

## **Nest-site selection and nest success of an Arctic-breeding passerine, Smith's Longspur, in a changing climate**

Authors: McFarland, Heather R., Kendall, Steve, and Powell, Abby N.

Source: The Condor, 119(1) : 85-97

Published By: American Ornithological Society

URL: <https://doi.org/10.1650/CONDOR-16-87.1>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



RESEARCH ARTICLE

## Nest-site selection and nest success of an Arctic-breeding passerine, Smith's Longspur, in a changing climate

Heather R. McFarland,<sup>1\*</sup> Steve Kendall,<sup>2</sup> and Abby N. Powell<sup>1,3,4a\*</sup>

<sup>1</sup> Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, Alaska, USA

<sup>2</sup> U.S. Fish and Wildlife Service, Hakalau Forest National Wildlife Refuge, Hilo, Hawaii, USA

<sup>3</sup> U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, Fairbanks, Alaska, USA

<sup>4</sup> Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska, USA

<sup>a</sup> Current address: U.S. Geological Survey, Florida Cooperative Fish and Wildlife Research Unit, Gainesville, Florida, USA

\* Corresponding authors: Heather McFarland, hrcraig@alaska.edu; Abby Powell, abbypowell@ufl.edu

Submitted May 16, 2016; Accepted December 4, 2016; Published February 8, 2017

### ABSTRACT

Despite changes in shrub cover and weather patterns associated with climate change in the Arctic, little is known about the breeding requirements of most passerines tied to northern regions. We investigated the nesting biology and nest habitat characteristics of Smith's Longspurs (*Calcarius pictus*) in 2 study areas in the Brooks Range of Alaska, USA. First, we examined variation in nesting phenology in relation to local temperatures. We then characterized nesting habitat and analyzed nest-site selection for a subset of nests ( $n = 86$ ) in comparison with paired random points. Finally, we estimated the daily survival rate of 257 nests found in 2007–2013 with respect to both habitat characteristics and weather variables. Nest initiation was delayed in years with snow events, heavy rain, and freezing temperatures early in the breeding season. Nests were typically found in open, low-shrub tundra, and never among tall shrubs (mean shrub height at nests =  $26.8 \pm 6.7$  cm). We observed weak nest-site selection patterns. Considering the similarity between nest sites and paired random points, coupled with the unique social mating system of Smith's Longspurs, we suggest that habitat selection may occur at the neighborhood scale and not at the nest-site scale. The best approximating model explaining nest survival suggested a positive relationship with the numbers of days above  $21^\circ\text{C}$  that an individual nest experienced; there was little support for models containing habitat variables. The daily nest survival rate was high (0.972–0.982) compared with that of most passerines in forested or grassland habitats, but similar to that of passerines nesting on tundra. Considering their high nesting success and ability to delay nest initiation during inclement weather, Smith's Longspurs may be resilient to predicted changes in weather regimes on the breeding grounds. Thus, the greatest threat to breeding Smith's Longspurs associated with climate change may be the loss of low-shrub habitat types, which could significantly change the characteristics of breeding areas.

**Keywords:** Smith's Longspur, *Calcarius pictus*, nest survival, temperature, habitat, climate change

### Sélection du site de nidification et succès reproducteur d'un passereau nichant dans l'Arctique dans un climat en évolution

#### RÉSUMÉ

Malgré les changements dans la couverture arbustive et les patrons météorologiques associés aux changements climatiques dans l'Arctique, on connaît peu les besoins en matière de reproduction de la plupart des passereaux des régions nordiques. Nous avons étudié la biologie de reproduction et les caractéristiques de l'habitat de nidification de *Calcarius pictus* dans deux zones d'étude de la chaîne Brooks, en Alaska. Nous avons d'abord examiné la variation dans la phénologie de nidification en fonction des températures locales. Nous avons ensuite caractérisé l'habitat de nidification et analysé la sélection du site de nidification pour un sous-ensemble de nids ( $n = 86$ ) en comparaison avec des points aléatoires appariés. Finalement, nous avons estimé le taux de survie quotidien de 257 nids trouvés en 2007–2013 relativement aux caractéristiques de l'habitat et aux variables météorologiques. L'initiation du nid a été retardée lors des années avec des chutes de neige, de fortes pluies et des températures sous le point de congélation tôt dans la saison de reproduction. Les nids étaient typiquement trouvés dans la toundra arbustive basse ouverte, et jamais dans les arbustes hauts (hauteur moyenne des arbustes aux nids de  $26,8 \pm 6,7$  cm). Nous avons observé de faibles patrons de sélection du site de nidification. Compte tenu de cette similarité entre les sites de nidification et les points aléatoires appariés, combinée au système d'accouplement social unique de cette espèce, nous suggérons que la sélection de l'habitat peut se produire à l'échelle du voisinage et non à l'échelle du site de nidification. Le meilleur modèle d'approximation expliquant la survie des nids suggérait une relation positive avec le nombre de jours au-dessus de  $21^\circ\text{C}$  qu'un nid a connu; il y avait peu d'appui pour les modèles contenant des variables d'habitat. Le taux de survie quotidien était plus élevé (0,972–0,982) que ceux de la plupart des passereaux dans des habitats forestiers ou de

prairie mais il était semblable à ceux de passereaux nichant dans la toundra. Compte tenu de leur succès de nidification élevé et de leur capacité à retarder l'initiation des nids lors de mauvaises conditions climatiques, *C. pictus* pourrait résister aux changements de régimes météorologiques prédits sur les aires de reproduction. Ainsi, la plus grande menace associée aux changements climatiques pour la reproduction de *C. pictus* pourrait être la perte d'habitats de type arbustive basse, ce qui peut changer significativement les caractéristiques des aires de reproduction.

*Mots-clés:* *Calcarius pictus*, survie des nids, température, habitat, changements climatiques

## INTRODUCTION

The Arctic is incredibly productive during the short summer season, with ~135 bird species breeding there annually (Johnson and Herter 1990). However, biodiversity in this region may be altered by climate change, which is occurring more rapidly at northern latitudes than in almost any place on earth (Arctic Climate Impact Assessment 2004, Anisimov et al. 2007). Landscapes are predicted to become shrubbier, with fewer open habitat types (Tape et al. 2006, Euskirchen et al. 2009). In addition to general warming trends (Hansen et al. 2006), weather conditions in the Arctic are becoming more erratic, with increased occurrence of storms during the spring and summer months (Parmesan and Galbraith 2004, Bengtsson et al. 2006). These changes may result in avian population declines through decreased reproductive success, as well as distributional shifts as some birds move to find more suitable conditions (Parmesan and Galbraith 2004, Wormworth and Mallon 2006, Sekercioglu et al. 2008). Baseline information on habitat selection and reproductive success, prior to further climate change, is needed to evaluate community-wide impacts within this quickly changing landscape.

Predictions of a shrubbier environment present concerns for many Arctic fauna (Sturm et al. 2001, Tape et al. 2006). Although these changes are expected to advance slowly, species tied to a more open, grassland-like habitat may shift their distribution or experience population declines (Tape et al. 2006, Seavy et al. 2008). Furthermore, habitat specialists are more likely to be negatively affected by environmental changes than generalists (Colles et al. 2009). In northern Alaska, USA, a recent study by Boelman et al. (2015) suggested that increasing shrub dominance will diminish the habitat quality for Lapland Longspurs (*Calcarius lapponicus*), which breed in open tundra. Although we cannot be certain how the predicted changes will affect other tundra-breeding birds, understanding the linkages between species and habitat use is key to predicting responses to environmental change (Hausner et al. 2003).

Perhaps of greater concern for Arctic birds than the conversion of tundra to shrubland is the rapid climatic shift currently taking place at northern latitudes. With only a narrow window of opportunity in which birds can

optimize their reproductive success, changes in storm patterns and temperature regimes could have a disruptive effect (Crick 2004, Bengtsson et al. 2006, Wormworth and Mallon 2006). For example, anecdotal evidence from Lapland Longspurs suggests that delayed nest initiation due to inclement weather can cause increased nest failure later in the breeding season (Astheimer et al. 1995). Although warming trends could cause a mismatch in food availability for some species (Visser et al. 1998, Sekercioglu et al. 2008), others may benefit from increased temperatures (e.g., from longer breeding seasons; Crick and Sparks 1999, Both and Visser 2005, McKinnon et al. 2013). For example, Snow Buntings (*Plectrophenax nivalis*) breeding in the High Arctic showed a positive correlation between temperature during incubation and reproductive success (Hoset et al. 2004). However, for most Arctic passerines, the impact of temperature and weather patterns on breeding success and timing is unknown.

The Smith's Longspur (*Calcarius pictus*) is an Arctic-breeding passerine that has been listed as a species of conservation concern, primarily because of threats on the winter and summer ranges (Rich et al. 2004, USFWS 2008, Zack and Liebezeit 2009). In Alaska, the species breeds in and is closely tied to open, low-shrub habitats in the Brooks Range (Wild et al. 2015), but little information is available on specific nesting requirements (Ehrlich et al. 1988, Briskie 2009). The goal of this research was to provide a baseline for evaluating impacts of future climate change on Smith's Longspurs breeding in the Brooks Range ecoregion. First, we examined the relationship between annual variation in nesting phenology and weather patterns, which could be altered significantly through climate change. Next, we described nest-site characteristics and examined how habitat features influenced nest-site selection. Lastly, we investigated whether nest survival was related to nest-site characteristics or weather variables. Specifically, we expected that nest sites would be characterized by fewer and shorter shrubs (Jehl 1968, Wild et al. 2015), but greater microhabitat structural variation (potentially hiding nests from predators), than those in random sites within the nesting area. Because vegetation and microtopographic features may help to camouflage nests from predators, we predicted that nest survival would be influenced by habitat selection (Harrison

et al. 2011, Murray and Best 2014) and nest visibility; changes to tundra habitats through increased presence and density of shrubs could lead to lowered productivity over time. Furthermore, changing weather patterns in the Arctic could provide either better (increased summer temperatures) or worse (increased and unpredictable storm frequency) conditions for nest survival. We expected nest survival rates to be affected by low and high temperatures (Jehl and Hussell 1966, Carey 2002, Hoset et al. 2004). We predicted lower survival at low temperatures, but increased survival at higher temperatures, when parents may have more time away from the nest to gather food for young.

## METHODS

### Study Area

We studied nest-site selection and nest success of Smith's Longspurs at 2 locations in the Brooks Range of northern Alaska, USA. Atigun Gorge, the more southerly study area, was located in a mountain valley (68.27°N, 149.21°W, elevation 846 m; studied in 2007–2013, excluding 2010), while Slope Mountain was 27 km north of the gorge in rolling foothills (68.41°N, 149.40°W, elevation 655 m; studied in 2011–2013). Both study areas were ~1,060 ha in size, intersected by the Dalton Highway and Trans-Alaska Pipeline, and characterized by treeless tundra. The study areas were chosen based on accessibility and presence of known breeding populations of Smith's Longspurs (T. Wild personal communication).

Within the Brooks Range ecoregion, Smith's Longspurs tend to breed in open, low-shrub areas of broad river valleys (Atigun Gorge) or in their rolling foothills (Slope Mountain; Wild et al. 2015). The most common vegetation types within these areas are willows (*Salix* spp.), ericaceous shrubs (*Rhododendron lapponicum*, *Vaccinium* spp., *Arcostaphylos* spp.), dwarf birches (*Betula* spp.), *Dryas integrifolia*, and sedges (*Eriophorum* spp. and *Carex* spp.). Mosses and lichens typically have close to 100% ground cover throughout the region. The area is also characterized by tussocks (clumps of *Eriophorum* spp.) and hummocks (earth features created by permafrost dynamics), which provide considerable structure to the landscape.

### Nest Searching and Monitoring

We searched for nests nearly every day (6–12 hr day<sup>-1</sup>) from early June to mid-July (a lesser effort was made during 2007, as the focus that year was on locating Smith's Longspurs through surveys; Craig et al. 2015, Wild et al. 2015). Because Smith's Longspurs are patchily distributed across the landscape (Wild et al. 2015), we located most nests using behavioral cues (e.g., alarm calls or nervous behavior by females; Martin and Geupel 1993). Nests were marked by placing plain popsicle sticks 1 m away on 2

opposing sides of the nest, and a fluorescent popsicle stick, which was aligned with the plain markers, ~20 m distant on an obvious structure (e.g., a hummock). This marking method allowed us to minimize the time spent relocating nests. Furthermore, to reduce the likelihood of attracting predators, we followed a new route during each nest visit, making sure that we left no dead-end paths to the nest. We monitored nests every 2–4 days until fledging or failure. The following evidence was used to determine successful nest fate: (1) cues such as adult(s) nearby uttering alarm calls, (2) fledglings seen or heard “peeping” in the area, and (3) fewer nestlings observed on consecutive nest visits when chicks were old enough to fledge (nestlings can fledge up to a day apart) and no visible signs of nest disturbance. Nest attempts were considered successful if at least 1 nestling fledged. Evidence of predator disturbance or activity near nests was also recorded and considered during nest fate determination.

We used weather data to examine relationships between temperature and nest success. During 2011–2013 we used Onset HOBO Micro Station Data Loggers (H21-002; Onset Computer Corporation, Bourne, Massachusetts, USA) to record temperature every 30 min in each study area. During 2007–2009, we used daily maximum and minimum temperatures reported at Toolik Field Station (68.38°N, 149.36°W), Institute of Arctic Biology, University of Alaska Fairbanks, which was located approximately halfway (23 km from Atigun Gorge, 24 km from Slope Mountain) between our 2 study areas (Environmental Data Center Team 2015). Although temperatures in Atigun Gorge and at Toolik Field Station (hereafter, Toolik) tracked each other, they tended to be cooler (by 0.8°C for maximum and 0.4°C for minimum daily temperatures) at Toolik. However, these slight differences were not consistent enough to assign an “offset” by which to adjust 2007–2009 Atigun Gorge temperatures. Snow-free periods and late-season snow event dates were identified from time-lapse imagery taken in Atigun Gorge (68.27°N, 149.22°W; Environmental Data Center Team 2016).

### Habitat Characteristics

To determine characteristics that influenced selection of nest sites within tundra, we measured microhabitat features at nests and paired random points. Habitat measurements were only taken during 2012 and usually within 2 weeks of either fledging or nest failure. Random locations were selected 5 to 30 m from the nest, within the area that we typically observed females defending, herein defined as a “territory.” To quantify vegetation structure, we used techniques similar to those described by Rotenberry and Wiens (1980). We placed a 1-m wooden rod on the ground at the outer edge of each nest or random point. In all 4 cardinal directions, we sampled vegetation at 10-cm intervals along the horizontal length of the rod for a total

of 40 points per sampling location. At each point, we recorded the height of the tallest contact of multiple vegetation types (erect willow, birch, blueberry, other ericaceous shrub, graminoid, and tussock or hummock). We recorded the presence or absence of moss, lichen, *Dryas*, dwarf willow, leaf litter, and bare ground, but did not measure their heights because they did not contribute to vertical cover. We also recorded slope, aspect, elevation, and specific habitat features associated with the placement of each nest (e.g., nest placed on the side or top of a hummock, between tussocks, under shrub). We accounted for circular distributions and examined directional trends of aspect using Rao's Spacing Test of Uniformity in the Circular package of R 3.1.1 (R Core Team 2014). For all measurements we report means  $\pm$  SD.

We assessed visibility at nest locations using a plastic disk (diameter = 6.5 cm) with a grid of alternating black and white 1-cm sections. Because we used a grid of squares in a circular disk, we estimated the number of visible sections to the nearest  $\frac{1}{3}$  of a square ( $\sim$ 16 total squares; similar to techniques described by Davis and Sealy 1998). The disk was placed inside the nest cup and the number of visible sections was assessed from 1 m directly above and from each of the 4 cardinal directions. Open nests scored higher (maximum = 80 sections observed) than nests that were well concealed (minimum = 0 sections observed).

### Nest-site Selection Analysis

We used conditional logistic regression to examine nest-site selection patterns of Smith's Longspurs. We chose this approach because it is more appropriate and powerful than standard logistic regression for analyzing paired data such as nest vs. random point within a nesting territory. Because we expected Smith's Longspurs to avoid tall vegetation, but to select areas with high variance in cover (thus hiding the nest from predators), we chose variables that were the most common features providing structure on the landscape. We tested the importance of mean height and the coefficient of variation (CV) of height (included as a proxy to examine heterogeneous cover) of erect willows and ericaceous shrubs, which were the 2 most common shrub communities in our study areas. We also included height and the CV of height for tussocks and hummocks, which we call "ground structure," because these features provided considerable structure in the treeless environment. To identify other potential patterns in nest-site selection, we also included slope and aspect as variables. We did not include study area effects in final models because preliminary testing suggested that site was of little importance.

Erect willows and ericaceous shrubs were patchily distributed across the landscape and not present at every sampling point. Thus, to avoid bias in our data by recording a mean and CV of zero for these missing values,

we included an interaction term (indicating either presence or absence) with each of the habitat variables. We also examined all variables within a correlation matrix and excluded those that would induce multicollinearity. We developed a candidate set of 25 models: null and global models, 4 single-factor models (mean ground structure height, CV of ground structure height, slope, aspect), 4 models with interaction terms examining habitat variables along with their indicator variable (mean erect willow height, CV of erect willow height, mean ericaceous shrub height, CV of ericaceous shrub height), 13 models examining additive effects of habitat and ground structure variables with slope or aspect, and 2 models exploring an additive relationship between the shrub types (erect willow and ericaceous shrub). We used Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) to identify the models that best fit the data. The top model was confirmed using the Hosmer-Lemeshow goodness-of-fit test (HL test), which was computed using the regular logit function (Hosmer and Lemeshow 2000). We computed the odds ratio by exponentiating the coefficient from the top logistic regression model. Conditional logistic regression models were implemented using the clogit function found within the survival package of R 3.1.1 (R Core Team 2014). The HL test was run using the Resource Selection package.

### Nest Survival Analysis

We used the nest survival module in program MARK (White and Burnham 1999) to determine the daily survival rate (DSR) of Smith's Longspur nests. We standardized season dates among years by using the earliest start date of nests with known fate from any year as the first day of the season, and the latest fledging or failure date of any year as the last day of the season (June 1–July 12; 1 nest was initiated as early as May 29, but its fate was unknown); thus, we defined the seasonal period to be 42 days in length (encounter occasions). We separated our data into 9 groups differentiated by year and study area. This structure allowed us to test for study area and year effects separately, as well as their interaction. We selected habitat covariates that we predicted could be related to predation risk, and weather variables that were most likely to influence egg and chick survival. Models are explained in full below.

We examined a candidate set of 16 models. Several models tested DSR in relation to temperature. First, we examined DSR in relation to the cumulative number of days below freezing that a given nest experienced (thus excluding freezing days when the nest was not active; designated as "Cold"). A similar model was built to examine DSR in relation to the number of "hot" days. We arbitrarily chose a temperature threshold of 21°C based on high temperatures typically reached during summer months in our study areas. Area-specific temper-

**TABLE 1.** Variation in Smith's Longspur nesting phenology as shown through nest initiation, hatching, and fledging dates during 6 yr at Atigun Gorge and 3 yr at Slope Mountain in northern Alaska, USA.

Site and year	<i>n</i>	Initiation		Hatching		Fledging	
		$\bar{x}$	Min-max	$\bar{x}$	Min-max	$\bar{x}$	Min-max
Atigun Gorge							
2007	6	Jun 6	Jun 4–10	Jun 20	Jun 19–25	Jun 28	Jun 25–Jul 2
2008	30	Jun 12	Jun 8–22	Jun 26	Jun 22–Jul 5	Jul 2	Jun 30–Jul 12
2009	28	Jun 9	Jun 7–17	Jun 24	Jun 22–Jul 7	Jul 1	Jun 30–Jul 6
2011	24	Jun 4	May 30–Jun 17	Jun 19	Jun 14–30	Jun 27	Jun 22–Jul 7
2012	40	Jun 7	Jun 3–16	Jun 21	Jun 18–30	Jun 28	Jun 25–Jul 7
2013	41	Jun 11	Jun 8–17	Jun 25	Jun 23–Jul 1	Jul 2	Jun 30–Jul 5
Slope Mountain							
2011	26	Jun 2	May 29–Jun 13	Jun 16	Jun 13–26	Jun 23	Jun 20–28
2012	46	Jun 6	Jun 3–19	Jun 21	Jun 18–30	Jun 28	Jun 26–Jul 7
2013	33	Jun 11	Jun 9–18	Jun 25	Jun 23–Jul 2	Jul 2	Jun 30–Jul 5

ature data were not available for 2007–2009, so constant survival was modeled for those years. Additionally, we tested whether the substitution of Toolik Field Station temperature during 2007–2009 would help to explain survival. For these models, we used a generic metric with the total numbers of days that temperatures were above 21°C or below 0°C at Toolik (designated as “Toolik”; Environmental Data Center Team 2015). We recognized that temperatures at Toolik were generally cooler, and thus that models examining “hot” temperatures were conservative, while those examining “cold” temperatures may have been biased high; however, the temperature differential between the 2 sites was <1°C. We also examined DSR in relation to the minimum and maximum daily temperature that each active nest experienced. Although daily temperature models included the entire 6-yr dataset, we examined the relationship between daily temperature and DSR in only the 3 yr (2011–2013) for which we had temperature data specific to each study area. Constant survival was modeled for each of the other years (2007–2009).

In addition to temperature, predation risk is another driver of nest survival for many passerines, thus nest-site selection commonly influences DSR. Consequently, we included several models to investigate DSR in relation to habitat and nest-site features. Because erect willow was the only habitat variable found to be important for nest-site selection, we included the CV of erect willow height (designated as “WillowCV”) and the erect willow indicator (presence or absence; “WillowInd”) in models to test whether nest-site selection influenced the nest survival of Smith's Longspurs. To further examine the influence of nest structure on survival, we included a nest visibility model (“Visibility”). Nesting habitat was only examined during 2012. Therefore, although we included all 6 yr of data in these models, the relationship between habitat features and DSR was only examined for 2012. Each of the other years was modeled with constant survival.

We were unable to model nest age because we could not accurately determine the initiation date of nests that failed prior to hatching. However, we did examine whether there was a difference in survival during the egg incubation period vs. the chick brooding period (designated as “Period”).

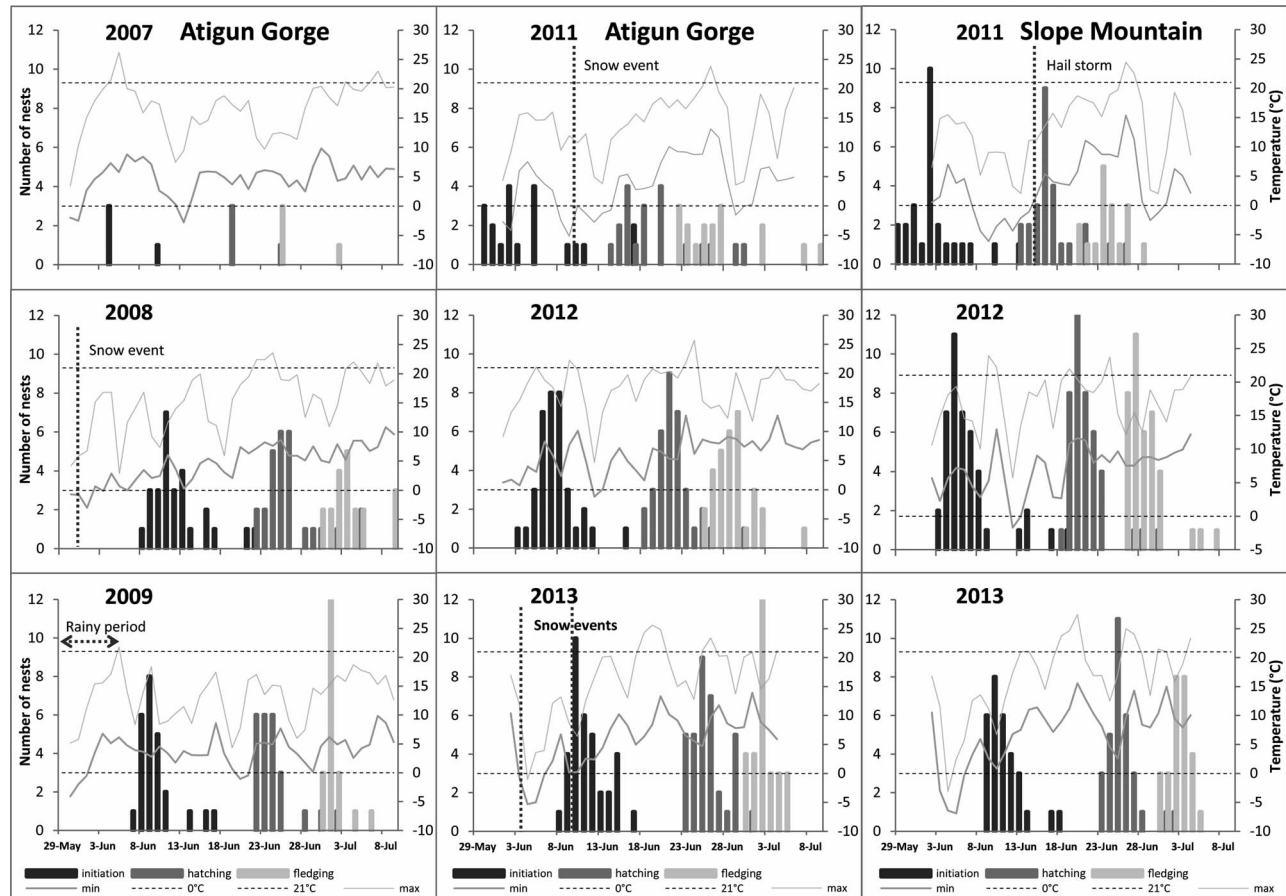
We used Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) to evaluate model fit. The model with the lowest  $\Delta AIC_c$  value was selected as the best model, although it was assumed that models with  $\Delta AIC_c$  of  $\sim 2$  or less were equally parsimonious if they did not differ from the more supported model by the addition of only uninformative parameters. We interpreted covariate effects by examining whether the 85% confidence intervals of coefficients overlapped 0 (Arnold 2010). Nest survival estimates were calculated using a 21-day nesting period.

## RESULTS

### Phenology

In the Brooks Range, Smith's Longspurs typically arrived on the breeding grounds during the last week of May or the first week of June. By the arrival date, study areas were generally free of snow (except in 2013, when snow remained on the ground until June 2); however, late-season snow events occurred in several years (June 1, 2008, June 13, 2011, and June 4 and 10, 2013; Figure 1; Environmental Data Center Team 2016).

We located a total of 274 Smith's Longspur nests during the 6 yr of our study (Atigun Gorge:  $n = 169$ ; Slope Mountain:  $n = 105$ ; Table 1). Earliest nest initiation ranged from May 29 (Slope Mountain;  $\bar{x} =$  June 2) in 2011 to June 9 (Slope Mountain;  $\bar{x} =$  June 11) in 2013 (Table 1). First nest initiations on Slope Mountain and in Atigun Gorge were generally within a day of one another. Due to the condensed breeding season in the Arctic, nests were



**FIGURE 1.** Daily maximum and minimum temperatures in relation to nest initiation, hatching, and fledging periods of Smith's Longspurs nesting at 2 study sites in the Brooks Range of Alaska, USA. Solid lines represent maximum (red) and minimum (blue) daily temperatures. Solid vertical bars represent the number of nests that were initiated (dark blue), hatched (red), or fledged (light blue) on a given day. Site-specific temperatures were not available in 2007–2009, and thus temperatures from Toolik Field Station were used for those years (Environmental Data Center Team 2015). In most years, snowmelt occurred at the end of May (in 2013, snow persisted until June 2). Late weather events are shown with vertical dotted gray lines and rainy periods are shown with horizontal dotted gray lines (Environmental Data Center Team 2016). Horizontal dashed lines indicate 0°C and 21°C for reference.

initiated almost immediately upon arrival or as soon as combined temperature and snow conditions allowed (Figure 1). For example, in 2008 and 2013, freezing temperatures and snow cover (Environmental Data Center Team 2016) delayed nest initiation until June 8. Similarly, in 2009, persistent rain (Environmental Data Center Team 2016) delayed nest initiation until June 7. The length of the nest initiation period ranged from 7 (Atigun Gorge in 2007) to 19 days (Atigun Gorge in 2011), with longer nest initiation periods occurring in years with more favorable conditions (warmer temperatures and fewer snow and rain events) early in the breeding season. Despite the variation in nest initiation dates, the nesting season, from initiation to fledging, was short (May 29–July 12), and nests were generally synchronous across all years. In total, there were only  $21 \pm 1$  days between average nest initiation ( $\bar{x}$  = June 7  $\pm$  4 days) and fledging dates ( $\bar{x}$  = June 28  $\pm$  4 days). Females

began incubating on the last day of laying, and incubation lasted  $11 \pm 1$  days, ranging from June 1 to July 5 throughout the study period. The nestling period was  $7 \pm 1$  days and lasted from June 20 to July 13. We did not document any renesting. Mean clutch size was  $3.7 \pm 0.9$  eggs (range = 1–5 eggs, with 1 nest containing 9 eggs;  $n$  = 274). From the one 9-egg nest, 6 chicks hatched and at least 4 fledged; the remaining 2 chicks were younger in age and had not fledged by the end of the study period. Only 1 female appeared to be attending the nest. The mean brood size at hatching was  $3.7 \pm 0.8$  chicks, and was  $3.1 \pm 1.1$  chicks at the last nest check prior to fledging.

#### Nest-site Characteristics

Nesting habitat consisted of sedge–shrub tundra (Wild et al. 2015). Within this habitat, Smith's Longspur nests were commonly located on the top (48%;  $n$  = 41) or side (24%;  $n$



**FIGURE 2.** Smith's Longspurs were found nesting in open, low-shrub tundra in the Brooks Range, Alaska, USA (left). Nests were typically found in open areas with little variation in erect willow height and usually placed under a low shrub (most commonly an erect willow), under a graminoid clump, or on the side of a tussock or hummock (right).

= 21) of hummocks, and only 28% ( $n = 24$ ) were placed on level ground. Many nests also had clumps of graminoids (44%;  $n = 38$ ) and shrubs (34%;  $n = 29$ ) located directly over them (Figure 2), but shrubs were generally <30 cm high. Only 22% of nests ( $n = 19$ ) had no direct association with nest canopy vegetation. The most common shrubs associated with nests were erect willows, followed by ericaceous species (*Vaccinium uliginosum*, *Rhododendron* spp.), and dwarf birches. Low shrubs (1.7–20.8 cm) were present at 88% of nests (Table 2). As expected, the mean elevation of nests in Atigun Gorge ( $\bar{x} = 846 \pm 26$  m) was higher than on Slope Mountain ( $\bar{x} = 655 \pm 49$  m). The slope of nest sites varied considerably, but tended to be steeper in Atigun Gorge ( $\bar{x} = 4^\circ \pm 3^\circ$ ; range = 0–10°) than on Slope Mountain ( $\bar{x} = 2^\circ \pm 2^\circ$ ; range = 0–9°). The aspect

of nests on Slope Mountain was uniformly distributed, with no sign of a directional trend, whereas nest aspect was not uniformly distributed in Atigun Gorge ( $\bar{x} = 160^\circ \pm 47^\circ$ ), with most nests aligned with the direction of the gorge. Nest visibility varied, but on average was  $28 \pm 10$  out of 80 possible points.

#### Nest-site Selection

We evaluated nest-site selection patterns at 86 Smith's Longspur nests relative to paired random points. Habitat at nest sites and random points was very similar, but, in general, shrubs tended to be taller with higher standard deviation at random points than at nests (Table 2). Among 25 conditional logistic regression models, only 1, which included the coefficient of variation for erect willow height

**TABLE 2.** Comparison of habitat characteristics at Smith's Longspur nests ( $n = 86$ ) and their paired random points within each territory in the Brooks Range of Alaska, USA, 2012. All measurements were taken within a 1-m radius of the nest or random point. Ground structure is also listed and represents the height, relative to the nest, of hummocks or tussocks within 1 m of the point. The height of prostrate vegetation and depth of leaf litter were not measured. Mean height and SD were calculated across all 40 subsamples at which the vegetation type was present.

Vegetation type	% sites vegetation type present		Height $\pm$ SD (cm)	
	Nest	Random point	Nest	Random point
Erect willow	65	62	11.4 $\pm$ 4.7	12.5 $\pm$ 5.3
Birch	30	33	8.2 $\pm$ 3.0	10.2 $\pm$ 4.8
Blueberry	49	41	4.9 $\pm$ 2.6	4.7 $\pm$ 3.3
Other ericaceous shrub	66	65	4.3 $\pm$ 2.8	4.1 $\pm$ 1.8
Graminoid	99	99	12.6 $\pm$ 8.4	11.5 $\pm$ 3.9
Tallest plant	100	100	26.8 $\pm$ 6.7	27.4 $\pm$ 8.5
Ground structure	93	95	10.9 $\pm$ 3.1	10.4 $\pm$ 3.2
Moss	100	99	—	—
Lichen	93	88	—	—
<i>Dryas</i>	79	73	—	—
Dwarf willow	78	79	—	—
Leaf litter	99	99	—	—
Bare ground	20	14	—	—



**TABLE 3.** Akaike's Information Criterion (AIC) ranking of logistic regression models used to predict Smith's Longspur nest-site selection (nest vs. random point within the territory) in the Brooks Range of Alaska, USA, 2012, as a function of microhabitat and nest features measured at each point. Only models with Akaike weights ( $w_i$ )  $\geq 0.01$  are listed. The model highlighted in bold font was the only supported model. Covariates included the coefficient of variation (CV) of erect willow height (WillowCV), mean erect willow height (WillowAvg), presence-absence of erect willow (WillowInd), CV of ericaceous shrub height (EricCV), mean ericaceous shrub height (EricAvg), presence-absence of ericaceous shrubs (EricInd), CV of ground structure height (GrndCV), mean ground structure height (GrndAvg), slope, and aspect. For each model that included the CV or average (Avg) of a vertical feature, the indicator variable (Ind) for that feature was also included (represented with a colon).  $K$  is the number of model parameters,  $\Delta AIC_c$  is the difference from the top model in AIC corrected for small sample size, and Log(L) is the log-likelihood.

Model name	Model description	$K$	$\Delta AIC_c$	$w_i$	Log(L)
<b>WillowCV</b>	<b>(WillowCV:WillowInd + WillowInd)</b>	<b>2</b>	<b>0.00<sup>a</sup></b>	<b>0.40</b>	<b>-53.97</b>
WillowCV + slope	(WillowCV:WillowInd + WillowInd) + slope	3	1.56	0.18	-53.71
ShrubCV	(WillowCV:WillowInd + WillowInd) + (EricCV:EricInd + EricInd)	4	1.81	0.16	-52.79
WillowCV + aspect	(WillowCV:WillowInd + WillowInd) + aspect	3	1.99	0.15	-53.93
GrndCV	Single factor model containing only GrndCV	1	5.93	0.02	-57.97
Full	Global model	10	6.03	0.02	-48.35
Null	Null model	0	7.21	0.01	-59.62
GrndCV + slope	GrndCV + slope	2	7.55	0.01	-57.76
GrndCV + aspect	GrndCV + aspect	2	7.93	0.01	-57.95
WillowAvg	(WillowAvg:WillowInd + WillowInd)	2	8.01	0.01	-57.98
Slope	Single factor model containing only slope	1	8.36	0.01	-59.18

<sup>a</sup> The  $AIC_c$  of the top model = 112.01.

(WillowCV; Akaike weight = 0.40), was supported in the candidate set. Three other additive models had a  $\Delta AIC_c < 2$  but differed from the WillowCV model only by uninformative parameters and were thus unsupported embellishments of the top-ranked model; together, these models garnered 89% of the support in the candidate set (Table 3). The top model indicated that, where erect willows were present, nest sites had less variability in shrub cover (lower CV of erect willow height) than random sites within the nest territory, but the effect size was small. The probability of a point being a nest site vs. a random site was reduced only slightly (odds ratio = 0.95) for every unit increase in the CV of erect willow height. We used regular logistic regression to examine the top model's goodness-of-fit using the Hosmer-Lemeshow test and found no evidence of poor fit ( $\chi^2 = 2.40$ ,  $P = 0.97$ ).

### Nest Survival

We were able to determine the fate of 95% of the nests that we located ( $n = 257$ ; 157 in Atigun Gorge and 100 on Slope Mountain). At least 1 chick fledged from 77% ( $n = 197$ ) of the nests. Among the failed nests, 53% ( $n = 32$ ) were lost to predation. The most common potential nest predators that we observed in the area were Arctic ground squirrels (*Urocyon parryii*), red foxes (*Vulpes vulpes*), and Common Ravens (*Corvus corax*). Four nests were abandoned, 2 (both in the chick stage) failed immediately after a snow or hail storm, and the remaining 22 (37%) failed for unknown reasons. At 12 of these nests, the chicks were too young to fledge, but the nest cup was empty, no adults were in the area, and there was no obvious sign of predation. Three nests were slightly disturbed, but

evidence of predation was inconclusive. One female incubated her nest for nearly twice the required incubation period 2 yr in a row; eggs in both nests never hatched. The remaining nests had dead chicks in the nest cup. We suspect that these nests may also have succumbed to weather, but we only reported weather as the cause of nest failure if we could directly link failure to a specific weather event (e.g., hail storm, unusually hot day). We did not record weather as the cause of nest failure when prolonged weather conditions (cold temperatures, rainy periods) had the potential to reduce adult feeding rates and induce starvation.

Daily survival rate was estimated from the 257 nests with known fates. The best approximating model (Hot; Akaike weight = 0.34; Table 4) indicated that DSR was positively related to the number of days above 21°C during the active period for each nest ( $\beta = 0.24 \pm 0.08$ ). The estimated DSR for years 2011–2013 (when area-specific temperature data were available) was 0.982 (85% confidence interval [CI]: 0.978–0.985), which corresponded to an average nesting success of 68% (85% CI: 63–73%). The same model used constant survival for years (2007–2009) when area-specific temperatures were not available and indicated a similar DSR (0.972; 85% CI: 0.965–0.979). Three other temperature models (Hot + Cold + HotToolik + ColdToolik, Hot + HotToolik, Hot + Cold) had  $\Delta AIC_c$  values  $< 2$ , but were not supported because they differed from the top model only by uninformative parameters (the 85% CI for all coefficients except "Hot" overlapped 0). Together, these 4 temperature models garnered 97% of the support in the candidate set (Table 4).

**TABLE 4.** Akaike's Information Criterion (AIC) rankings of daily nest survival models for Smith's Longspur nests at 2 breeding areas in northern Alaska, USA, 2007–2013. The model highlighted in bold font was the best-supported model in the candidate set. Covariates were minimum and maximum daily temperatures for a given nest while it was active (TempMin and TempMax, respectively), number of days above 21°C and below 0°C for each active nest (Hot and Cold, respectively), the coefficient of variation (CV) of erect willow height (WillowCV), presence-absence of erect willow (WillowInd), and nest visibility (Visibility). "Toolik" is the Toolik Field Station, which was used for measurement of climatic variables when site-specific information was not available.  $K$  is the number of model parameters,  $\Delta AIC_c$  is the difference from the top model in AIC corrected for small sample size,  $w_i$  is the Akaike weight, and Dev is the model deviance.

Model name	Model description	$K$	$\Delta AIC_c$	$w_i$	Dev
<b>Hot</b>	<b>2011–2013: No. of days &gt;21°C for each active nest; 2007–2009: Constant</b>	<b>2</b>	<b>0.00<sup>a</sup></b>	<b>0.34</b>	<b>420.62</b>
Hot + Cold + HotToolik + ColdToolik <sup>b</sup>	2011–2013: No. of days >21°C and <0°C for each active nest; 2007–2009: No. of days >21°C and <0°C per year (Toolik data used)	5	0.10	0.32	414.70
Hot + HotToolik <sup>b</sup>	2011–2013: No. of days >21°C for each active nest; 2007–2009: Total no. of days >21°C per year (Toolik data used)	3	1.47	0.16	420.09
Hot + Cold <sup>b</sup>	2011–2013: No. of days >21°C and <0°C for each active nest; 2007–2009: Constant	3	1.62	0.15	420.23
WillowCV	2012: CV of willow height; 2007–2009, 2011, 2013: Constant	2	7.42	0.01	248.04
WillowInd	2012: Willow present or absent; 2007–2009, 2011, 2013: Constant	2	8.41	0.01	429.03
Constant	Constant	1	8.44	0.01	431.06
Visibility	2012: Nest visibility; 2007–2009, 2011, 2013: Constant	2	9.75	0.00	430.37
Cold	2011–2013: No. of days <0°C for each active nest; 2007–2009: Constant	2	10.08	0.00	430.70
TempMax	2011–2013: Maximum daily temperature for each active nest; 2007–2009: Constant	2	10.28	0.00	430.90
StudyArea	Study area	2	10.32	0.00	430.94
TempMin	2011–2013: Minimum daily temperature for each active nest; 2007–2009: Constant	2	10.35	0.00	430.96
Period	Average egg vs. chick period by year and study area	10	10.59	0.00	415.13
Year	Year	6	11.39	0.00	423.98
Cold + ColdToolik	2011–2013: No. of days <0°C for each active nest; 2007–2009: No. of days <0°C per year (Toolik data used)	3	12.09	0.00	430.70
Year + StudyArea	Year and study area	9	13.25	0.00	419.81

<sup>a</sup>The  $AIC_c$  of the top model = 424.62.

<sup>b</sup>These models contained uninformative parameters and therefore were not supported.

In addition to the influence of temperature on nest survival, when we examined area-specific temperatures there appeared to be a relationship with both nest initiation date and synchrony among individuals (Figure 1). In 2013, snow and freezing temperatures in early spring delayed nest initiation until June 8 ( $\bar{x}$  = June 11). As a result, nest initiation, hatching, and fledging were highly synchronous. In contrast, in 2011 there was an early and warm spring and the average nest initiation dates were June 2 (Slope Mountain) and June 4 (Atigun Gorge), but synchrony was lower than in other years (Figure 1).

## DISCUSSION

We found that the timing and synchrony of nesting of Smith's Longspurs, as well as nest success, were strongly related to local weather. Like some other passerines, such as the Eurasian Great Tit (*Parus major*; Perrins and McCleery 1989), Smith's Longspurs seem to be able to

track seasonal changes and avoid initiating nests during harsh conditions (Figure 1). Advances in nest initiation dates correlated with warming temperatures and earlier snowmelt have been demonstrated in several Arctic-breeding species (McKinnon et al. 2012, Grabowski et al. 2013). In addition, there is evidence of flexibility in arrival dates in response to local temperatures and significantly earlier spring migration phenology for birds breeding along Alaska's central Arctic Coast over a 50-yr period (Ward et al. 2016). On that coastal plain, closely related Lapland Longspurs have advanced clutch initiation dates, with timing of snowmelt being the most important factor explaining this advancement (Liebezeit et al. 2014). Unfortunately, there are no long-term data on breeding Smith's Longspurs, so we cannot determine whether the timing of their breeding has changed in recent decades in response to warming temperatures in the Arctic. However, based on evidence of progressively earlier snowmelt in Alaska (Stone et al. 2002), we can infer that the average nest initiation has likely advanced for this species. Our data

for 6 yr of nesting phenology will serve as a baseline for future comparisons.

Based on the variables measured, we found only weak nest-site selection by Smith's Longspurs breeding in treeless tundra. The habitat variable that was the best predictor of nest location was the coefficient of variation of erect willow height, which tended to be lower at nest sites than at random points within the general nest area. We found no relationship, however, between this habitat variable and nest survival. This could indicate that Smith's Longspurs selected the best possible sites relative to the factors that influenced survival. However, weak nest-site selection is not unexpected considering that the random sites were only 30 m from nests and all habitat consisted of sedge–shrub tundra. The species may have strong nest-site selection, but at a larger spatial scale; for example, they may need some minimum-sized area away from dense shrubs or trees. Alternatively, we may have missed the variables that were most important for nest success.

Smith's Longspurs are generally tied to open, low-shrub habitat (Wild et al. 2015), and we found this relationship at the nest-site scale as well. We typically found nests under some low shrub or graminoid (Figure 2), and no nests were ever found among tall shrubs; the tallest plants associated with nests averaged only  $26.8 \pm 6.7$  cm (Table 2), suggesting that Smith's Longspurs prefer to nest in sites with good visibility. Considering the association with low-shrub habitat, invasion of tall deciduous shrubs (Hinzman et al. 2005) could reduce the availability of preferred nesting habitat. In addition, recent projected changes to wildlife habitats due to a warming climate in Alaska predict declines in low-shrub ecotypes in upland and alpine areas. The Smith's Longspur was listed as one of the species associated with low shrub that will likely lose habitat as a response to climate change (Marcot et al. 2015). Loss of open tundra is also expected to affect populations of the congeneric Lapland Longspur; it was predicted that by 2050 there could be a 20–60% decline in their breeding habitat (Boelman et al. 2015). However, Lapland Longspurs are more widely distributed and broader habitat generalists (Hussell and Montgomerie 2002) than Smith's Longspurs; thus, we might expect predicted changes in Arctic habitats to have a greater impact on Smith's Longspur populations.

Although Smith's Longspurs appear to avoid nesting in areas with tall or dense shrubs at the landscape scale (Wild et al. 2015), we found no relationship between nest-site selection and shrub height at the nest-site scale. The only predictor of nest location that we observed for Smith's Longspurs was variability of erect willow height, although it had such a small effect that it was likely of little biological significance. In contrast, for Lapland Longspurs nesting on the Arctic Coastal Plain of Alaska, both microrelief and variability of relief (surface roughness)

positively influenced nest-site selection and were thought to possibly afford greater food availability or crypsis from predators (Rodrigues 1994). For Smith's Longspurs, selecting territories with a plethora of potential, relatively uniform nest sites could be an alternative mechanism to reduce predation risk by increasing predator search effort (Martin 1993). Uniform shrub height near the nest could also reduce visual obstruction and allow a quicker escape from predators. Incubating females typically flushed quickly and quietly when disturbed without much of a distraction display, corroborating this theory. The nesting success of Smith's Longspurs was higher than that found generally for passerines in grassland or forested habitats (Martin 1995, Winter et al. 2005, Cox et al. 2012), and little loss (~12% of nests) was attributable directly to predation. Thus, predator-driven habitat selection in this system may not currently be as important as for ground-nesting species in other regions (Martin and Roper 1988, Hatchwell et al. 1996), but that could change with encroachment of taller shrubs and an influx of associated predators.

Although the habitat variables that we measured were not predictors of Smith's Longspur nest survival, we found a positive relationship between DSR and the number of days above 21°C. Considering that temperatures in the Arctic are increasing (Parmesan and Galbraith 2004, Ward et al. 2016), and that the frequency of warm days during the summer will likely increase, nest survival may be enhanced in the future. Although it is surprising that the number of freezing days had no influence on survival, Smith's Longspurs are well adapted to cold temperatures during the breeding season and may be relatively unaffected by freezing events. In addition, we found that Smith's Longspurs had the ability to delay nest initiation depending on local conditions. Our observation of high and consistent nest survival across all years, irrespective of nest initiation date, is contrary to the results of several studies documenting adverse effects of delayed nest initiation on Lapland Longspurs, including increased nest failure (Astheimer et al. 1995) and smaller clutch sizes (Fox et al. 1987).

We would expect that, in addition to temperature, precipitation (which is extremely variable spatially in the Brooks Range) would influence nest survival (Morrison and Bolger 2002), but unfortunately we did not record rainfall in our study areas. Anecdotal evidence from our study suggests that heavy precipitation early in the breeding season can delay nest initiation (Figure 1; Environmental Data Center Team 2016). Other studies suggest that, in addition to warming trends, the intensity and frequency of summer storms will increase (Hinzman et al. 2005), and erratic conditions are known to negatively affect the breeding success of birds (Hendricks and Norment 1992, Jones et al. 2001, Stenseth et al. 2002,

Dickey et al. 2008). Inclement weather has been linked to reductions in chick growth and survival of the Curlew Sandpiper (*Calidris ferruginea*) in Siberia (Schekkerman et al. 1998), and to reduced chick growth of Lapland Longspurs and Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) in sites near our study areas within Alaska's Brooks Range (Pérez et al. 2016). In Canada, the failure of 100% ( $n = 18$ ) of Smith's Longspur nests was attributed to a 4-day period of rain and cold temperatures (Jehl and Hussell 1966). Because harsh conditions are fairly common at northern latitudes, Arctic birds are relatively resilient. However, increased occurrence and severity of summer storms (Hinzman et al. 2005) could add additional stress to breeding birds and result in population declines over time, depending on the timing of those events.

The estimated DSR for Smith's Longspur nests was consistently high compared with that of Lapland Longspurs and Savannah Sparrows (*Passerculus sandwichensis*) breeding in the north (Weatherhead 1979, Martin et al. 2009, Liebezeit et al. 2011). We attribute the high and consistent rates of nest success of Smith's Longspurs in part to the species' polygynandrous mating system, in which females typically nest in neighborhoods and may benefit from soliciting copulations from multiple males, subsequently assuring additional care for offspring (Davies 1985). In the polygynandrous Alpine Accentor (*Prunella collaris*), which nests at high elevations, one of the main factors that influenced reproductive success was the extent to which females secured additional male mates, thus ensuring extra parental care (Nakamura 1998). For Smith's Longspurs, an increase in parental care from multiple males may offset potential negative impacts from harsh environmental conditions in the Arctic. Consequently, the effects of shifting local weather conditions on Smith's Longspur nest survival could be mediated to some degree by their unique mating system, although shrub encroachment could alter the large, open expanses of tundra typically selected for neighborhoods, and thus may influence social dynamics.

The current conservation status of Smith's Longspurs is largely based on an uncertain and likely small population size. Considering the changes that Arctic ecosystems are now undergoing, the potential long-term effects of climate change on Smith's Longspur populations are still unclear. Earlier snowmelt and warmer temperatures during the breeding season could result in a net increase in productivity over time. The relatively high and consistent nest success that we found across years suggests that Smith's Longspurs are resilient to harsh and unexpected conditions. Thus, the potential loss of large expanses of uniform, low-shrub habitats in upland and alpine areas may be of greater concern. Increased height, density, and occurrence of shrubs would change the characteristics of

breeding habitat, potentially increasing the pressure from nest predators and altering the social dynamics of this polygynandrous species. In conclusion, long-term climate-mediated impacts on Smith's Longspur breeding areas could result in increased reproductive success due to warmer temperatures, but overall population declines if habitats become shrubbier.

## ACKNOWLEDGMENTS

Nest survival data from 2007 to 2009 were collected by T. Wild. We thank E. Craig, J. Hughey, B. Higgins, C. Woodworth, N. Beauregard, and the numerous other volunteers who made field research possible, and T. Craig, E. Nol, and 2 anonymous reviewers for their reviews of the manuscript. We especially appreciate input from R. Barry and A. Blanchard on logistic regression techniques and from M. Lindberg on nest survival analysis. These individuals were instrumental in the success of this paper and we thank them for their expertise and willingness to share their knowledge.

**Funding statement:** This study would not have been possible without the financial and logistical support of a U.S. Geological Survey (USGS) and U.S. Fish and Wildlife Service (USFWS) Science Support Program grant; the USFWS Arctic National Wildlife Refuge; USGS Alaska Cooperative Fish and Wildlife Research Unit; and the Bureau of Land Management. Additional funding for H.R.M. was provided through an Arctic Audubon Grant, Ted McHenry Scholarship, Bergstrom Memorial Scholarship, John Marooney Scholarship, and CASE GK-12 Fellowship. The findings and conclusions of this article are those of the authors and do not necessarily represent the views of the USFWS. This paper has been peer-reviewed and approved for publication consistent with USGS Fundamental Science Practices (<http://pubs.usgs.gov/circ/1367>). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

**Ethics statement:** All field investigations were conducted in compliance with Institutional Animal Care and Use Committee protocol 172031 of the University of Alaska Fairbanks.

**Author contributions:** H.R.M., S.K., and A.N.P. conceived the idea and design, formulated the questions asked, and developed the methods. H.R.M. collected and analyzed the data. H.R.M. wrote the paper, with significant input from S.K. and A.N.P. S.K. contributed substantial materials, resources, and funding.

## LITERATURE CITED

- Anisimov, O. A., D. G. Vaughan, T. Callaghan, C. Furgal, H. Marchant, T. D. Prowse, H. Vilhjálmsson, and J. E. Walsh (2007). Polar regions (Arctic and Antarctic). In *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson, Editors). Cambridge University Press, Cambridge, UK. pp. 653–685.

- Arctic Climate Impact Assessment (2004). Impacts of a Warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press, Cambridge, UK. <http://www.acia.uaf.edu>
- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *The Journal of Wildlife Management* 74:1175–1178.
- Astheimer, L. B., W. A. Buttemer, and J. C. Wingfield (1995). Seasonal and acute changes in adrenocortical responsiveness in an arctic-breeding bird. *Hormones and Behavior* 29:442–457.
- Bengtsson, L., K. I. Hodges, and E. Roeckner (2006). Storm tracks and climate change. *Journal of Climate* 19:3518–3543.
- Boelman, N. T., L. Gough, J. Wingfield, S. Goetz, A. Asmus, H. E. Chmura, J. S. Krause, J. H. Perez, S. K. Sweet, and K. C. Guay (2015). Greater shrub dominance alters breeding habitat and food resources for migratory songbirds in Alaskan arctic tundra. *Global Change Biology* 21:1508–1520.
- Both, C., and M. E. Visser (2005). The effect of climate change on the correlation between avian life-history traits. *Global Change Biology* 11:1606–1613.
- Briskie, J. V. (2009). Smith's Longspur (*Calcarius pictus*). In *The Birds of North America* (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bna.34
- Carey, C. (2002). Incubation in extreme environments. In *Avian Incubation: Behaviour, Environment, and Evolution* (D. C. Deeming, Editor). Oxford Ornithology Series 13:238–253.
- Colles, A., L. H. Liow, and A. Prinzing (2009). Are specialists at risk under environmental change? Neocological, paleoecological and phylogenetic approaches. *Ecology Letters* 12:849–863.
- Cox, W. A., F. R. Thompson, III, and J. Faaborg (2012). Species and temporal factors affect predator-specific rates of nest predation for forest songbirds in the Midwest. *The Auk* 129: 147–155.
- Craig, H. R., S. Kendall, T. Wild, and A. N. Powell (2015). Dispersal and survival of a polygynandrous passerine. *The Auk: Ornithological Advances* 132:916–925.
- Crick, H. Q. P. (2004). The impact of climate change on birds. *Ibis* 146 (Suppl. 1):48–56.
- Crick, H. Q. P., and T. H. Sparks (1999). Climate change related to egg-laying trends. *Nature* 399:423.
- Davies, N. B. (1985). Cooperation and conflict among Dunnocks, *Prunella modularis*, in a variable mating system. *Animal Behaviour* 33:628–648.
- Davis, S. K., and S. G. Sealy (1998). Nesting biology of the Baird's Sparrow in southwestern Manitoba. *The Wilson Bulletin* 110: 262–270.
- Dickey, M.-H., G. Gauthier, and M.-C. Cadieux (2008). Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species. *Global Change Biology* 14: 1973–1985.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye (1988). *The Birder's Handbook: A Field Guide to the Natural History of North American Birds*. Simon & Schuster, New York, NY, USA.
- Environmental Data Center Team (2015). Meteorological monitoring program at Toolik, Alaska. Toolik Field Station, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, USA. [http://toolik.alaska.edu/edc/abiotic\\_monitoring/data\\_query.php](http://toolik.alaska.edu/edc/abiotic_monitoring/data_query.php)
- Environmental Data Center Team (2016). Snow-cover monitoring program at Toolik, Alaska. Toolik Field Station, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, USA. [http://toolik.alaska.edu/edc/abiotic\\_monitoring/image\\_library.php](http://toolik.alaska.edu/edc/abiotic_monitoring/image_library.php)
- Euskirchen, E. S., A. D. McGuire, F. S. Chapin, III, S. Yi, and C. C. Thompson (2009). Changes in vegetation in northern Alaska under scenarios of climate change, 2003–2100: Implications for climate feedbacks. *Ecological Applications* 19:1022–1043.
- Fox, A. D., I. S. Francis, J. Madsen, and J. M. Stroud (1987). The breeding biology of the Lapland Bunting *Calcarius lapponicus* in West Greenland during two contrasting years. *Ibis* 129: 541–552.
- Grabowski, M. M., F. I. Doyle, D. G. Reid, D. Mossop, and D. Talarico (2013). Do Arctic-nesting birds respond to earlier snowmelt? A multi-species study in north Yukon, Canada. *Polar Biology* 36:1097–1105.
- Hansen, J., M. Sato, R. Ruedy, K. Lo, D. W. Lea, and M. Medina-Elizade (2006). Global temperature change. *Proceedings of the National Academy of Sciences USA* 103:14288–14293.
- Harrison, M. L., N. A. Mahony, P. Robinson, A. Newbury, and D. J. Green (2011). Nest-site selection and productivity of Vesper Sparrows breeding in grazed habitats. *Journal of Field Ornithology* 82:140–149.
- Hatchwell, B. J., D. E. Chamberlain, and C. M. Perrins (1996). The reproductive success of Blackbirds *Turdus merula* in relation to habitat structure and choice of nest site. *Ibis* 138:256–262.
- Hausner, V. H., N. G. Yoccoz, and R. A. Ims (2003). Selecting indicator traits for monitoring land use impacts: Birds in northern coastal birch forests. *Ecological Applications* 13: 999–1012.
- Hendricks, P., and C. J. Norment (1992). Effects of a severe snowstorm on subalpine and alpine populations of nesting American Pipits. *Journal of Field Ornithology* 63:331–338.
- Hinzman, L. D., N. D. Bettez, W. R. Bolton, F. S. Chapin, M. B. Dyrurgerov, C. L. Fastie, B. Griffith, R. D. Hollister, A. Hope, H. P. Huntington, A. M. Jensen, et al. (2005). Evidence and implications of recent climate change in northern Alaska and other Arctic regions. *Climatic Change* 72:251–298.
- Hoset, K. S., Y. Espmark, A. Moksnes, T. Haugan, M. Ingebrigtsen, and M. Lier (2004). Effect of ambient temperature on food provisioning and reproductive success in Snow Buntings *Plectrophenax nivalis* in the High Arctic. *Ardea* 92:239–246.
- Hosmer, D. W., and S. Lemeshow (2000). *Applied Logistic Regression*, second edition. Wiley, New York, NY, USA.
- Hussell, D. J., and R. Montgomerie (2002). Lapland Longspur (*Calcarius lapponicus*). In *The Birds of North America* (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bna.656
- Jehl, J. R., Jr. (1968). The breeding biology of Smith's Longspur. *The Wilson Bulletin* 80:123–149.
- Jehl, J. R., Jr., and D. J. T. Hussell (1966). Effects of weather on reproductive success of birds at Churchill, Manitoba. *Arctic* 19:185–191.
- Johnson, S. R., and D. R. Herter (1990). Bird migration in the Arctic: A review. In *Bird Migration: Physiology and Ecophysiology* (E. Gwinner, Editor). Springer-Verlag, Berlin, Germany. pp. 22–43.
- Jones, J., R. D. DeBruyn, J. J. Barg, and R. J. Robertson (2001). Assessing the effects of natural disturbance on a Neotropical migrant songbird. *Ecology* 82:2628–2635.
- Liebezeit, J. R., K. E. B. Gurney, M. Buddle, S. Zack, and D. Ward (2014). Phenological advancement in arctic bird species:

- Relative importance of snow melt and ecological factors. *Polar Biology* 37:1309–1320.
- Liebezeit, J. R., G. C. White, and S. Zack (2011). Breeding ecology of birds at Teshekpuk Lake: A key habitat site on the Arctic Coastal Plain of Alaska. *Arctic* 64:32–44.
- Marcot, B. G., M. T. Jorgenson, J. P. Lawler, C. M. Handel, and A. R. DeGange (2015). Projected changes in wildlife habitats in Arctic natural areas of northwest Alaska. *Climatic Change* 130:145–154.
- Martin, M., A. F. Camfield, and K. Martin (2009). Demography of an alpine population of Savannah Sparrows. *Journal of Field Ornithology* 80:253–264.
- Martin, T. E. (1993). Nest predation among vegetation layers and habitat types: Revising the dogmas. *The American Naturalist* 141:897–913.
- Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.
- Martin, T. E., and G. R. Geupel (1993). Nest-monitoring plots: Methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507–519.
- Martin, T. E., and J. J. Roper (1988). Nest predation and nest-site selection of a western population of the Hermit Thrush. *The Condor* 90:51–57.
- McKinnon, L., E. Nol, and C. Juillet (2013). Arctic-nesting birds find physiological relief in the face of trophic constraints. *Scientific Reports* 3:1816. doi:10.1038/srep01816
- McKinnon, L., M. Picotin, E. Bolduc, C. Juillet, and J. Bêty (2012). Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. *Canadian Journal of Zoology* 90:961–971.
- Morrison, S. A., and D. T. Bolger (2002). Variation in a sparrow's reproductive success with rainfall: Food and predator-mediated processes. *Oecologia* 133:315–324.
- Murray, L. D., and L. B. Best (2014). Nest-site selection and reproductive success of Common Yellowthroats in managed Iowa grasslands. *The Condor: Ornithological Applications* 116:74–83.
- Nakamura, M. (1998). Multiple mating and cooperative breeding in polygynandrous Alpine Accentors. I. Competition among females. *Animal Behaviour* 55:259–275.
- Parnesan, C., and H. Galbraith (2004). Observed impacts of global climate change in the U.S. Pew Center on Global Climate Change, Arlington, VA, USA.
- Pérez, J. H., J. S. Krause, H. E. Chmura, S. Bowman, M. McGuigan, A. L. Asmus, S. L. Meddle, K. E. Hunt, L. Gough, N. T. Boelman, and J. C. Wingfield (2016). Nestling growth rates in relation to food abundance and weather in the Arctic. *The Auk: Ornithological Advances* 133:261–272.
- Perrins, C. M., and R. H. McCleery (1989). Laying dates and clutch size in the Great Tit. *The Wilson Bulletin* 101:236–253.
- R Core Team (2014). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. W. Demarest, E. H. Dunn, W. C. Hunter, E. E. Inigo-Elias, J. A. Kennedy, et al. (2004). Partners in Flight North American Landbird Conservation Plan. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Rodrigues, R. (1994). Microhabitat variables influencing nest-site selection by tundra birds. *Ecological Applications* 4:110–116.
- Rotenberry, J. T., and J. A. Wiens (1980). Habitat structure, patchiness, and avian communities in North American steppe vegetation: A multivariate analysis. *Ecology* 61:1228–1250.
- Schekkerman, H., M. W. J. van Roomen, and L. G. Underhill (1998). Growth, behavior of broods and weather-related variation in breeding productivity of Curlew Sandpipers *Calidris ferruginea*. *Ardea* 86:153–168.
- Seavy, N. E., K. E. Dybala, and M. A. Snyder (2008). Climate models and ornithology. *The Auk* 125:1–10.
- Sekercioglu, C. H., S. H. Schneider, J. P. Fay, and S. R. Loarie (2008). Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* 22:140–150.
- Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima (2002). Ecological effects of climate fluctuations. *Science* 297:1292–1296.
- Stone, R. S., E. G. Dutton, J. M. Harris, and D. Longenecker (2002). Earlier spring snowmelt in northern Alaska as an indicator of climate change. *Journal of Geophysical Research* 107:ACL 10. doi:10.1029/2000JD000286
- Sturm, M., C. Racine, and K. Tape (2001). Climate change: Increasing shrub abundance in the Arctic. *Nature* 411:546–547.
- Tape, K., M. Sturm, and C. Racine (2006). The evidence for shrub expansion in northern Alaska and the pan-Arctic. *Global Change Biology* 12:686–702.
- USFWS (U.S. Fish and Wildlife Service) (2008). Birds of Conservation Concern. U.S. Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, VA, USA. <https://www.fws.gov/birds/management/managed-species/birds-of-conservation-concern.php>
- Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen, and C. M. Lessells (1998). Warmer springs lead to mistimed reproduction in Great Tits (*Parus major*). *Proceedings of the Royal Society of London, Series B* 265:1867–1870.
- Ward, D. H., J. Helmericks, J. W. Hupp, L. McManus, M. Budde, D. C. Douglas, and K. D. Tape (2016). Multi-decadal trends in spring arrival of avian migrants to the central Arctic coast of Alaska: Effects of environmental and ecological factors. *Journal of Avian Biology* 47:197–207.
- Weatherhead, P. J. (1979). Ecological correlates of monogamy in tundra-breeding Savannah Sparrows. *The Auk* 96:391–401.
- White, G. C., and K. P. Burnham (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Wild, T. C., S. J. Kendall, N. Guldager, and A. N. Powell (2015). Breeding habitat associations and predicted distribution of an obligate tundra-breeding bird, Smith's Longspur. *The Condor: Ornithological Applications* 117:3–17.
- Winter, M., D. H. Johnson, and J. A. Shaffer (2005). Variability in vegetation effects on density and nesting success of grassland birds. *The Journal of Wildlife Management* 69:185–197.
- Wormworth, J., and K. Mallon (2006). Bird species and climate change: The global status report: A synthesis of current scientific understanding of anthropogenic climate change impacts on global bird species now, and projected future effects. Climate Risk, Fairlight, NSW, Australia.
- Zack, S., and J. Liebezeit (2009). New conservation priorities in a changing Arctic Alaska. Workshop summary. North America Program, Wildlife Conservation Society, Portland, OR, USA. <https://programs.wcs.org/carbon/climate-change/wcs-resources/publications.aspx>