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Article

Life-history tradeoffs revealed by seasonal declines in reproductive traits of Arctic-breeding shorebirds

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Seasonal declines in breeding performance are widespread in wild animals, resulting from temporal changes in environmental conditions or from individual variation. Seasonal declines might drive selection for early breeding, with implications for other stages of the annual cycle. Alternatively, selection on the phenology of nonbreeding stages could constrain timing of the breeding season and lead to seasonal changes in reproductive performance. We studied 25 taxa of migratory shorebirds (including five subspecies) at 16 arctic sites in Russia, Alaska, and Canada. We investigated seasonal changes in four reproductive traits, and developed a novel Bayesian risk-partitioning model of daily nest survival to examine seasonal trends in two causes of nest failure. We found strong seasonal declines in reproductive traits for a subset of species. The probability of laying a full four-egg clutch declined by 8–78% in 12 of 25 taxa tested, daily nest survival rates declined by 1–12% in eight of 22 taxa, incubation duration declined by 2.0–2.5% in two of seven taxa, and mean egg volume declined by 5% in one of 15 taxa. Temporal changes were not fully explained by individual variation. Across all species, the proportion of failed nests that were depredated declined over

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the season from 0.98 to 0.60, while the proportion abandoned increased from 0.01 to 0.35 and drove the seasonal declines in nest survival. An increase in abandonment of late nests is consistent with a life-history tradeoff whereby either adult mortality increased or adults deserted the breeding attempt to maximize adult survival. In turn, seasonal declines in clutch size and incubation duration might be adaptive to hasten hatching of later nests. In other species of shorebirds, we found no seasonal patterns in breeding performance, suggesting that some species are not subject to selective pressure for early breeding.

Introduction

Seasonal changes in reproductive success are widespread in wild animals, especially birds (Klomp 1970, Cooke et al. 1984, Daan et al. 1989, Rowe et al. 1994, Sandercock et al. 1999, Grant et al. 2005), but also other taxa (Hughes 1985, Landa 1992, Huber et al. 2001, Varpe et al. 2007). Early breeders tend to produce more, larger, or higher-quality offspring than individuals that breed later in the year. Selection for early breeding can influence other stages of the annual cycle, such as the timing or rate of migration or feather molt in migratory birds (Jonzén et al. 2006, Dietz et al. 2013).

The presence of seasonal declines seems disadvantageous if maintaining high reproductive output throughout the season would result in higher lifetime reproductive success. In some cases, inherent aspects of individual quality, such as age, are correlated with both breeding success and timing of breeding (Hochachka 1990, Christians et al. 2001). Lower-quality or less experienced individuals might be unable to breed early in the season. Among-individual variation can thus result in population-level seasonal declines in reproductive performance even if environmental conditions do not change.

In other cases, individuals that are adapted to average conditions during the breeding season might experience lower success when conditions change. Seasonal changes in environmental conditions, available resources, predation risk, or physiological condition of individuals can reduce the chance of success later in the season (Lepage et al. 1999). Similarly, selection acting on the phenology of nonbreeding stages can constrain reproductive output at the beginning or end of the breeding season. In birds, early fall migration can be critically important for avoiding predators, accessing abundant food, and completing wing molt (Schneider and Harrington 1981, Jamieson et al. 2014). Individuals that complete breeding earlier in the season may have an advantage at other times of the year. In some cases, individuals initiate but then curtail breeding attempts late in the season (Gratto-Trevor 1991, Jamieson et al. 2014), indicating a life-history tradeoff where adult survival is prioritized over reproductive success, as would be expected for iteroparous species with high residual reproductive value (Sæther and Bakke 2000). Like temporal patterns in conditions on the breeding grounds, selection for timing of departure on fall migration would be expected to affect all individuals in the population as conditions change. In birds, effects on seasonal performance of both among-individual variation and changing conditions are well supported and not mutually exclusive (Verhulst and Nilsson 2008, Pärt et al. 2017).

Long-distance migrants might face particular challenges in balancing the optimal timing of migration versus breeding, as a result of time constraints and distance from the environmental cues that could be used to optimize the timing of arrival at the breeding grounds (Coppack et al. 2003, Senner 2012, Winkler et al. 2014). Many birds migrate long distances to breed in the Arctic, where the period of clutch initiation is short and highly synchronous (Sandercock et al. 1999, Smith and Wilson 2010). Timing of breeding in the Arctic is thought to be driven by strong selection to coincide with an annual pulse of availability of food resources that are crucial for egg formation and chick development (Lepage et al. 2000, Schekkerman et al. 2003, Meltotte et al. 2007, Love et al. 2010, McKinnon et al. 2012). Long-distance migration and strong seasonality therefore make the Arctic an interesting system for investigating seasonality in breeding performance.

Previous studies have reported seasonality in reproductive parameters of several species of Arctic-breeding shorebirds (Maclean 1972, Reynolds 1987, Schamel and Tracy 1987, Sandercock 1997, 1998, Sandercock et al. 1999, Andersson 2005, Smith and Wilson 2010, Kwon 2016, Reneerkens et al. 2016). However, all previous studies have been conducted at single field sites. Site-specific conditions do not capture the full range of variation in drivers of reproductive traits and thus might not be representative of the species across its full geographic range (McCaffery and Ruthrauff 2004, Senner et al. 2017). Most Arctic-breeding shorebirds have broad geographic distributions, so multi-site studies are needed to make general inference about demographic rates and life-history traits. In 2008–2014, we used standardized protocols to collect field data on the breeding ecology of shorebirds at arctic field sites in Alaska, Canada, and Russia (Lancot et al. 2015). The field data were compiled by the Arctic Shorebird Demographics Network (ASDN) and represent one of the most geographically and taxonomically comprehensive sets of demographic data for any group of migratory birds.

We tested for seasonal changes in five major reproductive traits for 21 species of shorebirds across their breeding ranges. We applied Bayesian hierarchical models, which controlled for random effects and shared information across species and field sites, to test for seasonality in five components of reproductive performance: clutch size, egg volume, incubation duration, daily survival rate of nests, and cause-specific rates of nest failure. We predicted that strong selection on phenology of breeding and other stages of the annual cycle would result in seasonal declines in breeding performance. We also predicted that when seasonal declines were present,

they would indicate population-level selective pressure and would not be fully attributable to among-individual variation.

Methods

We monitored shorebirds at 16 field sites in arctic and subarctic habitats of North America and Russia (Fig. 1; Supplementary material Appendix 4 Table A1). In 2010–2014, all sites followed a common set of field protocols and data formats developed by the Arctic Shorebird Demographics Network (Brown et al. 2014). Data were also collected with similar field methods in 2008 and 2009 at a subset of three sites: Nome, Alaska (Sandercock et al. 1999), Barrow, Alaska (Saalfeld and Lanctot 2015), and Bylot Island, Nunavut (McKinnon and Bêty 2009).

Data collection

We located shorebird nests by walking across the tundra and observing distraction displays of attending parents or by rope-dragging to flush birds from nests. We estimated the age of each clutch at discovery based on the number of eggs for nests that were found during egg-laying, or

by floating the eggs in a small cup of water to estimate the stage of embryonic development for nests found after egg-laying was complete (Sandercock 1998, Liebezeit et al. 2007, Brown et al. 2014). We used the estimated clutch age and published estimates of incubation duration to predict the expected hatch date for nest-monitoring purposes.

We visited nests every 1–5 d during incubation. Arctic-breeding shorebirds typically lay one egg every 1–2 d (Colwell 2006), so when the number of eggs did not increase for > 2 d while the nest was active, we considered that number to be the final clutch size. Of 478 nests that were found during egg-laying, had a full clutch of four eggs, and hatched at least one egg, 8% were observed to lose part of their clutch during incubation (mean = 1.38 eggs, SD = 0.63), so observed clutch sizes represented the full number of eggs laid in most cases. Moreover, rates of egg loss did not change over the season (ASDN unpubl.), so partial clutch loss would not affect our assessment of seasonal trends in clutch size, even if the number we used for final clutch size was occasionally smaller than the number of eggs laid. In shorebirds, clutches with > 4 eggs usually result from joint egg-laying by more than one female, or are otherwise outliers (Arnold 1999), so we excluded nests with > 4 eggs (0.3% of all nests) from all analyses.



Figure 1. Locations of 16 study sites in arctic Russia, Alaska, and Canada. Breeding ecology of shorebirds was monitored for 3–7 yr per site as part of the Arctic Shorebird Demographics Network and earlier work (Supplementary material Appendix 4 Table A1).

For a subset of study sites and years, we used calipers to measure the length and width of each egg to the nearest 0.1 mm. We estimated egg volume as $V = kLB^2$, where L = length of the egg and B = breadth at the widest point (Hoyt 1976). Volume of the pyriform eggs of Arctic-breeding sandpipers and phalaropes can be accurately estimated using a shape coefficient of $k = 0.47$ (Sandercock et al. 1999, Governali et al. 2012). We used $k = 0.47$ for the plovers in our dataset as well; we were not making comparisons across species, so any variation among species in whether $k = 0.47$ was accurate would not affect our results. We used the linear measurements for all eggs in the final clutch to calculate the volume of each egg, and averaged across eggs to determine the mean egg volume for each nest.

We checked nests daily near the predicted hatch date and recorded a nest as hatched if at least one newly hatched chick was observed in the nest, or if eggshell fragments indicative of hatching were found in the nest within four days of the expected hatch date (Mabee 1997, Brown et al. 2014). We recorded the hatch date as 1) the day that downy chick(s) were first found in the nest, 2) the day after eggs were observed with pipped holes in the shells, or 3) two days after eggs were observed with star-cracks in the shells (Brown et al. 2014). We used a subset of nests that were found during egg-laying and observed to hatch on a known date to calculate the median duration of incubation for each species. We defined incubation duration as the number of days from the laying date of the last egg to the hatching date of the first egg. Previously published estimates of incubation duration were generally based on small numbers of nests, so we used our new estimates of median incubation duration for each species in all following analyses.

We classified nests as failed if we found evidence of predation, abandonment, or other causes of failure (detailed below). We recorded the cause of failure as predation when all eggs disappeared more than four days before the predicted hatch date or when large fragments of eggshells were present in the nest or abandonment when eggs were left unattended by parents for ≥ 3 visits. Other infrequent causes of failure included failure to hatch when eggs remained in the nest more than four days after the expected hatching date but were attended by parent(s), weather, trampling by ungulates, miscellaneous, or unclear cause of failure. Some uncertainty is expected when assigning causes of failure; for example, a nest that was abandoned but then depredated before the next visit by observers would have been recorded as failed to predation. Alternatively, adult mortality away from the nest may not have been observed, and the nest may have been recorded as abandoned given that it was unattended. We recorded nest fate as unknown if we found unclear or conflicting evidence of hatching versus failure at the nest site. Assigning all nests with unknown fate to any other category (hatched, failed, or failed to predation) did not change our conclusions (results not shown).

Many of the shorebirds attending nests were individually marked with color bands and leg flags (Brown et al. 2014,

Weiser et al. 2016). We recorded individual identities of parents when possible, and identified known re-nests when at least one parent was observed attending a different nest earlier in the season. In sandpipers with biparental incubation, if we knew the identity of only one parent, we assumed the breeding pair remained together between nesting attempts, as was typical in an experimental study of re-nesting in Dunlin (Gates et al. 2013). We expected our dataset to underestimate the frequency of re-nesting (Naves et al. 2008, Gates et al. 2013), but our intention was not to examine re-nesting propensity at a population scale. Instead, we used known re-nests to test for individual consistency in clutch size and mean egg volume and thus assess whether seasonal patterns may have resulted from among-individual variation versus temporal changes in environmental or physiological conditions.

Data deposition

All data used in our analyses are available from the NSF Arctic Data Center: <<http://dx.doi.org/10.18739/A2CD5M>> (Lanctot et al. 2016).

Statistical analyses

We used a Bayesian hierarchical framework to test for seasonal trends in each of the five components of reproductive performance. Unlike a maximum-likelihood approach, the Bayesian framework allows estimation of multiple random effects on the intercept for daily survival rate of nests (DSR; Rotella et al. 2004, Royle and Dorazio 2008). To provide statistical power for our tests of each response variable, we restricted each analysis to species with ≥ 20 nests with complete data. Each model also used hyperpriors ('priors of priors', i.e. priors that define the distribution of other prior distributions) to share information across species to improve precision while estimating species-specific seasonal trends (detailed in Supplementary material Appendix 1). We excluded a subset of nests that were experimentally manipulated for other studies from our estimates of incubation duration and nest survival. Clutch size and egg volume were not manipulated in any nest.

We adjusted the scale of three response variables to improve computational efficiency and statistical power. First, we categorized final clutch size as a binary variable: < 4 eggs (0) or 4 eggs (1), which we modeled with a logit link and a uniform prior in the interval -5 to 5 on the logit scale for the intercept, which corresponds to the interval 0 to 1 on the natural scale. Second, mean egg volume followed a multimodal distribution because egg size varied among species, so we converted the mean egg volume for each nest to the percent difference from the species-specific mean. The converted values followed a zero-mean normal distribution both within and among species, so we fixed the intercept at zero. Third, we modeled incubation duration on the natural scale (days) as the absolute difference from the species-specific

median, with a uniform prior in the interval -5 to 5 on the intercept. We modeled daily nest survival rate with a logit link and specified a uniform prior in the interval -5 to 5 on the logit scale for the intercept; the state of each nest on any given day was given as alive, predated, abandoned, failed to other causes, or unknown based on our field observations.

For each reproductive trait, we were interested in assessing how the timing of reproduction, relative to the local population, affected the trait. To define a metric of timing relevant to each reproductive trait, we used the estimated date of clutch initiation for our analyses of clutch size, mean egg volume, and incubation duration, and the day of each known nest state for DSR. We centered each date to the site-year mean for each response variable because we were interested in the effect of timing of breeding relative to the current season for the local population. We refer to the centered date value as ‘day-of-season’ hereafter, with negative values indicating a day earlier than the annual mean for each site. Before running the models, we standardized day-of-season to the mean and two standard deviations across all sites and years to ensure that the effects of day-of-season were comparable across all response variables (Gelman and Hill 2007). We then tested for linear ($\beta_{day[i]}$) and quadratic ($\beta_{day^2[i]}$) effects of day-of-season on each reproductive trait i , while controlling for random effects of species, site, and year nested within site. We estimated the effects with a varying-slopes model, where all species-specific estimates were drawn from one distribution defined by a single standard deviation, thus using the hierarchical modeling framework to share information among species. We provide a detailed description of our basic Bayesian model, which we used for clutch size, mean egg volume, and incubation duration, in Supplementary material Appendix 1.

To estimate DSR while correcting for potential bias introduced by nests that were lost before discovery by an observer, we adapted our basic model (Supplementary material Appendix 1) with daily nest survival models originally developed by Mayfield (1961) and extended by others (Johnson 1979, Bart and Robson 1982, Dinsmore et al. 2002, Rotella 2007). Bayesian implementations of daily nest survival models have been recently described (Royle and Dorazio 2008, Schmidt et al. 2010, Brown and Collopy 2012). We expanded the Bayesian DSR model to explicitly estimate cause-specific rates of nest failure so that we could test for seasonality in competing risks as well as DSR. We followed the conceptual approach of a risk-partitioning nest survival model previously developed in a maximum-likelihood framework (Etterson et al. 2007), which has recently been demonstrated in a Bayesian framework that allows the inclusion of random effects (Darrah et al. 2017). Our model differed from that of Darrah et al. (2017) in that we used a DSR model rather than a logistic-exposure model. Unlike Etterson et al. (2007) and Darrah et al. (2017), we also assessed the probability of each risk as conditional on failure; that is, the survival process was evaluated first (whether the nest survived or failed), and for nests that

failed, the probability of each cause of failure was then evaluated. Our approach allowed us to assess whether a covariate had an effect on the overall survival rate (survived versus failed) as well as whether any covariate of interest affected each competing risk for nests that failed (depredated versus abandoned versus failed to other causes). Our DSR model allowed for staggered entry and exit of nests and estimated effects of covariates on the probability of survival and two probabilities of cause-specific failure. We provide a detailed description and example code for the risk-partitioning DSR model in Supplementary material Appendix 2.

We partitioned the risks, which were conditional on nest failure, into three major causes of nest failure: predation, abandonment, and other causes. Each risk category had a smaller sample size than DSR because only a subset of nests failed, unsuccessful nests were further subdivided into causes of failure, and each unsuccessful nest had only one day of information for the failure event as opposed to multiple days that informed the DSR model. Rather than testing for species-specific effects of day-of-season on the probability of each cause of failure as we did for the survival process of the model, we therefore tested for effects across all species pooled to improve statistical power. The effects of interest for the partitioned risks were the linear or quadratic effects of day-of-season ($\beta_{day[j]}$ or $\beta_{day^2[j]}$) on the probability that an unsuccessful nest failed to each risk j : predation (p_{pred}) or abandonment (p_{aband}). Covariate effects were not estimable for the last risk category (other causes; Supplementary material Appendix 2), which included a variety of causes of failure that occurred rarely (detailed in Results).

From the model for each response variable, we obtained mean estimates with 95% Bayesian credible intervals (BCIs) for β_{day} , β_{day^2} , and the overall mean and the species-specific mean of the response variable (probability of a four-egg clutch, percent difference in mean egg volume, percent difference in incubation duration, DSR, p_{pred} , and p_{aband}). Within the DSR model, we also used the estimates of DSR, $\beta_{day[DSR]}$, and $\beta_{day^2[DSR]}$ to calculate expected nest success as the probability of nest survival from laying until hatching, depending on the day-of-season on which the nest was initiated (Supplementary material Appendix 3). We concluded that there was no linear or quadratic effect of day-of-season for a given species and response if the 95% BCI included zero for β_{day} or β_{day^2} , respectively. When the quadratic effect was not supported for a given response for any species, we reran the model with only the linear effect as our final model. Where a linear or quadratic effect was supported for a given species and response, we used the model to generate posterior probabilities for the expected value of the reproductive trait on each day of the season.

We implemented all Bayesian models in JAGS ver. 4.0 (Plummer 2003) with the package ‘runjags’ (Denwood 2016) in R ver. 3.2.2 (R Core Team). We discarded estimates from adaptation and burn-in periods (1000 and 2000 iterations, respectively) to produce good mixing across three chains. We then ran each model for a further 3000 iterations and saved the output from every third iteration to avoid autocorrelation,

resulting in 1000 saved iterations used to generate posterior distributions for estimates of the demographic parameters. For each model run, we checked that convergence was achieved as indicated by Gelman–Rubin statistics of < 1.10 for all parameters (Brooks and Gelman 2012).

Temporal changes vs among-individual variation

We used matched pairs of initial nests and renests attended by the same parents within a season to test for individual consistency in clutch size and mean egg volume within a breeding season. While we cannot be sure that the initial nest was actually the first clutch laid by that pair, as we may have missed a previous nest that failed, we never recorded more than two nests per season for any individual of any shorebird species. Whether or not the initial nest was the first nest of the season also would not affect our test for differences between the initial nest and renest. If parental quality, when covarying with the timing of the first breeding attempt (i.e. higher-quality birds often breed earlier), dictated any seasonal trends in breeding performance, we would expect that reproductive traits would not differ between initial nests and renests attended by the same individuals. In contrast, if traits such as clutch size or mean egg volume changed from the initial nest to the subsequent nest, that would indicate a temporal change within one individual. We used package `lme4` (Bates et al. 2014) in R to fit a generalized linear mixed effects model, including species as a random effect, to test if 1) clutch size depended on whether a clutch was an initial nest versus a renest, and 2) clutch size of a renest depended on the date of loss of the initial clutch. We also conducted a matched-pairs *t*-test in R to test for changes in mean egg volume between the initial nest and renest for each pair of birds.

To test for an effect of parental quality on DSR, we used our risk-partitioning DSR model but restricted the dataset to nests initiated on the mean day-of-season, which was also the modal day, for the corresponding site and year. If the seasonal pattern for these nests was the same as that for the full dataset, we concluded that the population-level seasonal decline was attributable to a temporal change that acted on individuals, rather than among-individual variation in parental quality that was related to the timing of breeding. Sample sizes were greatly restricted for nests initiated on the mean day-of-season, which reduced the precision of the posterior estimates. Thus, we checked whether the sign of the effect size for each species matched the full DSR model. If so, we concluded that seasonal patterns in DSR were not fully explained by among-individual variation in quality.

Results

We had sufficient sample sizes to include 25 taxa of Arctic-breeding shorebirds spanning seven genera in our demographic analyses (Table 1, Supplementary material Appendix 4 Table A2). Our dataset included five subspecies of dunlin and 20 other species (Table 1). Nests were initiated from

13 May to 17 July, spanning 17–44 d per field site. Taxa with biparental incubation (17 of 25 taxa; Table 1) tended to nest earlier than species with uniparental incubation (8 of 25 taxa; Table 1, Fig. 2a). Most nests were active within a narrowly defined window of the season (Fig. 2b). Across all taxa, mean clutch size was 3.85 eggs (SD=0.45, $n=7804$ nests), and 87.7% of nests had a final clutch size of four eggs, 9.9% had three eggs, 1.8% had two, and 0.5% had one. We recorded egg measurements for 3253 nests of 15 taxa, with mean egg volume ranging from 5.9 ml for red-necked phalaropes to 32.0 ml for black-bellied plovers (Table 1). We measured incubation duration for 532 nests across 21 taxa, and median incubation duration ranged from 19 d in semipalmated sandpipers and red phalaropes to 28 d in black-bellied plovers (Table 1).

We recorded the fate of 5743 nests of 22 taxa, of which 61% hatched, 30% failed, and 9% had an unknown fate. Modeled estimates of daily survival rate were similar across most taxa (Fig. 3a), with an overall mean DSR of 0.9813 (SD=0.0037) and corresponding probabilities of nest success (*S*) of 0.39–0.76 across taxa (Fig. 3b, dark gray triangles). Of all nests monitored, the raw proportion that survived each day-of-season declined over the season. Observed causes of nest failure were predation (86% of unsuccessful nests), abandonment (10%), and other causes (failure to hatch 1.5%, trampling by ungulates 0.9%, weather 0.2%, and miscellaneous causes 1.5%). The mean probabilities of failure to the three risks partitioned by our cause-specific model were $p_{pred}=0.94$ (SD=0.03), $p_{aband}=0.04$ (SD=0.02), and $p_{other}=0.01$ (SD=0.01) for nests that failed. The proportion depredated showed little seasonal change, while the proportion abandoned increased sharply near the end of the season (Fig. 2b).

Seasonality in breeding performance

We observed linear effects of day-of-season for at least one species in every reproductive trait, while quadratic effects were not supported (Supplementary material Appendix 4 Table A3, A4, Fig. 4). The linear effect of day-of-season was unambiguously negative for clutch size in 12 of 25 taxa, egg volume in one of 15 taxa, incubation duration in two of seven taxa, DSR in eight of 22 taxa, and one cause of nest failure for all species pooled. Where taxon-specific effects of day-of-season were not different from zero, the mean estimate was still often negative. The most extreme declines from the beginning to end of the season were 78% in probability of laying a four-egg clutch (0.96 to 0.21; semipalmated plover; Fig. 5c), 5% in mean egg volume (6.6 to 6.3 ml; semipalmated sandpiper; Fig. 5m), 2.5% in incubation duration (0.5 d; red phalarope; Fig. 5o), and 12% in DSR (0.9827 to 0.8662; long-billed dowitcher; Fig. 5u). In several cases with a large sample of nests ($n > 100$), we found no evidence for seasonal declines, such as clutch size of *hudsonia* dunlin; egg volume of American golden-plovers, *arcticola* dunlin, pectoral sandpipers, long-billed dowitchers, and red and

Table 1. Shorebirds included in the analysis of seasonal patterns in breeding performance. Species and subspecies are ordered by taxonomy following Clements et al. (2015). Demographic parameters were estimated by this study except where otherwise indicated.

Common name	Scientific name	Code	Incubation*	Clutch size		Egg volume		Incubation duration†		Nest survival	
				Mean ± SD	n	Mean ± SD	n	Median ± SD	n	Prop. hatched	n
Black-bellied plover	<i>Pluvialis squatarola</i>	BBPL	MF	3.87 ± 0.37	106	32.03 ± 2.55	38	28 ± 1.53	3	0.49	67
American golden-plover	<i>Pl. dominica</i>	AMGP	MF	3.92 ± 0.34	521	25.25 ± 1.97	160	26 ± 1.33	19	0.52	203
Common ringed plover	<i>Charadrius hiaticula</i>	CRPL	MF	3.83 ± 0.38	35	–	–	24	–	–	–
Semipalmated plover	<i>Ch. semipalmatus</i>	SEPL	MF	3.29 ± 1.15	67	–	–	25 ± 2.31	20	0.62	55
Whimbrel	<i>Numenius phaeopus</i>	WHIM	MF	3.58 ± 0.82	151	–	–	24 ± 1.58	10	0.47	120
Ruddy turnstone	<i>Arenaria interpres</i>	RUTU	MF	3.76 ± 0.65	87	15.44 ± 1.29	40	21 ± 0.00	3	0.53	57
Ruff	<i>Calidris pugnax</i>	RUFF	F	3.86 ± 0.40	50	–	–	21	1	0.54	26
Stilt sandpiper	<i>Ca. himantopus</i>	STSA	MF	3.96 ± 0.20	26	–	–	20	1	0.72	25
Temminck's stint	<i>Ca. temminckii</i>	TEST	U	3.75 ± 0.49	40	–	–	22	–	0.96	23
Dunlin‡	<i>Ca. alpina alpina</i>	DUNLalp	MF	3.91 ± 0.30	32	–	–	21	–	0.73	0
	<i>Ca. a. sakhalina</i>	DUNLsak	MF	3.85 ± 0.43	68	10.84 ± 0.87	35	22 ± 0.71	2	0.43	28
	<i>Ca. a. pacifica</i>	DUNLpac	MF	3.85 ± 0.39	89	10.95 ± 0.67	76	21 ± 0.98	16	0.61	54
	<i>Ca. a. arctica</i>	DUNLarc	MF	3.96 ± 0.22	491	11.24 ± 0.62	330	21 ± 2.34	33	0.67	382
	<i>Ca. a. hudsonia</i>	DUNLhud	MF	3.86 ± 0.46	150	10.7 ± 0.65	42	21 ± 0.63	6	0.73	129
Baird's sandpiper	<i>Ca. bairdii</i>	BASA	MF	3.97 ± 0.21	132	9.23 ± 0.68	68	21 ± 0.76	7	0.62	109
Little stint	<i>Ca. minuta</i>	LIST	U	4.00 ± 0.00	23	–	–	20	–	–	–
Least sandpiper	<i>Ca. minutilla</i>	LESA	MF	3.97 ± 0.18	31	–	–	21 ± 0.71	2	0.73	22
White-rumped sandpiper	<i>Ca. fuscicollis</i>	WRSA	F	3.84 ± 0.44	122	8.73 ± 0.67	36	20 ± 0.76	5	0.46	84
Buff-breasted sandpiper	<i>Ca. subruficollis</i>	BBSA	F	3.92 ± 0.40	25	–	–	24	–	0.35	20
Pectoral sandpiper	<i>Ca. melanotos</i>	PESA	F	3.94 ± 0.30	1027	12.19 ± 0.76	353	22 ± 1.02	44	0.63	794
Semipalmated sandpiper	<i>Ca. pusilla</i>	SESA	MF	3.86 ± 0.41	1770	6.44 ± 0.48	748	19 ± 1.05	143	0.65	1356
Western sandpiper	<i>Ca. mauri</i>	WESA	MF	3.67 ± 0.58	587	6.85 ± 0.46	284	20 ± 0.97	70	0.46	448
Long-billed dowitcher	<i>Limnodromus scolopaceus</i>	LBDO	MF	3.81 ± 0.54	177	19.31 ± 1.1	114	21 ± 0.65	11	0.48	155
Red-necked phalarope	<i>Phalaropus lobatus</i>	RNPH	M	3.83 ± 0.45	858	5.88 ± 0.43	275	20 ± 1.67	57	0.53	605
Red phalarope	<i>Ph. fulicarius</i>	REPH	M	3.83 ± 0.45	1139	7.45 ± 0.55	654	19 ± 2.10	78	0.70	981

*Biparental (MF), uniparental by either sex (U), female-only (F), or male-only (M) incubation of the nest (Hildén 1975, 1978, del Hoyo et al. 1996, Thomson et al. 2014, Rodewald 2015).

†For species where n is not given, none of the nests we found during the laying stage survived to hatch, so values are from the literature (Cramp and Simmons 1983, Lanctot and Laredo 1994, Visser et al. 1995, del Hoyo et al. 1996, Wallander 2003, Rönkä et al. 2006, Klima and Jehl 2012). Only species with ≥ 20 nests were included in the model testing for seasonal declines in incubation duration, but values for other species were used to estimate the exposure period in our calculations of expected nest success.

‡Five subspecies of dunlin occurred at our study sites: *alpina* (LKRL), *sakhalina* (CHAU), *pacifica* (NOME, CAKR), *arctica* (BARR, IKPI, COLV, PRBA, CARL), and *hudsonia* (CHUR, BURN, COAT, EABA, IGLO) (Cramp and Simmons 1983, Miller et al. 2015).

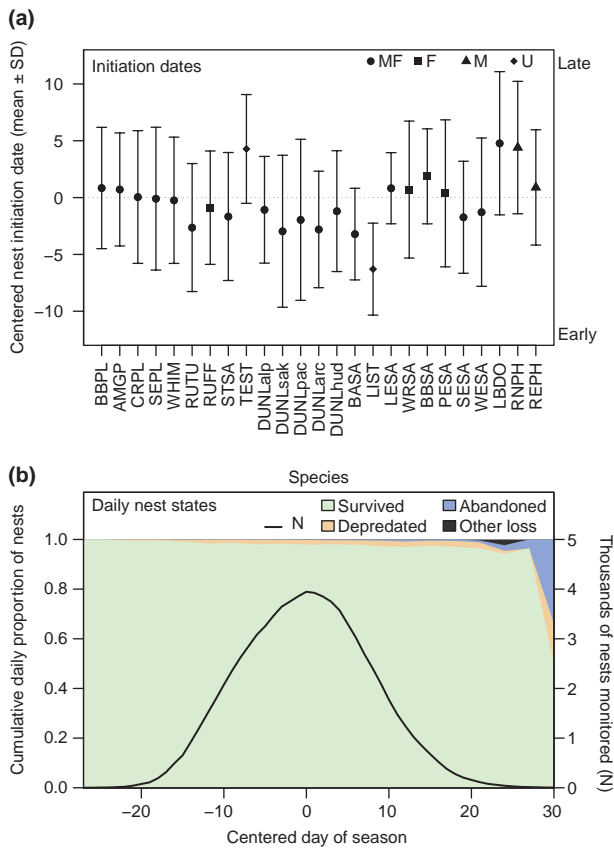


Figure 2. Breeding phenology of 25 taxa of shorebirds at 16 arctic sites. (a) Mean clutch initiation date for each species, relative to the site- and year-specific mean initiation date across all species. Species codes are defined in Table 1 and symbols indicate the incubation system of the species: MF=both sexes, F=female only, M= male only, and U=uniparental by either sex. (b) Cumulative proportion of active shorebird nests observed in each state on each day of the season, centered to the site-year mean date on which shorebird nests were monitored (shaded polygons), and the total number of nests monitored on each day-of-season (line).

red-necked phalaropes; and DSR of whimbrel, *hudsonia* dunlin, and Baird's and semipalmated sandpipers (Fig. 4).

For each taxon where the effect of day-of-season on DSR was different from zero, expected nest success through the exposure period (egg-laying and incubation) declined by 24–89% over the season (Fig. 3b). For all taxa pooled, the risk of each cause of failure also varied seasonally. For nests that failed, the probability of predation declined from 0.98 to 0.60 over the season, while the probability of abandonment increased from 0.01 to 0.35 and the probability of other risks increased from 0.01 to 0.05 (Fig. 5x).

Temporal changes vs among-individual variation

Of 4226 nests attended by at least one marked parent, 57 (1.3%) were known renests. We recorded the final clutch size for matched pairs of nests in 44 cases for five species: dunlin ($n=9$ nests across all subspecies), pectoral ($n=1$),

semipalmated ($n=21$), and western ($n=11$) sandpipers, and whimbrel ($n=2$). Across all species, the proportion of clutches with four eggs was lower for renests (0.65) than first nests (0.98), with a strong effect of nest sequence ($\beta_{\text{renest}} = -3.28$, $SE = 0.75$, $p < 0.001$). Within known renests, clutches tended to be smaller for nests that were laid later relative to those laid earlier in the season ($\beta_{\text{date}} = -0.09$, $SE = 0.06$, $p = 0.13$). Mean egg volume showed a tendency toward a small change between initial nests and renests, with a mean decline of -2% ($t = 1.57$, $p = 0.139$, $n = 15$ pairs of nests; taxa included four subspecies of dunlin, semipalmated sandpiper, and western sandpiper). When we restricted the DSR model to the subset of nests initiated on the mean day of the season ($n = 313$), declines in DSR over time were still evident, with a negative mean effect of day-of-season for all six species with ≥ 20 nests initiated on the mean day (Supplementary material Appendix 4 Table A4).

Discussion

We used a distributed research network with 16 field sites to conduct comprehensive tests for seasonal patterns in breeding performance of 25 taxa of Arctic-breeding shorebirds across their geographic ranges. Our demographic analyses provide two key insights into drivers of breeding phenology in migratory birds. First, for a subset of our study species, we found substantial seasonal declines in clutch size, incubation duration, and daily survival rate of nests (DSR), along with small declines in egg volume. Second, we found that the conditional probability of each cause of nest failure changed over the season for unsuccessful nests, with a strong decline in the risk of predation accompanied by a sharp increase in the risk of nest abandonment for nests that failed. Our results demonstrate that seasonal declines in breeding performance, and reveal that temporal changes in conditions, rather than among-individual variation in quality, drive seasonal trends in shorebirds.

Some of the strongest seasonal declines we found were in daily survival rates of nests, where 95% BCIs of the estimated effect of day-of-season excluded zero for eight of 22 taxa tested. Most other species also showed negative trends, indicating that seasonal declines in daily nest survival are common in Arctic-breeding shorebirds, as in other birds (Grant et al. 2005). Despite seasonal declines in nest survival, species such as phalaropes that nested late in the season did not have lower DSR than species that nested earlier in the season, suggesting that late-breeding species are adapted to late-season conditions. Alternatively, species unable to breed successfully late in the season may be constrained from evolving unusual mating systems, such as leks, polygyny, and polyandry, which are associated with breeding later in the season (Myers 1981).

In contrast to our finding of linear but not quadratic effects of day-of-season, earlier studies of shorebirds at two of our field sites found quadratic patterns, where daily nest

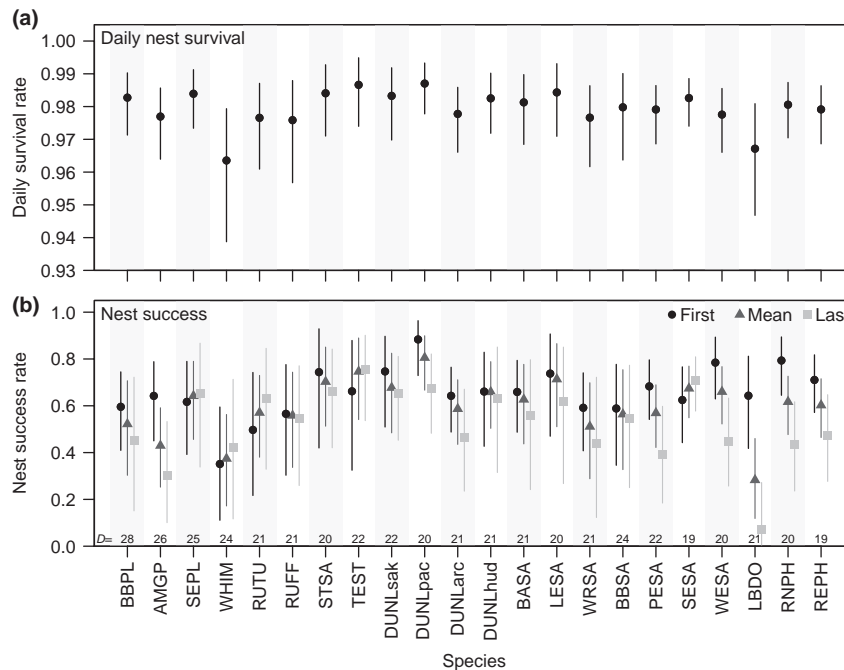


Figure 3. Modeled estimates of nest survival for 21 taxa of Arctic-breeding shorebirds. Estimates are shown for (a) mean daily nest survival rate, DSR, and (b) expected nest success to the end of the day-specific incubation period for nests initiated on the first, mean, or last day-of-season observed for that species. Values are from the posterior distributions from the Bayesian risk-partitioning model for daily survival rate (DSR) and error bars indicate 95% Bayesian credible intervals. Numbers along the horizontal axis in (b) indicate the median estimate of incubation duration for each species (D). Species codes are defined in Table 1.

survival was highest mid-season and lower for early or late nests (Smith and Wilson 2010, Senner et al. 2017). Our finding that daily survival rate declined over time, even within a subset of nests that were initiated on the same day-of-season, also contrasted with a previous study's finding that daily survival increased with nest age (Smith and Wilson 2010). Our analysis indicates that seasonal trends likely resulted at least partly from temporal changes rather than among-individual variation. Such differences in patterns of daily nest survival among studies could be attributable to high variability in breeding conditions among sites and years. While a linear trend described seasonality best in our multi-site, multi-year study, smaller, more specific datasets might find different patterns depending on current local conditions. Further study of the variation in seasonal patterns could shed light on the mechanisms that drive responses to changing conditions.

Predation is typically the main cause of nest failure in arctic shorebirds, so seasonal patterns in nest survival have previously been attributed to changes in predator numbers or activity (Sandercock 1998, Smith and Wilson 2010). In contrast, our results suggest an alternative explanation. We found that the proportion of unsuccessful nests that were depredated declined over the season, but the proportion of all monitored nests that were depredated remained relatively constant. At the same time, of all monitored nests, the proportion that survived declined and the proportion abandoned increased. This pattern of an increase in abandonment, accompanied by no change in the risk of predation, indicates

that the seasonal decline in daily survival rate in our study was largely driven by an increasing risk of nest abandonment by attending parents.

A sharp increase in nest abandonment near the end of the season could be explained by three different processes. First, the increase in abandonment could result from adults abandoning a breeding attempt in favor of maximizing their own survival, as would be expected for long-lived species with high residual reproductive value (Williams 1966). In some birds, parents minimize their own mortality risk by abandoning a breeding attempt upon reaching some physiological threshold, which may be more likely to occur later in the season (Bustnes et al. 2002, Spée et al. 2010). Body mass declines during incubation in shorebirds (Jamieson 2012) and incubation is energetically demanding in the Arctic (Piersma et al. 2003), so declining body condition could prompt an adult to abandon a breeding attempt. Second, for nests initiated relatively late in the season, the benefit of continuing a nesting attempt might be weighed against the optimal timing of migration. Selection for early departure on fall migration could result from predation pressure during migration or temporal trends in food availability at stopover or wintering sites (Schneider and Harrington 1981, Meltofte 1985, Lank et al. 2003, Jamieson et al. 2014). The nests in our study that failed to abandonment, which happened with increasing frequency over the course of the season, therefore could have been deserted by one or both parents to start migration. Individuals might base their decisions not only on

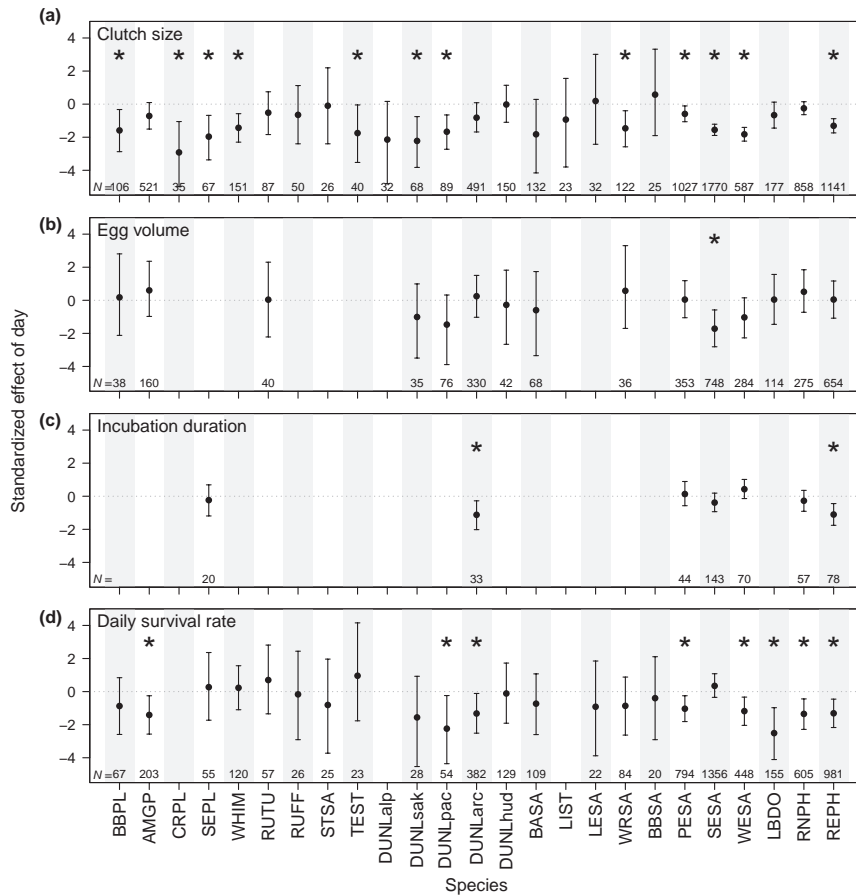


Figure 4. Standardized estimates of the taxon-specific effect of day-of-season on four reproductive traits for 25 taxa of shorebirds. A negative value of the linear effect of day-of-season indicates a seasonal decline in reproductive output. Error bars indicate 95% Bayesian credible intervals, asterisks indicate effects where 95% BCIs did not overlap zero, and numbers along horizontal axes are sample sizes (number of nests; *N*). Data were not available for all species for all analyses. Species codes are defined in Table 1.

the day-of-season, but also on the likelihood of successfully completing a breeding attempt under current conditions.

Third, apparent abandonment of nests could result from mortality of adults that was not detected by field observers. In species with uniparental incubation, predation of the attending adult would result in a nest appearing to have been abandoned. Even in biparentally incubating species, loss of one parent usually results in nest failure, as the remaining adult is unable to complete incubation and deserts the nest (Soikkeli 1967, Erckmann 1981, Miller 1985). Mortality could increase at the end of the season if predation pressure changes, perhaps as a result of increasing energetic demands of the growing offspring of predators or decreasing availability of nesting shorebirds as prey. Seasonal changes in predation pressure on adult shorebirds could also explain seasonal trends in apparent abandonment of nests. When seasonal declines are observed, either mortality of adults or a life-history tradeoff with starting migration at the expense of reproductive success would result in an increasing cost of reproduction as the breeding season progresses, indicating selective pressure to breed early in the season.

Selection for early breeding could in turn underlie seasonality in other reproductive traits. Clutch size showed a clear seasonal decline for 12 taxa and a negative trend where the 95% BCI included zero for another 10 taxa, indicating that seasonal declines in clutch size are nearly ubiquitous for Arctic-breeding shorebirds. Changes in clutch size were not driven by among-individual variation, because known renests had smaller clutches than the first nests laid by the same females, especially when laid later in the season. Previous studies of shorebirds have also reported that late or replacement clutches tend to have fewer eggs (Norton 1972, Sandercock et al. 1999, Jamieson 2011, Gates et al. 2013). Temporal changes were therefore likely driving the seasonal declines we observed. Small and mid-sized shorebirds are income breeders that rely on exogenous nutrients for egg formation (Klaassen et al. 2001), but invertebrate prey abundance generally increased through the egg-laying period for shorebirds at our study sites (Kwon 2016). Seasonal variation in clutch size is therefore unlikely to be driven by food availability in the Arctic. Instead, clutch size may be reduced as a life-history tradeoff, reducing the potential number of offspring but allowing incubation to begin a day or two earlier.

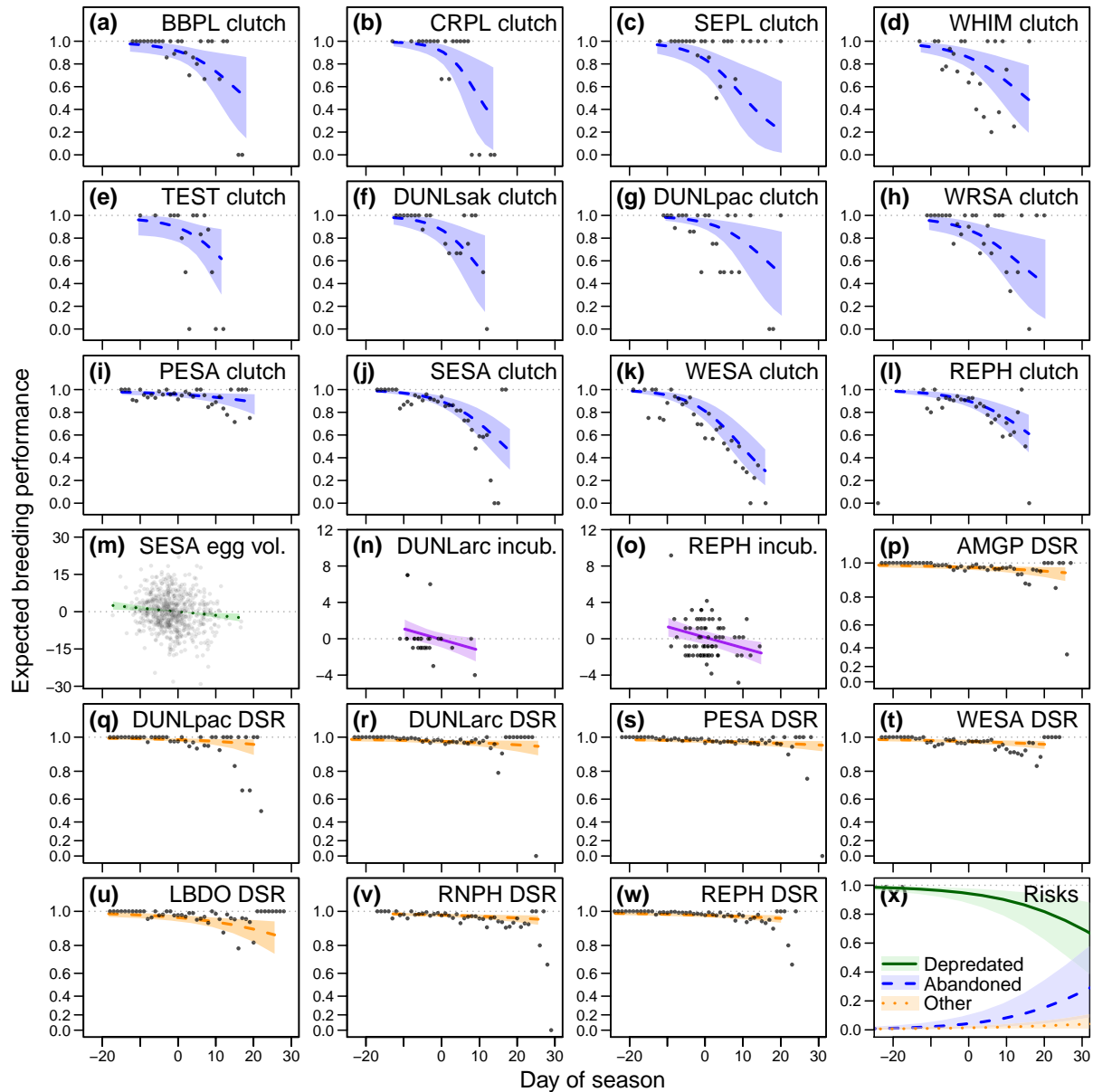


Figure 5. Estimates of seasonal changes in the breeding performance of Arctic-breeding shorebirds. Clutch size (a–l) is given as the probability of laying a four-egg clutch. Egg volume (m) is shown as the percent difference from the species mean. Incubation duration (n–o) is the difference in days from the species median. DSR (p–w) is the daily survival rate during the incubation period, plotted on the log scale for clarity. Risks (x) are the conditional probabilities of the cause-specific risks of failure for unsuccessful nests across all species pooled. Day-of-season is centered on the site- and year-specific mean clutch initiation date for egg volume, clutch size, and incubation duration or mean date of nest monitoring for DSR. Raw data are overlain on the predicted trends; for clarity, raw data were condensed to one value per day-of-season showing the proportion of nests with a four-egg clutch (a–l) or the proportion that survived that day for DSR (p–w). Raw data for egg volume (m) and incubation duration (n–o) are shown as one point per nest. Dotted reference lines on the vertical axis show the mean or median (zero) for egg volume and incubation duration, respectively, and the maximum (one) for clutch size, DSR, and risks. Species (one per panel) are shown only if the 95% BCI of the estimated effect of day-of-season did not overlap zero for a given reproductive trait, and the predicted relationship is shown only for the range of days during which each species nested. Species codes are defined in Table 1.

Advancing the hatch date of the nest would then improve the chance of nest success in the context of seasonal declines in DSR, and could also improve adult survival, especially if nest abandonment is due to adult mortality.

Shortening the incubation period later in the season to hasten the hatching date would also be adaptive given the seasonal declines in DSR and the potential seasonal increase in adult mortality indicated by nest abandonment. We

detected seasonal declines in duration of incubation for *arctica* dunlin and red phalaropes, with a 10–13% reduction from the earliest to latest nests. Seasonal declines in incubation duration have previously been reported for all three species of phalaropes, all of which employ uniparental incubation and thus may be more sensitive to ambient temperature or other extrinsic factors (Reynolds 1987, Schamel and Tracy 1987, Colwell and Oring 1988). In contrast, dunlin employ biparental incubation, which results in constant nest attendance and consistent rates of egg development (Norton 1972, Bulla et al. 2014, 2016). Shorebird parents can affect incubation duration by adjusting the temperature at which eggs are incubated (Cresswell et al. 2003, Reneerkens et al. 2011), so shortening the incubation period could be an adaptive response to seasonal conditions. If invertebrate prey emerge earlier when temperatures are warmer (Tulp and Schekkerman 2008), hastening hatching would improve the ability of chicks to find prey at a time when food limitation could reduce chick survival (Senner et al. 2017; but see also McKinnon et al. 2012). Late-hatched chicks in our study system are less likely to survive to fledging than earlier chicks (Ruthrauff and McCaffery 2005, Hill 2012), providing further support for an advantage of hastening hatching later in the season. However, our dataset also indicates that adjusting incubation duration is unusual among Arctic-breeding shorebirds, as most species showed no seasonal changes.

We detected a small seasonal decline in egg volume for only one species (semipalmated sandpiper). Arctic-breeding shorebirds might therefore primarily adjust clutch size in response to changing conditions, while keeping egg size nearly constant. We found some evidence for seasonal changes in egg volume within individual females, but individual changes (mean = -2%) did not fully account for the seasonal declines (mean = -5%). The small, nonsignificant decline we found between initial nests and renests is consistent with previous reports that within-individual variation in egg size is limited in most birds (Christians 2002). The seasonality we observed in egg volume for semipalmated sandpipers might therefore primarily reflect among-individual variation. Yearling semipalmated sandpipers lay later and produce smaller eggs than older females (Gratto et al. 1983), so female age could partly explain the seasonal declines we found. In small-bodied shorebirds, the total mass of the clutch can approach or equal the female's body mass (Colwell 2006), so egg volume may be more likely to be constrained by individual quality in small-bodied species than in the larger shorebirds in our dataset.

While most species showed evidence for a seasonal decline in clutch size, declines in other reproductive traits were not observed in the majority of species. In some cases, the lack of an effect could have resulted from low statistical power, as we had relatively small samples for some species. However, in some species with large sample sizes (> 100 nests), we still found no evidence of seasonality. Only one of 8 species with > 100 nests showed a seasonal decline in egg volume, suggesting that egg volume is relatively constant within species of Arctic-breeding shorebirds. Seven of 11 species with

> 100 nests showed seasonal declines in daily nest survival rates, but the other four showed no evidence of a negative trend. Our dataset therefore indicates among-species variation in how shorebirds respond to seasonal pressures. There was no apparent association between seasonal declines and other life history traits, such as parental care system, migration distance, or phylogeny. However, our findings indicate that some species are robust to changing conditions during the breeding season and are not under selective pressure to curtail breeding attempts later in the season, at least under the range of conditions that occurred during our study.

In conclusion, we show that seasonal declines in reproductive traits occur in many, but not all, species of Arctic-breeding shorebirds. When present, seasonal declines are likely primarily driven by temporal changes, rather than among-individual variation in quality. A seasonal decline in nest success, driven by an increase in the probability of nest abandonment revealed by our risk-partitioning model for nest survival, indicates a life-history tradeoff between reproduction and adult survival, either on the breeding grounds or later in the annual cycle. The fitness advantage of early breeding may also drive progressively smaller clutches and shorter incubation over the course of the season. Together, our findings provide some of the clearest evidence that migratory birds adjust multiple components of fecundity in response to selective pressures that may be acting on adult survival, resulting in life-history tradeoffs with consequences for reproductive success. However, seasonal declines were not observed in all species, so life-history tradeoffs might affect fecundity for only a subset of Arctic-breeding shorebirds.

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Supplementary material (Appendix JAV-01531 at <www.avianbiology.org/appendix/jav-01531>). Appendix 1–4.