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RESEARCH ARTICLE

Nestling growth rates in relation to food abundance and weather in the Arctic

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ABSTRACT

Raising nestlings to fledging is energetically demanding for songbirds, requiring parents to balance several major tradeoffs. Nestling growth rates are highly susceptible to variation in environmental conditions and parental investment, and highly variable environments with short breeding seasons such as the Arctic magnify these tradeoffs. Arctic-nesting passerines provide a good model system in which to explore variation within and between species in growth rates with regard to environmental conditions and the timing of clutch initiation. Here we investigated interannual and interspecies variation in nestling mass gain for 2 species of Arctic-breeding passerine, Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) and Lapland Longspur (*Calcarius lapponicus*), across 2 years. The nestling period of 2014 was both colder (with lower minimum and maximum temperatures) and wetter (with 73% more rainfall) than 2013. Arthropod biomass was also reduced in shrub tundra in 2014 compared to 2013. Both species showed reductions in rate of daily mass gain of nestlings in 2014 compared to 2013, but we observed no significant difference between species. Furthermore, we found that in 2014 early nesting birds had higher rates of nestling growth than those initiating clutches later in the season. These findings suggest that overall environmental conditions were more challenging for raising nestlings in 2014 compared to 2013 and that these differences were manifested in a reduced rate of nestling mass gain in both species. Furthermore, both species showed a negative correlation between precipitation and growth rates, whereas only Lapland Longspur showed a positive correlation between growth rates and temperature.

Keywords: arthropods, environment, temperature, clutch timing, climate change, phenology, White-crowned Sparrow, Lapland Longspur

Tasas de crecimiento de polluelos con relación a la abundancia de alimentos y el clima en el Ártico

RESUMEN

La cría de polluelos a volantones es energéticamente demandante para las aves canoras, requiriendo que los padres balanceen varios costos-beneficios importantes. Las tasas de crecimiento de los polluelos son altamente susceptibles a la variación en las condiciones ambientales y a la inversión parental; los ambientes altamente variables con estaciones reproductivas cortas como en el Ártico magnifican estos costos-beneficios. Las aves paserinas que anidan en el Ártico brindan un buen sistema modelo en el cual explorar la variación intra- e inter-específica en las tasas de crecimiento con respecto a las condiciones ambientales y a la fecha de inicio de la nidada. Aquí investigamos la variación inter-anual e inter-específica en el aumento de la masa de los polluelos para dos especies de aves paserinas que anidan en el Ártico: *Zonotrichia leucophrys gambelii* y *Calcarius lapponicus* a lo largo de dos años. El período de anidación de 2014 fue más frío (con temperaturas más bajas mínimas y máximas) y húmedo (con 73% más de precipitaciones) que el 2013. La biomasa de artrópodos también fue menor en los arbustales de la tundra en 2014 en comparación con el 2013. Ambas especies mostraron reducciones en la tasa de aumento de la masa de los polluelos en 2014 en comparación con el 2013, pero no observamos una diferencia significativa entre las especies. Más aún, encontramos que en 2014 las aves que anidaron más temprano tuvieron tasas de crecimiento de los polluelos más altas que las de aquellas que iniciaron sus nidadas más tarde en la estación. Estos hallazgos sugieren que las condiciones ambientales

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generales fueron más desafiantes para criar a los polluelos en 2014 en comparación con el 2013, y que estas diferencias se manifestaron en forma de una tasa reducida de aumento de la masa de los polluelos en ambas especies. Más aún, ambas especies mostraron una correlación negativa entre la precipitación y las tasas de crecimiento, mientras que solo *C. lapponicus* mostró una correlación positiva entre las tasas de crecimiento y la temperatura.

Palabras clave: ambiente, artrópodos, *Calcarius lapponicus*, cambio climático, fecha de inicio de la nidada, fenología, temperatura, *Zonotrichia leucophrys gambelii*

INTRODUCTION

Breeding birds face a multitude of challenges including finding a quality mate, avoiding predation, and successfully raising their offspring to independence. Life history theory predicts a tradeoff between investment in current reproduction, self-maintenance/survival, and future reproduction to maximize lifetime fitness (Williams 1966). Success or failure of the nest is often governed by the amount of parental investment that can be provided, which in turn determines growth rates and ultimately fledging success (Ricklefs 1968). The degree of parental investment during the incubation and nestling phases is dependent on both parental quality and environmental variation (Lack 1954, Conway and Martin 2000, Cresswell et al. 2004). Thus, differences in nestling growth rates between individuals and across years can be attributed to the environmental conditions, timing of clutch initiation, and parental quality.

Two key environmental factors play critical roles in determining the rate of nestling growth: weather conditions (Ricklefs 1968, Hedd et al. 2002) and food availability (Lack 1954, Drent and Daan 1980, Emlen et al. 1991, Gard and Bird 1992, Naef-Daenzer and Keller 1999, Tremblay et al. 2005). Major changes in weather conditions, such as storms or fluctuations in temperature, directly influence the allocation of energy by nestlings to growth (Williams and Prints 1986, Dawson et al. 2005), whereas variation in food availability can limit the rate at which parents can acquire and deliver food to nestlings. Parental provisioning of nestlings is dependent on the parents having the necessary energy and time to meet their own metabolic demands and those of their nestlings. In the event of low resource abundance (regardless of cause) and/or weather perturbations, there is an inherent tradeoff between self-maintenance (and potential future reproduction) vs. parental investment in the current brood (Williams 1966). Individual responses to low resource availability are highly variable and dependent on a large number of factors, but when environmental conditions deteriorate sufficiently, a threshold is reached, regardless of investment decisions by the parents, at which available resources prevent "adequate" investment in each nestling.

Parental investment tradeoffs are particularly acute in highly seasonal and/or unpredictable environments, thus heightening the importance of maintaining maximal nestling growth rates. Unpredictable weather conditions can alter food availability and costs associated with parental behavior (such as brooding or foraging efficiency) and self-maintenance for adults (Wingfield et al. 1983, Morton 2002, Ardia et al. 2010, Angelier et al. 2013, Ropert-Coudert et al. 2014). At high latitudes, short breeding seasons and highly variable environments combine to create rearing environments with conditions ranging from highly conducive to nearly impossible between years.

Variation in timing of clutch initiation may lead to variation in environmental conditions experienced by nestlings in a particular nest. For migrants, the arrival time hypothesis suggests that the time of arrival on the breeding grounds determines parental success, with early arriving individuals having first choice of breeding territories, leading to the acquisition of higher quality territories (Ketterson and Nolan 1976, Lozano et al. 1996, Morton 2002). Clutch initiation date can be a strong predictor of reproductive output, with early compared to late laying birds having higher reproductive success (Sydeman et al. 1991, Winkler and Allen 1996). Clutch initiation date has also been shown be a viable proxy for parental quality (Ardia and Clotfelter 2007).

Previous studies of nestling growth rates in Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) have been limited to geographic comparisons within and across subspecies/species (King and Hubbard 1981, Norment 1992). Similarly, previous work on Lapland Longspur (*Calcarius lapponicus*) has been limited to basic descriptions (Grinnell 1944), relation to onset of endothermy (Maher 1964), and parental behavior following experimental manipulation (Hunt and Wingfield 2004). Only Fox et al. (1987) examined nestling growth rates in Lapland Longspur in relation to environmental conditions, although their examination was limited. At present we are unaware of a study exploring multiple factors including environmental variation and clutch timing simultaneously in multiple species.

The aim of this study was to examine growth rates for nestlings of 2 species of Arctic-nesting passerines, the White-crowned Sparrow and the Lapland Longspur, with regard to multiple components of environmental variation. We hypothesized that variation in weather, food availability, and parental quality would affect nestling growth rates. Specifically, we predicted that: (1) variation in growth rates would be positively correlated with ambient temperature

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and/or arthropod availability and negatively correlated with precipitation during the nestling period; (2) nestlings from clutches laid earlier in the season would have higher growth rates than those from later clutches; and (3) Lapland Longspur would have higher rates of growth than White-crowned Sparrow (due to the Lapland Longspur's larger body size and its status as an Arctic specialist). This study provides a comparison of intraspecies and interspecies nestling growth rates under variable environmental conditions in the Arctic while exploring effects of clutch initiation date.

METHODS

Study Species and Sites

Long-distance migratory passerines Gambel's White-crowned Sparrow and Lapland Longspur typically arrive on their Arctic breeding grounds in mid to late May, beginning nesting by early June (N. T. Boelman personal communication). Both raise a single brood during the short Arctic summers, although re-nesting does occur following failure early in the season (Wingfield and Farner 1979, Hunt et al. 1999, Hussell and Montgomerie 2002). Both species are considered to be socially monogamous, with female-only incubation and biparental care (Chilton et al. 1995, Hunt et al. 1999, Hussell and Montgomerie 2002). Although both are ground-nesting species, they differ significantly in their preferred nesting habitats and breeding ranges. The White-crowned Sparrow nests in erect and riparian deciduous shrub communities (Oakeson 1954, Norment 1992, 1993, Boelman et al. 2014) from northern Washington state to the Arctic tundra (Chilton et al. 1995) whereas the Lapland Longspur is a circumpolar breeder (Hussell and Montgomerie 2002) that nests in tussock tundra communities dominated by graminoids, mosses, dwarf shrubs, and forbs (Rodrigues 1994, Boelman et al. 2014).

Our study nests were primarily located in the immediate vicinity of Toolik Lake Field Station on the North Slope of the Brooks Range, Alaska (68°38′N, 149°36′W), with additional nests observed at 3 nearby field sites along the Dalton Highway: Sagavanirktok Department of Transportation (68°45′N, 148°53′W), Imnaviat Creek (68°37′N, 149°17′W), and Roche Mountonee Creek (68°22′N, 149°18′W). Each site contained both "tussock tundra" and "shrub tundra" plots in which the arthropod sampling (described later) was conducted. The vegetation composition of both tussock tundra and shrub tundra plots has been described previously (Boelman et al. 2014).

Nests were found throughout the breeding season (early June through mid-July) in 2013 and 2014 by observation of female behavior. Briefly, nests were found either by flushing incubating birds from their nests or by following females until they returned to their nests. These data represent 246 individual nestlings, 110 Gambel's White-crowned Sparrow (2013: 19 fledged, 0 depredated, 0 dead other causes; 2014: 82 fledged, 0 depredated, 9 dead other causes) and 136 Lapland Longspur (2013: 19 fledged, 0 depredated, 2 dead other causes; 2014: 74 fledged, 4 depredated, 37 dead other causes). The nestlings came from 58 separate nests, with 30 of the 58 nests monitored daily from hatch through fledge. In 2013, 6 Lapland Longspur and 4 White-crowned Sparrow nests were monitored daily, and in 2014, 10 Lapland Longspur and 10 White-crowned Sparrow nests were monitored daily. Measurements for the remaining 28 nests were only made once when nestlings were 5 to 7 days of age. These additional nestlings were included because they improved, but did not change, model predictions.

Nestling Measurements

On the day of hatch, nestling age was defined as 0. Starting on day 1, nestling morphometrics were collected. Body mass was measured to the nearest 0.1 g using an electronic balance (YA Gold, Oshaus, Parsippany, NJ). Abdominal and furcular fat scores were assigned by visual estimation on a scale from 0 (no fat) to 5 (bulging deposits; Wingfield and Farner 1978). Skull size (back of the skull to the tip of the beak) and tarsus were measured to the nearest 0.1 mm with calipers.

Climate Data

Meteorological data were obtained from the Environmental Data Center at Toolik Lake Field Station (Environmental Data Center Team 2014). Wind speed (MET-ONE sensor: Campbell Scientific, Logan, UT), precipitation (Pluvio N Rain Gauge: OTT, Kempten, Germany), and temperature (Copper-Constantan wire: Omega Engineering, Stamford, CT) data were collected and saved using a CR3000 data logger (AM25T Multiplexer: Campbell Scientific, Logan, UT). All values are presented as daily means.

Arthropod Biomass

Ground-dwelling arthropod biomass was measured weekly during both years using pitfall traps at Toolik Lake Field Station. Each pitfall trap consisted of a plastic cup (~7.5 cm in diameter by 10 cm deep) buried in the ground so that the lip of the cup was flush with the surrounding ground surface (Norment 1987, Rich et al. 2013). Traps were filled 2 cm deep with 50% ethanol and were retrieved 48 hours after being set. At each plot there were two 100 m transects, each containing 10 pitfall traps spaced 10 m apart. On returning to the laboratory, each sample was placed in a 20 mL scintillation vial containing ~70% ethanol. To preserve the samples for future curation and entomological studies, pitfall biomass was determined using an alternative allometric approach, using published length–mass regression

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TABLE 1. The effects of age, mortality (final status), species and year on nestling mass from a linear mixed effects model. The random effect of nestling ID had a variance of 1.75 with standard deviation of 1.32, and the random effect of Nest had a variance of 1.71 with a standard deviation of 1.31; the residuals had a variance of 2.46 and standard deviation of 1.57. The variable Final Status is a dummy predictor coding whether an individual successfully fledged or died; the estimated effect is for nestlings that die prior to fledge. Species (LALO) indicates model predictions for Lapland Longspur.

Variable	Estimate	SE	df	T	*p*-value
Intercept	1.899	0.785	44	2.418	0.020
Final Status (Dead)	−0.500	0.480	403	−1.043	0.298
Age	2.500	0.068	872	36.734	<0.001
Species (LALO)	−1.885	1.027	46	−1.835	0.073
Year (2014)	0.896	0.876	47	1.023	0.312
Final Status * Age	−0.291	0.067	963	−4.358	<0.001
Age * Species (LALO)	0.178	0.089	878	1.993	0.047
Age * Year (2014)	−0.367	0.077	880	−4.757	<0.001
Species (LALO) * Year (2014)	0.533	1.160	51	0.459	0.649
Age * Species * Year	−0.026	0.105	900	−0.251	0.802

equations for each taxon captured as opposed to drying and weighing samples (see Appendix A).

A sweep net was used weekly at all 4 research sites to collect canopy-dwelling arthropods on both tussock and shrub tundra. The center point of each transect was marked with an iron rod. For every sampling session, a random direction for the sampling transect was chosen by spinning a pen. Ten samples consisting of 10 back-and-forth sweeps (20 passes in total) were collected every 10 m along the transect. The contents of each sample were placed in a plastic bag with a 1 cm^2 piece of Hot Shot No-pest strip (Spectrum Brands: Middleton, WI) to euthanize the arthropods and stored at –20°C until sorting. Arthropods were separated from debris; a subset of 2013 samples were analyzed using the allometric approach previously described, and the remainder were dried for 24 hours in Petri dishes at 40°C and then weighed to the nearest milligram.

Statistical Analyses

All statistical analyses were performed in R 3.1.1 (R Core Development Team 2014) with the lme4 (Bates et al. 2014), lmerTest (Kunznetsova et al. 2014), and lsmeans (Lenth and HervÃc 2015) packages.

For the primary comparison of nestling growth rates between species and years, nestling mass was assessed with a linear mixed-effects model in which nestling identity (ID) and nest were modeled as random to account for repeated measures and clustering. The model incorporated the main effects of species, year, nestling age ("age" hereafter), and all 2-way interactions as well as their 3-way interaction. Additionally, a predictor for final status of the nestling, either death or fledge, was tested. Final model selection was performed by Akaike Information Criterion (AIC). The best-fit model included random effects of individual and nest, a 2-way interaction between age by final status, and a 3-way interaction of age, species, and year (Table 1).

To assess the effects of reproductive timing on nestling growth rates, nests were divided into early and late groups based on clutch initiation date such that half the nests fell into each group. For each species, nestling mass was modeled with a linear mixed-effects model with fixed effects of age, timing, and their interaction. The analysis was conducted independently for each species. Nestling ID was again incorporated as a random effect to account for repeated sampling of individuals. This analysis was restricted to nests in 2014 that were monitored daily.

Temperatures across years were analyzed using linear regression models. Precipitation between years was compared by Welch Two Sample *t*-tests. All tests were conducted for the nestling period, a 28-day window defined as Julian dates 170 (June 19) to 198 (July 17) for 2013 and 165 (June 14) to 193 (July 12) for 2014. This period was chosen because it represents the maximum period each year during which eggs or nestlings are present in nests, based on known or estimated clutch initiation dates for all nests at all field sites.

Dry arthropod biomass was analyzed using linear mixed effects models following a natural log+1 transformation of the data. Pitfall and sweep-net biomass were analyzed independently using a linear mixed effects model with fixed effects of year, plot, and their interaction. Julian day and sample number were included as random effects to control for sampling location and the seasonal phenology of arthropods, respectively. As with previous analyses, the sampling window was restricted to the nestling period outlined previously for temperature. Least squared means contrasts were used to explore significant interactions.

The direct effects of temperature and precipitation on growth rates were assessed by linear mixed effect modeling of individual growth rates against observed environmental parameters. Individual nestling growth rates were generated by simple linear regression of mass against age for each bird observed for at least 3 days. The following

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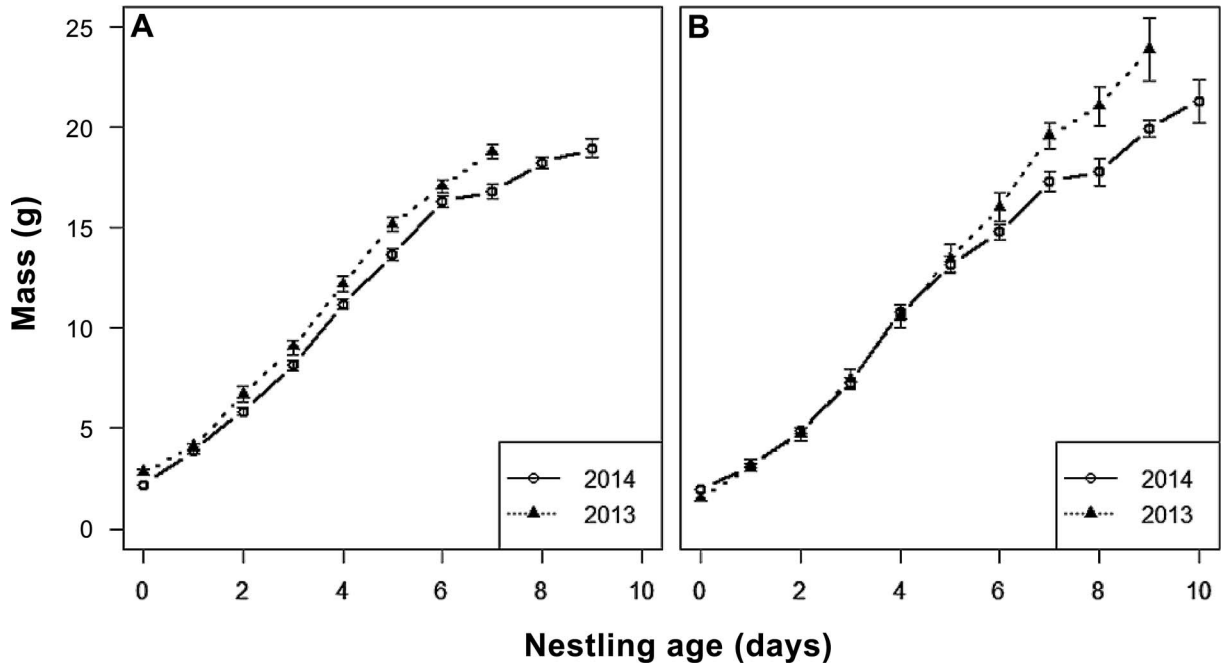


FIGURE 1. Daily nestling mass (g) for **(A)** Gambel's White-crowned Sparrow and **(B)** Lapland Longspur from hatch (Age = 0) to fledge in 2013 and 2014. Both species showed decreased rates of growth in 2014 compared to 2013. Data presented as means ± SEM.

environmental parameters were calculated for the observation window for each individual: mean daily maximum temperature, mean minimum daily temperature, mean daily rainfall, and total rainfall. Linear mixed effects models containing nest as random to account for clustering by nest were conducted for each variable independently. All values are reported as means ±SEM.

RESULTS

Nestling Growth Rates

The main effects of age and the interactions of final status by age, age by year, and age by species significantly predicted changes in nestling growth rates (Figure 1, Table 1). Estimated growth rates were significantly higher for both species in 2013 compared to 2014. Lapland Longspur had higher estimated growth rates than White-crowned Sparrow in both years (Table 2). Birds that died prior to fledge had lower growth rates than those that fledged.

TABLE 2. Estimated rates of daily mass gain (g d^{-1}) from linear mixed effects model for Gambel's White-crowned Sparrow and Lapland Longspur. Growth rates are estimated separately for nestlings surviving to fledge (Fledged) and those that died of non-predation related causes (Died).

	Gambel's White-crowned Sparrow		Lapland Longspur	
	2013	2014	2013	2014
Fledged	2.50	2.13	2.68	2.29
Died	2.21	1.84	2.39	1.99

Meteorological Conditions

Both maximum ($F_{1,54} = 4.27$, $p = 0.04$) and minimum daily air temperatures ($F_{1,54} = 7.54$, $p \leq 0.01$) were lower in 2014 than in 2013 (Figure 2). Both years had 14 days of rain during the nestling period and showed no difference in average daily rainfall ($t_{21} = -1.37$, $p = 0.19$); however, total rainfall during the nestling period was 73% greater in 2014 (68.8 mm) than in 2013 (39.8 mm).

Increases in maximum daily air temperatures had no effect on growth rates of White-crowned Sparrow ($t_{14} = 0.60$, $p = 0.56$; Figure 3A) but increased growth rates of Lapland Longspur ($t_{15} = 2.67$, $p = 0.02$). Minimum daily air temperature had no effect on growth rates in either species ($t_{30} = 0.81$, $p = 0.43$). Increased daily precipitation led to a decrease in growth rates for both species ($t_{65} = -3.72$, $p \leq 0.001$; Figure 3B).

Arthropod Biomass

Arthropod biomass caught using pitfalls was slightly lower during the 2014 nesting period relative to 2013, but this difference was not significant (Table 3). As evidenced by a significant year by plot interaction, the reduction in pitfall biomass due to conditions in 2014 depended on the plot

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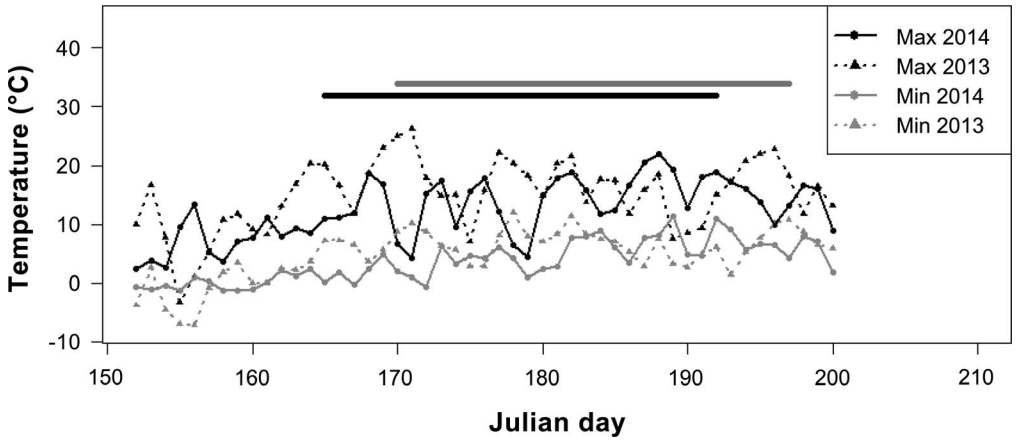


FIGURE 2. Daily min and max air temperatures (°C) for Toolik Lake, Alaska, for 2013 and 2014 from June 1 to July 19. The horizontal lines represent the defined "nesting period" for 2014 (black) and 2013 (gray).

(shrub tundra or tussock tundra; Table 3). In both years, shrub tundra plots tended toward lower arthropod biomass; however, this plot-to-plot difference was only significant in 2014 ($t_{76} = 3.51$, $p < 0.001$). The highest values for arthropod biomass in both years generally corresponded to a peak in activity-density of wolf spiders (family Lycosidae) and ground beetles (family Carabide; A. Asmus personal observation). The peak in pitfall arthropod biomass occurred ~1 week (1 sampling interval) later in 2014 relative to 2013 (Figure 4). In contrast with ground-dwelling arthropods, sweep-net biomass was significantly greater in shrub plots than tussock tundra (Table 4; $t_{169} = 2.13$, $p = 0.04$). A significant interaction of year and plot was also detected ($t_{169} = -2.64$, $p < 0.01$). The interaction of year and plot was explored via post hoc testing and found to only be significant for the shrub plot ($t_{170} = 2.84$, $p < 0.01$) and not the tussock tundra plot ($t_{170} = 0.54$, $p = 0.59$). In both years, sweep-net biomass peak generally corresponded to the mass emergence and activity of mosquitoes (A. Asmus personal observation). This peak was about 1 week later in 2014 relative to 2013 (Figure 3).

Timing of Clutch Initiation

A comparison of early vs. late nesting birds (clutch initiations) found significant effects of both nestling age ($t_{648} = 48.47$, $p < 0.001$) and early hatching by age

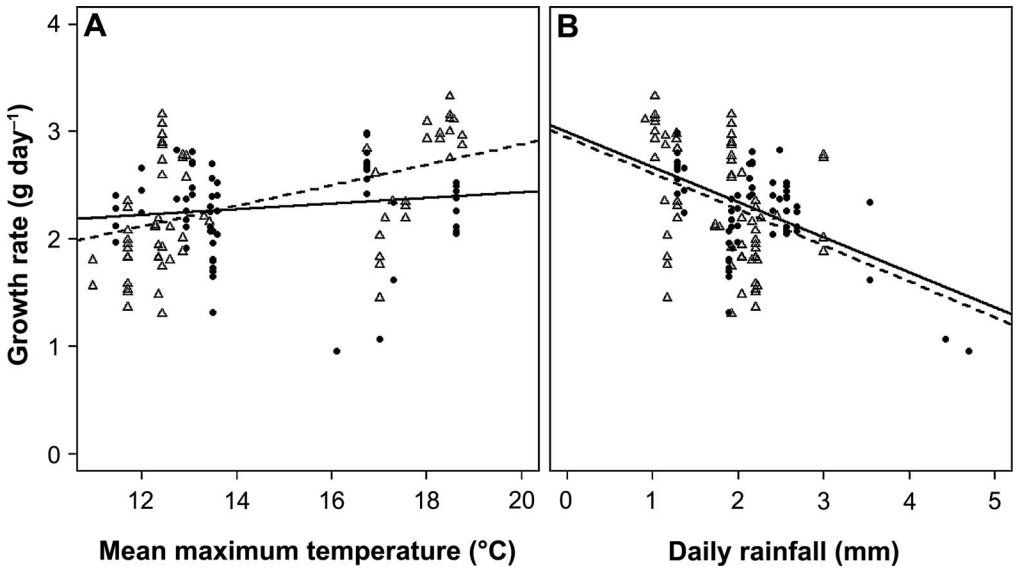


FIGURE 3. The relationship between daily growth rates and **(A)** maximum temperature and **(B)** mean precipitation for nestlings from Toolik Lake, Alaska, for Gambel's White-crowned Sparrow (filled circle and solid line) and Lapland Longspur (open triangles and dotted line). Fitted lines indicate predictions from linear mixed-effects models.

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TABLE 3. The fixed effects modeling pitfall arthropod biomass via linear mixed effects model.

Variable	Estimate	SE	df	T	*p*-value
Intercept	3.92	0.45	9	8.74	<0.001
Year 2014	0.24	0.64	8	0.37	0.72
Plot Shrub	−0.24	0.27	62	−0.88	0.38
Year 2014 * Plot Shrub	−0.76	0.28	309	−2.71	<0.01

interaction ($t_{645} = 5.63$, $p < 0.001$) on nestling mass (Table 5). Model estimates predicted a growth rate of 2.34 g d^{-1} for nestlings from early nests and only 1.99 g d^{-1} for those from late nests.

DISCUSSION

In alignment with our prediction that poorer conditions would lead to reductions in nestling growth rates, we found that conditions for nesting birds were harsher in 2014 than 2013. Both species showed significant reductions in growth rates in 2014 compared to 2013, correlated with lower temperatures, more rain, and lower arthropod biomass. This decrease persisted even when controlling for nonpredation-related mortality among nestlings. Furthermore, we found that across-year nestling growth rates were positively correlated with temperatures for Lapland Longspur and negatively correlated with precipitation.

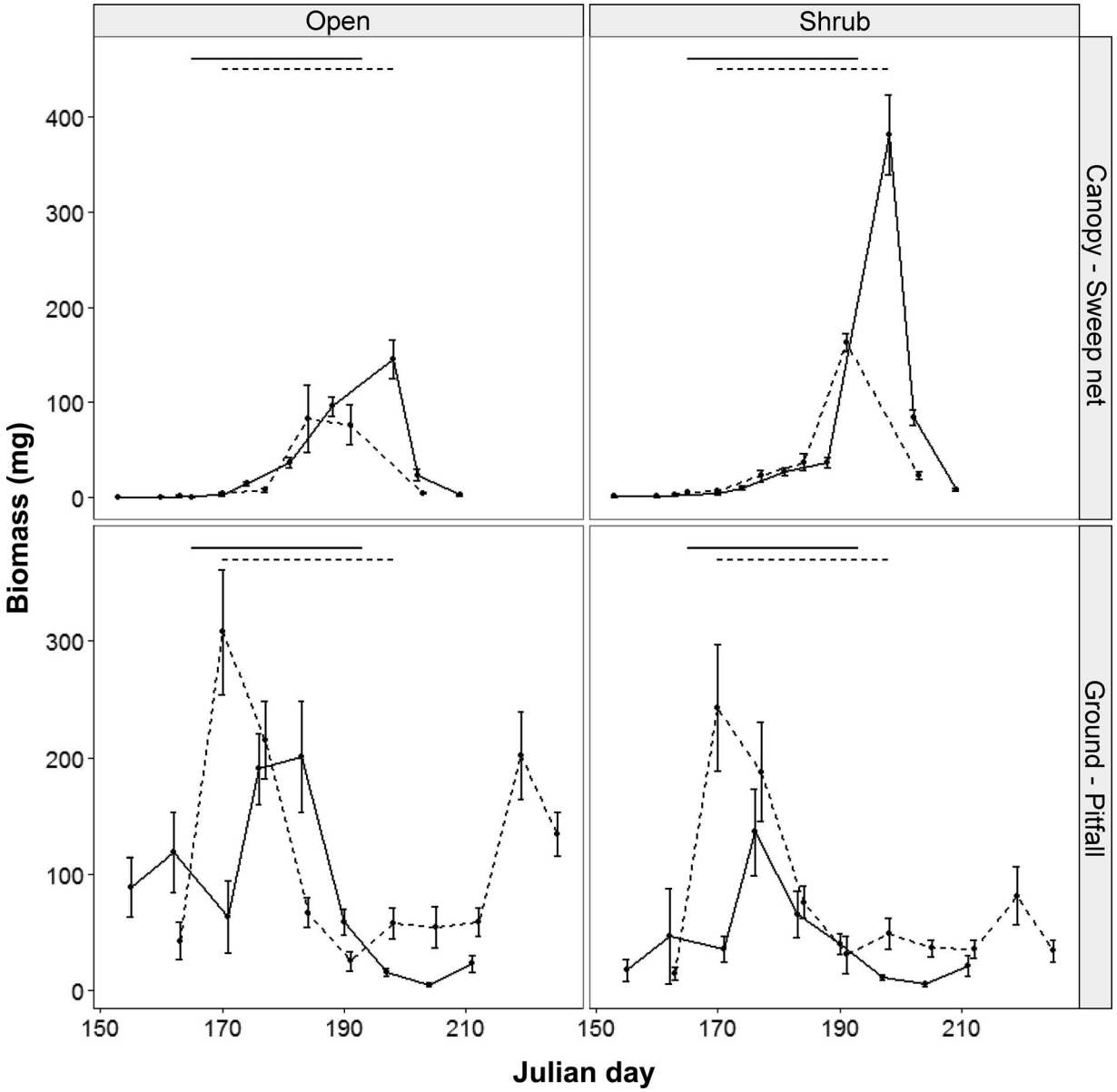


FIGURE 4. Arthropod biomass (mg) by Julian date for 2013 (dotted line) and 2014 (solid line) at Toolik Lake, Alaska. Data are presented for open and shrub tundra plots and for both pitfall and sweep-net sampling methods. Data presented as means ± SEM.

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TABLE 4. The fixed effects modeling sweep-net arthropod biomass via linear mixed effects model.

Variable	Estimate	SE	df	T	*p*-value
Intercept	3.19	0.43	8	7.40	<0.001
Year 2014	−0.15	0.28	170	−0.55	0.58
Plot Shrub	0.35	0.17	169	2.13	0.04
Year 2014 * Plot Shrub	−0.66	0.25	169	−2.64	<0.01

TABLE 5. The fixed effects modeling early vs. late nesting birds in 2014.

Variable	Estimate	SE	df	T	*p*-value
Intercept	2.36	0.29	256	8.08	<0.001
Age	1.99	0.04	648	48.47	<0.001
Early	−1.45	0.43	240	−3.35	<0.001
Age * Early	0.34	0.06	645	5.63	<0.001

These findings are consistent with nestling growth rates being dependent on environmental weather conditions (e.g., temperature and precipitation) and food availability, which are mediated through the quality and degree of parental investment provided.

Low temperatures result in tradeoffs with greater energy devoted toward self-maintenance as opposed to parental investment (McEwen and Wingfield 2003, Ardia et al. 2010, Wingfield and Ramenofsky 2011) for 2 reasons. First, reductions in ambient temperatures are known to result in increased costs of self-maintenance in adults because their thermoregulatory costs rise (Kendeigh 1969, Custer et al. 1986) Second, prior to the development of endothermy, nestlings are dependent on parental brooding to maintain appropriate body temperature, and therefore low temperatures require parents to spend more time brooding (Johnson and Best 1982, Lyon and Montgomerie 1987, Ardia et al. 2009). This investment reduces time available for both foraging for nestlings and for self-maintenance (Custer et al. 1986). Even after the onset of endothermy, low ambient temperatures still pose a thermal challenge because nestlings are predicted to require more food due to their own thermoregulatory costs (Geiser et al. 2008). Interestingly, our findings suggest that Gambel's White-crowned Sparrow is not affected by temperature while Lapland Longspur is, likely as a result of their different nesting habitats. The shrub-based nests of the White-crowned Sparrow may serve to reduce heat loss by providing a more sheltered microclimate, reducing the effects of temperature (Rauter and Reyer 2000). Our finding that maximum but not minimum temperatures were correlated with observed increased growth rates in Lapland Longspur suggests that consistently cold temperatures rather than short-term drops (daily or otherwise) are more important, likely a result of the ability of the parents to compensate for short term drops in temperature by brooding without major reductions in investment. Alternately, aerial insect activity has been shown to increase with temperature, particularly >18°C (Winkler et al. 2013).

Rain seems to be the primary environmental limiter of growth rates in both species, with increased precipitation resulting in decreased growth rates. Although we found no statistical differences in mean precipitation levels when comparing the nestling periods between years, total rainfall in 2014 was 73% higher than in 2013. This difference (29 mm over the nesting period), although small in absolute terms, may be highly relevant ecologically given that average rainfall for the Arctic is low; average annual rainfall for Toolik Lake from 1977 to 1994 was ~144 mm (Zhang et al. 1996). Furthermore, the historic precipitation data for the region reveals that June and July of both 2013 and 2014 were wetter than the previous 26-year average, with 2014 being significantly wetter than 2013. Higher precipitation has been shown to reduce nestling growth rates in Pied Flycatcher (*Ficedula hypoleuca*; Siikamäki 1996). Additionally, indirect effects of precipitation, through reduced parental foraging efficiency leading to reduced provisioning rates, have been observed in the Gray Catbird (*Dumetella carolinensis*; Johnson and Best 1982) and Eurasian Hoopoe (*Upupa eopops*; Arlettaz et al. 2010). Although we did not measure foraging efficiency directly in this study, we suspect that the combination of greater precipitation and lower temperatures in 2014 likely acted synergistically to reduce growth rates by negatively influencing arthropod activity and parental foraging efficiency.

The second major environmental factor that potentially affected nestling growth rates is food availability. Both Lapland Longspur and White-crowned Sparrow feed nestlings primarily on insects and spiders (Seastedt 1980, Chilton et al. 1995, Hussell and Montgomerie 2002, Norment 2003). Given the strong dependence of nestling growth on parental investment, the availability of sufficient arthropod prey is critical. For example, the White-fronted Bee-eater (*Merops bullockoides*) showed decreased nestling growth rates in response to food shortages, and severe food shortages lead to starvation (Emlen et al. 1991). Similar results have been found in seabirds (Bertram et al. 2001). Our prediction that arthropod biomass would be positively correlated with growth rates was only partially supported. Although biomass tended to be lower in 2014 across plots and sampling methods, these differences were only significant for sweep-net biomass in shrub plots. We acknowledge that our coarse weekly sampling interval may have been unable to resolve differences in arthropod availability at a scale meaningful to growth rates in nesting birds. Given the observed results, we believe shorter sampling intervals would likely detect significant differences between years in arthropod biomass during the

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critical nesting stage. In addition, these findings must be interpreted with caution because pitfall trap catches in the Arctic are known to vary with temperature and solar radiation (Hoye and Forchhammer 2008, Bolduc et al. 2013). Given the differences in weather between years and only 2 years of data, our analysis was unable to separate correlations between weather conditions and food availability with respect to their effects on nestling growth.

Assessment of timing of clutch initiation was limited by the availability of temporally spaced nestling measurements to a subset of nests in 2014, precluding a comprehensive understanding of how "clutch timing" or investment decisions may be modulated by environmental variation. However, our analysis was able to detect a strong effect of early vs. late clutch initiation on nestling growth rates. These findings are consistent with the generally observed pattern of decreasing nestling growth rates with later clutch initiation date (Birkhead and Nettleship 1982, Gaston et al. 1983, Winkler and Allen 1996, Morbey and Ydenberg 1997, Morton 2002). Although these findings support the arrival time hypothesis, our design does not allow the elimination of competing hypotheses regarding decreasing growth rates with later laying dates (Morbey and Ydenberg 2000). These findings are also consistent with the idea that early nesting birds may be higher quality parents than later nesting individuals.

Final status of nestlings (dead or fledged) was a significant predictor of nestling growth rates. Nestlings that ultimately died in the nest, presumably caused by starvation, sickness, or hypothermia, had lower rates of growth than those that survived until fledge. Because our model was unable to directly test for an interaction among final status, age, and species, we cannot test predictions for differences in effects of mortality on growth rates between species or years. We did observe a higher incidence of mortality in 2014 and, in particular, higher mortality among Lapland Longspur relative to White-crowned Sparrow; however, sample sizes were insufficient to draw firm conclusions (J.H. Pérez personal observation). We speculate that Lapland Longspur nestlings may be more severely affected by precipitation due to the lower abundance (or absence) of protective shrub cover. Exposure to rain would dramatically increase thermoregulatory costs if the nestlings became wet and may explain the higher nestling mortality observed in 2014. Although merely speculative at this point, future studies should directly assess the relationship among vegetation cover characteristics, precipitation, and nestling growth rates/fledging success. Potential methods include photographic assessment of percent vegetation cover overhanging the nest or other similar quantitative methods of assessing nest sites.

In keeping with our predictions, we found Lapland Longspurs to have higher estimated growth rates than White-crowned Sparrow in both years. This difference is likely due to the significantly larger body size of Lapland Longspur (27.27 g) compared to Gambel's White-crowned Sparrow (25.74 g; $t_{67} = 3.65$, $p < 0.001$) because variation in passerine growth rates has been attributed to differences in adult body size (Ricklefs 1968). Alternatively, the observed difference may be due to specialization to the Arctic (Confer and Knapp 1981). Lapland Longspur breeds exclusively in Arctic habitats (Hussell and Montgomerie 2002) and can be considered an Arctic specialist, whereas Gambel's White-crowned Sparrow is widely distributed, breeding predominately in boreal habitats except at the northern end of their range.

The dependence of nestling growth rates not only on parental investment decisions but on abiotic environmental factors, as demonstrated by our findings, is of particular concern with regard to the ongoing effects of global climate change. The Arctic has been warming at an accelerated rate (Anisimov et al. 2007). Although the predicted increases in spring temperatures (Serreze and Francis 2006, Overland et al. 2008) will favor higher nestling growth rates, provided breeding birds are able to maintain a phenological match to the timing of prey resources, the frequency of unpredictable storms and annual precipitation are predicted to increase (Finnis et al. 2007, Kattsov et al. 2007). Increased precipitation and occurrence of spring snow storms will presumably lead to reductions in nestling growth rates and perhaps increased mortality. Ultimately, the coupling of these two climate factors may lead to a system with boom–bust cycles, depending on the combination of environmental factors in any given year.

Conclusions

This study presents nestling growth rates for 2 species of Arctic nesting passerines in relation to variation in environmental conditions: weather and availability of arthropod prey. 2014 was shown to be a harsher year with lower temperatures and increased precipitation than 2013. These unfavorable environmental conditions were correlated with reduced rates of nestling growth for both the shrub-tundra–nesting White-crowned Sparrow and the tussock-tundra–nesting Lapland Longspur in 2014. Rainfall in particular seemed to drive the observed decreases in growth rates, suggesting that environmental variation is a major driver of nestling growth and, in turn, post-fledge survival in both Arctic-nesting species, regardless of their contrasting nesting habitat characteristics. This strong dependence on environmental conditions may be critical to species success in the future because environmental variability, especially rainfall in the Arctic, is predicted to increase. Future studies should investigate the relationship between weather conditions and food availability. Given the strong correlation

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between food and weather conditions, particularly for arthropods, longitudinal studies alone will likely prove ineffective. Experimental manipulations such as food supplementation or manipulation of nest microclimate may yield further insights.

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Appendix A: Pitfall allometry methods

To determine total pitfall sample biomass without drying and weighing the samples, we first counted and identified the arthropods in each sample. Arthropods were identified to family wherever possible; however, to expedite sample sorting, flies (Diptera) were lumped into 4 main groups: Tipulomorpha (Tipulidae and Trichoceridae), mosquitoes (Culicidae), other Nematocera (e.g., midges), and Brachyera (e.g., house flies). In addition, parasitic wasps were identified as such (Hymenoptera: Parasitica). Our samples also captured a terrestrial slug, which was identified as such (class Gastropoda).

During identification the total body length of the first 5 individuals of each taxonomic group were measured. To reduce biasing measurements (i.e. measuring only the largest individuals first), samples were spread in a large petri dish that was then rotated either clockwise or left-to-right while sorting. Body lengths were measured to the nearest 0.01 mm using a digital microscope camera and software (AmScope Mu035, www.amscope.com). The number of body measurements was limited to 5 for each taxon to expedite the process, but usually all the individuals of each taxonomic group were captured using this method, or an average 97% of individuals per sample.

Finally, the raw length and abundance data were processed to derive biomass estimates by taxonomic group. The 5 body lengths of each taxon were averaged for each sample. To these body length averages we applied published allometric (length–mass) equations (Collins 1992, Sample et al. 1993, Hódar 1997, Gruner 2003), producing the average biomass of an arthropod from a given taxonomic group and sample. These biomass averages were then multiplied by the total number of individuals captured in each sample, which generated the total biomass of each arthropod group in each sample. Values presented here represent total summed biomass of all taxonomic groups captured. All data processing steps were performed in R.

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