RESEARCH ARTICLE

Dispersal and survival of a polygynandrous passerine

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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 7-yr period at 2 areas in Alaska's Brooks Range. We used capture–recapture histories of 243 color-banded adults and 431 juveniles to estimate annual survival and determined dispersal patterns from 34 adults that were found breeding within the study areas over multiple years. Most adults (88%) returned to nest in the same breeding neighborhood as in previous years; mean dispersal distance was 300.9 ± 74.2 m and did not differ between sexes. Juveniles exhibited low natal philopatry; only 4% of banded hatch-year birds were resighted as adults during subsequent years. Those that did return dispersed, on average, 1,674.4 ± 465.8 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 that of males (60–63%); juvenile survival was 41% but was paired with a low (13%) encounter probability. We attribute the lack of sex bias in adult dispersal to this species' polygynandrous mating strategy. 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 that suggest a relationship between dispersal and mating strategy and provide some of the first insight into the demographic patterns of a polygynandrous passerine.

Keywords: Arctic, breeding-site fidelity, *Calcarius pictus*, mark–recapture, natal philopatry, Smith's Longspur

Dispersion et survie chez un passereau polygynandre

RÉSUMÉ
Bien que l'on croie que les biais liés au sexe dans la survie et la dispersion soient reliés aux systèmes de reproduction aviaires, on connaît peu de choses sur ces patrons démographiques dans les stratégies de reproduction moins communes, telles que la polygynandrie. Nous avons investigué la fidélité au site de reproduction, la philopatrie natale et la survie apparente d'une espèce polygynandre, *Calcarius pictus*, pendant une période de sept ans dans deux zones de la chaîne de Brooks, en Alaska. Nous avons utilisé les histoires de capture-recapture de 243 adultes et 431 juvéniles marqués avec des bagues de couleur pour estimer la survie annuelle, alors que les patrons de dispersion étaient déterminés à partir de 34 adultes se reproduisant dans les zones d'étude sur plusieurs années. La plupart des adultes (88 %) sont retournés pour nicher dans les mêmes environs que les années précédentes; la distance de dispersion moyenne était de 300,9 ± 74,2 m et ne différait pas entre les sexes. Les oiseaux juvéniles présentaient une faible philopatrie natale; seulement 4 % des oiseaux HY bagués étaient revus en tant qu'adultes au cours des années subséquentes. Ceux qui sont retournés se sont dispersés en moyenne à 1 674,4 ± 465,8 m de leur nid natal ($n = 6$). Les estimations de survie de la moyenne des modèles ont indiqué que la survie annuelle des femelles adultes (50-58 %) était légèrement inférieure à celle des mâles (60-63 %); la survie des juvéniles était de 41 %, mais elle était associée à une faible probabilité de rencontre (13 %). Nous attribuons l'absence de biais lié au genre dans la dispersion des adultes à la stratégie reproductive polygynandre de *C. pictus*. Dans ce système, plusieurs partenaires sont présents dans un même voisinage reproductif. Nous soutenons que la sélection naturelle a pu favoriser les femelles qui sont demeurées sur le même site de reproduction, qui leur était familier, car elles n'ont pas à se disperser vers une nouvelle zone pour trouver un partenaire approprié. La dispersion chez les populations reproductives semble se produire lorsque les juvéniles reviennent en tant qu'adultes. Nos résultats supportent les hypothèses qui suggèrent une relation entre la dispersion et la stratégie de reproduction et fournissent un premier aperçu des patrons démographiques d'un passereau polygynandre.

Mots-clés: *Calcarius pictus*, fidélité au site de reproduction, philopatrie natale, marquage-recapture, Arctique

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 sex 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 our knowledge is based on studies of taxa that are monogamous—the breeding strategy 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. By contrast, females return to the nesting grounds after males and select a territory on the basis of 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 Orians 1991).

Knowledge of dispersal patterns in nonmonogamous 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 or no male territory defense in Smith's Longspur (*Calcarius pictus*), a polygynandrous passerine. Instead, breeding "neighborhoods" of intermating 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). Because of the geographic limitations of most studies, long-distance dispersal events go undetected and are indistinguishable from mortality. This is particularly evident in HY passerines, in which dispersal distance tends to be greater and first-year survival is generally low (Paradis et al. 1998). Thus, to fully 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, USA. We hypothesized that because there was no resource defense by males, the species would not exhibit the usual female-biased dispersal seen in most passerines; instead, we predicted that adult dispersal rates would be equal between the sexes. Additionally, we predicted that compared to monogamous species, juvenile Smith's Longspurs would disperse greater distances than adults to ensure that young leave their natal neighborhood, where multiple related individuals likely exist (Briskie 1992). Finally, we expected to see lower annual survival of males than of females, because (1) early in the breeding season, male Smith's Longspurs have extreme energetic demands related to high copulation rates and intense mate guarding; and (2) later in the season, they help provision broods, as well as undergo molt during chick rearing (Briskie 1992, Briskie et al. 1998).

METHODS

Study Species

Smith's Longspur is a small (20–30 g) migratory songbird that breeds 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 the species can be locally abundant (Wild et al. 2014). Both sexes mate with as many as 3 individuals during a given breeding season; no pair bonds or defendable territories are established, and males "guard" females only during short periods of copulation (Briskie 1992). Because of 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 or no information on dispersal, philopatry, or annual survival.

Study Area

We studied breeding Smith's Longspurs from late May until the middle of July at 2 locations in the Brooks Range of northern Alaska (Figure 1). Atigun Gorge, the most southern study area, is located in a mountain valley (68.27°N, 149.21°W; 2007–2013), and Slope Mountain is 27 km north, in rolling foothills (68.41°N, 149.40°W; 2011–2013). Both study areas (~1,060 ha) were accessible from the Dalton Highway and characterized by treeless tundra habitat. Study areas were chosen on the basis of accessibility and presence of known breeding populations.

Field Techniques

We searched for nests every day (6–12 hr day^{-1}), except during inclement weather, for the entirety of the breeding season (late May through mid-July) over a period of 7 yr (2007–2013). Once nests were located, we monitored them every 2–4 days until they failed or chicks fledged. Capture, banding, and resighting were an offshoot of other studies on habitat associations of Smith's Longspurs during 2007, 2008, and 2010; 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 (approximately May 28 to June 10), we captured males, and occasionally females, using playback calls and decoys placed near the nets. During the incubation period (approximately 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 and 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.
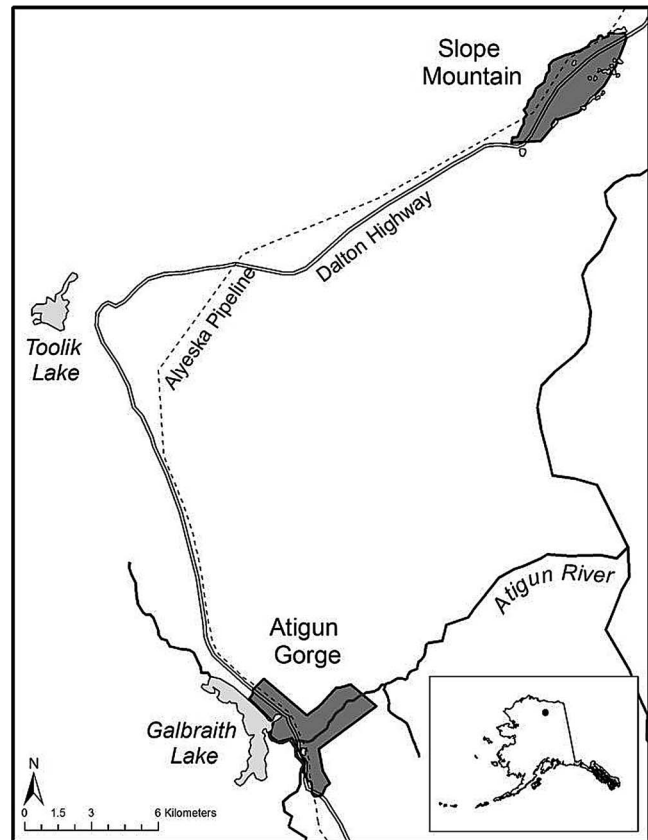

FIGURE 1. Study areas (Slope Mountain and Atigun Gorge) in the foothills of the Brooks Range, northern Alaska, USA, where Smith's Longspurs bred during 2007–2013.

We devoted approximately 30–40 hr yr^{-1} within each study area to resighting individuals. Resight effort was greatest (2–6 hr day^{-1}) during the first 2 wk of the breeding season, when birds were arriving and establishing breeding neighborhoods. Once this stage was complete, our resighting effort declined because 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.

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 version 10.1 (ESRI, Redlands, California, USA). We then selected nests of all individuals that nested within the study area in ≥2 yr (not necessarily consecutive). As an index of distance moved, we measured the distance between these nests, which we refer to as "interannual nest distance."

Given that Smith's Longspurs breed in neighborhoods rather than territories, we were also interested in determining neighborhood size. We developed an index of neighborhood size using the intra-annual nest distance

TABLE 1. Cormack-Jolly-Seber survival (ϕ) and recapture (p) models generated to fit Smith's Longspur resight data. Supported models are in bold. K = number of parameters, "effort" = difference in resighting efforts during some years, "age" = difference between hatch-year (HY) birds and adults, and "2a" = difference in survival between HY and second-year birds. Models that include "sex*age" examine sex effects only within adult groups because sex of HY birds was unknown.

Model	$\Delta QAIC_c$	$QAIC_c$ weights	Model likelihood	K	Deviance
ϕ sex*age p effort*age [a]	0.00	0.18	1.00	6	61.08
ϕ study area*sex*age p effort*age	0.52	0.14	0.77	9	55.48
ϕ age p effort*age	0.58	0.14	0.75	5	63.69
ϕ study area*age p effort*age	1.21	0.10	0.55	7	60.25
ϕ a2*age p effort*age	1.54	0.08	0.46	6	62.62
ϕ Trend*sex*age p effort*age	1.80	0.07	0.41	8	58.81
ϕ Trend*age p effort*age	2.49	0.05	0.29	7	61.54
ϕ sex*age p sex*age	2.50	0.05	0.29	6	63.58
ϕ sex*age p sex*effort*age	2.52	0.05	0.28	8	59.52
ϕ study area*2a*age p effort*age	2.93	0.04	0.23	8	59.94
ϕ sex*2a*age p sex*effort*age	3.49	0.03	0.18	9	58.45
ϕ study area*2a*age p sex*effort*age	3.81	0.03	0.15	10	56.72
ϕ study area*sex*2a*age p effort*sex*age	5.34	0.01	0.07	12	54.13
ϕ year*age p effort*age	6.49	0.01	0.04	10	59.40
ϕ Trend*sex*study area*2a*age p year*sex*age	6.88	0.01	0.03	13	53.61
ϕ year+sex*age p effort*age	8.68	0.00	0.01	12	57.47
ϕ year+sex*study area*2a*age p effort*sex*age	13.06	0.00	0.00	17	51.46
ϕ year*sex*age p effort*age	13.23	0.00	0.00	16	53.73
ϕ year*sex*study area*2a*age p effort*sex*age	19.34	0.00	0.00	21	49.34
ϕ year*sex*age*study area*a2 p year*sex*study area*age [b]	27.31	0.00	0.00	27	44.54
ϕ constant p constant [c]	70.13	0.00	0.00	2	139.30

[a] $QAIC_c$ value of best model was 340.89.
[b] Global model.
[c] Null model.

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 whether adult Smith's Longspurs exhibit even-sex dispersal, we compared mean inter-annual nest distance of males and females using a 2-tailed t-test (adjusted for unequal variance; $\alpha = 0.05$) in R version 3.0 (R Development 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 in >2 yr or (2) males that attended multiple nests in 1 yr, we randomly selected 1 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 1-tailed t-test. Values are presented as ranges and means ± SE.

Apparent Annual Survival and Detection Probability

Because dispersal and survival can 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 version 8.0 (White and Burnham 1999). We constructed a model set consisting of 21 possible models (Table 1). Because of relatively small sample sizes for juvenile and Slope Mountain birds, we separated our dataset into 6 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 across groups. 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 examined sex effects only within adult groups. We expected ϕ and p to differ between adult and HY birds, so we included age in every model. We also tested whether survival probability differed after the first year of life (denoted "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

TABLE 2. Distance (m) between nests of adult Smith's Longspurs returning to breed in multiple years after initial banding at Atigun Gorge and Slope Mountain, Alaska, USA, 2007–2013.

Number of years returned	n	Mean ± SE	Minimum	Maximum
Females				
4	3	406.4 ± 121.7	9.2	1,540.2
3	3	168.8 ± 46.3	40.4	414.3
2	18	322.3 ± 133.1	19.9	1,913.3
Total females	24	325.2 ± 72.6	9.2	1,913.3
Males				
2	10	240.3 ± 42.5	52.1	542.6
Grand total	34	300.9 ± 74.2	9.2	1,913.3

with a year effect in survival, so we included effort in nearly all detection models. We then tested for a year effect as well as for a temporal trend in adult survival.

We examined the most parameterized (global) model for goodness-of-fit using the median $\hat{c}$ approach ($\hat{c} = 2.5$; $n = 30$ replications). Moderate amounts of overdispersion are common in these models, and global models with a $\hat{c}$ value between 1 and 3 are considered to fit the data (Lebreton et al. 1992). We used quasi-Akaike's Information Criterion, adjusted for small sample sizes (QAIC$_c$), to assess model fit. The model with the lowest ΔQAIC$_c$ value was selected as the best model, although it was assumed that models with ΔQAIC$_c < 2$ (Burnham and Anderson 2002) were equally parsimonious. Models within 2 units of the best model that differed only by 1 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 because >1 of our models had ΔQAIC$_c < 2$.

RESULTS

Return Rates
We banded a total of 674 birds (243 adult and 431 juvenile) over the 7 yr of our study. Return rates of individuals in any subsequent breeding season were lower for females (37%; $n = 52$) than for 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 of the study areas was ever resighted in the other. The oldest documented female was ≥7 yr, and the oldest recorded male was ≥6 yr.

Adult Nest-site Fidelity
Among the returning birds, there were 34 instances (24 female and 10 male) in which the same individual's nest location was documented in multiple, but not always consecutive, years (range: 2–4 yr; Table 2).

Most returning adults nested within the same breeding neighborhood as in a previous season. We derived an index of mean neighborhood size (536.1 ± 133.5 m) from the intra-annual nest distances of 10 males that attended

multiple nests during the same summer. Only 4 individuals (17%; all females) returned to breed in locations outside of this proxy neighborhood size; their mean return nest distance was 1,443.6 ± 168.9 m.

The mean inter-annual nest distance of females was slightly farther than that of males (Table 2), but the difference was not significant (2-tailed t-test, $t_{30.15} = 0.57$, $P = 0.57$). Additionally, there was considerably more variability in dispersal distance of females than of males (Table 2). Despite high site fidelity in both male and female Smith's Longspurs, we observed only 1 instance of mate fidelity. There were 2 cases of male associations; these birds attended the same nest in 1 yr and were associated with each other again during following years.

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 and 3 male) of these returning birds' nests. Mean natal dispersal distance (1,674.4 ± 465.8 m) was significantly greater than adult dispersal (1-tailed t-test, $t_{5.25} = 3.01$, $P = 0.01$; Table 2). There was only 1 instance in which a male returned to breed within his natal neighborhood.

Apparent Annual Survival and Detection Probability
Model selection based on QAIC$_c$ indicated that the best-fitting model was $\phi_{sex*age}$, $p_{effort*age}$, in which survival differed by sex and age but was constant over time, and encounter probabilities differed between ages and between years of high or low search effort (Table 1). Apparent survival rate of females (0.50 ± 0.05) was lower than that of males (0.64 ± 0.04), and encounter probabilities were higher during high-effort years (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) were lower for HY returning as adults than for adults.

Five additional candidate models differed in ΔQAIC$_c$ values by <2 (Table 1). However, 3 of these differed from the best model by only 1 parameter and thus were not considered to be supported (Arnold 2010). When we modeled the effect of sex on survival at the 2 study areas

TABLE 3. Annual survival estimates $\pm$ SE (with 95% CI in parentheses) for adult Smith's Longspurs breeding at Atigun Gorge and Slope Mountain, Alaska, USA, calculated using program MARK by averaging the model weights of all models in the candidate set.

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

separately, adult survival rates were more similar between the sexes at Atigun Gorge (females: 0.57 ± 0.05; males: 0.62 ± 0.05) than at Slope Mountain (females: 0.39 ± 0.09; males: 0.71 ± 0.08). However, sample sizes and time spent were considerably lower for Slope Mountain than for Atigun Gorge; thus, model-averaged estimates that include Atigun Gorge may be more realistic. From the model-averaged estimates, the estimates (means + SE) of male and female survival overlapped at Atigun Gorge, whereas at Slope Mountain the SE did not overlap and there was an ~11% difference between male and female survival (Table 3).

DISCUSSION

Contrary to the female-biased dispersal pattern found in most adult passerines, we observed no sex 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*), in which resource competition is equal between the sexes, which suggests that 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 female Smith's Longspurs may not benefit from moving to unfamiliar areas. Monogamous systems, by contrast, show relatively greater female dispersal following failed breeding attempts (Dubois and Cézilly 2002). Dispersal costs of moving 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 1 of the 4 females that dispersed outside her previous breeding neighborhood had an unsuccessful breeding attempt in the previous year. Furthermore, we documented only 1 case of mate fidelity, which suggests that even within the same neighborhood, there is low occurrence of a female remating with a male with whom she previously had a failed nest. However, because so few adults 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 driven not by which specific male a female chooses, but rather by the quality of the habitat and of the collective group of males in 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 whether, 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 4 noncooperatively breeding passerines, median dispersal distances were at least the width of 4 territories (Zack 1990). We observed only 1 instance (out of 6) of an adult returning to breed within its natal neighborhood, and average natal dispersal distance was ~3 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 the present study is that we rarely searched for banded birds outside the study areas' 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 1 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 searched for nests only 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 their survival while on the breeding grounds. However, first-year survival also includes successful migration to and from wintering areas; unfortunately, information is not available on postbreeding-season movements of HY and 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 occurred. Methods have been developed to better estimate true survival and dispersal by combining dispersal distances with Cormack-Jolly-Seber models (Sandercock 2006, Schaub and Royle 2014); but, because of 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 1 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 life spans, there are few opportunities for long-distance dispersal following the first year of life. Considering short life expectancy, the 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.

There have been few studies 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%; Custer and Pitelka 1977) than what we found. However, these studies based survival estimates on cumulative returns and not on Cormack-Jolly models. Thus, the rates reported by Custer and Pitelka were likely lower than true survival. In general, there is a tradeoff between reproductive success and adult survival at high latitudes; nesting success is generally higher and adult survival 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 (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 for 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 have 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 it is rare, we have also documented males incubating eggs (H. R. Craig personal observation). 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 males' 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), the relationship between stress modulation and survival has seldom been tested (Breuner et al. 2008). It also might be argued that despite high energetic demands on male Smith's Longspurs, the cost of egg laying and incubation is still greater, resulting in lower female survival compared with males. However, the magnitude of the

difference between male and female survival in Smith's Longspurs was much less than is commonly found in other grassland passerines (Perlut et al. 2008, Perlut and Strong 2011). This reduction in the size of sex bias could provide support for our original hypothesis, suggesting that male survival is reduced by high energetic demands.

Although most studies on predation risk of ground-nesting birds have focused 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 a product either of high energetic demands during egg production or of mortality during the nonbreeding 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, this is 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 higher than those of females. Our results provide the first glimpse at demographic patterns of a polygynandrous passerine, but more long-term studies are needed to identify whether 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.

ACKNOWLEDGMENTS

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