

BREEDING ECOLOGY OF SMITH'S LONGSPURS (*Calcarius pictus*) IN THE
BROOKS RANGE, ALASKA

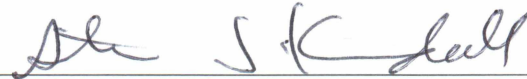
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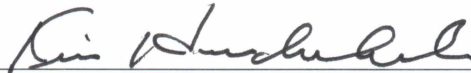
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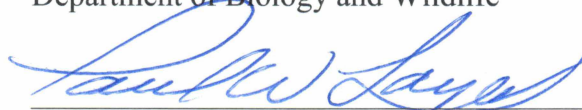


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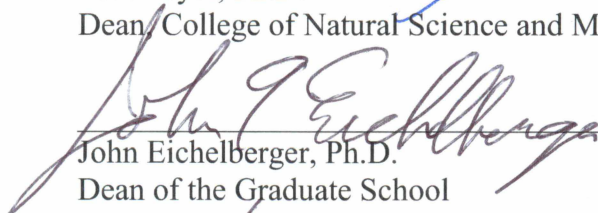


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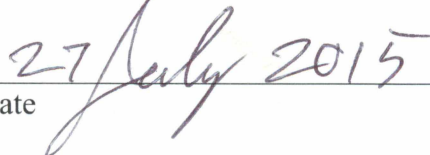
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BREEDING ECOLOGY OF SMITH'S LONGSPURS (*CALCARIUS PICTUS*) IN THE
BROOKS RANGE, ALASKA

A
THESIS

Presented to the Faculty
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MASTER OF SCIENCE

By

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Abstract

Alaska's arctic ecosystem provides critical habitat for nesting songbirds. However, within this region climate change projections indicate a shrubbier future, as well as major shifts in summer weather patterns. The polygynandrous Smith's Longspur (*Calcarius pictus*) is a little-known species that is closely tied to treeless tundra habitat in northern Alaska. I evaluated Smith's Longspur dispersal ability and annual survival rates using seven years of banding data, as well as breeding habitat requirements and reproductive success in two populations in the Brooks Range. Most adults (88%; $n = 34$) returned to nest in the same breeding neighborhood as previous years, and dispersal distance ($\bar{x} \pm SE = 301 \pm 70$ m) did not differ between sexes. Only 4% of juvenile birds were resighted as adults and dispersal distance ($\bar{x} = 1674 \pm 500$ m; $n = 6$) was significantly greater for juveniles than for adults. From 674 capture-recapture histories, I evaluated annual survival and found that adult female survival (50-58%) was only slightly lower than for males (60-63%); juvenile survival was 41%, but was also paired with a low (13%) encounter probability. I examined nest-site selection patterns by comparing habitat measurements from 86 nests to paired random points within the nest area. Nests were typically found in open low shrub tundra and never among tall shrubs (height of tallest shrub $\bar{x} = 26.8 \pm 6.7$ cm). However, the only predictor of nest location I found was variation in willow height, which was slightly lower at nests than at random points. Daily nest survival rates were estimated from 257 nests and found to be relatively high (0.97–0.99) and consistent across years, and the best approximating model indicated that nest survival was negatively related to the numbers of days below freezing and season date. Despite dispersal ability and resilience to harsh conditions, Smith's Longspurs' response to climate change is unknown. The lack of sex-bias in dispersal and the low sex bias in survival, as well as the weak nest-site selection, may be attributed to the

species' social mating system. Unlike most songbirds, multiple inter-mated individuals exist within each breeding neighborhood, altering social dynamics and likely demographic patterns. This is the first study to investigate the breeding biology of Smith's Longspurs at the western extent of their range and provides important conservation information as Arctic regions change.

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General Introduction

Climate change is occurring faster in the Arctic than anywhere else on earth, consequently threatening arctic ecosystems (Arctic Climate Impact Assessment 2004). Substantial changes in thermal regimes (Cox et al. 2000; Hansen et al. 2006), summer storm intensity (Parmesan and Galbraith 2004; Bengtsson et al. 2006), and habitat structure (Tape et al. 2006; Euskirchen et al. 2009) are underway, with some sensitive avian communities already responding (Wormworth and Mallon 2006). Further distribution shifts and extinctions are expected among the several hundred million migratory birds that breed in the Arctic (Malcolm et al. 2006; Wormworth and Mallon 2006). Passerine species tied to open tundra habitat types are expected to be among those affected by the northward advancement of deciduous shrubs, and may be displaced by shrub-breeding species (Tape et al. 2006; Euskirchen et al. 2009; Boelman et al. 2015). Changing weather patterns may also disrupt reproductive patterns that influence breeding success rates, and in turn, populations (Sanz 2003; Crick 2004).

Despite predictions of impacts from climate change, the breeding ecology of many Arctic passerines is understudied and poorly understood. As a result, patterns in sex- and age-specific survival and dispersal that are typically found in commonly studied species are often applied to all taxa, regardless of breeding strategy or geographic region. Because demographic parameters are highly variable across species (Greenwood 1980; Clarke et al. 1997; Dobson 2013), it is critical to identify breeding requirements, dispersal patterns, and survival rates of each taxon. Understanding demographic parameters at both the local and population level is essential to accurately and appropriately identify species response to changes in habitat and climate.

The Smith's Longspur (*Calcarius pictus*) is an arctic-breeding passerine with one of the most unique breeding strategies in North America. Contrary to most passerines, breeding pairs do not

form bonds or establish defensible territories (Jehl 1968). Furthermore, both sexes are promiscuous, mating with multiple individuals during a given breeding season (Briskie 1992). Strong social dynamics within these groups of interbreeding birds (neighborhoods) likely drive demographic parameters of the species. Despite Smith's Longspurs' fascinating breeding strategy, little is known about their breeding ecology (Ehrlich et al. 1988; Briskie 2009; Wild et al. 2014). Management agencies across Canada and Alaska have listed the Smith's Longspurs as a species of conservation concern (Rich et al. 2003; U.S. Fish and Wildlife Service 2008; Zack and Liebezeit 2009), highlighting a need to fill these knowledge gaps, particularly as climate change threatens their arctic breeding grounds.

Current understanding of Smith's Longspur breeding demographics is largely based on a small breeding population in Manitoba, Canada (Jehl 1968; Briskie 1992). Information on breeding requirements are almost completely lacking for Alaska populations. The only other study in Alaska examined Smith's Longspur distribution and large-scale breeding habitat associations, and found that within the Brooks Range ecoregion the species avoids breeding in areas with dense or tall shrubs (Wild et al. 2014). Considering this finding, and the advancement of deciduous shrubs across the Arctic, it is essential that we also identify microhabitat nest associations for the species. Furthermore, examination of Smith's Longspur survival and dispersal ability is important to determine the species' ability to respond to climate change.

The goal of my research was to provide a more complete understanding of Smith's Longspur breeding demographics in Alaska. I examined two breeding populations and used seven years of capture/resight data and nest monitoring to examine 1) adult and natal dispersal and apparent survival, and 2) nest habitat characteristics, nest-site selection, and reproductive success. This study is one of the first to examine the breeding ecology of Smith's Longspurs. Despite climate

change in the Arctic, little is known about survival, dispersal and breeding requirements of tundra nesting passerines, thus this study fills an important knowledge gap about demographic patterns of northern species. Furthermore, my findings shed light on the relationship between dispersal, nest-site selection, and social mating systems. Baseline data from my study will be useful for assessing future change to Smith's Longspur breeding populations, and for informing management decisions prior to more oil, gas, and mining development in Arctic regions. I encourage management agencies to continue to fund long-term studies such as this, as they are essential for identifying population trends.

Literature Cited

Arctic Climate Impact Assessment (2004). Impacts of a warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press. Cambridge, United Kingdom.

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.

Briskie, J. V. (1992). Copulation patterns and sperm competition in the polygynandrous Smith's Longspur. *The Auk* 109:563–575.

Briskie, J. V. (2009). Smith's Longspur (*Calcarius pictus*). In *Birds of North America Online*. Ithaca, New York. <http://bna.birds.cornell.edu/BNA>.

- Clarke, A. L., B.-E. Sæther, and E. Røskoft (1997). Sex biases in avian dispersal: a reappraisal. *Oikos* 79:429–438.
- Cox, P. M., R. A. Betts, C. D. Jones, S. A. Spall, and I. J. Totterdell (2000). Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408:184–187.
- Crick, H. Q. P. (2004). The impact of climate change on birds. *Ibis* 146:48–56.
- Dobson, F. S. (2013). The enduring question of sex-biased dispersal: Paul J. Greenwood's (1980) seminal contribution. *Animal Behaviour* 85:299–304.
- Ehrlich, P., D. S. Dobkin, and D. Wheye (1988). *Birder's Handbook: A Field Guide To The Natural History Of North American Birds*. Touchstone, London and New York.
- Euskirchen, E. S., A. D. McGuire, F. S. Chapin, 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.
- Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- 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* 103:14288–14293.
- Jehl, J. R. (1968). The breeding biology of Smith's Longspur. *Wilson Bulletin* 80:123–149.
- Malcolm, J. R., C. Liu, R. P. Neilson, L. Hansen, and L. Hannah (2006). Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology* 20:538–548.
- Parmesan, C., and H. Galbraith (2004). *Observed impacts of global climate change in the U.S.* Pew Center on Global Climate Change. Arlington, Virginia.

- Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. Demarest, E. H. Dunn, W. C. Hunter, and E. Iñigo-Elias (2003). Partners in Flight North American landbird conservation plan. Cornell Laboratory of Ornithology. Ithaca, New York.
- Sanz, J. J. (2003). Large-scale effect of climate change on breeding parameters of Pied Flycatchers in Western Europe. *Ecography* 26:45–50.
- Tape, K. E. N., M. Sturm, and C. Racine (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* 12:686–702.
- U.S. Fish and Wildlife Service (2008). Birds of Conservation Concern, p 85. United States Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management. Arlington, Virginia. <http://www.fws.gov/migratorybirds>.
- Wild, T. C., S. J. Kendall, N. Guldager, and A. N. Powell (2014). Breeding habitat associations and predicted distribution of an obligate tundra-breeding bird, Smith's Longspur. *The Condor: Ornithological Applications* 117:3–17.
- 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. Wildlife Conservation Society. Portland, Oregon.

Chapter 1. Dispersal and survival of a polygynandrous passerine.¹

1.1 Abstract

Although sex biases in survival and dispersal are thought to be linked to avian mating systems, little is known about these demographic patterns in less-common mating strategies such as polygynandry. We investigated breeding site fidelity, natal philopatry, and apparent survival of the polygynandrous Smith's Longspur (*Calcarius pictus*) over a seven-year period at two study areas in Alaska's Brooks Range. We used capture-recapture histories of 243 color banded adults and 431 juveniles to estimate annual survival, while dispersal patterns were determined from 34 adults who were found breeding within the study areas over multiple years. Most adults (88%) returned to nest in the same breeding neighborhood as previous years; mean dispersal distance was 301 ± 70 m and did not differ between sexes. Juvenile birds exhibited low natal philopatry; only 4% of banded HY birds were resighted as adults during subsequent years. Those that did return dispersed on average 1674 ± 500 m from their natal nests ($n = 6$). Model-averaged survival estimates indicated that annual survival of adult females (50-58%) was only slightly lower than males (60-63%); juvenile survival was 41%, but was paired with a low (13%) encounter probability. We attribute the lack of gender bias in adult dispersal to the polygynandrous mating strategy of Smith's Longspurs. Within this system, there are multiple mates within a breeding neighborhood. We argue that natural selection may favor females that remain on the same, familiar breeding site, because they do not have to disperse to a new area to find a suitable mate. Dispersal among breeding populations most likely occurs by juveniles returning as adults. Our findings support hypotheses suggesting a relationship between dispersal and mating strategy and provide some of the first insight of demographic patterns of a polygynandrous passerine.

¹ Craig, H.R., S. Kendall, T. Wild, and A. Powell (2015). Dispersal and survival of a polygynandrous passerine. Accepted to *The Auk: Ornithological Applications*.

1.2 Introduction

Dispersal and survival play important roles in the dynamics of species at both local and population levels (Brown and Kodric-Brown 1977, Comins et al. 1980, Wheelwright and Mauck 1998). However, within a species, not all individuals, sexes, or age classes disperse and survive uniformly. Studies of avian dispersal patterns have suggested a link with mating system (Greenwood 1980, Clarke et al. 1997); however, the relationship is still poorly understood (Sutherland et al. 2000, Dobson 2013, Mabry et al. 2013). In particular, almost nothing is known about gender differences in dispersal of adult and hatch-year (HY) birds with a polygynandrous breeding strategy. In this system both males and females pair and copulate with multiple individuals of the opposite sex (Briskie 1992).

Regardless of breeding strategy, dispersal patterns of adult versus HY passerines vary widely within populations (Sutherland et al. 2000). The most common trend is that the distance between an individual's natal site and the location of their first breeding attempt is much greater than the distance between subsequent breeding sites (Drilling and Thompson 1988). Whether a species disperses primarily through adult or HY movements, dispersal ability determines flexibility in response to habitat changes (La Sorte and Jetz 2010, Schloss et al. 2012). Understanding this flexibility is important in light of climate change predictions, particularly in the rapidly changing Arctic, where bird distributions may shift northward as currently suitable habitat becomes shrubbier (Seavy et al. 2008).

Despite the conservation implications of dispersal patterns, most of what is known is based on studies of monogamous taxa, the breeding strategy that is used by 93% of birds (Lack 1968). Within monogamous passerines, adult females commonly disperse farther than males (Greenwood 1980). It is generally thought that this female-biased dispersal in adults is a result of

resource defense behavior (Greenwood 1980, Cline et al. 2013). In these systems, males establish territories at a high energetic expense, thus they benefit from site familiarity. This familiarity allows males to forage more effectively and avoid previously identified predators. In contrast, females return to the nesting grounds after males and select a territory based on the male's defense ability. If a female's previous nest failed, she may be more inclined to disperse to a new territory in hopes of finding a mate with higher fitness. As a result, females exhibit higher dispersal rates than males (Beletsky and Gordon 1991).

Knowledge of dispersal patterns in non-monogamous mating systems is lacking. However, we can expect that if resource defense plays a key role in female-biased dispersal, then dispersal patterns should differ in taxa that do not utilize this strategy. In particular, there is little to no male territory defense in the polygynandrous passerine, the Smith's Longspur (*Calcarius pictus*). Instead, breeding "neighborhoods" of inter-mating males and females are formed (Briskie 1992). Because there are multiple options within each breeding neighborhood, even if a previous nesting attempt was unsuccessful, females may not have to disperse to unfamiliar areas to find alternative mates. As a result, in polygynandrous species it is likely that both sexes benefit equally from breeding site fidelity.

One of the difficulties in studying dispersal is that it is confounded by survival (Baker et al. 1995, Stenzel et al. 2007). Due to geographic limitations within most studies, long-distance dispersal events go undetected and are indistinguishable from mortality. This is particularly evident in HY passerines where dispersal distance tends to be greater and first year survival is generally low (Paradis et al. 1998). Thus, to better understand dispersal, survival patterns should be studied simultaneously. Unfortunately, information on survival is lacking for many species;

survival rates of polygynandrous passerines are generally unknown, as are survival rates of Arctic-breeding passerines, regardless of breeding strategy.

We examined breeding site fidelity, natal philopatry, and apparent survival of Smith's Longspurs in the Brooks Range of Alaska. We hypothesized that due to the absence of resource defense by males, the species would not exhibit the usual female-biased dispersal seen in most passerines; instead we predicted that sexes would exhibit equal dispersal rates for adult birds. Additionally, we predicted that compared to monogamous species, juvenile Smith's Longspurs would disperse greater distances than adults to ensure young leave their natal neighborhood where multiple related individuals likely exist (Briskie 1992). Finally, we expected to see lower annual survival of males than females, because (a) early in the breeding season, male Smith's Longspurs have extreme energetic demands related to high copulation rates and intense mate guarding, and (b) later in the season they help to provision broods, as well as undergo molt during chick rearing (Briskie 1992, Briskie et al. 1998).

1.3 Methods

1.3.1 Study species

The Smith's Longspur is a small (20–30 g), migratory songbird found breeding along the remote tundra-tree line of Alaska and Canada (Jehl 1968). This is an ideal study organism for investigating demographic patterns of polygynandrous species because they can be locally abundant (Wild et al. 2014). Both sexes mate with up to three individuals during a given breeding season; no pair bonds or defendable territories are established, and males only “guard” females during short periods of copulation (Briskie 1992). Due to the condensed Arctic breeding season, the mating period is only 5–8 days; as a result timing of nesting is fairly synchronous and

there is no renesting (Briskie 1992). Additionally, because most broods have mixed paternity, males share in parental care and often attend young at multiple nests (Briskie et al. 1998). Past studies suggest relatively high site fidelity in adults (Jehl 1968, Briskie 2009), but there is little to no information on dispersal, philopatry, or annual survival.

1.3.2 Study area

We studied breeding Smith's Longspurs from late May until the middle of July at two locations in the Brooks Range of northern Alaska (Figure 1.1). Atigun Gorge, the more southern study area, is located in a mountain valley (N 68.27°, W 149.21°; 2007–2013), while Slope Mountain is 27 km north in rolling foothills (N 68.41°, W 149.40°; 2011–2013). Both study areas were accessible from the Dalton Highway, ~1060 ha, and characterized by treeless tundra habitat. Study areas were chosen based on accessibility and presence of known breeding populations.

1.3.3 Field techniques

We searched for nests every day (6–12 hr d⁻¹), except during inclement weather, for the entirety of the breeding season (late May through mid July) over a period of seven years (2007–2013). Once nests were located, we monitored them every 2–4 days until they failed or chicks fledged. During 2007, 2008, and 2010 capture, banding, and resighting were an offshoot of other studies on habitat associations of Smith's Longspurs. As a result, banding and resighting efforts were not consistent among these years.

We captured adult birds using several mist-netting techniques, depending on period of breeding. In the early season (~May 28 to June 10) we captured males, and occasionally females,

using playback calls and decoys placed near the nets. During the incubation period (~June 10 to July 4), we captured both sexes in nets placed around the nest. In total, we banded 243 adults (142 female and 101 male) with a USGS metal band and a unique color combination of 3 plastic leg bands. Individuals were sexed using plumage characteristics (Pyle 1987), measured for body fat, body size (bill dimensions, wing and tail lengths) and weighed to the nearest 0.1 g following standard procedures. We banded HY birds ($n = 431$) in the nest just prior to fledging (usually 5–9 days of age) using a USGS metal band. In 2011 and 2012, we also banded HY birds with 1–2 color bands that were unique to the nest from which they hatched. Sex of HY birds was not determined unless they returned to the study area and were recaptured as adults, at which time we also added individual color band combinations.

To resight individuals, we devoted an additional ~30–40 hours year⁻¹ within each study area. Resight effort was greatest (2–6 hr d⁻¹) during the first two weeks of the breeding season when birds were arriving and establishing breeding neighborhoods. Once this stage was complete, our resight effort declined as most birds had already been identified. Determining mate association was of secondary importance to the main study goal and was done on an opportunistic basis.

1.3.4 Estimating breeding site fidelity and natal philopatry

To investigate breeding site fidelity, we plotted GPS coordinates of nest locations on a digital interactive map using ArcMap 10.1 (ESRI, Redlands, CA). We then selected nests of all individuals who nested within the study area in at least two, not necessarily consecutive, years. As an index of distance moved, we measured the distance between these nests, which we refer to as the inter-annual nest distance.

Smith's Longspurs breed in neighborhoods rather than territories, therefore, we were also interested in determining neighborhood size. We developed an index of neighborhood size using the intra-annual nest distance of all males associated with multiple nests during the same breeding season (representing a conservative estimate of area). We then compared the neighborhood size index with inter-annual nest distances; individuals were considered to have dispersed to a new neighborhood if their inter-annual nest distance exceeded the estimated mean neighborhood size + SE.

To determine if adult Smith's Longspurs exhibit even-sex dispersal, we compared mean inter-annual nest distance of males and females using a two-tailed *t*-test (adjusted for unequal variance; $\alpha = 0.05$) in program R 3.0 (R Core Team 2013). We combined data from both study areas because they were close enough (27 km) that dispersal behavior would not likely differ. To avoid bias associated with pseudoreplication of either (1) individuals that returned to nest more than two years, or (2) males that attended multiple nests in one year, we randomly selected one inter-annual nest distance from each of these birds, and used only that value in our analysis.

To examine natal philopatry, we calculated the distance from each natal location to its subsequent nest location as a breeding adult. Because we expected to find that natal dispersal would be greater than adult dispersal, we compared this distance to the inter-annual nest distances of adults using a one-tailed *t*-test. Values are presented as ranges and means \pm SE.

1.3.5 Apparent annual survival and detection probability

Because dispersal and survival may be confounded, we estimated apparent annual survival (ϕ) corrected for encounter probability (p) of adult and HY Smith's Longspurs using Cormack-Jolly-Seber mark-recapture models in program MARK (V 8.0; White and Burnham 1999). We

constructed a model set consisting of 21 possible models (Table 1.1). Because of relatively small sample sizes for juvenile and Slope Mountain birds, we separated our dataset into six groups: female and male adults and HY captured at Atigun Gorge and Slope Mountain. This structure allowed us to test for age, sex, and study area effects separately, as well as their interactions. However, for models with a time effect, we kept Slope Mountain adults and HY groups constant or grouped them with Atigun Gorge data. Furthermore, because we were unable to sex HY birds, we only examined sex effects within adult groups. We expected ϕ and p to differ between adult and HY birds, thus we included age in every model. We also tested whether survival probability differed after the first year of life (designated as “2a” in models). Because resighting efforts were not as vigorous during some years (2008 and 2010), we modeled differences in p depending on “high” or “low” resighting efforts (designated as “effort” in models). We recognized that this known source of variation could cause unwarranted support for models with a year effect in survival, so we included effort in nearly all detection models. Lastly, we tested for a year effect as well as for a trend in time in adult survival.

We examined the most parameterized (global) model for goodness of fit using the median \hat{c} ($\hat{c} = 2.5$) approach ($n = 30$ replications). Moderate amounts of overdispersion are common in these models, and global models with a \hat{c} of 1–3 are considered to fit the data (Lebreton et al. 1992). We used quasi-Akaike’s Information Criterion, adjusted for small sample sizes (QAICc) to assess model fit. The model with the lowest Δ QAICc value was selected as the best model, although it was assumed that models with Δ QAICc < 2 (Burnham and Anderson 1998) were equally parsimonious. Models within two units of the best model that differed only by one parameter were not considered to be supported (Arnold 2010). We used weighted model

averaging to make inferences of ϕ and p from the entire model set since more than one of our models had a ΔQAICc value <2 .

1.4 Results

1.4.1 Return rates

We banded a total of 674 birds (243 adult and 431 juvenile) over the seven years of our study. Return rates of individuals in any subsequent breeding season were lower for females (37%; $n = 52$) than males (53%; $n = 54$). Only 4% of HY birds were resighted within the local population as adults during subsequent years. No bird banded in one study area was ever resighted in the other study area. The oldest documented female was ≥ 7 years old, and the oldest recorded male was ≥ 6 years old.

1.4.2 Adult nest-site fidelity

Of the returning birds, there were 34 instances (24 female and 10 male) where the same individual's nest location was documented in multiple, but not always consecutive, years (range: 2–4 yr; Table 1.2).

Most returning adults nested within the same breeding neighborhood as in a previous season. We derived an index of mean neighborhood size (536 ± 100 m) from the intra-annual nest distances of ten males that attended multiple nests during the same summer. Only 4 (17%) individuals (all females) returned to breed in locations outside of this proxy neighborhood size; their mean return nest distance was 1444 ± 200 m.

The mean inter-annual nest distance of females was slightly farther than for males (Table 1.2); but the difference was not significant (two-tailed $t_{30.15} = 0.57$, $P = 0.57$). Additionally, there

was considerably more variability in dispersal distance of females than males (Table 1.2).

Despite high site fidelity in both male and female Smith's Longspurs, we only observed one instance of mate fidelity. There were two cases of male associations; these birds attended the same nest in one year, and were associated with each other again during following years.

1.4.3 Natal philopatry

Nineteen HY Smith's Longspurs were resighted during subsequent years as either second year (SY) or after-second-year (ASY) birds. We were able to locate 6 (3 female, 3 male) of these returning birds' nests. Mean natal dispersal distance (1674 ± 500 m) was significantly greater than adult dispersal (one-tailed $t_{5,25} = 3.01$, $P = 0.01$; Table 1.2). There was only one instance where a male returned to breed within his natal neighborhood.

1.4.4 Apparent annual survival and detection probability

Model selection based on QAICc indicated the best-fit model was where survival differed by sex and age but was constant over time, and encounter probabilities differed between age and high and low search effort years ($\phi_{sex*age}$, $P_{effort*age}$, Table 1.1). Apparent survival rate of females (0.50 ± 0.05) was lower than males (0.64 ± 0.04) and encounter probabilities during high effort years was higher (0.80 ± 0.06) than during low effort years (0.56 ± 0.08). Survival rate (0.41 ± 0.10) and encounter probability (0.13 ± 0.05) for HY returning as adults were lower than for adults.

Five additional candidate models differed in Δ QAICc values by <2 (Table 1.1). However, three of these differed from the best model by only one parameter and thus were not considered to be supported (Arnold 2010). When we modeled the effect of sex on survival at the two study

areas separately, adult survival rates were more similar between the sexes (females: 0.57 ± 0.05 ; males: 0.62 ± 0.05) at Atigun Gorge than at Slope Mountain (females: 0.39 ± 0.09 ; males: 0.71 ± 0.08). However, sample sizes and time spent at Slope Mountain were considerably lower than for Atigun Gorge; thus, model-averaged estimates that include Atigun Gorge may be more realistic. From the model-averaged estimates, the mean + SE estimates of male and female survival overlapped at Atigun Gorge, while at Slope Mountain the SE did not overlap and there was an ~11% difference between male and female survival (Table 1.3).

1.5 Discussion

Contrary to the female-biased dispersal pattern found in most adult passerines, we observed no gender bias in dispersal of adult Smith's Longspurs. Equal dispersal between sexes has also been found in the promiscuous Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*); however, DiQuinzio et al. (2001) attribute this pattern to habitat quality and not breeding strategy. In polygynandrous birds, even-sexed adult dispersal has not, to our knowledge, been investigated or observed. However, even-sexed dispersal has been associated with this breeding strategy in the collared pika (*Ochotona collaris*), where resource competition is equal between the sexes, suggesting the costs and benefits of dispersal are the same (Zgurski and Hik 2012).

We propose that an equal cost/benefit scenario may also explain why both sexes of adult Smith's Longspurs had high and equal site fidelity. Each neighborhood contains multiple available males, and there may be no benefit for female Smith's Longspurs to move to unfamiliar areas. Monogamous systems, by contrast, show relatively greater female dispersal following failed breeding attempts (Dubois and Cézilly 2002). Dispersal costs to more distant, new areas are outweighed by the benefit of finding a new, potentially better mate, while avoiding the old

mate (Dubois and Cézilly 2002, Beheler et al. 2003, Sedgwick 2004). This pattern was not readily apparent in our study because only one of the four females that dispersed outside her previous breeding neighborhood had an unsuccessful breeding attempt the previous year. Furthermore, we only documented one case of mate fidelity, suggesting that even within the same neighborhood there is low occurrence of a female re-mating with a male with whom she previously had a failed nest. However, because so few adult birds dispersed to new areas and apparent nest success was generally high (77%; H. R. Craig personal observation), more observations are needed to verify these findings.

An alternative explanation for the patterns we observed in Smith's Longspurs is that fitness of the neighborhood, rather than the individual, favors similarity in dispersal distances between the sexes. In this scenario, breeding success is not driven by which specific male a female chooses, but rather the quality of habitat and collective group of males making up her neighborhood. Female dispersal to a higher quality neighborhood could be beneficial following an unsuccessful nesting attempt. The variability seen in female dispersal distances may also be a consequence of small sample size; further study should identify if, with larger sample size, variability may be related to neighborhood quality.

Although adult Smith's Longspurs rarely returned to nest outside their previous breeding neighborhood, adults that were banded as HY dispersed significantly greater distances from their natal locations. If dispersal facilitates avoidance of inbreeding, we would expect natal dispersal from a breeding neighborhood to be farther than for dispersal from a much smaller breeding territory. For example, in a comparison of four non-cooperative breeding passerines, median dispersal distances were at least the width of four territories (Zack 1990). We observed only one

out of six instances of an adult returning to breed within its natal neighborhood, and average natal dispersal distance was approximately three times larger than estimated neighborhood size.

Low natal philopatry is regularly found in most passerines (Greenwood and Harvey 1982, Weatherhead and Forbes 1994), as is high juvenile and first-year mortality (Drilling and Thompson 1988). As a result, determining true dispersal and survival can be difficult (Koenig et al. 1996). One of the limitations of this study is that we rarely searched for banded birds outside the study area boundaries and may have missed returning birds if they moved long distances. However, our estimates of first-year survival were consistently high (41% at Atigun Gorge, and 32% at Slope Mountain), even with low return rates (4%) of HY birds. Low encounter probability (0.13) could indicate that SY birds breed in areas outside their natal neighborhood for their first breeding attempt before returning to breed closer to their natal area as ASY birds. We found one ASY male during his second breeding season (banded as a nestling) that had a different song variation than other birds within the neighborhood. Because song dialects are known to vary significantly between distant neighborhoods (Briskie 1999), this male likely spent his SY breeding season outside our study area. SY birds may also occupy less optimal habitat as young breeders. Considering that we only searched for nests within our study areas, which were chosen because they contained optimal Smith's Longspur habitat, we may have missed SY birds that actually survived but were not able to obtain a high-quality breeding site. Regardless, the survival rates we observed were slightly higher than expected for SY passerines; there is a largely untested assumption that first-year survival is approximately half that of adult survival (Temple and Cary 1988, Kershner et al. 2004). The high first-year survival rate we observed could be a product of neighborhood dynamics. Once young Smith's Longspurs leave the nest, it is common for groups of adults and their associated fledglings to join together (Jehl, 1968),

which could enhance survival while still on the breeding grounds. However, first year survival also includes successful migration to and from wintering areas; unfortunately information is not available on post-breeding season movements of HY/SY birds.

A common problem in demographic studies is that dispersal and survival are confounded. With finite study boundaries, it is nearly impossible to be sure that long-distance dispersal has not taken place. Methods have been developed to better estimate true survival and dispersal by combining distances dispersed with Cormack-Jolly-Seber models (Sandercock 2006, Schaub and Royle 2013), but because of the high breeding site fidelity (only 4 of 34 adults were observed dispersing outside their previous neighborhood) we did not use these techniques. Furthermore, we did not observe any birds crossing from one study area to the other, and in the rare event that we searched the surrounding areas for banded birds, none were found. Atigun Gorge is almost completely contained within geographic barriers, thus there was little suitable habitat surrounding it (Cooper et al. 2008); additionally, Smith's Longspurs are patchily distributed throughout the Brooks Range (Wild et al. 2014). As a result, few neighborhoods likely existed in close proximity to the study area. Finally, because Smith's Longspurs have short lifespans, there are few opportunities for long distance dispersal following the first year of life. Considering short life expectancy, geographic constraints of our study area, and the dispersal distances we observed, we believe that our estimates of survival and dispersal for adult birds are fairly accurate.

Few other studies exist on survival rates of arctic-breeding passerines. Briskie (2009) conducted a small-scale study of Smith's Longspurs in eastern Canada and reported return rates that were slightly higher than what we observed. Survival rates for the sympatric Lapland Longspur (*C. lapponicus*) in Barrow, Alaska were lower (females: 45.4%; males: 42.9%) than

what we found (Custer and Pitelka 1977). However, these studies based survival estimates on cumulative returns and not Cormack-Jolly models. Thus, the rates reported by Custer and Pitelka were likely lower than true survival. In general, at high latitudes there is a tradeoff between reproductive success and adult survival; nesting success is generally higher and adult survival is lower than at lower latitudes (Ricklefs and Wikelski 2002). Furthermore, some studies have found that because Arctic birds must travel such great distances between seasons, individuals that do not acquire adequate body stores prior to migration have reduced survival (Guy Morrison et al. 2007). However, Smith's Longspurs migrate relatively shorter distances than many other arctic breeders (Bairlein et al. 2012) and thus may have lower energetic demands.

We also expected to find that the unique energetic demands on male Smith's Longspurs during the breeding season would result in lower annual survival than females. Other studies have shown that survival may be negatively associated with high testosterone (Reed et al. 2006), as well as extreme levels of corticosterone, an indicator of stress (Brown et al. 2005). Because male Smith's Longspurs have enlarged reproductive organs with extremely high sperm production and thus likely increased testosterone levels (Briskie 1992, 1993), we expected to find reduced annual survival rates for males. In addition, during the early breeding season males have the highest reported corticosterone levels of any arctic passerine (Meddle et al. 2003). However, once males become invested in parental care there is a sharp drop in corticosterone level, despite this being the most energetically demanding period of the breeding season. Although rare, we have also documented males incubating eggs (H. R. Craig, personal observations). Later in the breeding season, males brood nestlings while simultaneously molting their feathers (Meddle et al. 2003). Despite these high energetic demands, and contrary to our original prediction, we found that male Smith's Longspurs had slightly higher survival rates than

females. We associate male survival with their ability to attenuate response to stress hormones (Meddle et al. 2003). Perhaps the ability to handle these stressful conditions provides male Smith's Longspurs with a survival advantage. Although stress modulation is a common trait among arctic birds (Hau et al. 2010), that breed despite the short erratic summer season (Astheimer et al. 1995, Wingfield and Hunt 2002), the relationship between stress modulation and survival has seldom been tested (Breuner et al. 2008). It also may be argued that despite high energetic demands on male Smith's Longspurs, the demands on females during egg laying and incubation is still greater, resulting in slightly lower survival rates than males.

Although most studies on predation risk of ground-nesting birds focus on egg and chick depredation (McKinnon et al. 2010), in some species incubating females are also at a greater risk of predation (Magnhagen 1991). However, we found little evidence of mortality on either sex during the breeding season in Alaska. Consequently, we suggest that the lower female survival rates we observed are either a product of high energetic demands during egg production, or of mortality during the non-breeding season. However, a basic understanding of the impact of migration versus breeding on apparent survival of Arctic birds is lacking (McKinnon et al. 2010).

In summary, we provide the first comprehensive study to examine both dispersal strategy and survival rates of a polygynandrous passerine. Our findings suggest that, despite the ongoing debate on the relationship between breeding strategy and dispersal, the even-sexed dispersal found in Smith's Longspurs is a result of their polygynandrous breeding strategy, in particular the formation of breeding neighborhoods. Additionally, we found that long distance dispersal events occur primarily through HY movements, which could have important conservation implications if climate change forces substantial range shifts within Arctic bird populations (Sekercioglu et al. 2008). Finally, contrary to our hypothesis, we found that despite the

presumably higher energetic demands on males, survival rates of males were slightly higher than females. Here we provide the first glimpse at demographic patterns of a polygynandrous passerine, however, more long-term studies are needed to identify if these dispersal and survival patterns exist in other Arctic or polygynandrous passerines. Future work on Smith's Longspurs should identify why survival rates differed between the sexes, and causes of mortality throughout their annual cycle.

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1.7 Literature Cited

- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178.
- Astheimer, L., W. Buttemer, and J. Wingfield (1995). Seasonal and acute changes in adrenocortical responsiveness in an Arctic-breeding bird. *Hormones and Behavior* 29:442–457.
- Bairlein, F., D. R. Norris, R. Nagel, M. Bulte, C. C. Voigt, J. W. Fox, D. J. Hussell, and H. Schmaljohann (2012). Cross-hemisphere migration of a 25 g songbird. *Biology Letters* 2012:505–507.
- Baker, M., N. Nur, and G. R. Geupel (1995). Correcting biased estimates of dispersal and survival due to limited study area: theory and an application using Wren Tits. *The Condor* 97:663–674.
- Beheler, A. S., O. E. Rhodes, Jr., and Harmon P. Weeks, Jr. (2003). Breeding site and mate fidelity in Eastern Phoebes (*Sayornis phoebe*) in Indiana. *The Auk* 120:990–999.
- Beletsky, L. D., and H. O. Gordon (1991). Effects of breeding experience and familiarity on site fidelity in female Red-Winged Blackbirds. *Ecology* 72:787–796.
- Breuner, C. W., S. H. Patterson, and T. P. Hahn (2008). In search of relationships between the acute adrenocortical response and fitness. *General and Comparative Endocrinology* 157:288–295.
- Briskie, J. V. (1992). Copulation patterns and sperm competition in the polygynandrous Smith's Longspur. *The Auk* 109:563–575.

- Briskie, J. V. (1993). Anatomical adaptations to sperm competition in Smith's Longspurs and other polygynandrous passerines. *The Auk* 110:875–888.
- Briskie, J. V. (1999). Song variation and the structure of local song dialects in the polygynandrous Smith's longspur. *Canadian Journal of Zoology* 77:1587–1594.
- Briskie, J. V. (2009). Smith's Longspur (*Calcarius pictus*). In *Birds of North America Online*. Ithaca, New York. <http://bna.birds.cornell.edu/BNA>.
- Briskie, J. V., R. Montgomerie, T. Pöldmaa, and P. T. Boag (1998). Paternity and paternal care in the polygynandrous Smith's Longspur. *Behavioral Ecology & Sociobiology* 43:181–190.
- Brown, C. R., M. B. Brown, S. A. Raouf, L. C. Smith, and J. C. Wingfield (2005). Effects of endogenous steroid hormone levels on annual survival in Cliff Swallows. *Ecology* 86:1034–1046.
- Brown, J. H., and A. Kodric-Brown (1977). Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445–449.
- Burnham, K. P., and D. R. Anderson (1998). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York, USA.
- Clarke, A. L., B.-E. Sæther, and E. Røskaft (1997). Sex biases in avian dispersal: a reappraisal. *Oikos* 79:429–438.
- Cline, M. H., A. M. Strong, T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes (2013). Correlates and consequences of breeding dispersal in a migratory songbird. *The Auk* 130:742–752.
- Comins, H. N., W. D. Hamilton, and R. M. May (1980). Evolutionarily stable dispersal strategies. *Journal of Theoretical Biology* 82:205–230.
- Cooper, C. B., S. J. Daniels, and J. R. Walters (2008). Can we improve estimates of juvenile dispersal distance and survival? *Ecology* 89:3349–3361.

- Custer, T. W., and F. A. Pitelka (1977). Demographic features of a Lapland Longspur population near Barrow, Alaska. *The Auk* 94:505–525.
- DiQuinzio, D. A., P. W. Paton, W. R. Eddleman, and J. Brawn (2001). Site fidelity, philopatry, and survival of promiscuous Saltmarsh Sharp-tailed Sparrows in Rhode Island. *The Auk* 118:888–899.
- Dobson, F. S. (2013). The enduring question of sex-biased dispersal: Paul J. Greenwood's (1980) seminal contribution. *Animal Behaviour* 85:299–304.
- Drilling, N. E., and C. F. Thompson (1988.) Natal and breeding dispersal in House Wrens (*Troglodytes aedon*). *The Auk* 105:480–491.
- Dubois, F., and F. Cézilly (2002). Breeding success and mate retention in birds: a meta-analysis. *Behavioral Ecology and Sociobiology* 52:357–364.
- Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- Greenwood, P. J., and P. H. Harvey (1982). The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1–21.
- Guy Morrison, R. I., N. C. Davidson, and J. R. Wilson (2007). Survival of the fattest: body stores on migration and survival in red knots *Calidris canutus islandica*. *Journal of Avian Biology* 38:479–487.
- Hau, M., R. E. Ricklefs, M. Wikelski, K. A. Lee, and J. D. Brawn (2010). Corticosterone, testosterone and life-history strategies of birds. *Proceedings of the Royal Society B* 277:3203–3212.
- Jehl, J. R. (1968). The breeding biology of Smith's Longspur. *Wilson Bulletin* 80:123–149.

- Kershner, E. L., J. W. Walk, and R. E. Warner (2004). Postfledging movements and survival of juvenile Eastern Meadowlarks (*Sturnella magna*) in Illinois. *The Auk* 121:1146–1154.
- Koenig, W. D., D. Van Vuren, and P. N. Hooge (1996). Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology & Evolution* 11:514–517.
- La Sorte, F., and W. Jetz (2010). Avian distributions under climate change: towards improved projections. *Journal of Experimental Biology* 213:862–869.
- Lack, D. (1968). *Ecological Adaptations For Breeding In Birds*. Methuen, London, UK.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Mabry, K. E., E. L. Shelley, K. E. Davis, D. T. Blumstein, and D. H. Van Vuren (2013). Social mating system and sex-biased dispersal in mammals and birds: a phylogenetic analysis. *PLoS ONE* 8:e57980.
- Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends in Ecology & Evolution* 6:183–186.
- McKinnon, L., P. Smith, E. Nol, J. Martin, F. Doyle, K. Abraham, H. Gilchrist, R. Morrison, and J. Bêty (2010). Lower predation risk for migratory birds at high latitudes. *Science* 327:326–327.
- Meddle, S. L., N. T. Owen-Ashley, M. I. Richardson, and J. C. Wingfield (2003). Modulation of the hypothalamic-pituitary-adrenal axis of an Arctic-breeding polygynandrous songbird, the Smith's Longspur (*Calcarius pictus*). *Proceedings of the Royal Society B: Biological Sciences* 270:1849.

- Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory (1998). Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67:518–536.
- Pyle, P. (1987). Identification guide to North American passerines: a compendium of information on identifying, ageing, and sexing passerines in the hand. Slate Creek Press Bolinas, California, USA.
- R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Reed, W. L., M. E. Clark, P. G. Parker, S. A. Raouf, N. Arguedas, D. S. Monk, E. Snajdr, J. Nolan, V., and E. D. Ketterson (2006). Physiological effects on demography: a long-term experimental study of testosterone's effects on fitness. *American Naturalist* 167:667–683.
- Ricklefs, R. E., and M. Wikelski (2002). The physiology/life-history nexus. *Trends in Ecology & Evolution* 17:462–468.
- Sandercock, B. K. (2006). Estimation of demographic parameters from live-encounter data: a summary review. *Journal of Wildlife Management* 70:1504–1520.
- Schaub, M., and J. A. Royle (2013). Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models. *Methods in Ecology and Evolution* 5:1316–1326.
- Schloss, C. A., T. A. Nuñez, and J. J. Lawler (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences* 109:8606–8611.
- Seavy, N. E., K. E. Dybala, and M. A. Snyder (2008). Climate models and ornithology. *The Auk* 125:1–10.
- Sedgwick, J. A. (2004). Site fidelity, territory fidelity, and natal philopatry in Willow Flycatchers (*Empidonax traillii*). *The Auk* 121:1103–1121.

- 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.
- Stenzel, L. E., G. W. Page, J. C. Warriner, J. S. Warriner, D. E. George, C. R. Eyster, B. A. Ramer, K. K. Neuman, and B. K. Sandercock (2007). Survival and natal dispersal of juvenile Snowy Plovers (*Charadrius alexandrinus*) in central coastal California. *The Auk* 124:1023–1036.
- Sutherland, G. D., A. S. Harestad, K. Price, and K. P. Lertzman (2000). Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* 4:16.
- Temple, S. A., and J. R. Cary (1988). Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* 2:340–347.
- Weatherhead, P. J., and M. R. L. Forbes (1994). Natal philopatry in passerine birds: genetic or ecological influences? *Behavioral Ecology* 5:426–433.
- Wheelwright, N. T., and R. A. Mauck (1998). Philopatry, natal dispersal, and inbreeding avoidance in an island population of Savannah Sparrows. *Ecology* 79:755–767.
- 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 (2014). Breeding habitat associations and predicted distribution of an obligate tundra-breeding bird, Smith's Longspur. *The Condor: Ornithological Applications* 117:3–17.
- Wingfield, J. C., and K. E. Hunt (2002). Arctic spring: hormone–behavior interactions in a severe environment. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* 132:275–286.

Zack, S. (1990). Coupling delayed breeding with short-distance dispersal in cooperatively breeding birds. *Ethology* 86:265–286.

Zgurski, J. M., and D. S. Hik (2012). Polygynandry and even-sexed dispersal in a population of collared pikas (*Ochotona collaris*). *Animal Behaviour* 83:1075–1082.

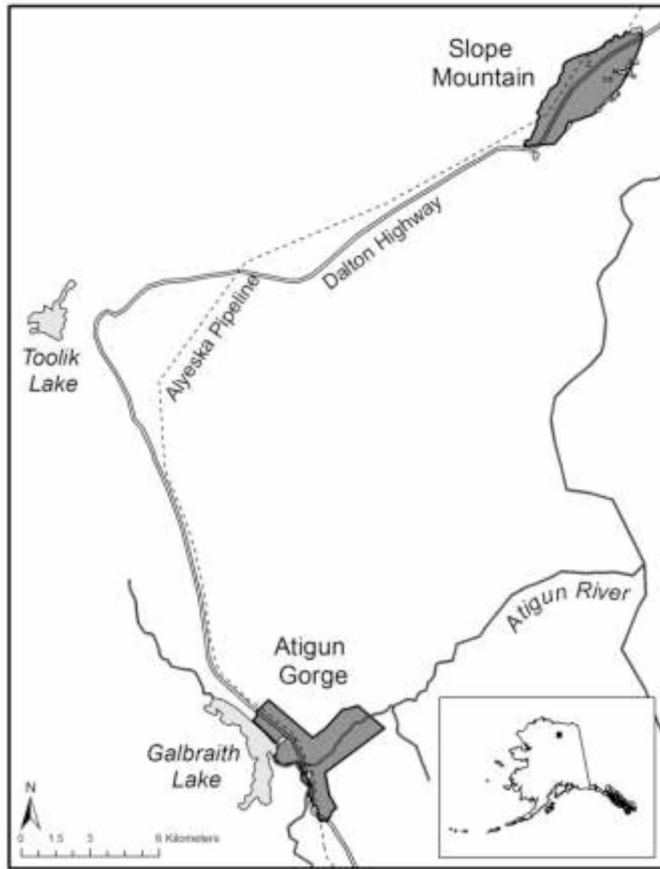


Figure 1.1. Study areas (Slope Mountain and Atigun Gorge) for Smith's Longspurs breeding in the foothills of the Brooks Range, northern Alaska, 2007–2013.

Table 1.1. Cormack-Jolly-Seber survival (ϕ) and recapture (p) models generated to fit Smith’s Longspur resight data. Bolded models are considered supported. K = number of parameters, “effort” = difference in resighting efforts during some years, “age” = difference between HY and adults, “2a” = difference in survival between HY and second year birds.

Model	Δ QAICc	QAICc weights	Model likelihood	K
^a $\phi_{\text{sex*age}} p_{\text{effort*age}}$	0.00	0.18	1.00	6
$\phi_{\text{study area*sex*age}} p_{\text{effort*age}}$	0.52	0.14	0.77	9
$\phi_{\text{age}} p_{\text{effort*age}}$	0.58	0.14	0.75	5
$\phi_{\text{study area*age}} p_{\text{effort*age}}$	1.21	0.10	0.55	7
$\phi_{\text{2a*age}} p_{\text{effort*age}}$	1.54	0.08	0.46	6
$\phi_{\text{Trend*sex*age}} p_{\text{effort*age}}$	1.80	0.07	0.41	8
$\phi_{\text{Trend*age}} p_{\text{effort*age}}$	2.49	0.05	0.29	7
$\phi_{\text{sex*age}} p_{\text{sex*age}}$	2.50	0.05	0.29	6
$\phi_{\text{sex*age}} p_{\text{sex*effort*age}}$	2.52	0.05	0.28	8
$\phi_{\text{study area*2a*age}} p_{\text{effort*age}}$	2.93	0.04	0.23	8
$\phi_{\text{sex*2a*age}} p_{\text{sex*effort*age}}$	3.49	0.03	0.18	9
$\phi_{\text{study area*2a*age}} p_{\text{sex*effort*age}}$	3.81	0.03	0.15	10
$\phi_{\text{study area*sex*2a*age}} p_{\text{effort*sex*age}}$	5.34	0.01	0.07	12
$\phi_{\text{year*age}} p_{\text{effort*age}}$	6.49	0.01	0.04	10
$\phi_{\text{Trend*sex* study area*2a*age}} p_{\text{year*sex*age}}$	6.88	0.01	0.03	13
$\phi_{\text{year+sex*age}} p_{\text{effort*age}}$	8.68	0.00	0.01	12
$\phi_{\text{year+sex*study area*2a*age}} p_{\text{effort*sex*age}}$	13.06	0.00	0.00	17

Table 1.1 continued.

$\phi_{\text{year*sex*age}} P_{\text{effort*age}}$	13.23	0.00	0.00	16
$\phi_{\text{year*sex*study area*2a*age}} P_{\text{effort*sex*age}}$	19.34	0.00	0.00	21
^b $\phi_{\text{year*sex*age*study area*2a}} P_{\text{year*sex*study area*age}}$	27.31	0.00	0.00	27
^c $\phi_{\text{constant}} P_{\text{constant}}$	70.13	0.00	0.00	2

^a QAICc value of best model was 340.89.

^{b,c} The global and null model, respectively.

* Models that include “sex*age” only examine sex effects within adult groups because the sex of HY birds was unknown.

Table 1.2. Distance (m) between nests of adult Smith’s Longspurs returning to breed in multiple years subsequent to banding at Atigun Gorge and Slope Mountain, Alaska, 2007–2013.

No. years returned	Distance (m)			
	<i>N</i>	Mean ± SE	Min	Max
Females				
4	3	406 ± 100	9	1540
3	3	169 ± 50	40	414
2	18	322 ± 100	20	1913
Total Females	24	325 ± 70	9	1913
Males				
2	10	240 ± 40	52	543
Grand Total	34	301 ± 70	9	1913

Table 1.3. Annual survival estimates \pm SE (95% CI in parentheses) for adult Smith's Longspurs breeding at Atigun Gorge and Slope Mountain, calculated using program MARK by averaging the model weights of all models in the candidate set.

Year	Female		Male	
Atigun Gorge				
2008	0.58 \pm 0.10	(0.37–0.76)	0.63 \pm 0.09	(0.45–0.78)
2009	0.57 \pm 0.09	(0.39–0.74)	0.62 \pm 0.08	(0.46–0.76)
2010	0.56 \pm 0.09	(0.39–0.72)	0.62 \pm 0.08	(0.47–0.75)
2011	0.56 \pm 0.08	(0.39–0.71)	0.61 \pm 0.07	(0.46–0.74)
2012	0.55 \pm 0.09	(0.38–0.70)	0.61 \pm 0.07	(0.46–0.74)
2013	0.54 \pm 0.09	(0.36–0.71)	0.60 \pm 0.08	(0.44–0.75)
Slope Mountain				
2012	0.51 \pm 0.11	(0.30–0.70)	0.61 \pm 0.10	(0.40–0.79)
2013	0.50 \pm 0.11	(0.29–0.70)	0.61 \pm 0.11	(0.39–0.79)

Chapter 2. Nest-site selection and reproductive success of an arctic-breeding passerine.¹

2.1 Abstract

Despite changes in shrub cover and climate regimes in the Arctic, little is known about breeding requirements of many passerines tied to these northern regions, including those species that are tundra obligates. We investigated breeding biology and nest habitat characteristics of the polygynandrous Smith's Longspur (*Calcarius pictus*) at two study areas in Alaska's Brooks Range. First, we characterized nesting habitat and analyzed nest-site selection for a subset of nests ($n = 86$) in comparison with paired random points within the nesting area. Second, we estimated daily survival rate of 257 nests found in 2007–2013 with respect to habitat characteristics and weather variables. Nests were typically found in open low shrub tundra, and were never found among tall shrubs (mean shrub height 26.8 ± 6.7 cm). We observed weak nest-site selection patterns, with the only predictor of nest location being variation in willow height, which was slightly lower at nests than at random points. Considering this similarity between nest-sites and paired random points, along with Smith's Longspurs social mating system, we suggest that habitat selection may occur at the neighborhood scale and not the nest-site scale. Models that included either the numbers of days below freezing within a season, or season date were the best approximating models we examined, and there was little support for models containing habitat variables. Despite this relationship, daily survival rates were relatively high (0.974–0.988) in all years. This is the first study to investigate the breeding biology of Smith's Longspurs at the western extent of their range, and sheds light on the relationship between demographic patterns and mating systems.

¹ Craig, H.R., S. Kendall, and A. Powell (2015). Nest-site selection and reproductive success of an arctic-breeding passerine. Prepared for submission to *The Condor: Ornithological Applications*.

2.2 Introduction

The Arctic is incredibly productive during the short summer season, with ~135 species of birds breeding there annually (Johnson and Herter 1990). However, biodiversity in this region may be threatened by climate change, which is occurring more rapidly at northern latitudes than 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 within 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 distribution 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 in order 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 declines (Tape et al. 2006; Seavy et al. 2008). Furthermore, habitat specialists are more likely to be negatively impacted by environmental changes than generalists (Colles et al. 2009). In northern Alaska, a recent study by Boelman et al. (2015) suggested that increasing shrub dominance will diminish the habitat quality of Lapland Longspurs (*Calcarius lapponicus*), which breed in open tundra regions. Although we cannot be certain how the predicted changes will impact other tundra birds,

understanding the linkages between species and habitat usage is key in predicting response to environmental change (Hausner et al. 2003).

Perhaps of greater concern for arctic birds than conversion of tundra to shrublands are the rapid climate shifts currently taking place at northern latitudes. With only a narrow window of opportunity for birds to optimize 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 of Lapland Longspurs suggested that delayed nest initiation due to inclement weather can cause nest failure later in the breeding season (Astheimer et al. 1995). Although warming trends could cause a mismatch in food availability in some species (Visser et al. 1998; Sekercioglu et al. 2008), others may benefit from increased temperature (e.g., from longer breeding season; Crick and Sparks 1999; Both and Visser 2005). For example, Snow Buntings (*Plectrophenax nivalis*) breeding in the High Arctic had 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 (*C. 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. 2003; U.S. Fish and Wildlife Service 2008; Zack and Liebezeit 2009). In Alaska, they breed in and are closely tied to open low shrub habitats in the Brooks Range (Wild et al. 2014), 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 within the Brooks Range ecoregion. First, we aimed to describe nest-site characteristics and examine how habitat features influence nest-

site selection. Second, we investigated the relationship between nest-site characteristics and weather variables on nest survival. Specifically, we expected that nest-sites would be characterized by fewer and shorter shrubs (Jehl 1968; Wild et al. 2014), but greater microhabitat structural variation (potentially hiding nests from predators), than random sites within the nesting area. Because vegetation and microtopographic features may help camouflage nests from predators, we predicted that nest survival would be influenced by habitat selection patterns (Harrison et al. 2011; Murray and Best 2014) and nest visibility. We also expected that rates of nest survival would be affected by extreme temperatures, particularly those below freezing and above 21°C (Jehl and Hussell 1966; Carey 2002, Hoset et al 2004).

2.3 Methods

2.3.1 Study area

During six years we studied nest-site selection and reproductive success of Smith's Longspurs breeding at two locations in the Brooks Range of northern Alaska. Atigun Gorge, the more southern study area, is located in a mountain valley (N 68.27°, W 149.21°; elevation 846 m; 2007–2013, excluding 2010), while Slope Mountain is 27 km north in rolling foothills (N 68.41°, W 149.40°; elevation 655 m; 2011–2013). Both study areas were ~1060 ha, intersected by the Dalton Highway and Trans-Alaska Pipeline, and characterized by treeless tundra habitat. Study areas were chosen based on accessibility and presence of known breeding populations of Smith's Longspurs.

Within the Brooks Range ecoregion, Smith's Longspurs tend to breed in open low-shrub areas of broad river valleys (Atigun Gorge) or in the rolling foothills (Slope Mountain; Wild et al. 2014). The most common vegetation types within these areas are willow (*Salix* spp.),

ericaceous shrubs (*Rhododendron lapponicum*, *Vaccinium* spp., *Arctostaphylos* spp.), birch (*Betula* spp.), *Dryas integrifolia*, and sedges (*Eriophorum* spp. and *Carex* spp.). Mosses and lichen 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.

2.3.2 Nest searching and monitoring

We searched for nests nearly every day (6–12 hr day⁻¹) from early June to mid-July (a lesser effort was made during 2007, as the focus was on locating Smith's Longspurs through surveys; Wild et al. 2014). Because Smith's Longspurs are patchily distributed across the landscape (Wild et al. 2014), 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 on either side of the nest, and a fluorescent popsicle stick, which was aligned with the plain markers, ~20 m distant on an obvious structure (e.g., hummock). This marking method allowed us to minimize time spent relocating nests. Furthermore, to reduce attracting predators, we followed new routes during each nest visit, making sure no dead-end paths were left. We monitored nests every 2–4 days until fledge 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) no visible sign of nest disturbance and fewer nestlings observed on consecutive nest visits when chicks were old enough to fledge. Nest attempts were considered successful if at least one nestling fledged. Evidence of predator disturbance/activity near nests was also recorded and considered during fate determination.

We used weather data to examine relationships between temperature and reproductive parameters. During 2011–2013 we used Onset HOBO Micro Station Data Loggers (H21-002) to record temperature every 30 min at each study area. During 2007-2010, we used daily maximum and minimum temperatures reported by Toolik Field Station (N 68.38°, W 149°36'), Institute of Arctic Biology, University of Alaska Fairbanks, which is located approximately halfway (23 km from Atigun Gorge, 24 km from Slope Mountain) between our two study areas.

2.3.3 *Habitat characteristics*

To determine characteristics that influence selection of nest-sites within tundra habitats, we measured microhabitat features at nests and paired random points. Habitat measurements were only taken during 2012 and usually two weeks after either fledge or nest failure. Random locations were selected 5 to 30 m from the nest, within the area we typically observed females defending, herein defined as "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 four 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 (graminoid, ericaceous shrubs, willow shrubs, birch shrubs, and tussocks/hummocks), and the presence or absence of dwarf willow, *Dryas*, moss, lichen, and leaf litter. We also recorded slope, aspect, elevation and specific habitat features associated with placement of each nest (e.g., nest placed on side or top of hummock, between tussocks, under shrub). For all measurements we report means \pm SD.

We assessed visibility at nest locations using a plastic disk with a grid of alternating black and white sections (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 in each of the four cardinal directions. Open nests scored higher (maximum = 80 sections observed) than nests that were well concealed (minimum = 0 sections observed).

2.3.4 Nest-site selection analysis

We used logistic regression to examine nest-site selection of Smith's Longspurs. Because we expected Smith's Longspurs to avoid tall vegetation, but select for areas with high variance in cover (thus hiding the nest from predators), we chose variables that were the most common features to provide structure on the landscape. We tested the importance of mean height and standard deviation of height (included as a proxy to examine heterogeneous cover) of willow and ericaceous shrubs, which were the two most common shrub communities at our study areas. We also included height and standard deviation of tussocks/hummocks because they also provide considerable structure in the treeless environment. To identify other potential patterns in nest-site selection, we also examined three nest characteristic variables: slope, aspect and study area (categorical).

Due to the patchy distribution of some vegetation types, not all habitat variables were present at every nest. To avoid bias in our data by recording a height/SD 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 to make sure they were not correlated. We developed a candidate set of 28 models including null and full models. We used Akaike's Information Criterion corrected for small sample sizes (AICc) to identify

models best fitting the data. The top model was confirmed using the Hosmer-Lemeshow goodness-of-fit test. We computed the odds-ratio by exponentiating the coefficient from the top logistic regression model. Data analysis was conducted using R 3.0 (R Core Team 2013) and the Resource Selection package.

2.3.5 Nest survival analysis

We used the nest-survival module in program MARK (White and Burnham 1999) to determine 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 (1 June–12 July), 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 interactions. We evaluated 85 individual covariates related to vegetation structure, nest visibility, and temperature.

We used three years of study area-specific temperature data to examine the influence of daily maximum and minimum temperature on DSR. Because temperatures commonly drop below freezing during the arctic summer and we assumed nests were susceptible to failure during these periods, we also included a model with the total number of days per season that temperatures were below freezing (designated as “freezing” in models). Additionally, because temperatures within our study areas rarely rose above 21°C degrees during the breeding season, we included a model with the total number of days per season $> 21^{\circ}\text{C}$ to represent warmer conditions.

Because willow was the only habitat variable found to be important for nest-site selection, we included the standard deviation of willow height + willow indicator (presence or absence) to test if nest-site selection influences nest survival. To further examine the influence of nest structure on survival, we included a nest visibility model.

We also included several models with nest stage effects. We were unable to model nest age because we could not accurately determine initiation date for nests that failed prior to hatch. However, we did model a trend in season date (designated as “season” in models). Considering the condensed Arctic summer with high breeding synchrony, we considered the “season” model to be an adequate proxy for nest age. We also examined whether there was a difference in survival during the egg incubation period versus the chick brooding period (designated as “period” in models).

We used Akaike’s Information Criterion corrected for small sample size (AICc) to evaluate model fit. The model with the lowest ΔAICc value was selected as the best model, although it was assumed that models with $\Delta\text{AICc} < 2$ were equally parsimonious.

2.4 Results

2.4.1 Phenology

We found that in the Brooks Range, Smith’s Longspurs typically arrive on the breeding grounds during the last week of May or the first week of June. Due to the condensed breeding season in the Arctic, nests were initiated almost immediately upon arrival or as soon as temperatures and snow conditions allowed (Figure 2.1). We located a total of 271 Smith’s Longspur nests during the six years of our study (2007–2013, no data from 2010). Across all years, the breeding season, from initiation to fledge, was short (30 May–12 July) and nests were

generally synchronous. There are only ~22 days between average initiation ($\bar{x} = 7$ June) and fledge ($\bar{x} = 28$ June) dates, and we did not document any re-nesting. Clutch size typically ranged from 1–5 eggs, except for one nest that contained 9 eggs ($\bar{x} = 3.7 \pm 0.9$). In the 9-egg nest, 6 chicks hatched and at least 4 fledged; the remaining 2 chicks were younger in age and their fate was unknown. This nest appeared to be attended by only one female.

2.4.2 Nest habitat characteristics

We found that Smith's Longspur nests were commonly located on the top (48%; $n = 41$) or side (24%; $n = 21$) of hummocks. Many nests also had clumps of graminoid (44%; $n = 38$) and shrubs (34%; $n = 29$) located directly over them. The most common shrub species associated with nests was willow, followed by ericaceous species (*Vaccinium uliginosum*, *Rhododendron* spp.), and dwarf birch. 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 (Table 2.1). Furthermore, low shrubs (1.7–20.8 cm) were present at 88% of nests and 91% of random points (Table 2.1).

2.4.3 Nest-site selection

We evaluated nest-site selection patterns at 86 Smith's Longspur nests relative to paired random points. Of 28 logistic regression models evaluated as predictors of Smith's Longspur nest-site selection, only one was supported (WillSD; $P = 0.008$, Table 2.2). This model, which accounted for 45% of AICc weight, suggests that where willow is present, nest-sites will have less variability in shrub cover (lower standard deviation of willow height) than random sites within the nest territory. If the standard deviation of willow height increased by 1 unit, the odds

of a nest being present decreased by 0.16-fold. We examined the model of willow variability for goodness-of-fit using the Hosmer-Lemeshow test and found no evidence that the model fit poorly ($\chi^2 = 5.74$, $P = 0.68$). The next three models only differed from the top model by one parameter, and made up 86% of the cumulative AICc weight.

2.4.4 Nest survival

We were able to determine the fate of 95% of the nests we located ($n = 257$; 157 at Atigun Gorge and 100 at Slope Mountain). At least one chick fledged from 77% ($n = 197$) of the nests. Of the failed nests, 53% ($n = 32$) were lost to predation. The most common nest predators we observed were arctic ground squirrels (*Spermophilus parryii*), red foxes (*Vulpes vulpes*), and Common Ravens (*Corvus corax*). Four nests were abandoned, two (both in the chick stage) failed immediately after a snow or hail storm, and the remaining 37% ($n = 22$) failed for unknown reasons. We suspect that some of the unknown-failure nests may have also succumbed to weather, but we only reported weather as the cause of nest failure if we could directly link it to a specific weather event (e.g., hail storm, unusually hot day). We did not record weather as the cause of failure when prolonged weather conditions (freezing temperatures, rainy periods) had the potential to weaken chicks and reduce adult feeding rates.

Daily survival rate was estimated from the 257 nests with known fates. The best-approximating model (AICc weight = 0.246) indicated an inverse relationship between DSR and the number of days per breeding season below freezing (Table 2.3). For example, DSR was lowest (0.97) during 2011, when 26% of days during the breeding season were below freezing. One other model, trend in season date, had ΔQAICc values < 2 (Table 2.3). In this model, DSR declined from the beginning (0.99) to the end (0.96) of the nesting season. Because multiple

models were supported, we used model-averaged coefficients to calculate daily survival estimates (Figure 2.2) (Burnham and Anderson 1998).

Although nest survival models including daily temperature were not supported, there appeared to be a relationship between temperature and both initiation date and synchrony among individuals (Figure 2.1). During 2013, snow and freezing temperatures in the early spring delayed nest initiation until 11 June. As a result, initiation, hatch, and fledge were highly synchronous. Despite a late spring, temperatures remained above freezing for the rest of the breeding season and DSR (0.99) was higher than any other year (Figure 2.1). In contrast, during 2011 there was an early and warm spring and the average initiation date was 4 June, but synchrony was lower than in other years. However, as mentioned previously, temperatures dropped below freezing throughout the breeding season and survival was low (Figure 2.1).

2.5 Discussion

To date there have been no studies on the breeding ecology of Smith's Longspurs in their western range. Compared to Smith's Longspurs breeding in Churchill, Manitoba, Canada (Jehl 1968; Briskie 2009), we observed similar clutch size (~4), incubation (~7 days) and nesting (~12 days) periods in Alaska. However, average nest initiation dates were considerably earlier in the Brooks Range (\bar{x} initiation date: Alaska = 7 June, Canada = 21 June). We also document similar nest-site characteristics to those reported in Canada. At both study areas, nests were found among dry sedge meadows and commonly placed at the base or on top of hummocks, protected by a dwarf shrub (*Rhododendron lapponicum.*, *Vaccinium* spp., *Dryas integrifolia* and *Salix* spp.) or overhanging sedge (Jehl 1968).

Based on the variables measured, we found only a weak preference in nest-site selection by Smith's Longspurs breeding in treeless tundra. The habitat variable that was the best predictor of nest location was the standard deviation of 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. Instead, we found that reproductive success was negatively associated with the number of days per season with freezing temperatures and season date.

Smith's Longspurs display a unique breeding system in which both sexes mate with up to three individuals during a given breeding season (Briskie 1992). These "neighborhoods" of interbreeding birds have loose territorial boundaries and exhibit strong social dynamics. Within the breeding area, Smith's Longspurs are generally tied to open low shrub habitat (Wild et al. 2014), and we found this relationship at the nest scale as well. Although we typically found nests under some low shrub or graminoid clump (Figure 2.3), no nests were ever found among tall shrubs; the tallest plants associated with nests averaged only 26.8 ± 6.7 cm (Table 2.2), 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 availability of preferred nesting habitat. Loss of open tundra types is also expected to impact 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). Breeding Lapland Longspurs are more widely distributed and they are more habitat generalists (Hussell and Montgomerie 2002) than Smith's Longspurs, thus we might expect predicted changes in tundra habitats to have a greater impact on Smith's Longspur populations. However, if suitable open

low shrub habitat advances northward onto the coastal plain, Smith's Longspur populations may be capable of northward expansion (Wild et al. 2014).

Although Smith's Longspurs appear to avoid breeding in areas with tall or dense shrubs (Wild et al. 2014), we found no relationship between nest-site selection and shrub height at the 1-m scale. In contrast, grassland-nesting Chestnut-collared Longspurs (*C. ornatus*) typically select territories in exposed areas with shorter vegetation than other local species. However, within these short and sparse vegetation patches, Chestnut-collared Longspurs select nests sites with taller and denser vegetation (Davis 2005). The only predictor of nest location that we observed in Smith's Longspurs was variability of willow height; which, although significantly lower at nest-sites than at random points, had such a small effect (0.16 increase in odds) that it may be of little biological significance. Shrub height within tundra regions is generally low (Table 2.2), so we would not expect large differences between nest-sites and random points. Other studies have shown that within tundra areas, nest-site selection may be related to microhabitat structural variation. For example, both micro-relief and variability of relief (surface roughness) positively influenced nest-site selection of Lapland Longspurs on the Arctic Coastal Plain, Alaska (Rodrigues 1994). In our study, selecting nest-sites with less variable shrub height could be a selection mechanism to reduce predation risk (Martin 1993). Uniform shrub height near the nest (with only a small shrub or other structure directly over the nest to hide it; Figure 2.3) could reduce visual obstructions, thus incubating females may be more vigilant and have a quicker escape from predators. Early detection seems to be important for Smith's Longspurs, as we observed that incubating females typically flushed quickly and quietly when disturbed without much of a distraction display. Predator dynamics could also help to explain why no other habitat variables were indicators of nest-site selection. In the Arctic, both avian and mammalian species

are common nest predators (Liebezeit and Zack 2008), yet they possess very different search techniques. Consequently, it may be difficult for birds to select for optimal nest-sites that encompass both of these predator strategies. Visual obstruction from above is important for hiding nests from aerial predators, while horizontal obstruction is necessary to hide from ground predators. Still, only 12% of Smith's Longspur nests were depredated, thus predator-driven habitat selection in this system may not be as important as for ground-nesting species in other regions (Martin and Roper 1988; Hatchwell et al. 1996).

Strong nest-site selection is often associated with the habitat patchiness found in forested or disturbed landscapes (Johnson and Temple 1990; Harrison et al. 2011; Murray and Best 2014), thus, we would not expect to find the same level of selection in tundra habitats that are comparatively homogenous (Figure 2.3). Furthermore, Smith's Longspurs are not likely habitat-limited in the Brooks Range ecosystem (Wild et al. 2014). Thus, if there is an abundance of available breeding habitat in a relatively pristine environment, habitat selection may not play an important role in Smith's Longspur nest placement. Instead, we suggest that Smith's Longspurs' polygynandrous mating behavior may be the driving factor in nest-site selection. Unlike monogamous breeders with distinct nesting territories, Smith's Longspurs typically nest in neighborhoods where social factors may influence nest-site selection. The benefit of such dynamics may encourage females to choose and build nests near one another. Nesting in close proximity may increase chances of soliciting copulations from multiple males and subsequently incurring additional care for offspring (Davies 1985). To our knowledge, there have been no studies of nest-site selection in other polygynandrous passerines.

Although the habitat variables we measured were not predictors of Smith's Longspur nest survival, there was a negative relationship between DSR and the number of days below freezing.

However, no other temperature models were supported. Considering that temperatures in the Arctic are expected to increase, the frequency of days below freezing during the summer will likely decrease, thus enhancing nest survival. However, some studies suggest that in addition to warming trends, summer storm intensity will increase (Hinzman et al. 2005), and erratic conditions are known to negatively impact breeding success of birds (Hendricks and Norment 1992; Jones et al. 2001; Stenseth et al. 2002; Dickey et al. 2008). We found that local weather had a strong relationship with timing and synchrony of breeding, as well as on reproductive success. Like other species such as the Great Tit (*Parus major*; Perrins and McCleery 1989), Smith's Longspurs seem to be able to "track" seasonal change and avoid initiating during harsh conditions (Figure 2.1). Because of this ability to delay initiation, extreme temperatures early in the season did not impact survival of Smith's Longspur nests. However, survival was influenced by freeze events later in the season, when young chicks were particularly susceptible to cold temperatures (Hendricks and Norment 1992) and decreased feeding rates by adults. We would expect that in addition to temperature, precipitation (which is extremely variable spatially in the Brooks Range) would also influence survival (Morrison and Bolger 2002), but unfortunately we did not record rainfall at our study areas. Inclement weather has been linked to reductions in chick growth and survival of other Arctic species such as the Curlew Sandpiper (*Calidris ferruginea*) in Siberia (Schekkerman et al. 1998). In Canada, the failure of 100% ($n = 18$) of Smith's Longspur nests was attributed to a four-day period of rain and cold temperatures (Jehl and Hussell 1966). Because harsh conditions are fairly common at northern latitudes, Arctic birds are fairly resilient. However, increased occurrence and severity of summer storms could add additional stress to breeding birds and over time result in population declines.

Mean apparent nest success was slightly higher in our study (77%, $n = 197$) than in eastern Canadian populations (66%, $n = 79$; Briskie 2009). Both Jehl (1968) and Briskie (2009) found that nest success in Canada was highly variable among years (33–90%); however, neither estimated DSR for Smith's Longspurs. In fact, few studies have identified factors that influence DSR of tundra-nesting passerines. In alpine-nesting Savannah Sparrows (*Passerculus sandwichensis*) in northern British Columbia, DSR varied from 0.85–0.98, with significant variation among years (Martin et al. 2009). Conversely, we observed low variability in survival among years (Figure 2.2), and DSR only changed ~0.1 unit from the lowest survival year (2011, 0.97–0.98) to the highest survival year (2013, 0.98–0.99). Although year was not an important covariate in our survival models, we did find that season date influenced DSR (Table 2.3). Considering the condensed and fairly synchronous breeding season, this is likely an indication that nests initiated later in the season were less successful than those initiated earlier, but unfortunately, we were unable to include initiation date in our models. We observed that older female Smith's Longspurs (based on banding data) were among the first to initiate nests each year. Previous breeding experience could provide them with an advantage with regard to reproductive success (Nol and Smith 1987), thus DSR might be a function of female age. Further study should examine nest survival in relation to female age. On the Arctic Coastal Plain, estimated DSR (ranging from ~0.94–0.97) of Lapland Longspur nests had a positive relationship with season date, which was attributed to an abundance of nest predators early in the season (Liebezeit et al. 2011). In comparison to Lapland Longspurs and Savannah Sparrows breeding in the north (Martin et al. 2009; Liebezeit et al. 2011), estimated DSR for Smith's Longspurs was consistently high. We attribute these high rates of reproductive success to the species' unique mating system; the increase in parental care from multiple males may offset potential negative

impacts from harsh environmental conditions in the Arctic. For example, in the polygynandrous Alpine Accentor (*Prunella collaris*), one of the main factors influencing reproductive success was the extent to which females secured additional male mates, thus incurring extra parental care (Nakamura 1998). Unfortunately, we did not quantify the number of males attending each nest, and thus cannot evaluate the effect of increased paternal care on reproductive success of Smith's Longspurs.

Despite evidence that DSR of Smith's Longspurs is related to the number of days each season below freezing, the relatively high and consistent nest success across years suggests that Smith's Longspurs are resilient to harsh and unexpected conditions. Furthermore, because habitat is not saturated and juveniles as well as a small proportion of females disperse (Chapter 1, Wild et al. 2014), Smith's Longspurs may be capable of shifting their distribution northward as their current breeding areas become shrubbier. However, we question whether Alaska's coastal plain will be suitable, considering that it is a water-dominated landscape and we rarely observed Smith's Longspurs nesting in areas with open water. Although increases in temperature could provide opportunity for re-nesting (Wormworth and Mallon 2006) and increased nesting success, the potential impacts of climate-related changes on breeding Smith's Longspurs remain unknown. Thus, it is essential that management agencies monitor Smith's Longspur populations as northern regions continue to change in response to climate change. Future study should also compare habitat within and outside neighborhoods to determine if nest-site selection is occurring at the landscape scale rather than at the nest-site scale. Social behaviors within neighborhoods may also influence nest survival, so studies should investigate a possible relationship between number of male nest attendants and DSR. This information will help us to better understand the impact of social mating strategy on breeding demographics.

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2.7 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). *Climate Change* 15:653–685.

Arctic Climate Impact Assessment (2004). *Impacts of a warming Arctic: Arctic Climate Impact Assessment*. Cambridge University Press. Cambridge, United Kingdom.

- Astheimer, L., W. Buttemer, and J. 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. (1992). Copulation patterns and sperm competition in the polygynandrous Smith's Longspur. *The Auk* 109:563–575.
- Briskie, J. V. (2009). Smith's Longspur (*Calcarius pictus*). In *Birds of North America Online*. Ithaca, New York. <http://bna.birds.cornell.edu/BNA>.
- Burnham, K. P., and D. R. Anderson (1998). *Model selection and inference: a practical information theoretic approach*. Springer–Verlag, New York.
- Carey, C. (2002). Incubation in extreme environments. *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.
- Crick, H. Q. P. (2004). The impact of climate change on birds. *Ibis* 146:48–56.

- Crick, H. Q. P., and T. H. Sparks (1999). Climate change related to egg-laying trends. *Nature* 399:423–423.
- Davies, N. B. (1985). Cooperation and conflict among Dunnocks (*Prunella modularis*) in a variable mating system. *Animal Behaviour* 33:628–648.
- Davis, S. K. (2005). Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *The Condor* 107:605–616.
- Davis, S. K., and S. G. Sealy (1998). Nesting biology of the Baird's Sparrow in southwestern Manitoba. *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., D. S. Dobkin, and D. Wheye (1988). *Birder's Handbook: A Field Guide To The Natural History Of North American Birds*. Touchstone, London and New York.
- Euskirchen, E. S., A. D. McGuire, F. S. Chapin, 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.
- 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* 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., N. Bettez, W. R. Bolton, F. S. Chapin, M. Dyurgerov, C. Fastie, B. Griffith, R. Hollister, A. Hope, H. Huntington, A. Jensen, G. Jia, T. Jorgenson, D. Kane, D. Klein, G. Kofinas, A. Lynch, A. Lloyd, A. D. McGuire, F. Nelson, W. Oechel, T. Osterkamp, C. Racine, V. Romanovsky, R. Stone, D. Stow, M. Sturm, C. Tweedie, G. Vourlitis, M. Walker, D. Walker, P. Webber, J. Welker, K. Winker, and K. Yoshikawa (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.
- Hussell, D. J. T., and R. D. Montgomerie (2002). Lapland Longspur (*Calcarius lapponicus*). In *Birds of North America Online*. Ithaca, New York. <http://bna.birds.cornell.edu/BNA>.
- Jehl, J. R. (1968). The breeding biology of Smith's Longspur. *Wilson Bulletin* 80:123–149.
- Jehl, J. R., 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, p. 22–43. In E. Gwinner [ed.], *Bird migration: physiology and ecophysiology*. Springer-Verlag, Berlin.
- Johnson, R. G., and S. A. Temple (1990). Nest predation and brood parasitism of tallgrass prairie birds. *Journal of Wildlife Management* 54:106–111.
- 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., G. 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.
- Liebezeit, J. R., and S. Zack (2008). Point counts underestimate the importance of Arctic Foxes as avian nest predators: evidence from remote video cameras in Arctic Alaskan oil fields. *Arctic* 61:153–161.
- 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. *American Naturalist* 141:897–913.
- 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. *Condor* 90:51–57.
- Morrison, S., and D. 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.
- Nol, E., and J. N. M. Smith (1987). Effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. *Journal of Animal Ecology* 56:301–313.
- Parmesan, C., and H. Galbraith (2004). Observed impacts of global climate change in the U.S. Pew Center on Global Climate Change. Arlington, Virginia.
- Perrins, C. M., and R. H. McCleery (1989). Laying dates and clutch size in the Great Tit. *Wilson Bulletin* 101:236–253.
- R Core Team (2013). 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. Demarest, E. H. Dunn, W. C. Hunter, and E. Iñigo-Elias (2003). Partners in Flight North American landbird conservation plan. Cornell Laboratory of Ornithology. Ithaca, New York.
- 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. 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* 25:1–10.
- 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.
- Sturm, M., C. Racine, and K. Tape (2001). Climate change: increasing shrub abundance in the Arctic. *Nature* 411:546–547.
- Tape, K. E. N., M. Sturm, and C. Racine (2006). The evidence for shrub expansion in northern Alaska and the pan-Arctic. *Global Change Biology* 12:686–702.
- U.S. Fish and Wildlife Service (2008). *Birds of Conservation Concern*, p 85. United States Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management. Arlington, Virginia. <http://www.fws.gov/migratorybirds>.
- Visser, M., A. J. Noordwijk, J. Tinbergen, and C. Lessells (1998). Warmer springs lead to mistimed reproduction in Great Tits (*Parus major*). *Proceedings of the Royal Society of London. Series B: Biological Sciences* 265:1867–1870.
- 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 (2014). Breeding habitat associations and predicted distribution of an obligate tundra-breeding bird, Smith's Longspur. *The Condor: Ornithological Applications* 117:3–17.
- 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. Wildlife Conservation Society. Portland, Oregon.

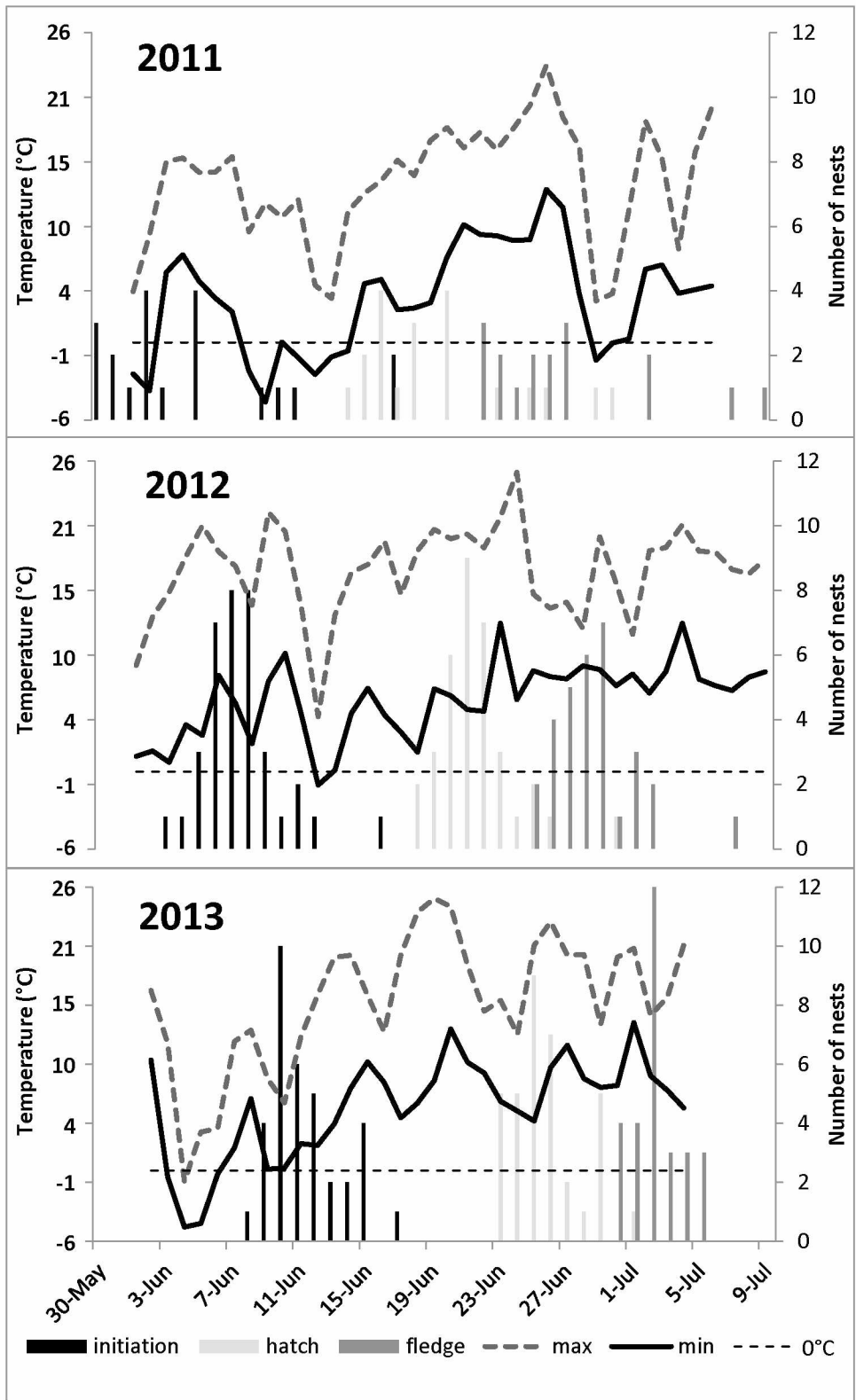


Figure 2.1. Daily maximum and minimum temperature compared to initiation, hatch, and fledge periods of Smith’s Longspurs nesting in the Brooks Range of Alaska, (2011–2013).

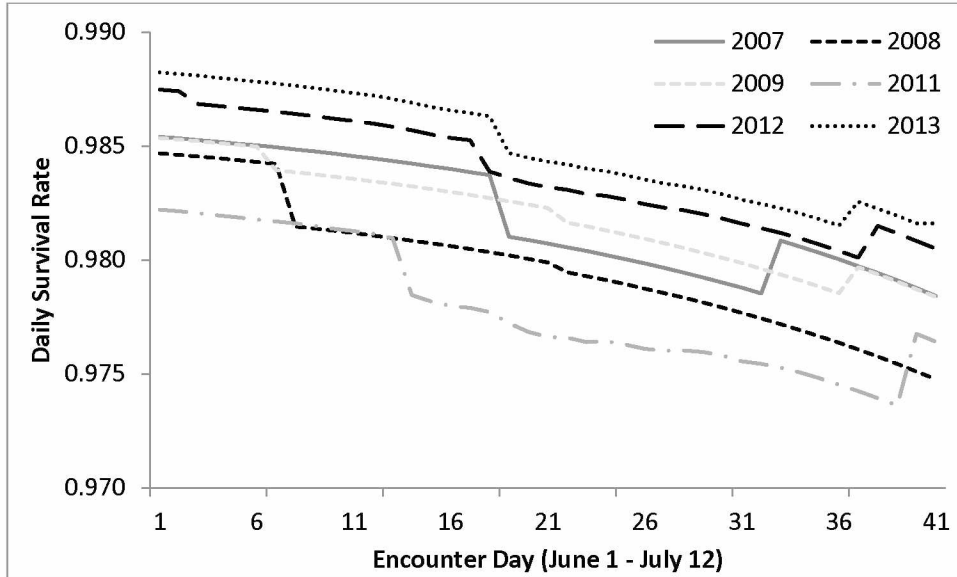


Figure 2.2. Model-averaged daily nest survival estimates for Smith's Longspurs breeding in the Brooks Range of Alaska (2007–2013). Shown here are data from Atigun Gorge only; Slope Mountain data were removed because survival estimates were very similar to those at the other study area.



Figure 2.3. Smith's Longspurs are found breeding in open low shrub tundra in the Brooks Range, Alaska (left). Nests are typically found in open areas with little variation in willow height and placed under a low shrub (most commonly willow), graminoid clump or on the side of a tussock or hummock (right).

Table 2.1. Comparison of habitat characteristics (percentage of sites with vegetation type, mean height (cm) \pm SD) at Smith’s Longspur nests ($n = 86$) and their paired random points within each territory. Because percent cover was overlapping, vegetation types could add up to $>100\%$. All measurements were taken within a 1-m radius of the nest or random point.

Vegetation type	% sites with vegetation type		Height \pm SD (cm)	
	Nest	Non-nest	Nest	Non-nest
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	66	65	4.3 \pm 2.8	4.1 \pm 1.8
All shrubs	88	91	7.3 \pm 4.2	7.8 \pm 4.8
Graminoid	99	99	12.6 \pm 8.4	11.5 \pm 3.9
Ground Structure	93	95	10.9 \pm 3.1	10.4 \pm 3.2
Moss	100	99	–	–
Lichen	93	88	–	–
Dryas	79	73	–	–
Dwarf Willow	78	79	–	–
Leaf Litter	99	99	–	–
Tussocks	47	49	–	–
Hummocks	97	98	–	–
Bare ground	20	14	–	–
Tallest Plant	–	–	26.8 \pm 6.7	27.4 \pm 8.5

Table 2.2. AIC ranking of logistic regression models used to predict Smith’s Longspur nest-site selection (nest vs. random point within the territory) as a function of microhabitat and nest features measured at each point. Only models with weights >0.00 are listed, plus the full model, which is provided for reference. The model in bold was best supported. Covariates were willow standard deviation, mean willow height, ericaceous standard deviation, mean ericaceous height, shrub standard deviation, mean shrub height, ground structure standard deviation, mean ground structure height, slope, aspect and study area. AICc of top model was 234.13.

Model Name	K	Δ AICc	Weight
WillSD	3	0.00	0.45
WillSD.aspect	4	1.97	0.17
WillSD.slope	4	2.09	0.16
ShrubSD	5	3.53	0.08
Null	1	5.23	0.03
WillAvg	3	6.51	0.02
Slope	2	6.94	0.01
Aspect	2	7.27	0.01
Study area	2	7.27	0.01
GrndSD	3	7.47	0.01
Full	13	16.33	0.00

Table 2.3. AIC rankings of daily nest survival models generated using program MARK and Smith's Longspur nest survival data collected at two breeding areas in northern Alaska. Models in bold are the best supported models in the candidate set. AICc of top model was 424.13.

Model Name	K	Δ AICc	Weight
Freezing	2	0.00	0.26
Season	2	0.46	0.21
Constant	1	2.10	0.09
Period	10	2.21	0.09
Willow*Study area	5	3.08	0.06
MinTemp*Year	7	3.49	0.05
Study area	2	3.85	0.04
21°C	2	4.09	0.03
Indicator	3	4.23	0.03
Freezing*MinTemp*Year	8	4.23	0.03
Year	6	4.73	0.02
Willow	3	4.84	0.02
Visibility	3	5.17	0.02
Study area*Year	9	5.52	0.02
MinTemp	3	5.52	0.02
MaxTemp	3	5.77	0.01
Willow*Indicator	4	6.04	0.01
Visibility*Willow	4	6.82	0.01
MinMaxTemp	4	7.27	0.01

General Conclusions

Despite rapid climate change across arctic regions (Serreze et al. 2000), little is known about breeding requirements of northern songbirds. As a result, understanding how increases in shrub height and abundance (Tape et al. 2006) and changes in weather patterns (Crick 2004; Wormworth and Mallon 2006) might impact breeding populations is unclear. To help fill this knowledge gap, I examined the breeding ecology of Smith's Longspurs in the Brooks Range, Alaska. Until now, information on Smith's Longspur populations has been sparse in general (Jehl 1968; Briskie 1992, 1993; Briskie et al. 1998; Briskie 1999), and virtually non-existent in their western range. This study is the first to highlight the unique way that Smith's Longspurs polygynandrous mating strategy influences breeding demographics. As a species of conservation concern (U.S. Fish and Wildlife Service 2008), information on Smith's Longspurs general breeding requirements may also be important for managers, particularly as the Arctic changes.

In total I banded 674 adult and juvenile Smith's Longspurs, from which I determined adult and juvenile nest-site fidelity and natal philopatry as well as apparent annual survival. Additionally, I monitored 257 nests with known fate, which I used to describe microhabitat associations, identify nest-site selection patterns, and examine temporal and physical factors influencing daily survival rate. Few studies on arctic passerines have monitored as many nests or attained a banded population of this size, making my estimates (particularly of juvenile survival and dispersal) some of the most comprehensive.

My study suggests that mating strategy is integrally connected to all aspects of Smith's Longspur breeding ecology. Contrary to many studies of monogamous taxa (Greenwood 1980), I found no sex-bias in dispersal patterns of adult Smith's Longspurs. I attribute this to the availability of multiple mates within a breeding neighborhood, so females do not have to

disperse in order to find alternative mates. With only a few exceptions, adults of both sexes returned to nest in the same breeding neighborhood as the previous year, while juveniles returning as adults dispersed to areas outside of their natal neighborhoods. In this way, Smith's Longspur populations maintain genetic diversity, while still maximizing the benefits of nesting in a familiar breeding site.

Contrary to my original predictions, I found that adult males had slightly higher annual survival than females. Decreased female survival is common in other passerines due to energetic demands and predation risk during egg laying, incubation, and feeding young (Low et al. 2010). However, I expected the reverse scenario, considering that male Smith's Longspurs have high energetic demands from enlarged testes and high sperm production, which is related to their extremely high copulation rates. Furthermore, males assist with brood rearing at multiple nests while simultaneously molting (Briskie 1992; Meddle et al. 2003). It is likely that the high male survival I observed is a consequence of an adaptive ability to attenuate response to stress (Meddle et al. 2003). This evolutionary trait would be particularly beneficial to polygynandrous Smith's Longspurs, considering they breed in such a harsh unpredictable environment. Despite male Smith's Longspurs exhibiting slightly higher survival than females, the magnitude of the difference was much less than what is commonly found in other grassland passerines (Perlut et al. 2008, Perlut and Strong 2011). Although we found that this sex-bias still existed, the reduction in magnitude could provide support for our original hypothesis that male Smith's Longspur survival is impacted by their unique energetic demands.

In many ground-nesting passerines, strong nest-site selection is associated with predator dynamics of fragmented landscapes (Harrison et al. 2011; Murray and Best 2014); thus, I suggest that habitat quality as well as neighborhood dynamics may contribute to the low levels of nest-

site selection I observed. In contrast to the fragmented habitats that characterize many studies of avian nest-site selection, the Brooks Range offers an abundance of suitable (Wild et al. 2014), relatively pristine and homogenous breeding habitats for Smith's Longspurs. Furthermore, I found that reproductive success of Smith's Longspurs was higher than what has been reported for other arctic passerines (Martin et al. 2009; Liebezeit et al. 2011). Consequently, predator-driven patterns of nest-site selection may not exist in this system. Considering these factors, nest-site selection may be driven by habitat or social variables at the neighborhood scale rather than the nest scale that I used. For example, polygynandrous females may choose to nest in the presence of other individuals rather than near specific habitat features. By nesting in close proximity to other females, multiple mates become accessible thus maximizing potential for extra paternal care, which likely increases reproductive output in this harsh environment (Davies 1985).

Although I found that nest success was negatively influenced by the number of days each season below freezing, daily survival rate of Smith's Longspur nests was relatively high with low variability across seasons. This resilience to local weather extremes suggests that breeding populations are well adapted to harsh weather conditions. However, considering Smith's Longspurs' tendency to avoid breeding in areas with tall shrubs, increases in shrub abundance throughout the Arctic (Tape et al. 2006) could result in population declines or distribution shifts (Wild et al. 2014). Northward expansion of Smith's Longspur populations, although plausible, could increase inter-specific competition with the closely related Lapland Longspurs that already breed on the coastal plain (Hussell and Montgomerie 2002).

In summary, I provide the first comprehensive study to examine dispersal strategy, survival rates, nest-site selection and reproductive success of a polygynandrous passerine, and one of the

few studies on arctic-breeding passerines. I propose that mating strategy influenced many aspects of the species' breeding ecology, and suggest that other polygynandrous songbirds should be examined to see if similar patterns arise. This study also contributes a basis for assessing the response of Smith's Longspurs and other tundra breeding songbirds to changes within open shrub tundra habitats in Alaska's Brooks Range.

Literature Cited

- Briskie, J. V. (1992). Copulation patterns and sperm competition in the polygynandrous Smith's Longspur. *The Auk* 109:563–575.
- Briskie, J. V. (1993). Anatomical adaptations to sperm competition in Smith's Longspurs and other polygynandrous passerines. *The Auk* 110:875–888.
- Briskie, J. V. (1999). Song variation and the structure of local song dialects in the polygynandrous Smith's longspur. *Canadian Journal of Zoology* 77:1587–1594.
- Briskie, J. V., R. Montgomerie, T. Pöldmaa, and P. T. Boag (1998). Paternity and paternal care in the polygynandrous Smith's Longspur. *Behavioral Ecology & Sociobiology* 43:181–190.
- Crick, H. Q. P. (2004). The impact of climate change on birds. *Ibis* 146:48–56.
- Davies, N. B. (1985). Cooperation and conflict among Dunnocks (*Prunella modularis*) in a variable mating system. *Animal Behaviour* 33:628–648.
- Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- 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.

- Hussell, D. J. T., and R. D. Montgomerie (2002). Lapland Longspur (*Calcarius lapponicus*). In Birds of North America Online. Ithaca, New York. <http://bna.birds.cornell.edu/BNA>.
- Jehl, J. R. (1968). The breeding biology of Smith's Longspur. *Wilson Bulletin* 80:123–149.
- Liebezeit, J., G. 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.
- Low, M., D. Arlt, S. Eggers, and T. Pärt (2010). Habitat-specific differences in adult survival rates and its links to parental workload and on-nest predation. *Journal of Animal Ecology* 79:214–224.
- Martin, M., A. F. Camfield, and K. Martin (2009). Demography of an alpine population of Savannah Sparrows. *Journal of Field Ornithology* 80:253–264.
- Meddle, S. L., N. T. Owen-Ashley, M. I. Richardson, and J. C. Wingfield (2003). Modulation of the hypothalamic-pituitary-adrenal axis of an Arctic-breeding polygynandrous songbird, the Smith's Longspur (*Calcarius pictus*). *Proceedings of the Royal Society B: Biological Sciences* 270:1849.
- 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.
- Perlut, N. G., and A. M. Strong (2011). Grassland birds and rotational-grazing in the northeast: breeding ecology, survival and management opportunities. *The Journal of Wildlife Management* 75:715–720.
- Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley (2008). Grassland songbird survival and recruitment in agricultural landscapes: implications for source-sink demography. *Ecology* 89:1941–1952.

- Serreze, M., J. Walsh, F. Chapin Iii, T. Osterkamp, M. Dyrgerov, V. Romanovsky, W. Oechel, J. Morison, T. Zhang, and R. Barry (2000). Observational evidence of recent change in the northern high-latitude environment. *Climatic Change* 46:159–207.
- Tape, K. E. N., M. Sturm, and C. Racine (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* 12:686–702.
- U.S. Fish and Wildlife Service (2008). *Birds of Conservation Concern*, p 85. United States Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management. Arlington, Virginia. <http://www.fws.gov/migratorybirds>.
- Wild, T. C., S. J. Kendall, N. Guldager, and A. N. Powell (2014). Breeding habitat associations and predicted distribution of an obligate tundra-breeding bird, Smith's Longspur. *The Condor: Ornithological Applications* 117:3–17.
- 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.

APPENDIX. Potential relationship between nest predation and predator corridors.

Predation is one of the most common causes of nest failure in ground nesting passerines (Martin 1993), and landscape features can increase this rate (Yosef 1994; Willson et al. 2001; Weldon 2006). Use of roads and other corridors by predators can increase efficiency of hunting through maximizing travel distance and speed. As a result, predators such as foxes have been known to focus their hunting efforts along linear corridors (Frey and Conover 2006). In Florida, reproductive success of the Loggerhead Shrike (*Lanius ludovicianus*) was lowest near fence lines that were commonly traveled along by mammalian and avian predators (Yosef 1994). Several potential predator corridors also exist in my study, including the Dalton Highway, Trans-Alaska Pipeline, and creeks and rivers. On several occasions, I observed both red foxes (*Vulpes vulpes*) and Common Ravens (*Corvus corax*) utilizing these corridors. Other studies in northern Alaska have found that behavior of mammalian and avian nest predators have been altered by anthropogenic structures (Eberhardt et al. 1982; Liebezeit et al. 2009). On the Arctic Coastal Plain, nesting success of passerines was lower within 5 km of oil field infrastructure that provided nesting, perching or denning sites for predators (Liebezeit et al. 2009). Consequently, I expected that rates of predation on Smith's Longspur nests near the pipeline, highway, and waterways would be higher compared to the rest of the study area.

Using ArcMap 10.1 (ESRI, Redlands, CA) and data layers provided by Toolik Field Station I created a 100 m buffer around the highway, pipeline, and streams/rivers/lakes. I then examined the number of nests that failed (during egg or chick stage) due to predation within each of these buffered regions and compared them to the rest of the study areas. In total, I examined 271 nests that were located and monitored over a seven-year period. Only one nest was depredated within either the water ($n = 29$) or the highway ($n = 19$) buffer. However, nests within the 100 m buffer

of the Trans-Alaska Pipeline were depredated (19%, $n = 5$ of 27 nests) 1.6 times as often as nests throughout the rest of the study area (12%, $n = 27$ of 230 nests).

As one of the tallest structures in a treeless landscape, I observed that the pipeline was a common perch for ravens and other avian species. Unlike the Dalton Highway, the pipeline has very little human activity so predators, whether avian or mammalian, are rarely disturbed (personal observation). Considering the relatively small number of nests within the corridor buffers, and the lack of statistical testing, future studies should verify the relationship between nest survival and proximity to the pipeline. Furthermore, the Trans-Alaska Pipeline covers a relatively small footprint, thus the increased predation rate we observed is not likely at a scale that will impact the population. However, these findings should be considered prior to further petroleum development in the Arctic.

Literature Cited

- Eberhardt, L. E., W. C. Hanson, J. L. Bengtson, R. A. Garrott, and E. E. Hanson (1982). Arctic fox home range characteristics in an oil-development area. *The Journal of Wildlife Management* 46:183–190.
- Frey, S. N., and M. R. Conover (2006). Habitat use by meso-predators in a corridor environment. *Journal of Wildlife Management* 70:1111–1118.
- Liebezeit, J. R., S. J. Kendall, S. Brown, C. B. Johnson, P. Martin, T. L. McDonald, D. C. Payer, C. L. Rea, B. Streever, A. M. Wildman, and S. Zack (2009). Influence of human development and predators on nest survival of tundra birds, Arctic Coastal Plain, Alaska. *Ecological Applications* 19:1628–1644.

- Martin, T. E. (1993). Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* 141:897–913.
- Weldon, A. J. (2006). How corridors reduce Indigo Bunting nest success. *Conservation Biology* 20:1300–1305.
- Willson, M. F., J. L. Morrison, K. E. Sieving, T. L. De Santo, L. Santisteban, and I. Díaz (2001). Patterns of predation risk and survival of bird nests in a Chilean agricultural landscape. *Conservation Biology* 15:447–456.
- Yosef, R. (1994). The effects of fencelines on the reproductive success of Loggerhead Shrikes. *Conservation Biology* 8:281–285.