Correlates of Annual Stopover Counts in Two Species of Arctic-Breeding Shorebirds: Roles of Local, Breeding, and Climatic Drivers

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Correlates of Annual Stopover Counts in Two Species of Arctic-Breeding Shorebirds: Roles of Local, Breeding, and Climatic Drivers

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Abstract.—Long-term surveys at stopover sites provide measures of abundance (counts) that are commonly used to assess the status of shorebird populations. We analyzed a 29-year time series of counts of Western Sandpiper (*Calidris mauri*) and Least Sandpiper (*C. minutilla*) conducted during southward migration from 1990 to 2018 at a small stopover site on Sidney Island, British Columbia, Canada, and examined correlations between counts and conditions local to the site, on the breeding grounds, and large-scale climatic indices. Annual counts varied from 0 to ~4,000 birds, and did not show strong long-term trends over the study period. Counts were most strongly associated with conditions on breeding grounds or large-scale climatic indices, rather than local weather variables, suggesting counts of juvenile shorebirds could serve as an index of reproductive success. Further, counts of juveniles and adults were positively correlated in the same year for both Western and Least sandpipers, indicating a common underlying process determining the abundances of the two age classes at this site. Across the 29-year study period, Sidney Island has remained a consistently used and locally important stopover site for both adults and juveniles of both shorebird species. *Received 31 October 2019, accepted 5 October 2020.*

Key words.—Arctic-breeding shorebirds; hierarchical modelling; fall migration; migratory surveys; stopover counts; wader migration

Standardized and structured long-term monitoring of migratory stopover sites can provide valuable information for conservation efforts (Gilchrist *et al.* 2005; Likens and Lindenmayer 2018). The value of such programs includes the ability to put any annual or short-term changes into a broader temporal context, and thus help differentiate cyclical processes from population declines (Catry *et al.* 2011). Counts of shorebird abundance conducted at stopover sites are commonly used to assess population size or trends, as they allow the opportunity to survey large proportions of a population in a limited amount of space and time. However, such counts can be shaped by factors other than population size (Ydenberg *et al.* 2004; Hope 2018; Hope *et al.* 2020), and such effects must be disentangled before inferences can be made about population trends.

Western (*Calidris mauri*) and Least (*C. minutilla*) sandpipers are small shorebirds (~ 25 g) that breed in the Arctic, tundra, and boreal regions of North America and Russia (Nebel and Cooper 2008; Franks *et al.* 2014). Western Sandpipers have a re-stricted breeding distribution in northwestern Alaska (Franks *et al.* 2014), whereas Least Sandpipers have a broad breeding distribution that extends from inland Alaska across northern Canada to Atlantic Canada (Nebel and Cooper 2008). The two species have different rankings of conservation concern (Hope *et al.* 2019). Western Sandpiper is a species of high conservation concern due to declines from the 1980s to 2010s at both migration and non-breeding areas (Canham *et al.* 2020; Warnock *et al.* 2020), whereas Least Sandpipers appear to have a more stable population trends (Andres *et al.* 2012). The two age classes (adult and juvenile) of both species migrate southward during different months of the year. Following nesting on the breeding grounds, adults abandon their young around fledging to depart southward (Nebel and Cooper 2008; Jamieson *et al.* 2014), and juveniles follow about one month later, with little overlap between age classes at stopover sites (Butler *et al.* 1987; Butler and Kaiser 1995). As a reduced adult population likely will produce fewer juveniles, the number of adult and juvenile birds counted

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per year at southward staging sites should be linked. However, adult and juvenile behavior while at stopover sites can be very different, due in part to differences in morphology, physiology, individual levels of experience, and conditions through which different age classes migrate (Lank *et al.* 2003; Hope *et al.* 2011; Hope *et al.* 2014), as well as the final destinations of juveniles and adults in non-breeding locations (O'Hara *et al.* 2005; Nebel 2006; Mathot *et al.* 2007). Therefore, it remains uncertain if abundances of adults and juveniles at stopover sites should covary or be independently shaped by differing factors.

Counts of adult and juvenile shorebirds at stopover sites are affected by local weather, conditions on the breeding grounds, and broad-scale climatic conditions. Local weather such as temperature and precipitation can affect food availability at foraging areas, and wind strength and direction will affect birds' decision to settle or keep moving. Annual conditions on the breeding grounds and on migration that precedes arrival to stopovers also vary widely (Niehaus and Ydenberg 2006; Mellone *et al.* 2011; Jamieson *et al.* 2014; Kwon *et al.* 2018). For Western Sandpipers, cooler temperatures during pre-laying periods can lead to later clutch initiation dates (Kwon *et al.* 2018). Female Western Sandpipers will abandon late-hatching clutches, and this effect is strongest in cooler years or those with late snowmelt dates (Jamieson *et al.* 2014). Longer, earlier breeding seasons have been associated with greater breeding success (Meltofte *et al.* 2007), and lower average temperatures have been associated with higher energy demands, reduced food availability, and higher mortality for young shorebirds (Schekkerman *et al.* 1998; Tulp and Schekkerman 2008). Snowmelt dates can influence migratory decisions by sandpipers. Earlier snowmelt is linked with earlier migration of Peregrine Falcons (*Falco peregrinus*), important predators for shorebirds, making the juvenile migration much more dangerous, which may make a small dangerous site less favourable in years when snowmelt is earlier (Niehaus and Ydenberg 2006; Hope *et al.* 2011; Hope *et al.* 2014; Hope 2018).

Snowmelt dates can also affect the chance of an individual sandpipers' or population-level phenological mismatch (Kwon *et al.* 2019). Poor breeding conditions could lead to a reduced number of juveniles surviving to migration, increased early abandonment of young by adults, or even reduced adult survival (Nol *et al.* 1997; Meltofte *et al.* 2007; Smith and Wilson 2010). The annual conditions can also affect migratory strategies and stopover site selection and will affect stopover counts (Hope 2018).

In this paper, we examined annual counts of Western and Least sandpipers during southward migration at a small stopover site in British Columbia, Canada, from 1990 to 2018. In particular, three questions around abundances of Least and Western sandpipers at our monitoring site on Sidney Island were examined: (1) Has there been any systematic change in counts across the 29-year period of surveys? (2) Are annual counts of each age-class and species driven by local conditions, conditions on the breeding grounds, or broad-scale climatic conditions? (3) Is there a correlation between annual variation in counts of adults and juveniles of the two species? We used hierarchical models to answer these questions and an information-theoretic approach to assess support for each of the factors affecting annual counts at stopover.

METHODS

Study Site

Sidney Island (48° 37′ 48″ N, 123° 19′ 48″ W) is in the unceded traditional territories of the Coast Salish peoples, known as Á,LEṈEṈEȻ ȽTE (W̱SÁṈĆ; Elliott 1990; Wong *et al.* 2020; use of capital letters in Indigenous names (SENĆOŦEN alphabet)), and lies 4 km off the coast of Vancouver Island in southwestern British Columbia, Canada (Fig. 1). Southbound Western and Least sandpipers stopover at SK̓ŦÁMEN (Sidney Island Spit) and SK̓ELT-ÁMEN (north end of Sidney Island) within Sidney Spit Marine Park, part of the Gulf Islands National Park Reserve, roosting and feeding along the sandspit and within a 96 ha lagoon that encompasses mudflats, beds of eelgrass (*Zostera marina*), and saltmarsh at the northwest end of the island (Butler *et al.* 1987). These two species are the most numerous shorebirds using the area during southward migration. Adults precede juveniles, arriving at the end of June
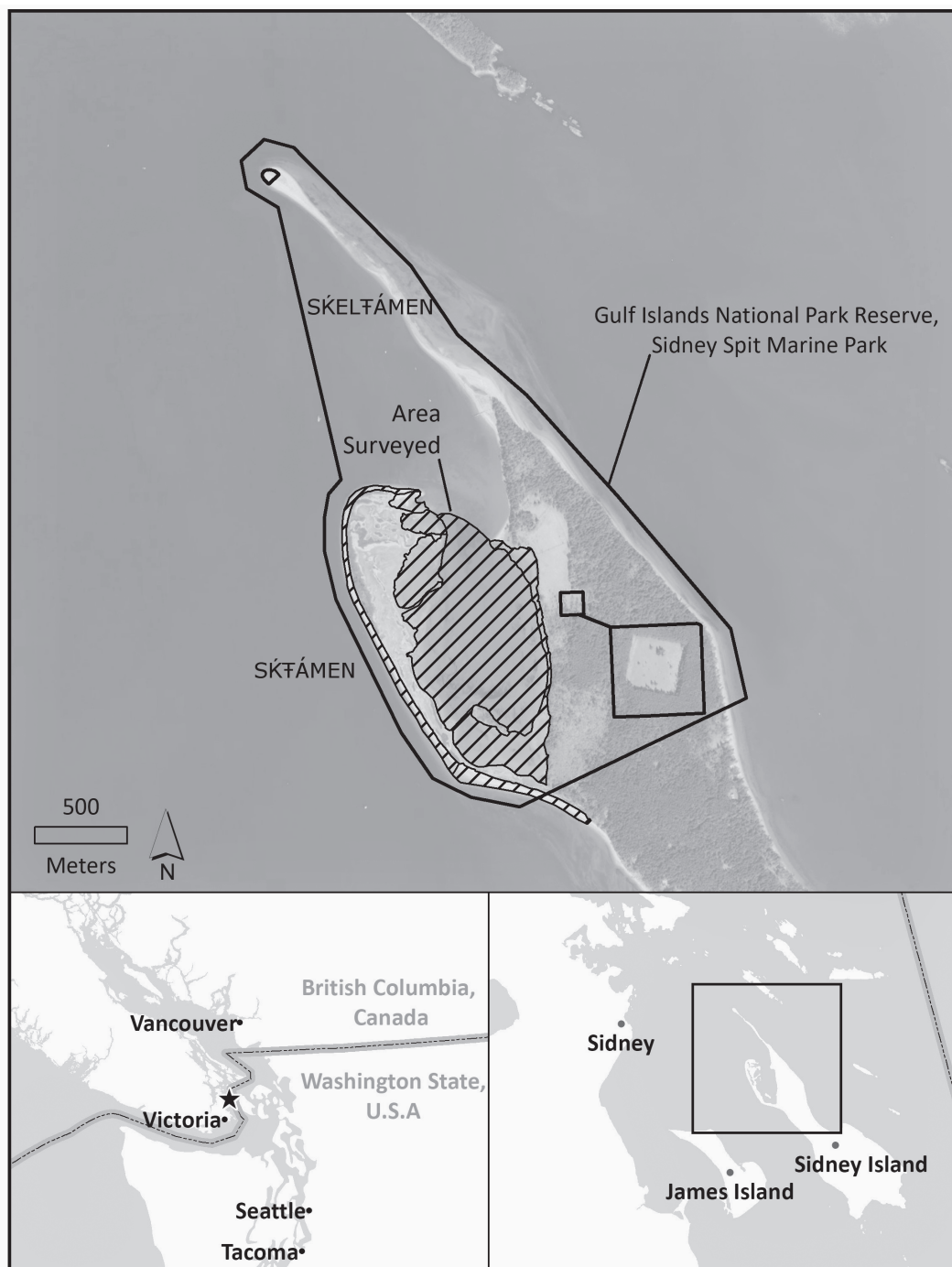
Figure 1. Map of study site on Sidney Island, British Columbia, Canada, where Western (*Calidris mauri*) and Least (*C. minutilla*) sandpipers were counted during southward migration, July and August, from 1990 to 2018. Lower left panel indicates location of study site within the broader Salish Sea area; star denotes location of Sidney Island. Lower right panel indicates location of study site with nearby geographical features noted. Upper panel indicates survey area, and park boundaries. Indigenous place names are included; note use of capital letters in the SENĆOŦEN alphabet.

and throughout July and remaining for 4-12 days (Hope *et al.* 2011); few adults remain by end of July. Juveniles reach the site in late July and early August with their numbers trailing off in early September. As a result, the site experiences a transition from purely adult to purely juvenile flocks over the course of the season.

In Western Sandpipers, residence time (length of stay) of birds at the site show two distinct patterns. First, within each season, adult lengths of stay increase throughout July, with lengths of stay at the end of July being almost double that of the birds that arrive at the start of July. Juvenile lengths of stay decrease seasonally, with the later arriving birds having the shortest lengths of stay (Hope *et al.* 2011). Secondly, between 1992 and 2001, average lengths of stay decreased from 8.4 days to 2.7 days; no length of stay information exists for the site since 2001 (Ydenberg *et al.* 2004).

Survey Methods and Effort

Counts were conducted in 27 of the 29 years from 1990-2018. No counts occurred in 1991 or 2014. Counts were conducted daily during the migration period between 1990 and 2001. Survey effort from 2002 onwards

was then reduced to counts conducted weekly. The typical survey window within each year extended from 15 July-26 August, but varied each year due to logistical considerations (start range: 7 July-15 July; end range: 26 August-9 September). In 6 years (1994, 2001, 2003, 2004, 2006, 2011), surveys began in the last week of July or the first week of August and covered the tail end of adult migration and the entire juvenile migration (Fig. 2).

Counts were conducted during the low tide of the day, when shorebirds were feeding in the exposed mudflat of the lagoon, though the amount of mudflat exposed varied based on the tidal heights. Observers walked along the shore of the lagoon, stopping periodically at vantage points to look for birds, with the aim of conducting a complete area search. Counts were made with the unaided eye, through binoculars, and with a 20-60X zoom spotting scope, depending on the proximity of the birds. All individuals in small flocks were counted, and numbers of birds in large flocks were estimated by counting in groups of 5, 10, 50 or 100 according to flock size in each successive field of view across a scan of the entire flock. Given the geography of the site, all individuals within the lagoon could be counted.
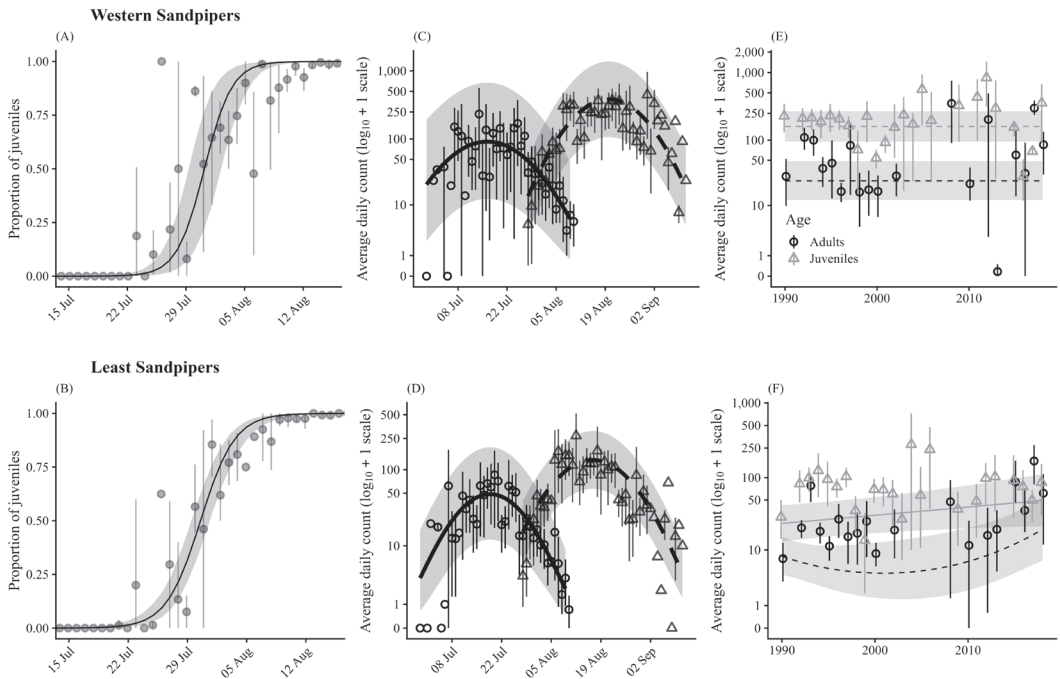
Figure 2. Seasonal patterns and interannual trends in counts of Western Sandpipers (*Calidris mauri*) and Least sandpipers (*C. minutilla*) at Sidney Island, British Columbia, Canada, from 1990 to 2018. Panels (A) and (B) depict the seasonal turnover in age classes of birds, as proportion of juveniles in flocks. Panels (C) and (D) depict seasonal patterns of abundance of adults (circles) and juveniles (triangles). Mean annual estimated abundances are shown on a log10 + 1 scale to include zero counts. Panels (E) and (F) depict interannual trends in counts for adults (circles) and juveniles (triangles). Mean annual estimated abundances are shown on a log10 + 1 scale to include zero counts. Lines show trend in abundance with associated 95% confidence intervals, estimated from top models. In all panels, points indicate mean ± 95% confidence intervals of observed values, and lines show the mean estimated trend with associated 95% confidence intervals.

From 1990 to 2001, counts were occasionally conducted more than once in a day, and the largest total count was used as the daily estimate for these days.

For smaller flocks, we were able to identify all individual birds to species and age-class. Sub-samples from larger flocks were also aged (adult or juvenile) and identified to species. Birds were aged by plumage characteristics (Prater *et al.* 1977). Adult Western Sandpipers were distinguished from juveniles by the dark chevron markings present along the sides and breast. Juvenile Least Sandpipers have a buffy breast compared to the distinct, darker one of the adult, and juveniles have bright rufous scapulars compared to the drab feather-edges of the adults. In both species, juvenile plumage appears brighter and cleaner than adult plumage, which is more worn and tattered.

Species Composition within Unknown Flocks

Identification of birds to species was not always possible for flocks of birds seen at a distance. We did not expect the relative proportion of Least to Western sandpipers to follow any pattern over the course of the migratory period, and therefore these were not modelled, and we used the observed species proportions of identified birds for each count-day to infer total flock composition on that day (Bishop *et al.* 2000; Drever *et al.* 2014). Estimated counts were added to the number of known birds to produce a total estimated species count for the given count-day. Based on a sensitivity analysis, we limited subsequent analyses to surveys where at least 20% of birds counted were identified to a species level. The sensitivity analysis involved running all the models described below while adjusting the threshold to include surveys between all birds identified to species and none of the birds identified to species. We determined that limiting included surveys to those with at least 20% identified to species avoided strongly biasing parameter values.

Modeling Age-Class Composition

The proportion of known-age adults and juveniles of each species recorded on a given count-day was used to model the age-class turnover for each year and species. Generalized linear mixed-effects (GLMM; Bates *et al.* 2015) models were fit to the dataset using a binomial distribution to model the probability of a bird being a juvenile as a function of day-of-the-year (DOY; fixed effect) that was allowed to vary by year (by including both DOY and year as random factors). Model fit was assessed by arcsin transforming observed and predicted proportions, regressing them against each other and visually assessing the residuals. We used the modeled probability of a bird being a juvenile on a given date and year to predict the proportion of adults and juveniles of each species within surveyed flocks across all count-days in the dataset. The model average was used to impute proportions for four years where age-class data for both species was inadequate (1998, 1999, 2012, and 2013; online Appendix Fig. A1.1). In our analyses, we modelled species and age classes independently and did not propagate error between the age class models

(Equation 1) and the model of abundances (Equation 2). Additionally, we do not quantify a measure of error around our estimates of daily species proportions. These decisions were driven by data limitations, but could lead to underestimates of error in our models and have the potential for biases in results. We examined the patterns of proportions species and age-classes observed across the data set and determined them to be unlikely to cause biases in the results.

Modelling seasonal variation in abundance

We modelled seasonal variation in abundances separately for each species and age class. Age and species counts for each date were generated by taking the total number of birds counted (both identified and non-identified birds), multiplied by the proportion of birds identified to species that were identified as that species, multiplied by the estimated daily proportion of a given age class for each species, such that:

$$z_{saij} = y_{ij} \, p^*_{sjt} \, p_{saij}$$

$$p^*_{sjt} = \frac{y^*_{\{s\}ji}}{y^*_{\{s=0\}ji} + y^*_{\{s=1\}ji}} \tag{1}$$

The estimated abundance (z_{saij}) for each species (s) and age class (a) on a given DOY (j) and in a particular year (i) was calculated from the total count y_{ij} (which includes both individuals identified to species and those not identified to species). The total number of birds counted (y_{ij}) was multiplied by the modelled proportion (p_{saij}) of species s in age class a as described in the previous section and by the proportion of all birds identified to a species which were classified to species s on that date (p^*_{sjt}). The daily proportion of birds identified to species (p^*_{sjt}) is calculated as the total number of birds on a day and year identified to a given species (s) divided by the total number of birds identified as either Western Sandpipers ($y^*_{\{s=0\}ji}$) or Least Sandpipers ($y^*_{\{s=1\}ji}$). These values do not include birds counted, but which could not be distinguished between Western and Least sandpipers.

To avoid biasing our results from variation in survey effort, we eliminated a portion of the data. We eliminated the tails of each migration period by limiting the data for each age group to dates that included the 99th quantiles of all birds counted (adults before 8 August (DOY = 221); juveniles after 27 July (DOY = 207)). Data were bounded on the outer ends of the migratory curve by survey timing, so we did not filter the data for early adults or late juveniles. As survey effort was lower after 2001, we limited the analysis to years with at least three surveys within each age group's migration period (adult vs. juvenile), which resulted in the inclusion of more years for juveniles ($n = 24$) than for adults ($n = 19$).

The baseline model for each species and age class included a quadratic trend in DOY and a random intercept parameter for each year.

$$z_{saij} \sim NB(\lambda_{saij}, \phi_{sa})$$
$$\log(\lambda_{saij}) = \beta_{2sa} x_{saij} + \beta_{2sa} x^2_{saij} + \alpha_{sai} \tag{2}$$
$$\alpha_{sai} = N(\mu_{asa}, \sigma^2_{asa})$$

Where z_{saij} is the daily estimated count for a given species *s*, age class *a*, year *i*, and day of year *j* as described in Equation 1, x_{saij} is the DOY, and α_{sai} is the annual random effect of year. It is important to note that independent models were run for each age class and species. We centered and rescaled the day of year (*x*) value within each age and species group by subtracting from the average date and dividing by twice the standard deviation of the survey dates within that group. Counts were modelled using a negative binomial distribution (NB) with a log link due to strong overdispersion (ϕ) and a tendency for the variance to increase quadratically with the mean. Adult Western Sandpiper counts were zero-inflated, and therefore we included a zero-inflation parameter in their model ($z_{saij} \sim ziNB(p_{sa}, \lambda_{saij}, \phi_{sa})$ replaces the first line of Equation 2). The other age and species groups were not zero-inflated enough to warrant inclusion in the model. We compared the support for alternative distributions (Poisson; Zero-inflated Poisson), but found the negative binomial to be the most appropriate for the data based on patterns of variance in residuals from the baseline model.

In subsequent analyses, we modified the baseline model (Equation 2) by adding a parameter for an interannual trend across years and parameters associated with annual conditions to identify the conditions that impact annual counts of each age-class and species. Each modified model therefore included the baseline model plus one or more additional additive parameters. We visually inspected the residuals for each year to ensure years with fewer surveys were not driving any of the patterns associated with annual conditions.

Question 1: Annual Trends in Abundance

We tested whether annual abundances of shorebirds at the site showed trends over the study period. A previously documented decline in counts at the site occurred from 1990-2001 (Ydenberg *et al.* 2004). We examined whether counts had continued to decline since 2001 (linear) or recovered (quadratic). For both species and age classes, we examined trends in counts across years using (1) a linear change between 1990 and 2018; or (2) a quadratic fit ('Year' + 'Year^2'). The linear and quadratic models are essentially the baseline model (Equation 2), plus a linear or quadratic terms.

Question 2: Drivers of Shorebird Abundance (Local, Breeding, Global)

We examined a set of broad hypotheses to explain annual variation in abundances for adult and juvenile Western and Least sandpipers, which were considered in 18 models (Table 1). Each explanatory variable was deemed likely to affect a number of factors, including reproductive success, timing of breeding, migrant flight trajectory between Alaska, USA and British Columbia, Canada, or stopover decisions within the local region around Sidney Island, Canada (Table 1). Patterns across the period of surveys are shown in online Appendix Fig. A2.1. Each model included the baseline parameters (Equation 2), plus one or more additional parameters depending on the hypothesis under consideration.

Local climate conditions. To explore the role of local conditions around Sidney Island in shaping annual counts, we ran six models that used weather data collected from the Victoria International Airport at Sidney, British Columbia, Canada located 8 km from the study site (48° 38′ 50″ N, 123° 25′ 33″ W; Environment and Climate Change Canada (ECCC) 2018). We ran one model that included each of the mean estimates of the wind component vectors ("u" and "v") and that included both variables and their interaction. Positive

Table 1. Suite of models relating migration counts of adult and juvenile Western (*Calidris mauri*) and Least (*C. minutilla*) sandpipers to local conditions at the stopover site, conditions on the breeding grounds, and broad-scale climate indices. Counts were conducted at Sidney Island, British Columbia, Canada, from 1990 to 2018.

Number	Model Name	Model Type
1	Baseline (seasonal) model (no interannual trend)	Interannual
2	Linear interannual trend	Interannual
3	Quadratic interannual trend	Interannual
4	Local temperature	Local
5	Local total precipitation	Local
6	Local horizontal wind vector (u)	Local
7	Local vertical wind vector (v)	Local
8	Local wind vectors (u & v)	Local
9	Full local weather model (wind, temperature, precipitation)	Local
10	Day of Alaskan snowmelt	Breeding
11	Mean daily minimum temperature (2nd half May)	Breeding
12	Mean daily minimum temperature (June)	Breeding
13	Full breeding conditions (snow melt, temperature May, temperature June)	Breeding
14	Arctic Oscillation (AO) index	Global
15	Pacific Decadal Oscillation (PDO) index	Global
16	Pacific/North American teleconnection (PNA) index	Global
17	Aleutian Low Pressure index (ALPI)	Global
18	Full climate indices model	Global

'u' vectors indicate the strength of wind moving towards the east, whereas positive 'v' vectors indicate the strength of wind moving towards the north. We calculated wind components hourly and then averaged across the months of July and August. We ran one model that added temperature to Equation 2. We used the mean hourly temperature and averaged it within the months of July and August. We also ran a model that used the monthly total precipitation, which was calculated daily and then summed across each month. We used weather data from July of each year for the adult analyses and from August for the juvenile analyses. We predicted favourable local winds could push migrants further south or east toward larger sites at the Fraser River Estuary or in Puget Sound, lowering numbers at Sidney Island. A cold season could lead to changes in refuelling rates locally, shifting counts higher if longer refuelling times were required. Changes in precipitation could also potentially influence birds' decision to stay or move onward in a given year, again shifting the counts upwards if lengths of stay increased. Finally, we ran a global model for this hypothesis that included the baseline model plus the wind, temperature, and precipitation variables.

Climate conditions on breeding grounds. To examine the role of conditions on the breeding grounds, we explored three variables related to the breeding area of Western and Least sandpipers: (1) mean date of snowmelt; (2) mean daily minimum temperature in the last two weeks of May; and (3) mean daily minimum temperature in June. We used the average values calculated from three weather stations in Alaska, USA at the Nome, Bethel, and Kotzebue airports (Kotzebue: 66° 52′ 00″ N, 162° 37′ 60″ W (GHCND:USW00026616); Nome: 64° 30′ 40″ N, 165° 26' 24" W (GHCND:USW00026617); Bethel: 60° 47′ 06″ N, 161° 49′ 45″ W (GHCND:USW00026615); Menne *et al.* 2012). We defined the date of snowmelt as the last date between 19 February and 19 July (18 July in leap years) where greater than 12.5 mm of snow was recorded at the site (Niehaus and Ydenberg 2006). We predicted these variables would have a reduced effect on numbers of Least Sandpipers, which have a much broader breeding distribution than Western Sandpipers. We did not derive alternative weather variables for Least Sandpipers, as the breeding ground of origin for the birds that use Sidney Island is unknown. Given regional similarities in annual conditions across the Arctic, and the link between snowmelt in Western Alaska with timing of falcon migration (Niehaus and Ydenberg 2006), we expected Least Sandpipers should also be partially influenced by annual snowmelt dates from changes in their exposure to predators. We ran three models that included the baseline model plus one of the breeding area variables and one model that included all the three variables plus the baseline model.

Global climate indices. We evaluated correlations between broad scale metrics of climate and annual variation counts of Least and Western sandpipers stopping-over at Sidney Island. Climate indices integrate weather conditions over large areas. Four climate indices were selected that vary with air pressure, temperature, and strength of the jet stream over large areas between the breeding grounds and southern British Columbia during the months of breeding and early migration: the Arctic Oscillation (AO), Pacific Decadal Oscillation (PDO), the Pacific/North American teleconnection (PNA) and the Aleutian Low Pressure Index (ALPI). The AO, PDO, and PNA were calculated as the average of monthly index values for the breeding period only: May-July (National Oceanic and Atmospheric Administration (NOAA) 2018)). The ALPI is an annual index calculated using data from November in the previous year to March in the year of interest (Surry and King 2015). We ran four models adding each variable separately to the baseline model, plus a full model that included all four broad scale metrics plus the baseline model.

We predicted negative AO values, positive PDO values, and positive PNA would be associated with higher counts of juveniles. In years where the ALPI is strongest (most positive), weather conditions should favour southward flights (Gill *et al.* 2005), and we predicted numbers at Sidney Island to be lower as more migrants fly further south.

Examination of competing hypotheses. For each age-class and species, we compared 18 models (Table 1) using an information theoretic approach (Burnham and Anderson 2002). In all models, we included the baseline model parameters (a quadratic DOY trend fixed-effect, and annual random intercept). For most models, we added one additional parameter described above or added all the parameters in a hypothesis in a full model for that hypothesis. All explanatory variables were rescaled and centered by subtracting values from the mean and dividing by two times the standard deviation of the value across the dataset. A full model that included all variables from all hypotheses overfit the annual variation in the data, and so was excluded from the analysis.

The support for the models from the data was assessed using Akaike's Information Criterion, corrected for small sample sizes AICc (Burnham and Anderson 2002). We compared the support for the hypotheses to explain annual variation in counts by summing the Akaike weights for each hypothesis for each species and age class. We also examined the assumptions for the models and estimated a 10-fold cross-validation estimate of the Mean Absolute Error (MAE) for the top model for each group.

Question 3: Correlations between Counts of Adults and Juveniles

To examine the correlations between adults and juvenile migrations, we used the annual random intercept estimates from the baseline models (Equation 2) for adult Western and Least sandpipers as measures of the annual abundance in adults. We then included the adults' random intercept (α_i) as an annual variable in the juvenile model. Under this expectation, we predict that years with low adult counts would have low juvenile counts also and vice versa. As fewer years were included in the analysis for adults than juveniles, we could not compare this model with others, but instead examined the relationship between adult and juvenile migrations separately.

All data analyses were run in R (R Core Team 2020). Models were fit using lme4 (Bates *et al.*, 2015), and glmmTMB (Brooks *et al.* 2017). Code from the analyses is available at the project repository (Hope *et al.* 2021). Count data from 1990-2013 are available through the Government of Canada data portal (Drever 2013). Data for 2014-2018 is planned to be added to the data portal in the near future (Drever 2020). Until then, data is available upon request.

RESULTS

Daily and Seasonal Variation in Shorebird Counts

Counts of both species varied widely from year to year. The average number of birds, including both Western and Least sandpipers, counted per year at Sidney Island was 7,251 (range: 1,808-17,468; *n* = 24 years). Of these birds, 4,914 (range: 938-13,226) were Western Sandpipers, and 2,337 (range: 234-6,753) were Least Sandpipers. Counts of juveniles were higher than adults for both species across years and Western Sandpipers were more abundant than Least Sandpipers in both age classes (Fig. 2).

A variable number of birds were identified to species during each survey. Of the 183,616 sandpipers counted during the 29-year survey period, 43% were identified to species level in the field. The median percentage of birds identified to species per count-day was 61% (range: 0-100%; *n* = 610 count-days). The median number of Western Sandpipers identified to age on any given count-day was 56 birds (range: 1-1,892; *n* = 294 survey-days with at least one Western Sandpiper identified to age); the median number of Least Sandpipers was 22 individu-

als (range: 1-616; *n* = 303 survey-days with at least one Least Sandpiper identified to age).

Composition of age-classes in counts varied in a predictable manner through the migration period for both Western and Least sandpipers with a seasonal transition from all adults to all juveniles (Fig. 2, online Appendix Fig. A1.1, Fig. A1.2). Modeled values of daily age class proportions fit the data well (Western Sandpiper: marginal r^2 = 0.79, conditional r^2 = 0.97, *n* = 457; Least Sandpiper: marginal r^2 = 0.88, conditional r^2 = 0.96, *n* = 457). On average, the model estimated that the proportion of juvenile Western Sandpipers in counts was less than 1% before 22 July (21 July in leap years), and then rose within 16 d to over 99% after 7 August (6 August in leap years). For Least Sandpipers this trend was almost identical (from 1% to 99% juveniles between 20 July and 8 August).

Baseline Model for Seasonal Variation

Our baseline model provided a reasonable fit to the seasonal variation in counts at Sidney Island in all groups. Across species and age classes, there was a strong quadratic effect of DOY. Allowing this DOY effect to vary randomly by year provided a better fit in some years. However, in later years, there was insufficient data to justify using this more complex model, and the simple model provided a reasonable fit to the seasonal trend across all years (online Appendix Fig. A3.1, Fig. A3.2). With a random intercept, the mean absolute error from the 10-fold cross validation was equivalent to the original model fitting, and was estimated to be from the same distribution between training and test runs (Table 2).

Table 2. Results of 10-fold cross-validation runs on baseline models of seasonal trends in counts of adult and juvenile Western (*Calidris mauri*) and Least (*C. minutilla*) sandpipers on southward migration from 1990 to 2018. Mean absolute errors (MAE) are shown for the baseline model, the average of the training datasets and the average from the test models. Paired Wilcoxon signed rank test *P*-values test the alternative hypothesis that the training and test come from different distributions.

Species	Age	Mean absolute error			
		Model	Training runs	Test Runs	Wilcoxon test p-value
Western Sandpiper	Adults	61.63	61.62	61.68	0.92
Western Sandpiper	Juveniles	192.46	192.46	192.45	1.00
Least Sandpiper	Adults	26.10	26.10	26.10	0.92
Least Sandpiper	Juveniles	77.85	77.85	77.84	0.49

Question 1: Annual Trends in Abundance

Annual abundances for both species and age classes, as indexed by the random intercepts of trend models, varied widely between 1990 and 2018 (Fig. 2). For Western Sandpipers, we found little support for a linear or quadratic trend across years ($\sum w_i < 0.03$ for both age-classes). The trend model that received the most support for both adults and juveniles was the baseline model with no temporal trend (adults $w_i = 0.08$, ΔAICc = 2.28; juveniles $w_i = 0.06$, ΔAICc = 3.97; Fig. 2). For Least Sandpipers, there was some support for interannual trends in both age-classes (adults $\sum w_i = 0.12$; juveniles $\sum w_i = 0.15$). In adults, the top trend model included a quadratic term for year, although it was not more parsimonious than the top overall model ($w_i = 0.07$, ΔAICc = 4.33). This model indicated mean abundances decreased over time during the study period with a low around 2003 and a subsequent recovery (Fig. 2). For juvenile Least Sandpipers, the top supported model was the simple linear trend, although it was not more parsimonious than the top overall model ($w_i = 0.08$, ΔAICc = 1.55), and showed a positive trend in abundance over time (Fig. 2).

## Question 2: Drivers of Shorebird Abundance (Local, Breeding, Global)

Differing factors appear to be shaping annual variation in counts of the two species and age classes, and in general, factors from the breeding grounds or global climate indices had more support than local variables in explaining shorebird counts at Sidney Island (Table 3). Variables from the breeding grounds had the most support for affecting both adult and juvenile Least Sandpipers ($\sum w_i = 0.74$, and $\sum w_i = 0.4$, respectively) and juvenile Western Sandpipers ($\sum w_i = 0.61$). Adult Western Sandpiper counts were most affected by global indices ($\sum w_i = 0.63$). There was much lower support for local variables affecting counts in any of the age-classes or species ($\sum w_i < 0.15$ for all species/age groups).

For adult Western Sandpipers, support for a response to the PNA index was strongest in the suite of models considered ($w_i = 0.24$), though there was also comparable support for models that included other climate indices (ΔAICc < 1.34; online Appendix Table A4.1). The baseline model also had some support ($w_i = 0.07$; ΔAICc = 2.28), indicating inclusion of the environmental covariates in general should be viewed as exploratory. Most standardized model effects for adult Western Sandpipers had confidence intervals that broadly overlapped zero (Fig. 3), consistent with the model selection uncertainty. There was a strong positive effect of the PNA index, which did not overlap 0, indicating higher counts of adult Western Sandpipers in years when the PNA was positive (Fig. 4). The ALPI index had the opposite effect on abundances, with higher abundances observed in years where the ALPI was negative (Fig. 3). For the three models with strong support from the data (ΔAICc < 2), the mean absolute error was similar to that in both the training models and the full model (Table 4).

Table 3. Sum of AIC weights ($\sum w_i$) for hypotheses examined to explain annual variation in counts of adult and juvenile Western (*Calidris mauri*) and Least (*C. minutilla*) sandpipers on southward migration at Sidney Island, British Columbia, Canada, from 1990 to 2018. Top model group in bold.

| Hypothesis | Number of Models | Western Sandpiper | | Least Sandpiper | |
| | | Adults | Juveniles | Adults | Juveniles |
		$\sum w_i$	$\sum w_i$	$\sum w_i$	$\sum w_i$
Interannual	3	0.12	0.12	0.12	0.15
Local	6	0.15	0.11	0.03	0.13
Breeding	4	0.10	**0.61**	**0.74**	**0.43**
Global	5	**0.63**	0.16	0.12	0.30
Total	18	1	1	1	1
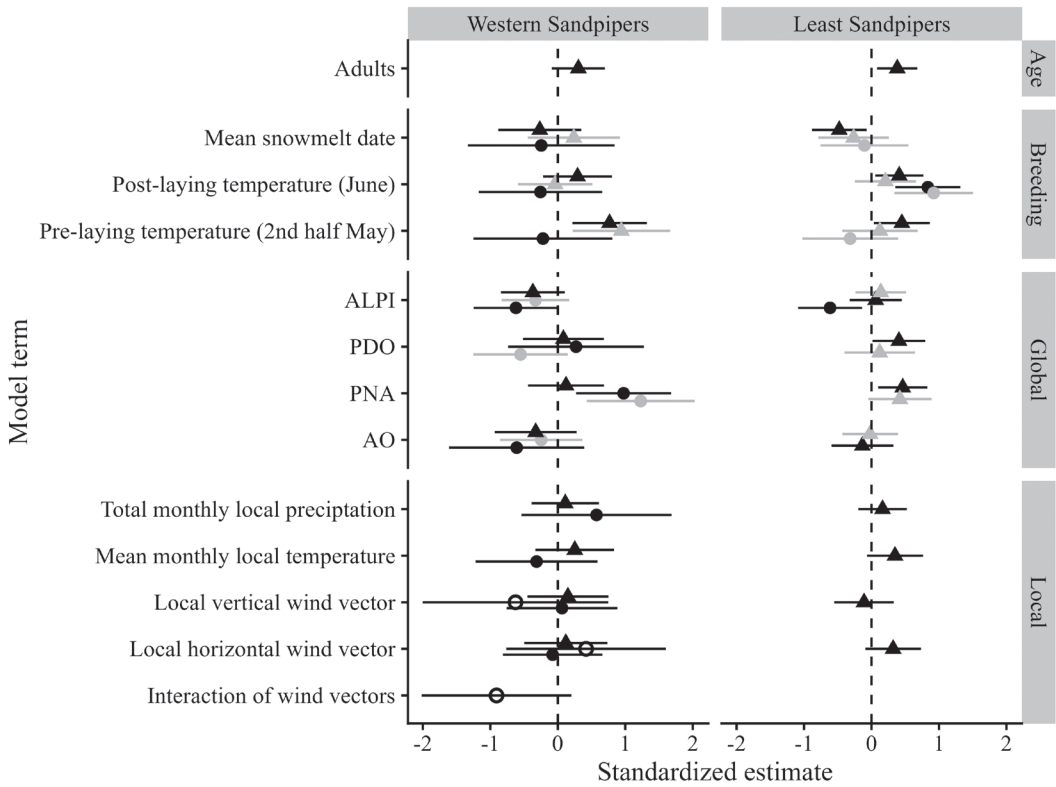
Figure 3. Standardized estimates of fixed effects for correlates explaining interannual variation in counts of Western (*Calidris mauri*) and Least (*C. minutilla*) sandpipers, at Sidney Island, British Columbia, Canada. Symbols indicate age classes of birds: adult (circles) and juvenile (triangles). Estimates show the value ± 95% CI derived from either models with a single value added above the baseline seasonal trend (black) or in a full model for a particular hypothesis (grey). Only models that have moderate support from the data (ΔAICc< 6; online Appendix 4) are shown. We did not include the interannual trend models in this figure. Acronyms refer to climate indices: ALPI = Aleutian Low Pressure index; PDO = Pacific Decadal Oscillation; PNA = Pacific/North American teleconnection; AO = Artic Oscillation.

For juvenile Western Sandpipers, the model with strongest support included pre-laying temperatures (w_i = 0.46; online Appendix Table A4.2), indicating counts on Sidney Island were positively correlated with temperatures during the pre-laying period on the breeding grounds. When the temperature in Alaska was warmer in the second half of May, abundances at Sidney Island were higher in August (Fig. 4). This model fared well in the cross-validation with mean absolute error comparable between test and training data sets (Table 4).

For adult Least Sandpipers, the top supported model was the model including mean June daily minimum temperature (w_i = 0.61). When June mean daily minimum temperatures were higher in Alaska, so too were abundances of adult Least Sandpipers

at Sidney Island (Fig. 4). The role of ALPI also had moderate support from the data (w_i = 0.08; ΔAICc = 4.07) as did the full breeding conditions model (w_i = 0.10; ΔAICc = 3.54). The relationship between adult Least Sandpipers and the ALPI was very similar to that in adult Western Sandpipers (Fig. 4), with higher abundances when ALPI was negative, that is, when the semi-permanent low-pressure system over the North Pacific was weak.

For juvenile Least Sandpipers, model selection did not identify a clear top model. Support for a response to the PNA index was strongest for all models (w_i = 0.18), although there was also support for several other models that included other climate indices and Alaska weather variables (ΔAICc < 1.66; online
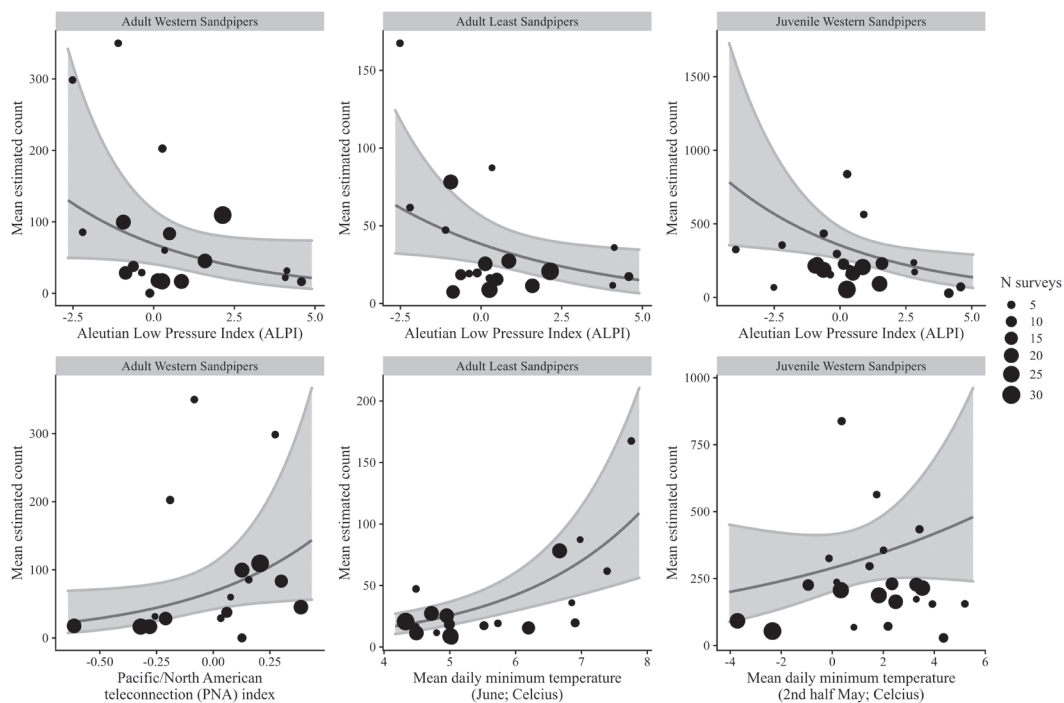
Figure 4. Relationships between relevant weather variables, climate indices and average annual abundances of Western (*Calidris mauri*) and Least (*C. minutilla*) sandpipers, at Sidney Island, British Columbia, Canada. Only variables from the top models within each group are shown, as identified in covariate modelling. Juvenile Least Sandpipers did not have a clear top model, and their covariate patterns are shown in online Appendix Figure A5.1. Size of point indicates the number of surveys conducted in each year.

Appendix Table A4.1). While effect sizes in these models with parameters from the breeding grounds were smaller than other groups, many of the confidence intervals did not overlap zero (Fig. 3). Both mean daily minimum temperatures in June and in the second half of May had positive effects on juvenile abundance, and the date of snowmelt had a negative effect on abundances. As colder years will likely have later snowmelt, these correlations all suggest the same climactic mechanism with juvenile abundances. The PDO and PNA indices also had positive relationships with juvenile Least Sandpiper abundances, with higher abundances when the PDO or PNA were positive. The top models all performed well across all groups in the cross validation runs (Table 4). The mean absolute errors were largest for juvenile Western Sandpipers, due to their higher mean abundances relative to the other species and adult Western Sandpipers.

Question 3: Correlations Between Counts of Adults and Juveniles

Counts of juveniles were positively correlated with counts of adults in the same year for both Western and Least sandpipers (Fig. 5). Overall, a doubling of adult abundance led to a 28% increase in Western Sandpiper juvenile numbers and 36% increase in juveniles for Least Sandpipers.

DISCUSSION

Annual abundances of Western and Least sandpipers on Sidney Island varied widely from 1990 to 2018. Adult Western Sandpipers showed the largest amount of variation between years, while juvenile Least Sandpipers showed the least variation. Across all years, juvenile abundance was consistently higher than adult abundance in both species. This difference in counts likely reflects real differences in overall abundance of

Table 4. Results of 10-fold cross-validation runs on best supported models (ΔAICc < 2; online Appendix 4) of seasonal trends in counts of adult and juvenile Western Sandpiper (WESA; *Calidris mauri*) and Least Sandpiper (LESA; *C. minutilla*) on southward migration at Sidney Island, British Columbia, Canada, from 1990 to 2018. Mean absolute errors (MAE) are shown for best supported models, the average of the training datasets and the average from the test models. Models that have good predictive capacity have mean absolute error with similar values between training and test runs. Within a species and age group, models with smaller MAE will have a stronger fit to the data. Paired Wilcoxon signed rank test p-values test the alternative hypothesis that the training and test come from different distributions. Acronyms under Model Name column refer to climate indices: ALPI = Aleutian Low Pressure index; PNA = Pacific/North American teleconnection; PDO = Pacific Decadal Oscillation.

| Species | Age | Akaike weight | Model Name | Mean absolute error | | | Wilcoxon test p-value |
				Model	Training runs	Test Runs	
WESA	Adults	0.24	ALPI	61.65	61.63	61.70	0.92
WESA	Adults	0.18	Global variables	61.68	61.68	61.74	0.85
WESA	Adults	0.12	PNA	61.67	61.66	61.73	0.92
WESA	Juveniles	0.46	Pre-laying temperature	192.45	192.42	192.43	1.00
LESA	Adults	0.61	Post-laying temperature	26.1	26.09	26.16	0.92
LESA	Juveniles	0.18	PNA	77.84	77.83	77.93	1.00
LESA	Juveniles	0.17	Day of Alaskan snowmelt	77.85	77.84	77.94	1.00
LESA	Juveniles	0.13	Post-laying temperature	77.85	77.84	77.94	1.00
LESA	Juveniles	0.09	Pre-laying temperature	77.85	77.84	77.94	1.00
LESA	Juveniles	0.08	PDO	77.84	77.83	77.93	1.00
LESA	Juveniles	0.08	Year	77.85	77.84	77.94	1.00
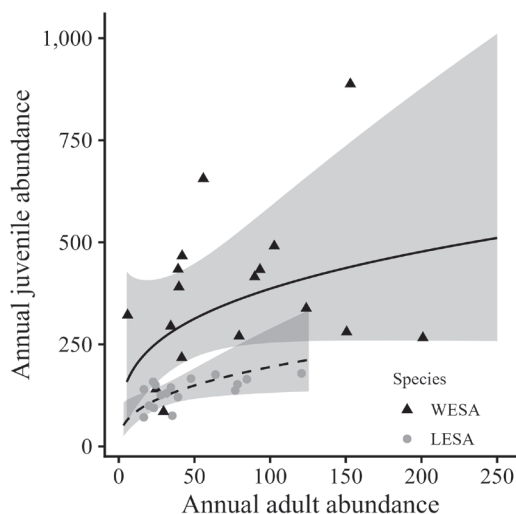
Figure 5. Correlation between counts of two age classses of Western Sandpipers (*Calidris mauri*) and Least Sandpipers (*C. minutilla*), at Sidney Island, British Columbia, Canada. Western Sandpipers (WESA) are shown in solid line, dark triangles, and Least Sandpipers (LESA) shown in dashed line, light circles. Lines show the estimated trend in abundance with associated 95% confidence intervals from a model that predicted the abundance of juveniles in each year as a function of the adult random intercept from the baseline model. Abundances and trends for both adults and juveniles are estimated using log-counts and back transformed to linear scale for presentation.

the two age classes at the site, as estimated lengths of stay in Western Sandpipers are similar between age groups (Hope *et al.* 2011). Juvenile abundances were often far more than the expected two-fold abundance difference that would occur if every adult that passed through Sidney Island had produced two chicks that both survived and passed through the site (Ruthrauff and Mc-Caffery 2005). As seasonal productivity cannot account for the observed difference in counts between age groups, these counts are likely driven by differing site selection or migratory routes between adults and juveniles, with juveniles being relatively more drawn to the site than adults.

Despite the previously reported decline in counts from 1990 to 2001 (Ydenberg *et al.* 2004), there was little support for any trend in abundances of Western Sandpipers over the whole study period from 1990 to 2018. The decline in usage over the early years

was apparent in the mean counts (Fig. 2), but across the entire time period, sandpiper counts have remained stable or recovered despite the continued increase in falcon populations (Ydenberg *et al.* 2017). Adult and juvenile Least Sandpipers both showed an increase in numbers since the early 2000s, and juveniles remained more abundant than adults across the study period. Despite the annual variation in counts, it is clear that Sidney Island remains an important and consistently used local stopover site on southward migration for adult and juvenile Western and Least sandpipers.

Annual abundance of shorebirds at Sidney Island was not strongly driven by local weather conditions. Across all groups, models representing climate indices and weather conditions on the breeding grounds had more support than those derived from local weather variables, suggesting a partial role of conditions at the breeding grounds in shaping migratory counts at Sidney Island. For both species, years with warmer conditions on the Alaska breeding grounds were positively related with survey abundance. For Western Sandpipers, mean nest initiation date in Alaska is positively correlated with temperature on the breeding grounds, and later nests have lower survival (Kwon *et al.* 2018). This effect of temperature and snowmelt could be the result of phenological mismatch, both within individuals and within populations, between demand by shorebirds and supply from insect prey, although the effect appears smaller in western arctic breeders, which are likely the population that moves through Sidney Island, rather than eastern breeders (Kwon *et al.* 2019). Years with later snowmelt dates show lower abundances of juveniles, either because later snowmelt lowers Western Sandpiper productivity, or due to links between snowmelt and the timing of falcon southward migration, which can affect staging site choices by migrating shorebirds (Ydenberg *et al.* 2002; Niehaus and Ydenberg 2006; Hope 2018).

Adult Western Sandpiper counts were most strongly influenced by the PNA index. As positive PNA years are related to warmer temperatures and reduced precipitation,

these conditions could allow adults to initiate nests and complete their breeding earlier. A testable prediction from this hypothesis would be that a greater proportion of adult females should be found at this stopover site in years with positive PNA, given that females depart the breeding grounds sooner than the males (Jamieson *et al.* 2014). As predicted, ALPI was negatively related to adult abundances in both species and to juvenile Western Sandpiper abundances. However, as the index refers to a low-pressure system that forms during the winter months and it covaries to some degree with the PNA (Overland *et al.* 1999), the link may be also related to climatic conditions experienced by birds on the breeding grounds.

We found a positive correlation between the adult and juvenile counts (Fig. 6), however, there was very large variation around this relationship, especially in Western Sandpipers. While the size of the adult population will influence the annual production of juveniles, observed abundances at this migratory stopover appear to be strongly influenced by the differing conditions that the two age classes experience as they migrate through. Juveniles migrate through the same site a month later, by which time both the predation risk and food abundance are higher than when adults make the journey (Lank *et al.* 2003). This trade-off between food and safety should make juveniles particularly sensitive to annual conditions when they are deciding to use a relatively dangerous stopover site (Hope 2018). Additionally, adults must moult after completing migration and generally have differing migratory destinations than juveniles (Page 1974; O'Hara *et al.* 2002; O'Hara *et al.* 2006; Nebel 2006). Therefore, these differing pressures on the two age classes are consistent with the weak correlation we found between abundances of adult and juvenile birds.

Our analysis required that we interpolate information about flock composition by age and species. The interpolation for ages was robust and consistent, with a rapid transition from adults to juveniles at the site (Fig. 2), and as such, this interpolation should not affect results. The inclusion of mixed species flocks did have the potential to influence the results as these flocks occurred across all years and dates. While the threshold for inclusion of species identification did affect the parameter estimates from the models, the effect was minor so long as we identified at least 30% of the flock to species. This variation highlights the importance for surveyors to identify to species as much as possible in mixed species flocks.

Changing survey effort throughout the time series also complicated interpretation of results. The reduction in total effort and focus on effort in August led us to exclude several years of surveys, and weakened interpretation from later years. When examining annual trends or impacts that have a large amount of within-season variation, it is important to have enough survey effort within migratory periods to ensure annual effects are not driven by a single count. On southward migration when distributions of birds are spread across many sites of variable sizes, it is important to survey across multiple sites to disentangle the difference in counts that may result from changes in site choice and from overall numbers of birds (Hope 2018).

In summary, Sidney Island remains a well-used stopover site on southward migration for both Western and Least sandpipers. Annual variability appears to be driven in part by conditions that both adults and juveniles experience on the breeding grounds as well as variation in overall population size. These correlations between shorebird counts and conditions at breeding areas indicate that migration monitoring programs could provide insight into reproductive success of shorebird populations. Sidney Island remains the best-surveyed site in Pacific Canada during southward migration for both species, but we suggest increased survey effort to allow for an examination of the role of seasonal variation in counts. Therefore, while counts at Sidney Island may serve as an approximate index of population trends, more region-wide surveys and higher species identification rates would improve inferences about underlying mechanisms for wide fluctuations in abundance that occur there.

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