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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 23 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 decline 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 for maintaining high reproductive output throughout the season. 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 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). 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 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 the time of the year. In some cases, individuals initiate but curtail breeding attempts late in the season (Gratto-Trepano 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 residual reproductive value (Sæther and Bakke 2000). Temporal patterns in conditions on the breeding grounds and 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 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 in response to environmental cues that could be used to optimize the timing of arrival at the breeding grounds (Coppack et al. 2003, 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 for maintaining high reproductive output throughout the season. 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 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). 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 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 the time of the year. In some cases, individuals initiate but curtail breeding attempts late in the season (Gratto-Trepano 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 residual reproductive value (Sæther and Bakke 2000). Temporal patterns in conditions on the breeding grounds and 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 are well supported and not mutually exclusive (Verhulst and Nilsson 2008, Pärt et al. 2017).

Previous studies have reported seasonality in reproductive parameters of several species of Arctic-breeding shorebirds (Mclean 1972, Reynolds 1987, Schamel and Tracy 1987, Sandercock 1997, 1998, Sandercock et al. 1999, Andersson et al. 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 (McCaery and Ruthrau 2004, Senner et al. 2017). Most Arctic-breeding shorebirds have broad geographic distributions, so multi-site studies are needed to constrain 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 field sites in Alaska, Canada, and Russia (Lanctot 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 the 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 by incubating 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.

## Methods

We monitored shorebirds at 16 field sites in arctic and subarctic habitats of North America and Russia (Figure 1, Supplementary material Appendix 4 Table A1). In 2012 and 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 with a 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 and analyses.



Figure 1. Locations of 16 study sites in arctic Russia, Alaska, and Canada. Breeding ecology of shorebirds was monitored for 3–7 years 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 (Weiser et al. 2016). We recorded individual identities of parents when possible, and identified known renests when at least one parent was observed attending a different nest earlier in the season. In sandpipers with biparental incubation, 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 renesting in Dunlin (Gates et al. 2013). We expected our dataset to underestimate the frequency of renesting (Naves et al. 2008, Gates et al. 2013), but our intention was not to examine renesting probability at a population scale. Instead, we used known renests 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.

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 determined 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 own 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, were not 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 retended as abandoned given that it was unattended. We recorded the 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 to predation) did not change our conclusions (results not shown).

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 parameters based on small numbers of nests, so we used our own estimates of median incubation duration for each species to provide statistical power for our tests of each response variable. We restricted each analysis to species with complete data. Each model also used hyperpriors ('prior priors', i.e. priors that define the distribution of other priors) 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 nest clutch size as a binary variable (0 or 1) based on whether a nest contained 4 or fewer 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 multivariate normal 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

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

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, or failed to other causes, or unknown based on our observations. We modeled 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 on any given day was given as alive, predated, abandoned, or failed to other causes, or unknown based on our observations. Our DSR model allowed for staggered entry and exit of nests and estimated

For each reproductive trait, we were interested in assessing the effect of covariates on the probability of survival and two 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 trait 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 refactored the centered date value as 'day-of-season' hereafter, with day of

multiple 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 and quadratic 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 was 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 Johnson (1979, Bart and Robson 1982, Dinsmore 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 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 (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 on any given day was given as alive, predated, abandoned, or failed to other causes, or unknown based on our observations. Our DSR model allowed for staggered entry and exit of nests and estimated success of covariates on the probability of survival and two 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 trait 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 refactored the centered date value as 'day-of-season' hereafter, with day of multiple 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 and quadratic 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 was 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 Johnson (1979, Bart and Robson 1982, Dinsmore 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 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 (whether the nest survived or failed), and for nests that

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 by Gelman–Rubin statistics of 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 the 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 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 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

19 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 = 0.35, n = 7804 nests), and 87.7% of nests had a natal 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 11 taxa, and median incubation duration ranged from 19 d for 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. Multiple 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 of 0.39–0.76 across taxa (Fig. 3b, dark gray triangles). Of 532 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), nest abandonment (10%), and other causes (failure to hatch a egg, 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  $p_{\text{pred}} = 0.94$  (SD = 0.03),  $p_{\text{aband}} = 0.04$  (SD = 0.02), and  $p_{\text{other}} = 0.01$  (SD = 0.01) for nests that failed. The proportion of nests predated 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 (> 100), we found no evidence for seasonal declines, such as clutch size of dunlin; mean egg volume of American golden-plover; and incubation duration of 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  $\geq 20$  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).

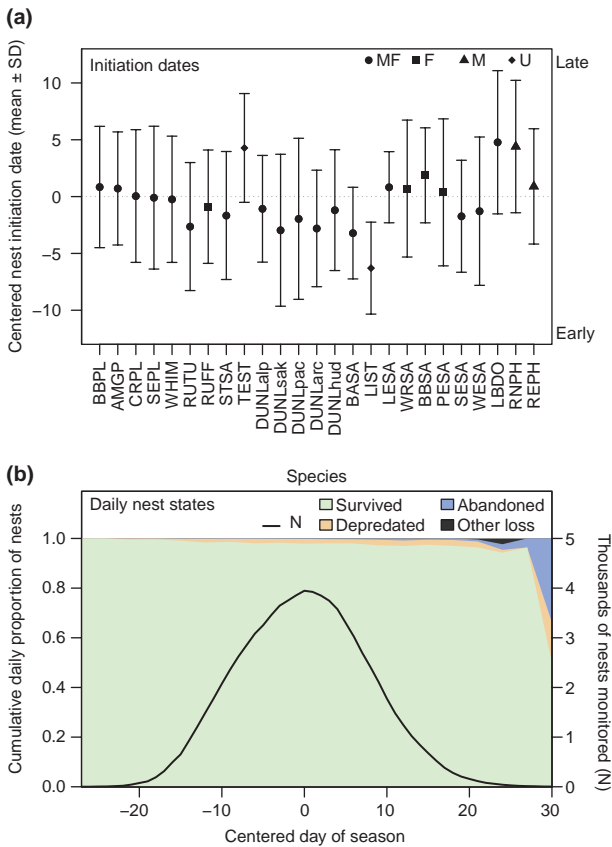


Figure 2. Breeding phenology of 25 taxa of shorebirds at 16 arctic sites. (a) Mean clutch initiation date for each species, relative to the site- and year-specific mean initiation date across all species. Species codes are defined in Table 1 and symbols indicate the incubation system of the species: 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, 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, 53 (1.3%) were known renests. We recorded the natal clutch size for matched pairs of nests in 44 cases for five species (dunlin (n=9 nests across all subspecies), pectoral

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  $-2\%$  ( $\beta = -1.57$ ,  $p = 0.139$ ,  $n = 15$  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=13), 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 are widespread but not ubiquitous in Arctic shorebirds, 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 sites found quadratic patterns, where daily nest



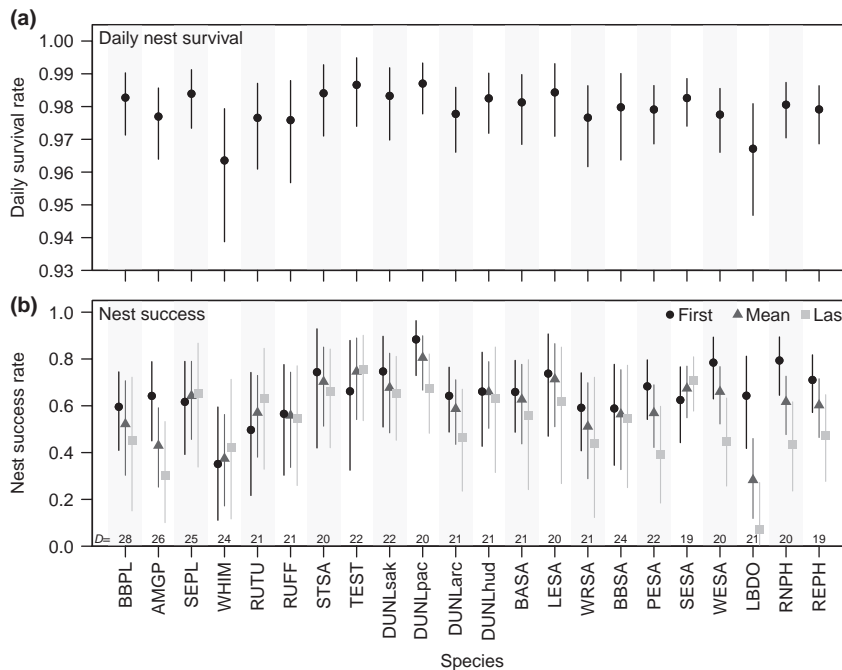


Figure 3. Modeled estimates of nest survival for 21 taxa of Arctic-breeding shorebirds. Estimates are shown for (a) mean daily nest survival rate, DSR, and (b) expected nest success to the end of the day-specific incubation period for nests initiated on the first, mean, or last day of-season observed 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 incubation duration for each species. Species codes are defined in Table 1.

survival was highest mid-season and lower for early or late in the season. The seasonal decline in daily survival rate in our study was largely driven by an increasing risk of nest abandonment over time, even with attending parents.

Our results contrast with a previous study's finding that daily survival increased with nest age (Smith and Wilson 2010). 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 cases, 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 the 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 previously been attributed to changes in predator numbers or activity (Sandercock 1998, Smith and Wilson 2010). Optimal timing of migration. Selection for early departure on migration could result from predation pressure during wintering sites (Schneider and Harrington 1981, Meltofte 1985, Lank et al. 2003, Jamieson et al. 2014). The nests in the study that failed to abandonment, which happened with an 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

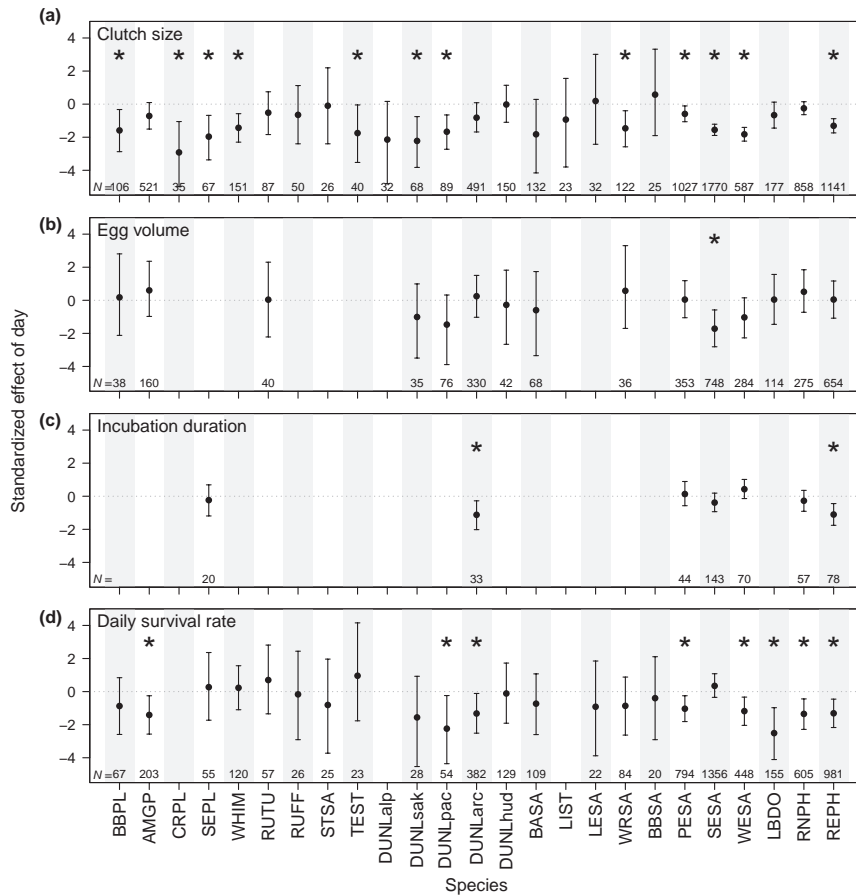


Figure 4. Standardized estimates of the taxon-specific effect of day-of-season on four reproductive traits for 25 taxa of shorebirds. A negative value of the linear effect of day-of-season indicates a seasonal decline in reproductive output. Error bars indicate 95% Bayesian credible intervals, asterisks 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 successful selection for early breeding could in turn underlie seasonal changes in other reproductive traits. Clutch size showed a seasonal decline for 12 taxa and a negative trend where apparent abandonment of nests could result from a seasonal decline in clutch size for another 10 taxa, indicating that mortality of adults that was not detected by field observations. In species with uniparental incubation, predation on the attending adult would result in a nest appearing to be abandoned. Even in biparentally incubating species, loss of one parent usually results in nest failure and the remaining adult is unable to complete incubation and the same females, especially when laid later in the season, deserts the nest (Soikkeli 1967, Erckmann 1981, Milne 1985). Mortality could increase at the end of the season if replacement clutches tend to have fewer eggs (Norton 1972, Gates et al. 1999, Jamieson 2011, Gates et al. 2013). Temporal changes were therefore likely driving the seasonal trends or decreasing availability of nesting shorebirds as prey becomes scarce. Small and mid-sized shorebirds are often the 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 mortality of adults or a life-history trade-off 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. Instead, clutch size may be reduced as the breeding season progresses, indicating selective pressure to breed early in the season but allowing incubation to begin a day or two earlier.

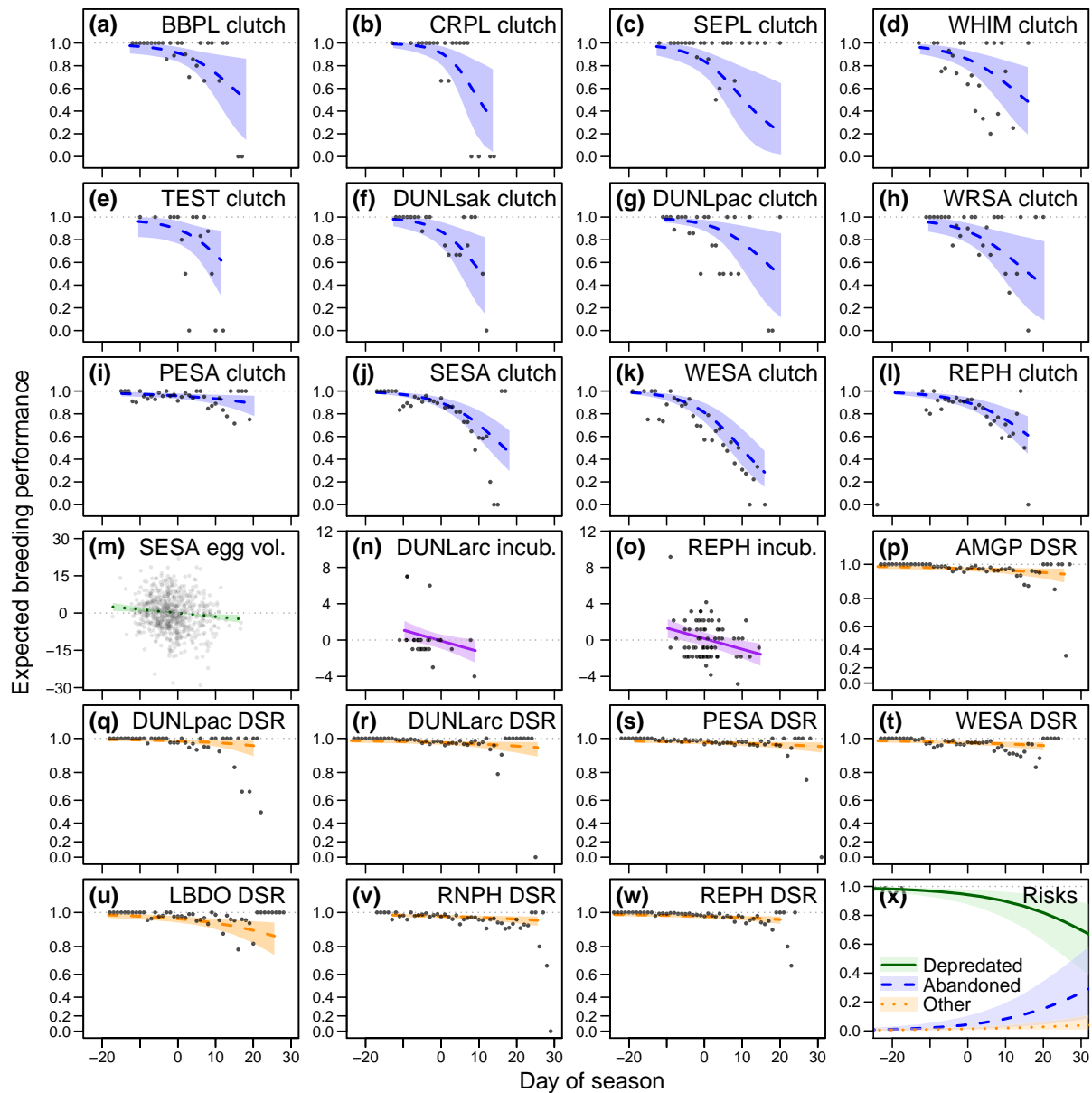


Figure 5. Estimates of seasonal changes in the breeding performance of Arctic-breeding shorebirds. Clutch size (a–l) is given as the proportion of laying a four-egg clutch. Egg volume (m) is shown as the percent difference from the species mean. Incubation duration (n–o) is shown as the difference in 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. The day of season is centered on the site- and year-specific mean clutch initiation date for egg volume, clutch size, and incubation duration or the 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 DSR. 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 nest later in the season 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  $> 100$  nests showed seasonal declines in daily nest survival (mean = -10%, range = -13% to -5%), but the other four showed no evidence of a negative trend. 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, Schamelle 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 (North 1972, Bulla et al. 2014, 2016). Shorebird parents can adjust 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 (Tuljapur 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 McKinnon et al. 2012). Late-hatched chicks in our study system are less likely to survive to fledging than earlier chicks (Ruthra and McCaery 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 in egg volume.

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 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 ( $n \geq 100$  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

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Supplementary material (Appendix JAV-01534) at [www.avianbiology.org/appendix/jav-01534](http://www.avianbiology.org/appendix/jav-01534). Appendix 1–4.