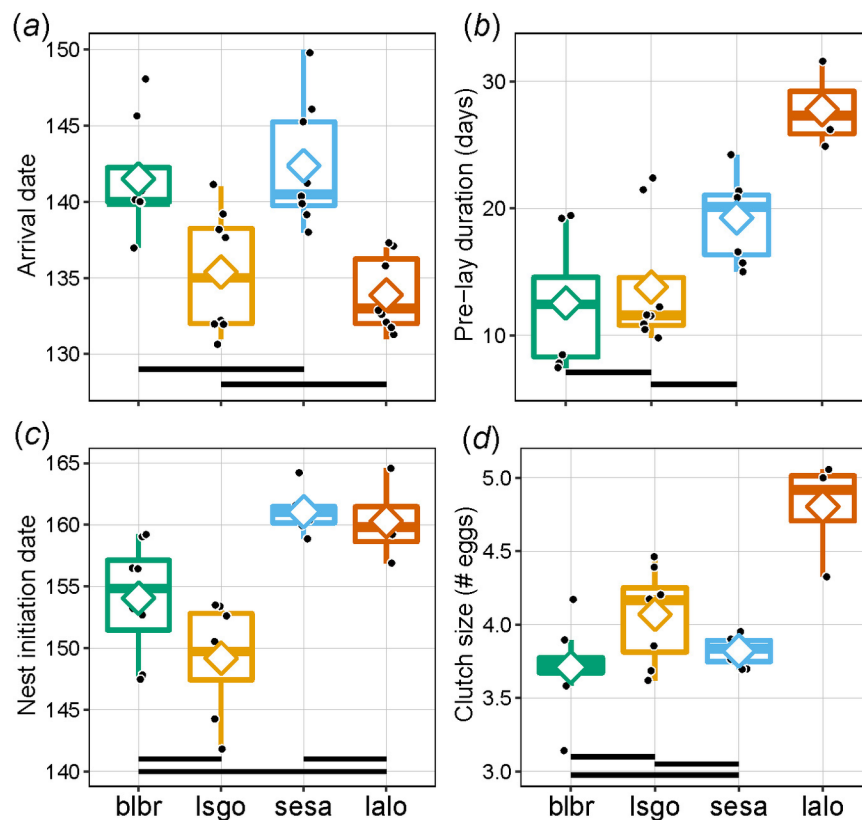
Adjustments to the timing of reproduction in response to snow cover and spring temperature varied by species (Fig. 2; Table 3). The four species arrived at the Colville River Delta earlier with advancing snow melt (Fig. 2a), but this relationship was only significant for semipalmated sandpipers (0.55 days earlier arrival for each day of advancing snowmelt; Table 3). Earlier snowmelt resulted in a reduced pre-lay period for brant (Fig. 2c; Table 3) and earlier nest initiation for all four species (Fig. 2e), although the magnitude of the effect varied among species and was greatest in brant and snow geese (Table 3). For assessments of reproductive investment, earlier snowmelt resulted in larger clutches for brant and snow geese (Fig. 3a; Table 3) and increased nesting efforts by semipalmated sandpipers (Fig. 3c; Table 3). In general, the effect of spring temperatures on reproductive phenology and investment were less pronounced than snow cover. Warmer spring temperatures resulted in earlier nest initiation for brant and snow geese (Fig. 2f; Table 3), and larger clutch sizes for brant (Fig. 3b; Table 3) and increased nesting efforts for semipalmated sandpipers (Fig. 3d; Table 3). Spring temperature did not influence any of the reproductive metrics for longspurs (Fig. 2 and 3, Table 3).

TABLE 3 Response of black brant (BLBR), lesser snow geese (LSGO), semipalmated sandpipers (SESA), and Lapland longspurs (LALO) to snow cover (a; date of 50% snow cover each year) and temperature (b; accumulated thaw-degree days from 1 January–10 June each year), 2011–2018, Colville River, Alaska. Values represent statistically significant slope parameters ($\pm 95\%$ confidence intervals) from linear least-squares regression models with date of site arrival, duration of pre-lay period, date of nest initiation, clutch size, and number of nests as response variables. There was no support for species-specific differences in site arrival or pre-lay duration as a function of temperature, but all other assessments had at least one significant species-specific response. Significance levels represented by * (P [?] 0.05), ** (P [?] 0.01), and *** (P [?] 0.001); n.s. indicates $P > 0.05$

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	species	species	species	species
	BLBR	LSGO	SESA	LALO
(a) snow cover	(a) snow cover	(a) snow cover	(a) snow cover	(a) snow cover
site arrival	n.s.	n.s.	0.55 (0.06–1.05)*	n.s.
pre-lay duration	0.59 (0.04–1.14)*	n.s.	n.s.	n.s.
nest initiation	0.84 (0.59–1.08)***	0.74 (0.50–0.98)***	0.28 (0.03–0.52)*	0.38 (0.09–0.67)*
clutch size	-0.04 (-0.07– -0.01)*	-0.04 (-0.07– -0.00)*	n.s.	n.s.
number of nests	n.s.	n.s.	-6.14 (-9.82– -2.45)**	n.s.
(b) temperature	(b) temperature	(b) temperature	(b) temperature	(b) temperature
site arrival	n.s.	n.s.	n.s.	n.s.
pre-lay duration	n.s.	n.s.	n.s.	n.s.
nest initiation	-0.22 (-0.36– -0.07)**	-0.21 (-0.36– -0.07)**	n.s.	n.s.
clutch size	0.02 (0.00–0.03)*	n.s.	n.s.	n.s.
number of nests	n.s.	n.s.	1.64 (0.38–2.92)*	n.s.

FIGURE 2 Effect of interannual differences in the date of 50% snow cover (left column) and accumulated thaw-degree days on 10 June (right column) on the arrival date (a and b), pre-lay interval (c and d), and mean date of nest initiation (e and f) of black brant, snow geese, semipalmated sandpipers, and Lapland longspurs at a site on the Colville River, Alaska, 2011–2018. Circles represent year-specific values (±SE for nest initiation), and solid lines represent the best-fit least-squares regression ±95% prediction interval (dashed lines). Species-specific colored triangles to right of figures represent slope parameters that significantly differ from zero. See Table 4 for estimates (±95% confidence interval) of slope parameters
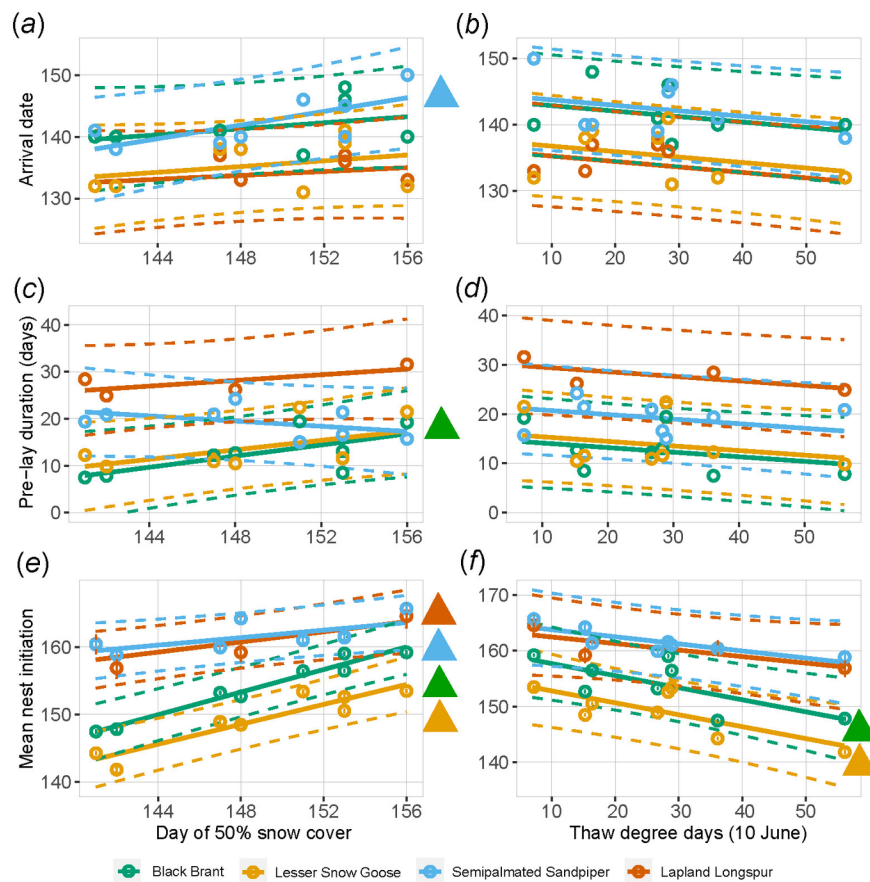
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FIGURE 3 Effect of interannual differences in the date of 50% snow cover (left column) and accumulated thaw-degree days on 10 June (right column) on the clutch size (*a* and *b*) and number of nests (*c* and *d*) of black brant, snow geese, semipalmated sandpipers, and Lapland longspurs at a site on the Colville River, Alaska. Clutch sizes were monitored for brant, snow geese, and semipalmated sandpipers from 2011–2018, and Lapland longspurs from 2015–2018. Nesting effort was monitored on known-area plots for all four species from 2015–2018. Circles represent year-specific values (±SE for clutch size), and solid lines represent the best-fit least-squares regression ±95% prediction interval (dashed lines). Species-specific colored triangles to right of figures represent slope parameters that significantly differ from zero. See Table 4 for estimates (±95% confidence interval) of slope parameters. Ordinal date 148 is 28 May
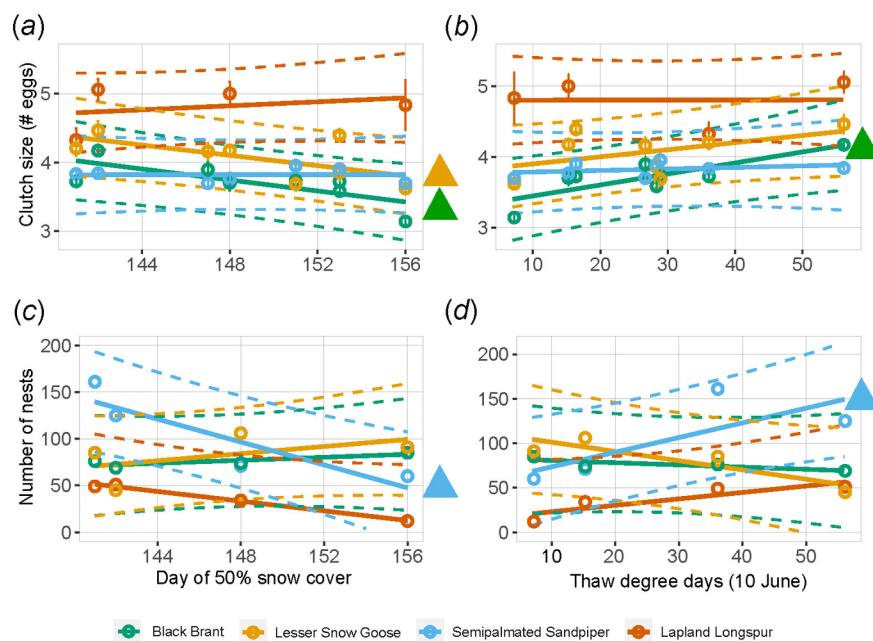
3.2 Chick growth

We modeled the growth of 166 brant goslings (99 females, 67 males) from 105 nests, 390 snow goose goslings (195 females, 195 males) from 215 nests, 250 observations of 188 semipalmated sandpiper chicks from 94 nests, and 118 observations of longspur broods from 56 nests. Excluding the intercept-only null models, conditional R^2 values ranged from [?]0.73 (snow goose) to [?]0.97 (longspur) and marginal R^2 ranged from [?]0.31 (snow goose) to [?]0.92 (longspur) across all model sets (Tables S1–S4), indicating that the combinations of fixed and random variables in our model sets satisfactorily accounted for variation in avian growth. For all species, null models received no support ($w_i = 0$) in multimodel comparisons, and models with only age and sex (herbivores) or age alone (insectivores) as covariates were likewise poorly supported ($w_i = 0$; Tables S1–S4) except for longspurs, where a model fitting only age had the second-highest model weight ($w_i = 0.14$; Table S4) in the model set. For all species, the model-averaged parameter estimates for juvenile age were positive (Table 4), unsurprisingly indicating the strong influence of age on body mass. Additionally, the model-averaged parameter estimates of sex for both goose species (Table 4) indicated that male goslings weighed more than females of the same age, as expected (Ankney, 1980; Hupp et al., 2017).

TABLE 4 Model-averaged predictor variables ($\pm 95\%$ confidence interval) from analysis of factors affecting the mass of chicks of black brant (BLBR), snow geese (LSGO), semipalmated sandpipers (SESA), and Lapland longspurs (LALO) at the Colville River, Alaska, 2012–2017. Values in bold highlight variables with confidence intervals that do not overlap 0. All predictor variables except age and sex were standardized prior to analysis; see Table 2 for species-specific variables

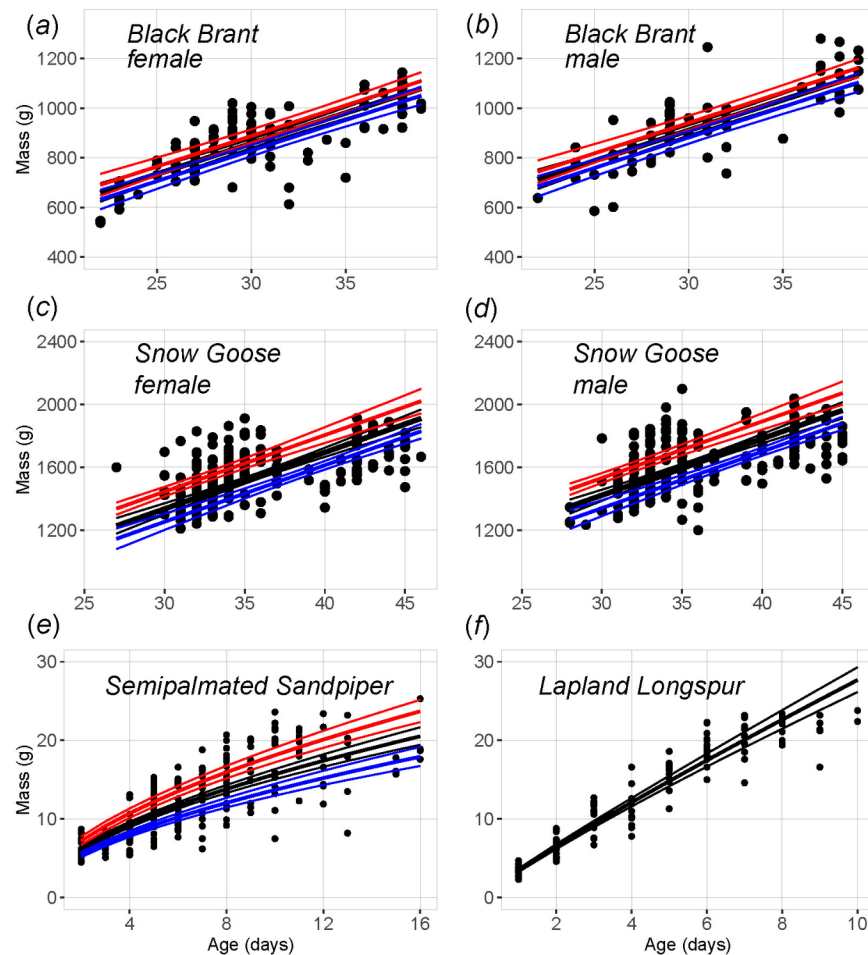|	species	species	species	species
variable	BLBR	LSGO	SESA[a]	LALO[a]
age	**24.611 (21.040–28.182)**	**35.983 (30.796–41.170**	**0.571 (0.529–0.614)**	**0.899**
sex[b]	**52.972 (30.970–74.975)**	**86.932 (64.734–109.130)**	n.a.	n.a.
resource abundance	**-17.964 (-35.706– -0.223)**	8.891 (-11.490– 29.273)	-0.004 (-0.022–0.013)	0.003 (
nest timing	**-33.357 (-51.022– -15.692)**	**-19.845 (-37.296– -2.395)**	**-0.058 (-0.074– -0.042**	-0.016
temperature	-6.398 (-24.816–12.019)	**-107.347 (-134.796– -79.898)**	**0.022 (0.012–0.033)**	0.008 (
wind	4.234 (-11.483–19.951)	15.699 (-1.679–33.077)	0.008 (-0.001–0.018)	-0.001

[a] For SESA and LALO, age was $\log_{10}$-transformed in all models to control for heteroscedasticity.

[b] Females are the reference level; sexes unknown for SESA and LALO.

The effect of the environmental covariates on chick growth varied by species (Table 4). For brant and snow geese, age-specific body mass of goslings increased with earlier nest timing (nest incubation date – date of 50% snow cover; Table 4). For brant, lower resource abundance (g m^{-2} *subspathacea* biomass at 15 days of age; Table 4) was associated with increased gosling mass, and the body mass of snow goose goslings declined as thaw-degree days increased (Table 4). For semipalmated sandpipers, higher age-specific chick masses were associated with warmer temperatures and nests that were initiated early with respect to the date of 50% snow cover (Table 4). For longspurs, all model-averaged parameters for environmental variables were small and with confidence intervals that broadly overlapped zero (Table 4), indicating that none of the environmental variables that we included in our models meaningfully predicted the mass of chicks of this species. Finally, wind speed (all species) and arthropod abundance (insectivores) did not meaningfully influence chick mass as indicated by confidence intervals on parameter estimates that overlapped zero (Table 4).

For environmental covariates that influenced chick growth (Table 4), we estimated age-specific chick masses for each species using values of the 25th and 75th quartiles of these predictors to assess the effect of optimal and sub-optimal (see Methods: Analysis) values of these variables on chick mass. Across the ages and sexes of chicks for which we modeled growth, the difference between optimal and sub-optimal chick-growth conditions resulted in body mass differences of 5.0–8.5% for brant, 9.1–14.3% for snow geese, and 24.4% for semipalmated sandpipers. For snow geese (Figs 4c, 4d) and semipalmated sandpipers (Fig. 4e), the 95% confidence intervals on estimates derived under optimal conditions did not overlap those derived under sub-optimal conditions, but those for brant overlapped slightly (Figs 4a, 4b).

FIGURE 4 Model-averaged predictions of chick growth of female (*a*) and male (*b*) black brant, female (*c*) and male (*d*) snow geese, semipalmated sandpipers (*e*), and Lapland longspurs (*f*) at the Colville River, Alaska. Brant and snow goose goslings measured from 2012–2017, semipalmated sandpiper and Lapland longspur chicks from 2015–2017. Measured values are represented by black circles, and black lines represent estimates under average environmental conditions. Red and blue lines for brant, snow geese, and semipalmated sandpipers represent body-mass estimates of chicks under optimal (red lines) and sub-optimal (blue lines) environmental conditions based on variation in biologically meaningful predictor variables (see Table 3 for species-specific variables). For all colors, heavy lines represent model-averaged estimates, and fine lines represent the associated 95% confidence intervals

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4. DISCUSSION

The four species of Arctic-breeding birds in our comparison exhibited strong variation, both within years across species and within species across years, in multiple metrics related to the timing of and investment in reproduction. This variation was also expressed during the period of chick growth, but the species-specific responses during this phase of the breeding cycle often contrasted with those expressed during the pre-lay and nesting phases. Our prediction that spring temperatures and snow cover would have a greater effect on the timing of nest initiation and clutch size in geese compared to semipalmated sandpipers and longspurs was generally supported and may reflect the differing role that endogenous reserves play among the taxa during reproduction (see below). Our prediction that arthropod abundance would have relatively little effect on the growth of altricial longspur chicks was also supported, but we found no evidence that resource abundance influenced the growth of semipalmated sandpiper chicks or snow goose goslings. Furthermore, the effects of *subspathacea* biomass on the growth of brant goslings were opposite of our predictions, emphasizing the role of factors other than resource abundance in juvenile growth.

4.1 Annual adjustments to reproductive phenology and investment

Of the four species in our comparison, only semipalmated sandpipers meaningfully adjusted their arrival date in response to environmental conditions (snow cover), likely a reflection of the species' dependence on exogenous reserves derived from arthropod prey that only become available as snow melts and temperatures

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warm (Holmes & Pitelka, 1968; MacLean & Pitelka, 1971). In contrast, snow geese and longspurs consistently arrived the earliest at our study site each spring. Snow geese employ their robust bill and specialized foraging techniques to access nutritious sub-surface roots and shoots (Iacobelli & Jefferies, 1991), while longspurs can subsist on seeds (Custer & Pitelka, 1978) prior to the emergence of arthropods. Brant are relatively dependent on food resources that emerge only as temperatures warm and melting snow exposes appropriate foraging substrates (Lewis et al., 2020), but unlike semipalmated sandpipers, brant also carry significant endogenous reserves that can serve as buffers when food resources are inaccessible (Hupp et al., 2018).

Subsequent phases of the reproductive cycle of the species in our comparison further reflected the species' positions on the endogenous-exogenous continuum. Larger bodied geese are capable of carrying comparatively larger endogenous reserves to the Arctic that they can then invest in egg production and incubation (Klaassen et al., 2006). Conversely, shorebirds and passerines derive virtually all egg nutrients and reserves for self-maintenance after their arrival to the breeding area. All species advanced nest initiation with earlier snowmelt, but the effect was strongest for geese. Likewise, warmer spring temperatures resulted in earlier nest initiation by geese, but not for semipalmated sandpipers and longspurs. In years when Arctic phenology is advanced, geese can use their reserves to begin egg development in late migration or shortly after their arrival on the nesting area so as to initiate nests early and better time the hatch of offspring with peak nutrient availability (Klaassen et al., 2006; Nolet et al., 2020). Compared to the large-bodied goose species that can rely on endogenous reserves, the pre-lay periods for semipalmated sandpipers and longspurs were relatively long, reflecting the fact that individuals of both species must first forage to acquire the necessary exogenous resources prior to producing eggs. Relative to snow geese, brant invest more exogenous nutrients into eggs, and in years when spring is advanced are more likely to initiate follicle development during migration (Hupp et al., 2018). The shorter pre-lay durations in brant during years of earlier snowmelt likely reflected the species' tendency to initiate follicle development prior to arrival on the nesting area. Follicle development in snow geese breeding on the Colville River Delta mainly occurs after arrival in the Arctic (Hupp et al., 2018), and their pre-lay interval is less variable relative to environmental conditions.

Although endogenous investment in eggs gives geese an advantage in advancing egg development and nest initiation when Arctic phenology is advanced, female geese may use reserves for self-maintenance at the expense of reproductive investment in years when snow and cold temperatures persist (Barry, 1962; Raveling, 1978; Reed et al., 2004). We detected reduced clutch size in response to delayed snowmelt in both brant and snow geese, and to lower temperatures in brant (Fig. 3). Because brant invest relatively more endogenous reserves into eggs than the other species we studied, they are more likely to reduce clutch sizes in colder springs or when late snowmelt delays nest initiation and induces females to use reserves for self-maintenance (Barry, 1962). Late springs likely delayed new plant growth that brant also rely on for egg nutrients (Hupp et al., 2018). In contrast, phylogenetic constraints (MacLean, 1972) likely preclude semipalmated sandpipers from varying clutch sizes (Sandercock et al., 1999), although previous research indicates that shorebirds can regulate egg size within clutches in response to seasonal variation (Martin et al., 2018; Sandercock et al., 1999). Longspurs exhibited the greatest variation in clutch size during our study (1–7 eggs), but this variation was not related to environmental conditions. Such variation may instead reflect the influence of other factors (e.g., female age or breeding experience; Sæther, 1990; Stearns, 1976) that we did not measure.

In addition to adjusting investment in clutches, Arctic-breeding birds may forego breeding altogether in response to extreme environmental conditions (Ganter & Boyd, 2000; Schmidt et al., 2019), a response believed to reflect a trade-off between current reproductive investment and future survival (Linden & Møller, 1989; Roff, 2002). The nesting effort of semipalmated sandpipers was greatest in years with warm temperatures and early snow melt, but the other three species did not meaningfully moderate nesting efforts in response to these variables. This variation again suggests the likely role of exogenous reserves in modulating the reproductive output of semipalmated sandpipers. Shorebirds lay clutches that constitute a relatively high proportion of their body mass (Rahn et al., 1975; Ricklefs, 1984), and semipalmated sandpiper females at our study site were apparently unable to acquire sufficient arthropod resources to initiate nests in cold springs with extensive snow cover. In contrast, brant and snow geese could rely on endogenous reserves, and longspurs seed resources in lieu of arthropods, to ensure nesting opportunities.

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Notably, the four species in our study share the overarching life-history trait of being migratory animals. Previous research has suggested that migratory species are more vulnerable to climate change due to the potential decoupling of relevant seasonal cues across a species' range (Both et al., 2010; Møller et al., 2008; Robinson et al., 2009). We documented interannual responses among these four migratory species, however, that demonstrated a high degree of interspecific response to shared stimuli among diverse taxa. The species at our study site use two flyways (Pacific [brant and snow geese] and Central [snow goose, semipalmated sandpiper, and longspur] Americas flyways) across a mix of marine (brant and semipalmated sandpiper), seasonal wetland (snow goose and semipalmated sandpiper), and agriculture/prairie landscapes (snow goose and longspur) to migrate to Arctic breeding grounds. Despite the use of varied migratory routes and habitats, these species nonetheless adjusted their timing of breeding in ways that tracked spring environmental conditions at the breeding site. Indeed, long-term information for these and other species at this site exhibit a general advancement of arrival dates in concert with warming spring conditions (Ward et al., 2016), patterns noted more broadly in other studies (Jonzén et al., 2006; Thorup et al., 2007; Van Buskirk et al., 2009). Migratory birds exhibit life histories that are predicated on exploiting diverse, ephemeral landscapes (Greenberg & Marra, 2005; Newton, 2008), and employ flexible physiologies that permit the rapid hypertrophy and subsequent atrophy of respiratory, digestive, and circulatory functions (Piersma & van Gils, 2011). Such behavioral and physiological adjustments enable large-scale movements and undoubtedly also serve as buffers in a changing world. So although migratory species may theoretically be predisposed to a decoupling of seasonal cues across their large ranges, these four species responded predictably to prevailing environmental conditions by adjusting their reproductive timing and investment. Migratory birds, by virtue of their intrinsic life histories, may thus accommodate the effects of a warming Arctic better than previously appreciated.

4.2 Variation in chick growth

Interannual adjustments in the timing of and investment in breeding may reflect adaptive responses to prevailing environmental conditions, but nests must hatch and chicks must grow and survive in order for such adjustments to be propagated in an evolutionary context (see Charmantier & Gienapp, 2014). The rate of chick growth provides insights into fitness-related variables (e.g., survival, recruitment, lifetime reproductive output) that are otherwise extremely difficult to measure in most bird species. Curiously, resource abundance was not a meaningful predictor of chick mass of either insectivore species in our study. Obviously, food abundance directly affects chick growth, which suggests that either we did not measure arthropod abundance in a way that reflected real abundance or that the range of abundances that we measured at our site did not limit growth. For the former supposition, this same sampling protocol has been successfully employed by others (see Kwon et al., 2019 for overview), and Saalfeld et al. (2019) specifically determined that this sampling technique described variations in arthropod abundance that predicted the chick mass of two shorebird species (dunlin *Calidris alpina* and pectoral sandpiper *Calidris melanotos*) that are closely related to semipalmated sandpipers. Thus, it is more likely that arthropod abundances were not limiting during our period of study. Despite measuring a nearly 300-fold variation in arthropod abundance (1.5–427.3 mg 3-day^{-1} sample) during periods of chick growth from 2015–2017, our measurements did not apparently reflect conditions that affected the growth of insectivore chicks. For semipalmated sandpipers, warmer temperatures in the 3-day period prior to recapture were associated with larger same-age chicks, and there was a positive relationship between temperature and arthropod abundance at our study site (Pearson's r = 0.62, $P < 0.001$). In general, arthropod abundance was low at lower temperatures and increased at temperatures >5°C, but, importantly, we also documented periods of high temperature that coincided with low arthropod abundance (see Results) during which we nonetheless observed high age-specific chick masses. Further, we documented mass loss or static growth of recaptured semipalmated sandpiper chicks during a period of unusual cold (average 3.4°C from 7–13 July 2015), and encountered dead and emaciated chicks of red phalaropes (*Phalaropus fulicarius*) that presumably had starved. This suggests a thermogenic trade-off for semipalmated sandpiper chicks at higher temperatures wherein the high cost of thermogenesis (Bakken et al., 2002; Schekkerman et al., 2003) may be minimized and growth maximized (McKinnon et al., 2013), permitting rapid chick growth even during periods of relatively low food abundance.

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Resource abundance was a meaningful predictor of the growth of only brant, but the negative parameter estimate of this metric (Table 4) was counterintuitive. Previous research has demonstrated an inverse relationship between forage biomass and forage quality (i.e., nitrogen content) in graminoids like *subspathacea* (Doiron et al., 2014; Lameris et al., 2017), a relationship which may account for this finding. There is a strong positive relationship between nitrogen content and demographic variables like gosling growth and survival (Doiron et al., 2015; Manseau & Gauthier, 1993; Person et al., 2003; Sedinger & Raveling, 1986), and in our study it may be that periods of high *subspathacea* biomass had correspondingly low values for nitrogen content. The NDVI-based techniques of Hogrefe et al. (2017) are not suitable for detecting the small but meaningful differences in the nitrogen content of *subspathacea* . Anecdotally, Hogrefe et al. (2017) determined the biomass and percent nitrogen of 221 samples of *subspathacea* from 2012–2015 at our study site, and although NDVI values could not accurately predict the nitrogen content of these samples, there was a strong negative relationship between biomass and nitrogen content (Pearson's r = -0.52, P <0.001). Thus, higher age-specific body mass of brant goslings associated with lower forage biomass may reflect aspects of forage quality that we were unable to measure. In contrast, we did not find that higher *subspathacea* biomass negatively affected the growth of snow goose goslings. The larger snow goose goslings may be able to accommodate lower quality *subspathacea* compared to smaller brant goslings due to a greater intake and processing capacity (e.g., Lesage & Gauthier, 1997; Manseau & Gauthier, 1993; Richman et al., 2015). Further, larger snow goose goslings were associated with cooler temperatures, a result contrasting with semipalmated sandpipers. This may again indirectly reflect aspects of food quality (Dickey et al., 2008) rather than thermal constraints on growth per se (but see Fortin et al., 2000), as *subspathacea* responds to warm temperatures with increased vegetative growth (i.e., resource biomass) and decreased nitrogen content (i.e., resource quality; Doiron et al., 2014; Lameris et al., 2017). Although we do not fully understand the mechanisms, our study does demonstrate that warmer temperatures during brood rearing can differentially affect growth rates of avian herbivores versus insectivores.

Of note, none of the environmental covariates that we assessed meaningfully predicted the mass of longspur chicks, the only altricial species in this comparison. Previous research at a nearby site in Arctic Alaska documented seasonal declines in the growth of longspur chicks, as well as negative effects of low arthropod abundance and cold temperatures (Pérez et al., 2016). At our study site, however, other factors were apparently more important in modulating the growth of longspurs. It may be that aspects of parental quality that we did not measure (e.g., nest-site selection [Martin et al., 2000, Lloyd & Martin, 2004], chick provisioning [Davies, 1986; Limmer & Becker, 2009]) buffered deleterious effects of temperature and resource abundance that affected the chicks of precocial species at our site.

An environmental variable that received wide support across our comparisons was the timing of nest initiation with respect to snow cover. For brant, snow geese, and semipalmated sandpipers, chicks from nests that were initiated before or near the annual date of 50% snow cover were larger than chicks from nests that were initiated relatively later (Table 4). The positive effect of early initiation on chick growth has been documented in other studies of Arctic-breeding birds (Cooch et al., 1991; Ruthrauff & McCaffery, 2005; Sedinger & Flint, 1991), and indicates that early nest initiation rather than resource abundance is a more important factor in regulating chick growth at our study site. This suggests the role of potential factors (e.g., parental quality [Clutton-Brock, 1984; Forslund & Pärt, 1995], carry-over effects [Harrison et al., 2011]) that we could not measure. Other researchers, however, have specifically detected seasonal declines in the growth of snow goose goslings related to food abundance (Lepage et al., 1999; Lindholm et al., 1994). These studies were conducted at breeding sites with degraded grazing lawns and low-quality food compared to that on the Colville River (Hupp et al., 2017), emphasizing how spatial variation in ecological factors—in this case, food quality and abundance—can differentially affect the demographic response of the same populations (Sedinger et al., 2001).

4.3 Conclusion

Life-history traits that afford flexible responses to variable environmental conditions are favored in highly seasonal and unpredictable environments like the Arctic. Traits that in turn promote evolutionary changes in

a population are further expected to be subject to strong selection pressure under climate-warming scenarios (Berteaux et al., 2004; Hoffmann & Sgrò, 2011; Williams et al., 2008). Temperatures across all seasons are projected to increase on Alaska's Arctic Coastal Plain due to climate change (IPCC, 2013), and increases in warming have already led to long-term advances in snow melt and longer snow-free seasons in Arctic Alaska (Cox et al., 2017; Hinzman et al., 2005; Stone et al., 2002). Brant and snow geese generally responded more flexibly to variation in temperature and snowmelt during the pre-lay and nesting periods than did semipalmated sandpipers and longspurs. In contrast, we detected potentially deleterious effects of increased temperature on brant and snow goose goslings, while semipalmated sandpiper chicks responded favorably to warmer conditions. Thus, brant and snow geese may possess traits that are beneficial during one phase of the reproductive cycle (e.g., relative flexibility along the endogenous-exogenous spectrum) and others which may be detrimental at another phase (e.g., temperature-mediated sensitivity to food quality during juvenile growth). For the Arctic-breeding birds in our study, these contrasting responses underscore the importance of assessing the effects of climate variability across multiple phases of the reproductive cycle (Nolet et al., 2020).

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AUTHORS' CONTRIBUTIONS

J.H. and D.W. initiated the study, which D.R. and V.P. managed after 2014; D.R. analyzed the data with assistance from V.P.; D.R. led the writing, and all authors contributed to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data collected in support of this manuscript are publicly available at the U.S. Geological Survey Alaska Science Center's data archive: https://doi.org/10.5066/F72J692N, https://doi.org/10.5066/F7M907KT, and DOI pending for Colville collection release.

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