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Author(s): David D. Hope, Mark C. Drever, Joseph B. Buchanan, Mary Anne Bishop, George Matz, and Moira J. F. Lemon

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RESEARCH ARTICLE

# Trends in timing of spring migration along the Pacific Flyway by Western Sandpipers and Dunlins

**David D. Hope,[1]* Mark C. Drever,[2] Joseph B. Buchanan,[3] Mary Anne Bishop,[4] George Matz,[5] and Moira J. F. Lemon[2]**

[1] Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada
[2] Canadian Wildlife Service, Environment and Climate Change Canada, Pacific Wildlife Research Centre, Delta, British Columbia, Canada
[3] Cascadia Research Collective, Olympia, Washington, USA
[4] Prince William Sound Science Center, Cordova, Alaska, USA
[5] Kachemak Bay Birders, Homer, Alaska, USA
* Corresponding author: dhope@sfu.ca

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## ABSTRACT

Long-distant migrants timing their arrival on the breeding grounds face a tradeoff between optimal timing for breeding and optimal timing for survival. For many shorebird species, the flyway northward spans thousands of kilometers, and both conditions encountered en route and priorities of individuals can affect the timing of migration. We used data from spring migration surveys of Western Sandpipers (*Calidris mauri*) and Pacific Dunlins (*Calidris alpina pacifica*) along the Pacific Flyway of North America to determine whether the timing of their northward migration changed from 1985 to 2016. We compiled survey data for both species from 6 sites of varying size along the northern portion of the flyway from Washington, USA, through British Columbia, Canada, to Alaska, USA, and estimated interannual trends in the timing of passage through each site. Peak passage dates at the sites closest to the species' breeding grounds in Alaska became later by 1–2 days over the study period, while dates of peak passage at sites farther south became ~3 days earlier. A post hoc analysis suggested that local temperatures affected peak passage dates at most sites, with warmer temperatures related to earlier passage. Discerning patterns of movement by Dunlins at southern sites was complicated by the presence of winter residents. Simulation analyses of sandpiper movement through a stopover site highlighted both length of stay and timing of arrival as important factors shaping peak passage estimates. We suggest that Western Sandpipers appear to be arriving earlier at southern sites and staying longer at larger stopover sites, such as Alaska's Copper River delta. Our methodology generated specific predictions of peak passage dates on northward migration that may be useful in other systems for which historical count data are available.

*Keywords:* migratory progression, Pacific Flyway, shorebird monitoring, spring migration, migration simulation, individual-based model, migration phenology, calidrid

### Tendances dans la chronologie de la migration printanière de *Calidris mauri* et *Calidris alpina pacifica* dans la voie migratoire du Pacifique

## RÉSUMÉ

Les migrateurs de longue distance qui synchronisent leur arrivée sur les sites de reproduction font face au compromis entre le moment optimal pour la reproduction et le moment optimal pour la survie. Pour plusieurs espèces de limicoles, la voie migratoire s'étend sur des milliers de kilomètres vers le nord et les conditions rencontrées en chemin de même que les priorités des individus peuvent affecter la chronologie de la migration. Nous avons utilisé des données d'inventaires de la migration printanière de *Calidris mauri* et de *Calidris alpina pacifica* le long de la voie migratoire du Pacifique, en Amérique du Nord, afin de déterminer si la chronologie de leur migration vers le nord a changé entre 1985 et 2016. Pour les deux espèces, nous avons examiné 5 sites de taille variable le long de la portion nordique de la voie migratoire dans l'État de Washington, en Colombie-Britannique et en Alaska, et nous avons estimé des tendances interannuelles dans le moment de passage à chaque site. Le pic de passages aux sites les plus près des lieux de reproduction de ces espèces en Alaska est passé à 1-2 jours plus tard au cours de la période étudiée, alors que les dates de pic migratoire aux sites plus au sud sont passées à ~3 jours plus tôt. Une analyse post hoc a suggéré que la température locale a aussi affecté les dates de pic migratoire à la plupart des sites, avec des températures plus chaudes reliées à un passage plus hâtif. La présence d'individus résidents hivernaux a compliqué la distinction des patrons de migration par *C. alpina pacifica* aux sites méridionaux. Des analyses de simulations des déplacements des bécasseaux dans une halte migratoire ont mis en évidence que la durée du séjour et la chronologie d'arrivée sont des facteurs importants qui façonnent les estimations des pics de passage. Nous suggérons que *C. mauri* arrive plus tôt sur les sites méridionaux et reste plus longtemps aux grandes haltes migratoires telles que le delta de la rivière Copper, en Alaska. Notre méthodologie génère des prédictions spécifiques des dates de pic migratoire vers le nord qui peuvent être utiles dans d'autres systèmes où des mentions historiques sont disponibles.

*Mots-clés:* progression migratoire, voie migratoire du Pacifique, suivi des limicoles, migration printanière, simulation de la migration, modèle basé sur l'individu, phénologie de la migration, bécasseaux

## INTRODUCTION

The phenology of movement along a migratory flyway can strongly affect a migrant's fitness. Migrants that move into seasonally available habitats for breeding must make tradeoffs that involve arriving at a time and in a condition optimal for breeding while not compromising survival during migration or on the breeding grounds. Changes in conditions along a flyway or on the breeding grounds should result in shifts to the timing of movement along a flyway (Hüppop and Hüppop 2003, Lank et al. 2003, Gill et al. 2014). The timing of migration along a flyway can be influenced by food (van der Graaf et al. 2006, Duriez et al. 2009), predation (Clark and Butler 1999, Lank et al. 2003, Taylor et al. 2007, Hope et al. 2011), and climatic variables (Both and te Marvelde 2007, Coppack et al. 2008, Knudsen et al. 2011, Lameris et al. 2017). Predator populations have increased along the Pacific Flyway in recent decades, as they have globally (Ydenberg et al. 2017). Climate change has also had demonstrated impacts on the timing of breeding and arrival of birds using the Pacific Flyway (Niehaus and Ydenberg 2006, Grabowski et al. 2013, Ward et al. 2016, Saalfeld and Lanctot 2017). These changes lead us to expect that the timing of migration along the Pacific Flyway of North America has also changed in recent decades.

Counts of abundance of migratory shorebird species present an opportunity to estimate the timing of migration along flyways and to observe changes over time. Species that aggregate in large numbers at major stopover sites can easily be observed and counted. The passage of individual birds through a stopover site involves arriving, staying for a few days to refuel, and then departing onward. Across the duration of migration, passage through stopover sites comprises as much as 88% of the time spent on migration (Hedenström and Alerstam 1997), and the total time spent on stopovers during migration explains 66% of the variation in the total speed of migration across avian taxonomic groups (Schmaljohann and Both 2017). Therefore, understanding the processes involved in passage through stopover sites and estimating changes in the timing of progression through multiple stopover sites will help us to assess the general timing of the progression of a population along a migratory flyway between the nonbreeding and the breeding grounds (hereafter, 'migratory progression').

Western Sandpipers (*Calidris mauri*) and Pacific Dunlins (*C. alpina pacifica*) encounter a series of potential stopover sites while moving northward to their Alaskan breeding grounds each spring. Stopover duration has been shown to vary between 1 and 4 days at each site (Iverson et al. 1996, Warnock and Bishop 1998, Warnock et al. 2004b), but there has been no long-term monitoring to determine whether this duration has changed. The intent of this study was to evaluate the extent to which we can infer changes in stopover duration and migratory progression based on comparisons of trends in the timing of migration across a range of sites within a flyway. The specific objectives were to generate estimates of dates of peak passage of migrants at 6 stopover sites, and to analyze trends within and among these sites to determine whether the rate of northward progression has changed in this system over a ca. 30-yr period between the late 1980s and 2016. Specifically, we addressed 2 basic questions: (1) Has the date of peak passage of Western Sandpipers and Dunlins changed at these 6 sites over the study period? (2) Is the interannual trend consistent across the flyway? In addition, we explored whether available climatic data explained observed changes across the flyway. Finally, we simulated migrant passage through a stopover site to quantify the effect on our peak passage measure of changes in length of stay, arrival date, and the mixing of differing migration and nonbreeding strategies.

## METHODS

### Survey Sites

Survey counts were compiled from 6 sites on the northern Pacific Flyway (Figure 1, Table 1), from 5 stopover areas. Four of the 5 areas are designated sites under the Western Hemisphere Shorebird Reserve Network (WHSRN): the Copper River delta (encompassing the Copper River Delta and Hartney Bay survey sites) and Fraser River delta (encompassing the Roberts Bank survey site) are classified as being of 'Hemispheric Importance' (at least 500,000 shorebirds annually or at least 30% of the biogeographic population of a species); Kachemak Bay is considered to be of 'International Importance' (at least 100,000 shorebirds annually or at least 10% of the biogeographic population of a species); and Tofino Mudflats is ranked of 'Regional Importance' (at least 20,000 shorebirds annually or at least 1% of the biogeographic population of a species). These sites' designations represent, at least in part, their importance to migrating Western Sandpipers and Dunlins.

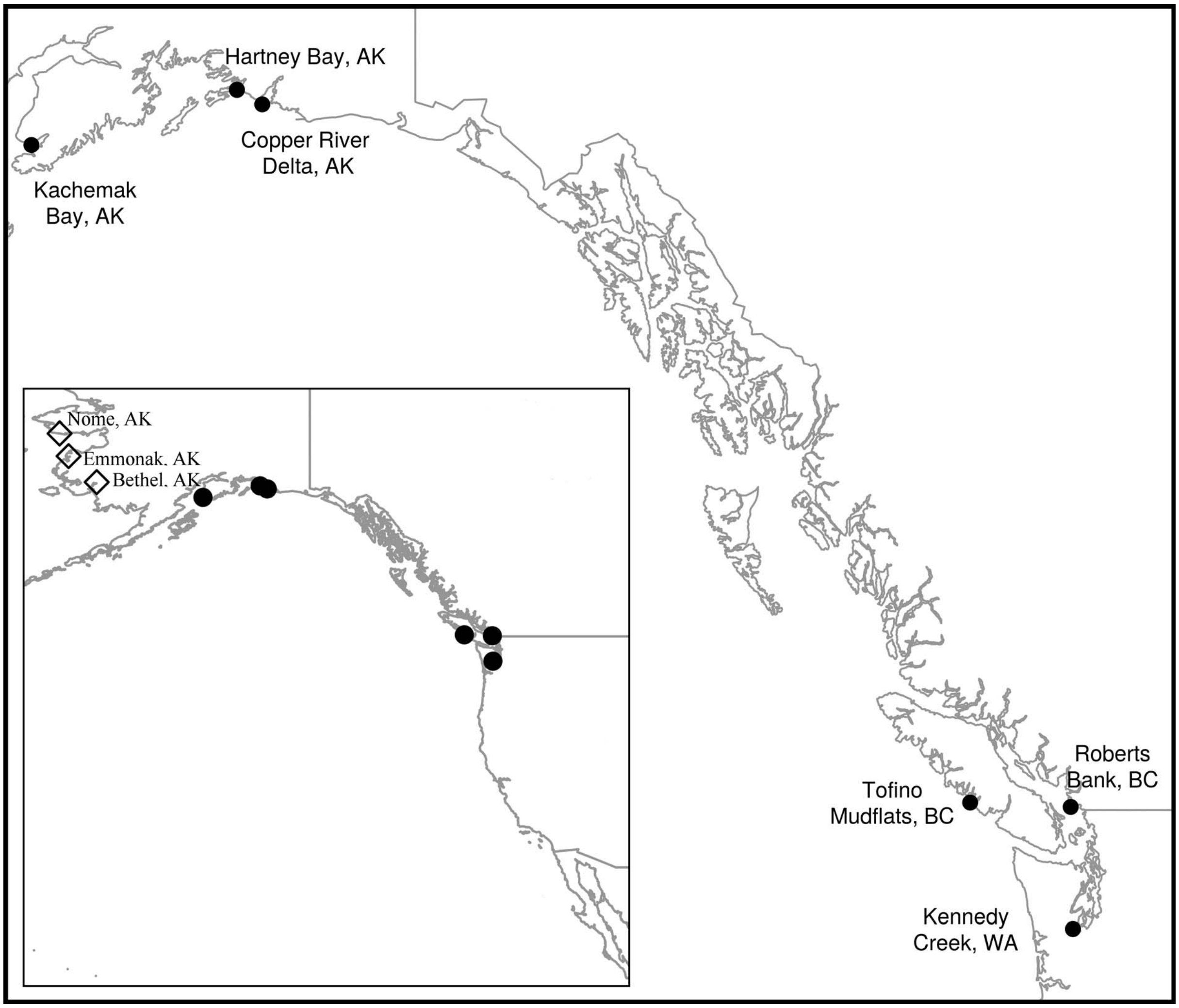

**FIGURE 1.** Map of the northeastern coast of the Pacific Ocean from Washington (WA) to Alaska (AK), USA, showing the northern portion of the Pacific Flyway in North America. To determine whether the timing of northward migration of Western Sandpipers and Dunlins changed along the flyway between 1985 and 2016, we used data from spring migration surveys at 6 sites: Kennedy Creek, WA; Roberts Bank, British Columbia (BC), Canada; Tofino Mudflats, BC; Hartney Bay, AK; Copper River Delta, AK; and Kachemak Bay, AK. The inset shows the survey sites (black dots) within a larger context, with breeding locations (open diamonds) of Western Sandpipers and Dunlins also shown.

**TABLE 1.** Geographic positions of surveyed stopover sites along the northern portion of the Pacific Flyway in North America included in our analysis of changes in the timing of migration between 1985 and 2016 by Western Sandpipers and Dunlins. The distance from each survey site to the breeding area is represented by distance to 3 locations within the area and their average. All distances are measured in great arc distance. Latitude (N) and longitude (W) are given in decimal degrees. Sites are ordered from the farthest to the closest to the breeding grounds. WA = Washington, USA; BC = British Columbia, Canada; and AK = Alaska, USA.

| | Geographic location | | Distance (km) | | | |
|---|---|---|---|---|---|---|
| Site | Latitude | Longitude | Bethel | Emmonak | Nome | Mean |
| Kennedy Creek, WA | 47.10°N | 123.08°W | 2,900 | 3,100 | 3,170 | 3,057 |
| Roberts Bank, BC | 49.05°N | 123.14°W | 2,740 | 2,930 | 2,994 | 2,888 |
| Tofino Mudflats, BC | 49.12°N | 125.88°W | 2,590 | 2,790 | 2,860 | 2,747 |
| Copper River Delta, AK | 60.27°N | 145.17°W | 910 | 1,060 | 1,120 | 1,030 |
| Hartney Bay, AK | 60.50°N | 145.86°W | 868 | 1,018 | 1,095 | 994 |
| Kachemak Bay, AK | 59.62°N | 151.46°W | 580 | 780 | 880 | 747 |

The most southerly survey site, the Kennedy Creek estuary (47.098°N, 123.083°W), is located at the head of Totten Inlet in southern Puget Sound, Washington, USA (Buchanan 1988). It consists of a small, ~1 km$^2$ mudflat surrounded on 3 sides by vegetative cover. Counts of Western Sandpipers and Dunlins have been conducted at this site 1–7 days per week since 1980, with more regular counts conducted since 1985. The entire area can be viewed by a single observer from a single vantage point. In the past, peak counts of Western Sandpipers and peak counts of Dunlins have both exceeded 5,000 (Buchanan 1988), making this small estuary one of the most productive in southern Puget Sound (Evenson and Buchanan 1997). More recently, peak numbers have dropped to ~2,000 Dunlins and fewer than 100 Western Sandpipers in some years.

Moving north, Roberts Bank (49.058°N, 123.163°W) is a large mudflat (8 km$^2$) situated within the Fraser River delta, British Columbia, Canada. Regular spring surveys of Western Sandpipers and Dunlins have been conducted at Roberts Bank since 1991 (Drever et al. 2014). Observers used a spotting scope or binoculars to count shorebird numbers at a series of stops along a dike adjacent to the mudflat. Counts of individual species were then calculated by multiplying total flock counts by the proportion of Western Sandpipers to Dunlins for each day, determined from a subsample of the flock (Drever et al. 2014). Peak counts averaged >210,000 Western Sandpipers and >56,000 Dunlins for the years surveyed. The median population estimate for birds using this site during northward migration is 600,000 Western Sandpipers (14%–21% of the total flyway population) and 200,000–250,000 Dunlins (30%–50% of the flyway population; Drever et al. 2014).

Tofino Mudflats (49.117°N, 125.867°W) are a complex of mudflats (55.3 km$^2$ in total) on the west coast of Vancouver Island in British Columbia. The Canadian Wildlife Service of Environment and Climate Change Canada surveyed the site in 1988, 1995, and 2011 through a combination of boat- and road-based counts. Counts are the sums of the daily counts at all sites within the mudflat complex (Butler et al. 1992, Butler and Lemon 2001, Drever et al. 2016). Peak counts averaged 17,000 Western Sandpipers and 1,520 Dunlins for the years surveyed.

Alaska's Copper and Bering river deltas (60.310°N, 145.000°W; this study site hereafter referred to as the Copper River Delta) are on the northern coast of the Gulf of Alaska, USA. This large estuary covers ~80,000 ha of tidal and submerged lands and intertidal and freshwater wetlands that are protected from the Gulf of Alaska by barrier islands. The numbers of Western Sandpipers and Dunlins at the site were estimated from 1992 to 1995 using a combination of aerial- and airboat-based surveys to derive total numbers of shorebirds and species composition (Bishop et al. 2000). There were 2 days that were missing species composition data, so for these dates we interpolated the species ratio using the methodology described by Drever et al. (2014). Peak counts averaged 560,000 Western Sandpipers and 130,000 Dunlins for the years surveyed. It has been estimated that ~60% of the global population of Western Sandpipers uses this site on northward migration (Bishop et al. 2000).

We separated the Copper River Delta into 2 separate sites to allow for the inclusion of recent counts. No repeat of the large-scale survey of the Copper River Delta has occurred since 1995. However, since 2013, smaller-scale surveys have been conducted on mudflats in the southern Orca Inlet by volunteers working on the Migratory Shorebird Project, the Copper River International Migratory Bird Initiative, and the Environment for the Americas' Migratory Bird Program. These surveys have followed a standardized protocol developed as part of the Migratory Shorebird Project (Point Blue Conservation Science 2014). We used counts from 2013 to 2016 gathered in Hartney Bay (60.50°N, 145.86°W), a small mudflat southwest of Cordova. Hartney Bay is part of the WHSRN Copper River delta site, but lies >10 km to the north of the main mudflats in the region, and is used later in migration (on or after May 1, compared with April ~20 for the Copper River Delta; M. A. Bishop personal observation). Counts from this location included many estimates that did not specify species. We utilized the proportion of Western Sandpipers and Dunlins counted each day and the methodology of Drever et al. (2014) to interpolate these counts and added them to the species-specific counts. Daily ground transects for shorebirds had previously been conducted at Hartney Bay in the 3 springs of 1991–1993. While the methodology varied between the earlier ground transects and the more recent Hartney Bay surveys, we feel that the earlier surveys are useful for giving us a reliable measure of any shift in the timing of migration at this site. The alternatives would be to compare the earlier counts from the broader Copper River Delta site with the recent counts from the much smaller Hartney Bay site, or to exclude the sites from analysis.

The site closest to the breeding grounds is Kachemak Bay (59.625°N, 151.456°W), a 64-km long inlet near Homer on the Kenai Peninsula of Alaska, USA. Surveys were conducted in spring in 1986 and from 1989 to 1994 by a single individual driving between sites (Matz et al. 2012). Surveys with multiple observers were conducted from 2009 to 2013 and involved simultaneous visits to the sites. These latter surveys were conducted every 5 days during a 2-hr period on an outgoing tide and covered a larger portion of the migratory period (Matz et al. 2012). To ensure that counts at Kachemak Bay included the peak count for each year, we also included supplementary counts collected between the survey periods. These supplementary counts did not have a standardized protocol, so we compared our results with and without the supplementary counts. We found that their inclusion did not change the results substantially, but did substantially increase the number of survey dates included in the analysis, so we retained them in our study. The supplementary data for Kachemak Bay were available for 2010 through 2016, and peak counts with the supplementary data included averaged 9,100 Western Sandpipers and 1,100 Dunlins for all years surveyed.

While we attempted to obtain all available data from all major stopovers along the northern portion of the Pacific Flyway, there has been no long-term monitoring at Grays Harbor, Washington, Stikine River, Alaska, or Yaktuat Forelands, Alaska, all of which have been identified as potentially important stopover sites along the northern portion of the flyway (Warnock and Bishop 1998, Bishop et al. 2004). There are also vast unmonitored areas of intertidal mudflats sites around the Fraser River delta and Puget Sound that are potential stopover sites. The coast between British Columbia and Alaska has many smaller estuaries that are unmonitored and could potentially host some birds each spring. Radio-tagged Western Sandpipers and Dunlins have been shown to move between the Fraser River delta, Copper River delta, and Kachemak Bay (Iverson et al. 1996, Warnock and Bishop 1998, Warnock et al. 2004b). These patterns suggest that observed changes across our study sites will be representative of the patterns of migration of birds that use the flyway.

### Estimating Dates of Peak Passage

We generated estimates of the dates of peak passage from survey counts for each site in each year. For an individual, passage through a site involves arriving, staying for a few days, and departing. The passage of a population of birds is the combined passages of all birds using a specific site. We defined an individual's passage date as the midpoint of their stay at a site. The date of peak passage was then the average of passage dates for all individuals using that site. As we did not observe individual movements through a site, we used counts of abundance as a proxy, with the date of the peak count being an indicator of peak passage timing. We did not have complete coverage for each date within the migratory period; therefore, we determined the date of peak passage of Western Sandpipers and Dunlins for each year and site by fitting truncated normal distributions to the daily count data, based on methods from Jenni and Kéry (2003). We used package gamlss (Rigby and Stasinopoulos 2005) in R (R Core Team 2016) to fit the distributions. The distributions were truncated at the first and last day of the counts for each year and site. Dates used here were the ordinal day of the year, so in leap years the day of the year was one higher than in nonleap years. This method iteratively fits a partial normal distribution that is clipped at the truncation points in the data. By fitting a truncated distribution it is still possible to estimate an accurate peak even if survey dates change between years or are initiated after migration begins (Jenni and Kéry 2003, Rigby and Stasinopoulos 2005). The truncation allows the peak of the distribution to be estimated as within or outside the truncation points. The model does assume variance to be symmetrical around the mean (Stasinopoulos and Rigby 2007), and so we examined results using Student's $t$ distributions, but found the estimates to be similar ($r = 0.99$). Therefore, the normal distribution was kept as the more parsimonious model.

We defined the mean of the truncated distribution as the date of peak passage for the population of birds migrating through a site (Jenni and Kéry 2003). Estimates for which the model did not converge within 400 iterations were not used for subsequent trend analyses. Every estimate that required more than 400 iterations could also be excluded for other reasons (i.e. unrealistically early or late estimates, estimation of confidence intervals failed, or fewer than 7 survey dates in a year; Supplemental Material Table S1). We generated confidence intervals around the estimates of peak passage dates using a jackknife analysis that involved sequentially dropping each survey date at a site and reestimating the date of peak passage without that data point. We then calculated the 2.5% and 97.5% confidence limits from the jackknifed estimates. Estimates for which the confidence intervals failed to converge during the jackknife procedure were also excluded from further analyses. Because the numbers of counts in some years were low and the jackknifed estimates were not normally distributed, the confidence intervals are likely inaccurate as confidence intervals, but instead act as indicators of how dependent an estimate is on a single day of counts.

Owing to large variation in survey effort within and among sites, we used a simulation analysis to explore how the peak passage date estimates were affected by survey effort. The simulations and their results are described in Supplemental Material Appendix A.

### Trends in Peak Passage Dates

Our analysis focused on changes in the timing of migration across the migratory flyway. We expected dates of peak passage and any trends in migratory timing to be related to each site's distance to the breeding grounds, but we also had a large amount of variation in the number of birds passing through the sites and the survey effort at each site. We used a hierarchical modeling approach that estimated peak passage dates based on the distance to the breeding grounds. This ensured a flyway-scale analysis that allowed interannual trends to be estimated at sites with few years surveyed (Gelman and Hill 2007). While our modeling approach constrained the trends within some sites relative to all of the sites, we developed the final model using a standardized approach that considered other potential random and fixed effects before arriving at the most parsimonious model (Zuur et al. 2009).

To understand how the migratory progression northward of Dunlins and Western Sandpipers might have changed, we developed a mixed-effects model that modeled date of peak passage as a function of distance to the breeding grounds, year of study (for temporal trends), and their interaction, expressed as:

$$\mu_{ij} = \alpha_j + \beta_1 \cdot year_i + \beta_2 \cdot \varphi_j + \beta_3 \cdot \varphi_j \cdot year_i + \varepsilon_{ij}, \qquad \text{(equation 1)}$$

where

$$\alpha_j = N(\mu_\alpha, \sigma_\alpha^2). \qquad \text{(equation 2)}$$

In equation 1, $\mu_{ij}$ is the estimated peak passage date at a given site $j$ and year $i$, and $\varphi_j$ is the average distance from a given site to the breeding grounds (described below). The $\beta$ parameters are the effects of year ($\beta_1$), distance to the breeding grounds ($\beta_2$), and their interaction ($\beta_3$). The intercept ($\alpha_j$) is assumed to be site specific ($j$) and is drawn from a normal distribution (Gelman and Hill 2007). Year and distance to the breeding grounds were centered by subtracting the mean value from the variable and standardized by dividing by twice the standard deviation of all estimates.

We used a composite of distance to the breeding grounds instead of latitude for each site along the flyway, as distance to the breeding grounds was a better indicator of the timing of migration along the flyway. Birds move more westward than northward along the northern portion of the flyway in Alaska (Table 1). For example, the Copper River Delta lies at a more northerly latitude than Kachemak Bay, but Iverson et al. (1996) and Warnock et al. (2004b) showed that birds move from the Copper River Delta toward Kachemak Bay. For both species, we used the mean great circle distance from each site to Bethel, Emmonak, and Nome, Alaska. Birds of both species do breed farther north than Nome, but this centroid represents the core breeding range of both species (Warnock and Gill 1996, Franks et al. 2014). While distance to the breeding grounds provided a better fit to the data, using latitude did not substantially change the overall results. We also found no support for an effect of leap year on the date of peak passage and so it was not included in the analyzed models.

We modeled the migrations of Western Sandpipers and Dunlins separately to allow for differing patterns between species. We excluded any year in which the number of survey occasions (dates) was <7, based on survey effort simulations (see Supplemental Material Appendix A Figure S6). For Western Sandpipers, 8 site-years either failed to converge or had fewer than 7 survey dates and therefore were not included in the analysis. We removed 2 outlier estimates of peak passage date from Kennedy Creek (2007, 2016) that we considered implausible for that site. For Dunlins, 22 site-years were excluded because of lack of convergence or too few counts within a season. We also removed 6 estimates of peak passage date from Kennedy Creek that occurred before April 1 (1985, 2004, 2010, 2011, 2012, and 2014). As described in the simulation analysis below, these early estimates may have a biological explanation related to the population of winter residents, but remained as strong outliers that would have violated model assumptions and exerted strong influence on the results. The removed data are shown in Supplemental Material Table S1. After outlier removal, the mixed-effects models for both species had normally distributed residuals and random effects, and we found little indication of heterogeneity of residuals across any of the predictors.

To assess whether adding additional parameters to the model was justified given the data, we compared the full model to a model without a year effect, and to a null model with only the random site effect. The models used in these comparisons were fit with maximum likelihood estimation to allow comparisons between models with differing fixed effects (Zuur et al. 2009). The final model was refit using restricted maximum likelihood (REML) to allow for better estimation of effect sizes. Confidence intervals around the parameter estimates were calculated using a parametric bootstrap evaluation.

Survey methodology changed after 2009 at Hartney Bay (Copper River Delta) and Kachemak Bay. For both sites, we also refit models without the recent Hartney Bay data and without the supplementary counts from Kachemak Bay described above. We compared the results of the models with and without these counts to ensure that the change in methodology had not biased the results. We found that effect sizes did not vary substantially between datasets with and without the additional data, and we therefore included the supplementary data in the final analysis. Across the dataset, some confidence intervals around the estimated dates of peak passage were large, suggesting a high sensitivity to a single day of counts. We refit the models without these data points, but did not find a difference in the final model results.

### Post Hoc Analysis Including Temperature

Based on the results of the flyway-scale analysis, we examined potential causes of the divergent trends in peak passage dates by assessing support for models that included a local temperature variable in shaping the peak passage date at each of the sites. While external factors that shape migratory progression may include, among others, climate, food availability, and predation, we were limited by data availability in the effects that we could consider. We obtained temperature data for all sites across all years using publicly available data from the National Oceanic and Atmospheric Administration's (NOAA) Climate Information (https://www.ncdc.noaa.gov/) and Environment and Climate Change Canada's Historical Climate Data (http://climate.weather.gc.ca) sites. We downloaded climatic data from the monitoring stations nearest each site for which there were data available for all years in the analysis. We used the minimum daily temperature as this was available for the complete dataset, whereas mean temperature was not. For each site and year, we calculated the mean minimum daily temperature across the range of that site's survey dates across all years. Therefore, the range of days differed between sites, but within sites was held constant across years.

There was no consistent trend in local warming or cooling across the sites (Supplemental Material Figure S1). Across all years, most sites showed a slight decrease in the local minimum temperature, but there was a large amount of variation between years. We did not expect that such small-scale local temperature changes would explain the observed interannual trends in peak passage dates, but that annual local temperatures could explain some of the variation at individual sites around the broader interannual trend.

We developed a set of candidate models that included mean minimum temperature at a site as a fixed effect to explain within-site variation in peak passage date. We compared these models with the original models after finding that using the random intercept of site was the most parsimonious random effect structure with and without temperature data (Zuur et al. 2009). The modified version of the original model was described as follows:

$$\mu_{ij} = \alpha_j + \beta_1 \cdot year_i + \beta_2 \cdot \varphi_j + \beta_3 \cdot \varphi_j \cdot year_i + \beta_4 \cdot \tau_{ij} \cdot \eta_j + \beta_5 \cdot \tau_{ij} + \beta_6 \cdot \eta_j + \varepsilon_{ij}, \quad \text{(equation 3)}$$

where the first portion of the equation remains equivalent to the previous model described above in equation 1. The additional parameter $\tau_{ij}$ is the average of the minimum daily temperature for a given site and year across the range of survey dates for a specific site. It is presented as the deviation from the mean of that value and standardized by dividing by twice the standard error of the value. The added parameter $\eta_j$ is a modifying parameter for the temperature effect that separates southern sites (Kennedy Creek, Roberts Bank, and Tofino Mudflats,) from northern sites (Copper River Delta, Hartney Bay, Kachemak Bay). The additional $\beta$ parameters are the effects of temperature ($\beta_5$), categorical location ($\beta_6$), and their interaction ($\beta_4$).

### Simulation Analysis: Effects of Behavior on Estimates of Peak Passage Dates

We conducted a simulation analysis to assess the effect of migration decisions on our measure of the peak passage date at a site. We simulated count data from a simple individual-based model of birds passing through a stopover site. Simulated migrants arrived at a stopover location, spent a given number of days at the site, and then departed onward. The actions of individual birds generated a distribution of counts from which we extracted a peak passage date. Specifically, the arrival date and length of stay of migrants were stochastically chosen from a log normal distribution (Limpert et al. 2001) with a mean value of length of stay based on the literature (Warnock and Bishop 1998, Bishop et al. 2004, Warnock et al. 2004a). The model was developed in Python 3.4 using NumPy (Jones et al. 2001, van der Walt et al. 2011). The full Overview, Design concepts, and Details (ODD) description (Grimm and Railsback 2005, Grimm et al. 2010) of the model is available in Supplemental Material Appendix B.

We simulated 2,000 birds moving through a site for each simulation run. We performed 10 baseline runs to get an estimate of natural variation in the model. Each subsequent analysis had 10 model runs for each parameter adjustment. The model generated the abundance of birds at each site daily. We estimated peak passage dates at each site using the same truncated distribution method described above for the stopover site survey data. We then examined individual parameter effects on passage using a global 'one at a time' sensitivity analysis across the realistic range of that parameter (Grimm and Railsback 2005). We calculated the magnitude of change in peak passage dates in response to changes in lengths of stay, population size, and timing of arrival at the site.

We also modified this basic model to address 2 potential sources of bias that can complicate the understanding of migratory progression along a flyway. First, distinct migratory populations can have different migration strategies, which might be reflected in spatial or temporal variability in the passage of cohorts based on factors such as geographic location of overwintering areas, age, or sex (Warnock and Bishop 1998, Bishop et al. 2004). To understand how the presence of multiple migration strategies could affect the estimate of the date of peak passage, we simulated a population that used 2 strategies: the baseline strategy described above, and a strategy wherein migration was initiated later but progressed more quickly (Taylor et al. 2007). The later-migrating birds arrived at the simulated site on average 4 days later and had a mean length of stay 3 days shorter than those that used the baseline strategy (Supplemental Material Appendix B). The proportion of the population using the baseline strategy was adjusted from 0 to 1 to understand

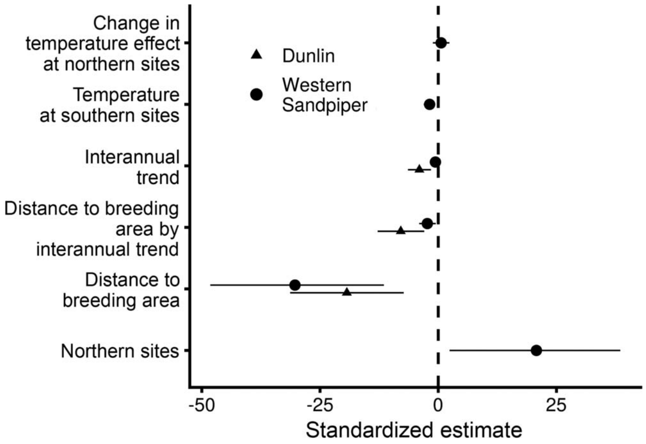

**FIGURE 2.** Standardized fixed effect parameter estimates and their associated bootstrapped 95% confidence intervals for the best supported models describing trends in peak passage dates during spring migration along the Pacific Flyway from 1985 to 2016 for Western Sandpipers and Dunlins. The interannual trend, distance to breeding area, and temperature have been centered by subtracting the mean from the variable and then standardized by dividing by twice the standard deviation. Changes in temperature have also been centered around the site's mean minimum temperature. The model for Western Sandpipers included additional variables of mean minimum site temperature and its interaction with northern sites (Copper River Delta, Hartney Bay, and Kachemak Bay, Alaska, USA) and southern sites (Kennedy Creek, Washington, USA, and Roberts Banks and Tofino Mudflats, British Columbia, Canada).

how mixing the 2 strategies affected the estimate of peak passage date.

Second, the timing of migration may be affected by the proportion of birds that are already present at each stopover site before the migration period begins (Warnock and Gill 1996, Franks et al. 2014). To examine how the presence of and changes in the size of a wintering population at one site could affect peak passage dates, we added a term to denote the proportion of an overwintering population that was present at the stopover site before surveys began. The count window for the model was set to begin on the date when the first migrant bird arrived. This was a numerical technique to ensure standardization of surveys to the actual migration period, but assumed that the survey design incorporated knowledge of when migrants began to arrive. We examined the impact that this assumption had on the first analyzed survey date, and found no change in the first date included in the estimation of peak passage as the proportion of wintering birds increased or as the arrival date of migrants changed. This is likely because the distribution of migrant arrivals means that even if mean arrival is on day 4, there is still at least 1 bird arriving on day 1.

## RESULTS

### Interannual Trends in Peak Passage Dates

Estimated peak passage dates (μ) varied by species, year, and site (Supplemental Material Table S1).

**Western Sandpipers.** The mean peak passage date ranged from April 28 (day of year 118 [scaled to nonleap years]; Kennedy Creek) to May 10 (day of year 130; Kachemak Bay; Table 2). The full model that included the interaction between distance to the breeding grounds and year had moderate support from the data ($w_i = 0.47$) when compared with models without the interaction or without any fixed effects (Table 3A). The model without the interannual trend had almost equal support ($w_i = 0.36$).

As is expected in a northward migration, the date of peak passage occurred earlier at the more southerly sites farther from the breeding grounds (Kennedy Creek and Roberts Bank) and later at sites closer to the breeding grounds (Copper River Delta, Hartney Bay, and Kachemak Bay). The shift in peak passage dates over the years was strongly divergent with distance from the breeding grounds, with peak passage dates becoming earlier at the southern sites and slightly later at the northern site of Kachemak Bay.

**Dunlins.** The migration of Dunlins generally began earlier and lasted longer than that of Western Sandpipers. On average, peak passage dates (scaled to nonleap years) ranged from April 10 (day of year 100; Kennedy Creek) to May 9 (day of year 129; Kachemak Bay and Hartney Bay; Table 2). For the trend analysis, the full model with the interaction between year and distance to the breeding grounds received strong support from the data ($w_i = 0.97$; Table 3B, Figures 2 and 3C).

The interannual trends in peak passage dates were similar to those of Western Sandpipers, but the interaction between year and distance to the breeding grounds suggested that the divergence of the interannual trend with distance to the breeding grounds changed more rapidly in Dunlins, driven by earlier peaks at southern sites. For Dunlins, none of the modeled effects had confidence intervals that overlapped zero (Figure 2). The interannual trend in peak passage dates at southern sites would have been stronger had we included years with peak passage estimates before April 1, as these years tended to occur later in the time series of Kennedy Creek and Roberts Bank. There was also greater uncertainty in the modeling results, driven by the years with early estimates of peak passage dates at Kennedy Creek and Roberts Bank.

### Post Hoc Analysis Including Temperature

**Western Sandpipers.** There was strong support for the inclusion of temperature in the models of Western Sandpiper peak passage dates. All models that included temperature received more support than those without

**TABLE 2.** Average timing and survey effort between 1985 and 2016 at 6 stopover sites (see Figure 1 and Table 1 for locations) on the Pacific Flyway, listed south to north. Dates of peak spring migration passage for both Western Sandpipers and Dunlins were estimated from the mean of a truncated normal distribution fit using iterative maximum likelihood estimation. The mean standard deviation (SD) of this distribution describes the shape of the fitted distribution and is a value in days. Values are means ± SE.

| Site | Years (*n*) | Survey days | Survey initiation date | Survey termination date | Estimated peak passage date | SD (days) |
|---|---|---|---|---|---|---|
| Western Sandpiper | | | | | | |
| Kennedy Creek, WA | 15 | 13.9 ± 0.9 | April 4 ± 0.6 | May 16 ± 1.6 | April 28 ± 0.6 | 4.7 ± 0.8 |
| Roberts Bank, BC | 23 | 20.6 ± 1.3 | April 18 ± 0.5 | May 11 ± 0.7 | April 29 ± 0.4 | 4.4 ± 0.3 |
| Tofino Mudflats, BC | 3 | 17.3 ± 4.1 | April 21 ± 0.9 | May 18 ± 5.5 | May 3 ± 1.1 | 4.2 ± 0.9 |
| Copper River Delta, AK | 4 | 10.0 ± 0.9 | April 24 ± 1.4 | May 16 ± 0.5 | May 5 ± 0.8 | 5.0 ± 0.5 |
| Hartney Bay, AK | 7 | 19.0 ± 2.5 | May 1 ± 0.6 | May 20 ± 2.6 | May 8 ± 0.7 | 2.9 ± 0.3 |
| Kachemak Bay, AK | 15 | 20.5 ± 1.5 | April 21 ± 1.6 | May 22 ± 1.1 | May 10 ± 0.4 | 3.7 ± 0.2 |
| Dunlin | | | | | | |
| Kennedy Creek, WA | 10 | 14.5 ± 1.2 | April 4 ± 0.7 | May 13 ± 0.7 | April 10 ± 1.6 | 10.9 ± 0.7 |
| Roberts Bank, BC | 15 | 19.7 ± 1.7 | April 18 ± 0.6 | May 12 ± 0.9 | April 21 ± 1.7 | 6.6 ± 0.6 |
| Tofino Mudflats, BC | 3 | 17.3 ± 4.1 | April 21 ± 0.9 | May 18 ± 5.5 | May 3 ± 1.5 | 5.2 ± 1.1 |
| Copper River Delta, AK | 3 | 9.7 ± 1.2 | April 25 ± 1.7 | May 16 ± 0.3 | May 4 ± 1.0 | 8.4 ± 2.1 |
| Hartney Bay, AK | 7 | 19.0 ± 2.5 | May 1 ± 0.6 | May 20 ± 0.9 | May 9 ± 0.9 | 2.4 ± 0.4 |
| Kachemak Bay, AK | 15 | 20.5 ± 1.5 | April 21 ± 1.6 | May 22 ± 1.1 | May 9 ± 0.5 | 4.2 ± 0.3 |

**TABLE 3.** Support for models predicting changes in peak passage date of migrating (**A**) Western Sandpipers ($n = 67$ observations) and (**B**) Dunlins ($n = 53$ observations) on northward migration along the Pacific Flyway of North America. Model variables include the distance from each stopover site to the breeding area (Dist), an interannual trend (Year), the mean minimum temperature (Temp), and the division of sites between those in Alaska vs. south of Alaska (NS). All models include a random intercept of site. $r^2$ values are the marginal fit to the model of the fixed effect parameters (Nakagawa and Schielzeth 2013). As temperature was added post hoc, model support prior to its addition is noted separately ($w_i$*). $K$ is the number of parameters in the model, $-2\ln L$ is negative 2 times the log-likelihood of the model, $\Delta\text{AIC}_c$ is the difference from the top model in Akaike's information criterion corrected for small sample size, and $w_i$ is the Akaike weight (which indicates support for the model within the candidate model set).

| Model description | $K$ | $-2\ln L$ | $\Delta\text{AIC}_c$ | $w_i$ | $r^2$ | $w_i$* |
|---|---|---|---|---|---|---|
| (**A**) Western Sandpipers | | | | | | |
| Year*Dist + Temp*NS [a] | 9 | 270.28 | 0.00 | 0.63 | 0.89 | — |
| Year*Dist + Temp | 7 | 277.43 | 1.90 | 0.25 | 0.82 | — |
| Dist + Temp | 5 | 284.63 | 4.18 | 0.08 | 0.78 | — |
| Year + Dist + Temp | 6 | 284.18 | 6.15 | 0.03 | 0.78 | — |
| Year*Dist*Temp | 10 | 276.31 | 8.80 | 0.01 | 0.81 | — |
| Year*Dist | 6 | 288.99 | 10.95 | 0.00 | 0.80 | 0.47 |
| Dist | 4 | 294.26 | 11.47 | 0.00 | 0.77 | 0.36 |
| Dist + Year | 5 | 293.62 | 13.17 | 0.00 | 0.77 | 0.16 |
| Temp | 4 | 295.90 | 13.11 | 0.00 | 0.02 | 0.16 |
| Null model | 3 | 305.65 | 20.60 | 0.00 | 0.00 | 0.00 |
| Year | 4 | 304.78 | 21.99 | 0.00 | 0.00 | 0.00 |
| (**B**) Dunlins | | | | | | |
| Year*Dist [b] | 6 | −154.72 | 0.00 | 0.58 | 0.71 | 0.97 |
| Year*Dist + Temp | 7 | −152.06 | 1.61 | 0.26 | 0.71 | — |
| Year*Dist + Temp*NS | 9 | −154.20 | 3.04 | 0.13 | 0.84 | — |
| Dist + Year | 5 | −153.96 | 7.78 | 0.01 | 0.66 | 0.02 |
| Dist | 4 | −159.89 | 9.12 | 0.01 | 0.65 | 0.01 |
| Year*Dist*Temp | 10 | −159.73 | 9.88 | 0.00 | 0.72 | — |
| Year + Dist + Temp | 6 | −161.78 | 10.00 | 0.00 | 0.66 | — |
| Dist + Temp | 5 | −161.55 | 11.10 | 0.00 | 0.65 | — |
| Year | 4 | −163.50 | 12.56 | 0.00 | 0.01 | 0.00 |
| Null model | 3 | −165.40 | 14.01 | 0.00 | 0.00 | 0.00 |
| Temp | 4 | −165.16 | 15.88 | 0.00 | 0.00 | — |

[a] Top model: $\text{AIC}_c = 291.44$.

[b] Top model: $\text{AIC}_c = 323.28$.

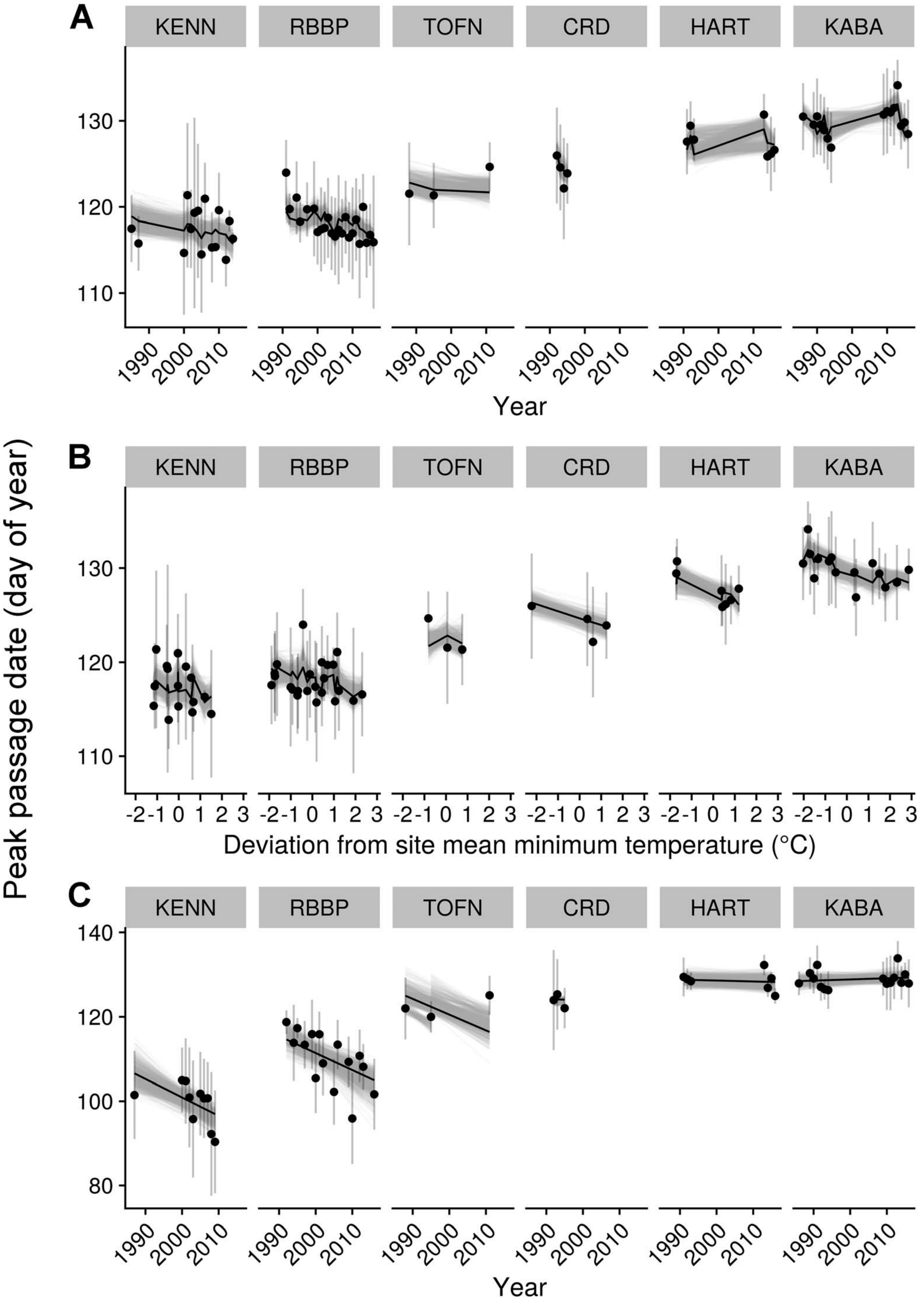

**FIGURE 3.** The predicted (**A**) interannual and (**B**) mean minimum local air temperature (in °C) effects on peak spring migration passage dates estimated from the best supported linear mixed model for Western Sandpipers, and (**C**) interannual trends for Dunlins at Kennedy Creek, Washington, USA (KENN), Roberts Bank, British Columbia, Canada (RBBP), Tofino Mudflats, British Columbia (TOFN), Copper River Delta, Alaska, USA (CRD), Hartney Bay, Alaska (HART), and Kachemak Bay, Alaska (KABA). Predicted model patterns across years at each site are shown with their associated bootstrapped prediction error (light gray lines). Estimated peak passage dates are shown with the estimated standard deviation of counts around that peak. The sites are arranged from left to right in decreasing distance from the breeding grounds. Only the interannual trend is shown for Dunlins because there was little support from the data for a model that included temperature.

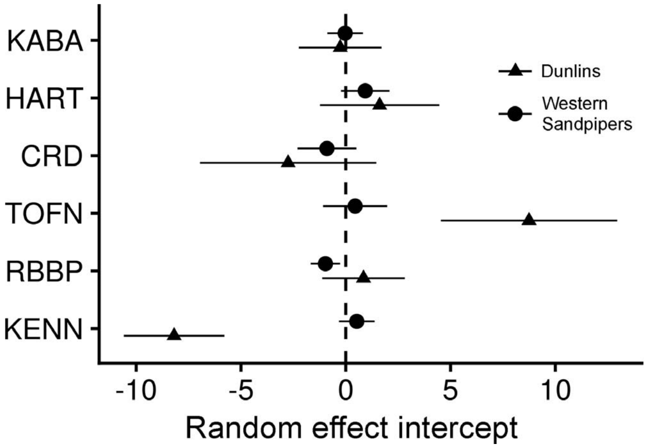

**FIGURE 4.** Random effect deviations in days, with associated 95% confidence intervals, from the expected model intercept for spring migration passage dates along the Pacific Flyway of Western Sandpipers and Dunlins based on distance from the breeding grounds alone for Kennedy Creek, Washington, USA (KENN), Roberts Bank, British Columbia, Canada (RBBP), Tofino Mudflats, British Columbia (TOFN), Copper River Delta, Alaska, USA (CRD), Hartney Bay, Alaska (HART), and Kachemak Bay, Alaska (KABA).

temperature (Table 3A). The model that received the most support from the data included variables from the previous top model plus a temperature parameter that varied based on whether a site was farther from or closer to 2,000 km from the breeding grounds ($w_i = 0.63$). This parameter divided sites into those within Alaska (Copper River Delta, Hartney Bay, and Kachemak Bay) and those south of Alaska (Kennedy Creek, Roberts Bank, and Tofino Mudflats). The second-ranked model, which received most of the remaining support from the data ($w_i = 0.25$), did not include the north–south interaction term. In the top model, only the effect of year (without the interaction with distance to the breeding grounds) and the difference in temperature effect between northern and southern sites had confidence intervals that overlapped zero (Figure 2).

Mean minimum temperature had different impacts on northern and southern sites (Figure 3B). An increase in temperature at southern sites led to earlier departure by 1.22 days per °C and at northern sites to earlier departure by 1.83 days per °C. There was still a strongly divergent trend in peak passage dates between northern and southern sites (Figure 3A).

After accounting for the impact of temperature, the divergent interannual trends between northern and southern sites remained (Figure 2). Peak passage dates through the 2 most southerly sites were estimated to have become 0.08 and 0.09 days year$^{-1}$ earlier, while estimated passage dates through the northern sites became 0.03, 0.04, and 0.05 days year$^{-1}$ later. The random effects related to site show how site-specific passage dates differ relative to what was expected from their distance to the breeding grounds and temperature. There were only small deviations from the expected mean site passage dates, with peak passage dates at Roberts Bank and Copper River Delta occurring earlier by ~1 day relative to their distance from the breeding grounds (Figure 4). Migration at Tofino Mudflats and Kennedy Creek occurred ~0.5 days later than expected from their distances to the breeding grounds alone. Hartney Bay appeared to have peaks that occurred ~2 days later than those at the main Copper River Delta site (Figure 4).

**Dunlins.** The inclusion of temperature in the models did not substantially change the results for Dunlins. The top model remained the model that included year, distance to the breeding grounds, and their interaction, though its support from the data was diminished with the inclusion of the additional models ($w_i = 0.58$; Table 3B). Although the second and third best-supported models included the divergent temporal pattern, they also include the temperature effect and the divergent temperature effect, respectively (Table 3B). The random effect of site showed greater variance in the Dunlin model than in the Western Sandpiper model in each site's mean peak passage date relative to that expected from the distance to the breeding grounds. Mean peak passage through Kennedy Creek was relatively early, and through Tofino Mudflats was comparatively late, compared with what was expected; however, peak passage through Roberts Bank, Copper River Delta (including Hartney Bay), and Kachemak Bay was closer to the mean expected date. The difference in relative passage intercepts for Dunlins at Hartney Bay and the geographically adjacent Copper River Delta was even larger than that for Western Sandpipers, with peaks separated by ~5 days (Figure 4).

### Simulation Analysis: Effects of Behavior on Estimates of Peak Passage

The baseline arrival day of the year was 110.0 ± 1.3 (all simulation parameters are mean ± SD of the distribution) and the baseline length of stay was 5.0 ± 1.1 days. Under these conditions, our simulated baseline estimated date of peak passage was 112.39 ± 0.01 (all simulation effects are reported as mean ± SE).

Unsurprisingly, changes in mean arrival date by 1 day resulted in changes to the peak passage estimate of ~1 day (1.11 ± 0.01 day), which was double the effect size of the length of stay. An increase in the length of stay of 1 day shifted the peak passage date later by one-half day (0.50 ± 0.02 day; Figure 5A). We found no interactive effect between length of stay and arrival date (0.00 ± 0.01 day). Changing the simulated population size had no effect on the peak passage date estimate above 500 birds using the site. Below this point, the variance between estimates

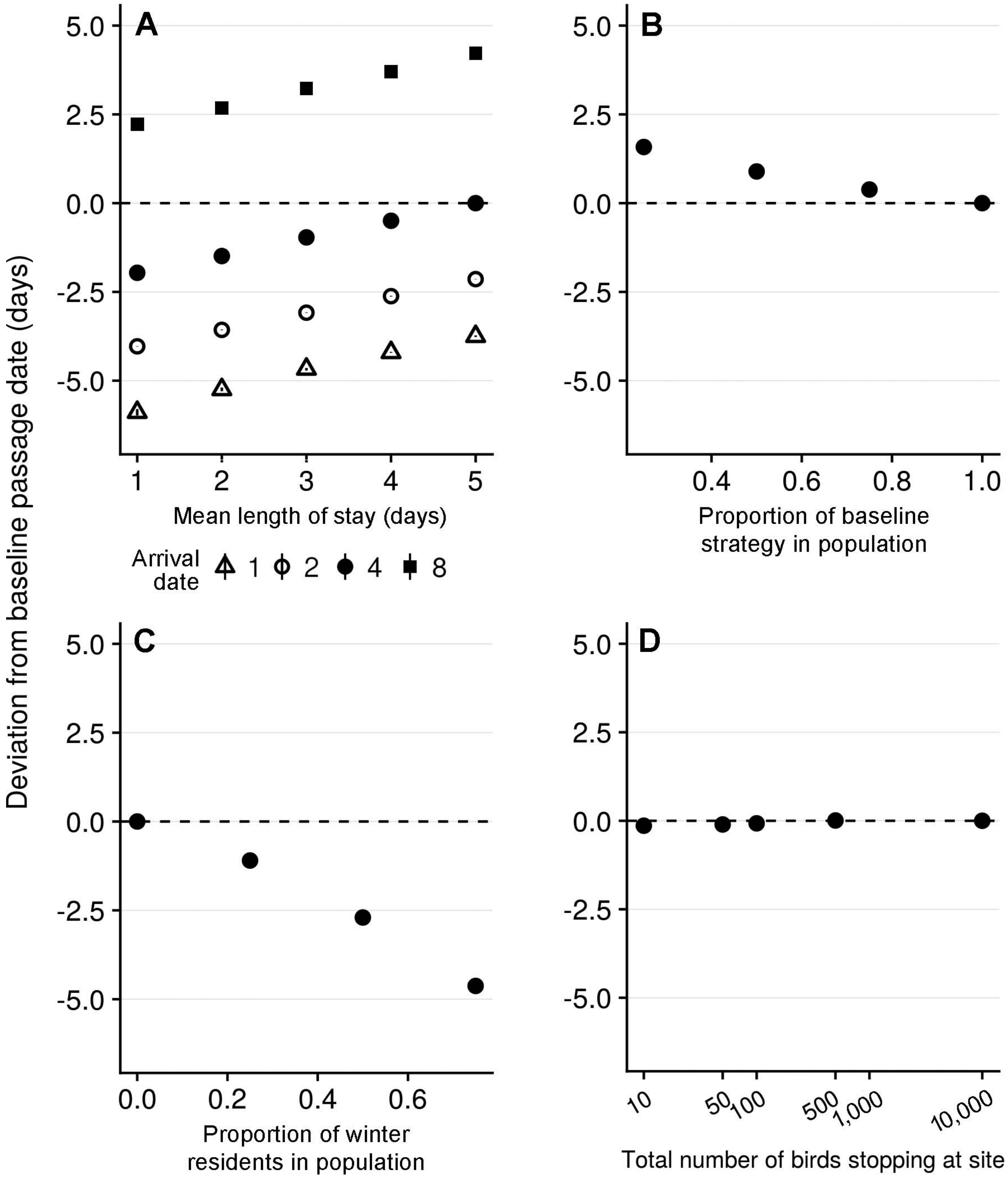

**FIGURE 5.** Effects of changes in simulated behavior of migrant birds passing through a stopover site on the estimated peak passage date at that stopover site. We plot the deviation from date of peak passage estimated in the simulation run with baseline parameters. All passage date estimates are means with 95% CI, which are masked by some points. (**A**) Effect of mean length of stay (in days) and mean arrival date (in days). (**B**) Effect of the relative proportion of 2 migration strategies in the population: Type A (baseline strategy), which is to arrive early, but stay longer; and type B, which is to arrive later but have a shorter length of stay. (**C**) Effect of the proportion of the total population that is present at the start of the simulation. This simulates a nonbreeding population that is resident at the start of counts. (**D**) Effect of changes in the total number of birds using the stopover site.

increased and the estimate became slightly earlier, although only by 0.15 day (Figure 5D).

The introduction of an alternative migration strategy had a small effect on the estimate of peak passage date. The alternative strategy involved arriving later and staying for a shorter time (arrival date: 114.0 ± 1.2 [mean ± SD]; length of stay: 2.0 ± 1.1 day [mean ± SD]). As the proportion of the population adopting the alternative strategy increased, the peak passage date became later (Figure 5B). A complete shift in strategy within the population using the site resulted in a shift in peak passage date of only 1.5 days.

The presence of a wintering population at the site prior to migration had a substantial effect on the peak passage date estimate. Under baseline conditions, increasing the proportion of wintering birds present at the start of surveys to 75% of the site's population shifted peak passage to occur >4 days earlier (4.63 days; 95% CI = 4.60–4.64; Figure 5C), but when wintering residents comprised 50% of the site's population, the peak passage date was only 2.69 days earlier (95% CI = 2.69–2.71). As the mean arrival date of migrants was adjusted, there were divergent impacts of adding winter residents on peak passage date estimates. An earlier mean arrival date seemed to flatten out the impact of winter residents. If the mean arrival date was set to day 1, meaning that many of the migrants had arrived when surveys were initiated, changing the proportion of birds that were winter residents had little effect on peak passage date (1 day for a change between 0% and 75% winter residents). Delaying the arrival date of migrants synergistically amplified the impact of increasing the proportion of winter residents in a site's population. When migrant arrival was delayed by 3 days (mean arrival date = day 4), shifting the site population from 0% to 75% winter residents resulted in a date of peak passage that was 22.8 days earlier.

Likewise, the mean length of stay modified the effect of winter residents. When the mean length of stay was 5 days, increasing the proportion of winter residents to 50% of the population moved the baseline peak passage date to occur 2.7 days earlier. If the length of stay was reduced to 1 day, the corresponding shift to 50% winter residents resulted in a peak passage date estimate that was 8.3 days earlier than the baseline value. The model failed to converge when the length of stay was short (1–2 days) and the proportion of winter residents was 75%. When the length of stay was shortened (3 days), arrival time was delayed (4 days late), and proportion of winter residents was high (75%), the peak passage date occurred 66 days earlier than the baseline value, far beyond our cutoff date for the Dunlin analyses.

## DISCUSSION

We analyzed patterns in the timing of the northward migration of Western Sandpipers and Dunlins along the North American Pacific Flyway. Our results indicated changes in the timing of migration that were differentiated across the flyway stopover sites. From 1985 to 2016, the peak passage date of Western Sandpipers at southern sites became earlier by >2 days, while at the sites closest to the breeding grounds it became later by >1 day. Much of the variation in the timing of peak passage was related to local temperatures, but temperature changes did not explain the broader interannual shift. A slowing of northward Western Sandpiper migration by 3.6 days across >2,000 km of flyway represents an unanticipated finding, but matches changes in migratory patterns in response to local climatic changes in other migratory systems (Strode 2003, Hüppop and Winkel 2006, Senner 2012). Dunlin migration showed a similar interannual pattern, but with greater differences between northern and southern sites, complicated by the presence of winter residents at southern sites.

### Comparisons with Tracked Radio-tagged Sandpipers

Our estimates of migratory progression are comparable with direct measures of the migrations of radio-tagged individuals. Dunlins radio-tagged in spring of 2001 at Grays Harbor, Washington (45.90°N, 124.04°W), took an average of 9.1 ± 5.9 days (mean ± SD; $n = 8$) to make the 2,140-km journey to the Copper River Delta (Warnock et al. 2004b). For Western Sandpipers that were radio-tagged in the springs of 1995 and 1996, the journey was estimated to have taken an average of 5.1 ± 2.2 days (Warnock and Bishop 1998, Bishop et al. 2004, Warnock et al. 2004b). Using the fixed effects from our models, we predicted the differences in dates of peak passage between these sites to be 12.4 days for Dunlins and 5.6 days for Western Sandpipers. Radio-tagged Western Sandpipers took 4.3 ± 0.7 days (mean ± SE; $n = 3$) to move between sites in the Fraser and Copper river deltas (~1,900 km) in 1992 (Iverson et al. 1996), compared with our estimate of migratory progression between these 2 sites of 5.6 days in that year. The radio-tracking estimates are the time between the last detection at the southern site and the first detection at the northern site, whereas our progression estimates are the differences in the mean timing of movement for the populations passing through the 2 sites, and therefore will include a portion of the stay lengths at both sites. Nonetheless, while our estimates are slower than the measures generated from the radio-tagged Western Sandpipers and Dunlins, they are comparable, especially if we consider that our estimates also include time spent at the 2 sites of comparison.

### Behavioral Mechanisms for Observed Trends in Peak Passage Dates

Our simulation modeling suggests that the most likely scenario to explain the divergent shift in peak passage dates is based around a shift to an earlier arrival date at the southern stopover sites. As we did not see a corresponding shift in the timing of passage through northern sites, migrants must now be spending longer at either the southern, northern, or some intermediate sites. The extra time could be spent at Roberts Bank if the shift in arrival dates is twice the change in the length of stay. Given that the measured length of stay at Roberts Bank was 3.6 ± 0.9

days in 1992 ($n = 5$; Iverson et al. 1996) and was 2.2 ± 1.2 days in 1995 and 1996 ($n = 25$; Warnock and Bishop 1998), and the model expectation is a 3-day reduction in length of stay to shift the peak passage date to occur 2 days earlier, this scenario seems unlikely. Alternatively, a shift in timing to arrive 4 days earlier at Roberts Bank could be masked by an increase in length of stay of 3–4 days at the site. We did see an increase in the standard deviation of the estimated distribution at the site, which is one of the diagnostic signs of a potential increase in length of stay, but Drever and Hrachowitz (2017) found no indication that stay lengths had changed over the time period of this study. We thus find a shift in timing to an arrival date of 2–4 days earlier to be a more likely explanation for the trends in peak passage date observed at Roberts Bank.

If arrival at Roberts Bank has become earlier and lengths of stay here have not changed, additional time must be spent elsewhere, closer to the breeding grounds. The most likely location is the Copper River delta, but unmonitored sites such as the Stikine River delta are also possible. Iverson et al. (1996) found that many radio-tagged birds stopped at the Stikine and Copper river deltas after departing from the Fraser River delta. Across all birds tracked, detection rates increased steeply between the Fraser, Stikine and Copper river deltas (9%, 29%, and 62%, respectively), suggesting that birds were less likely to skip the Copper River than the Stikine River delta. If the shift in migration timing is limited to Roberts Bank, early arrival could be masked or diluted by the large number of birds at the site. Alternatively, early arrival could be hidden from our peak passage date estimates if lengths of stay also increased at the Copper River Delta site. If this is a larger population-wide trend, the large Copper River delta provides an ideal location for stopover prior to departing northward to the breeding grounds. Conditions at northern sites, such as the Copper River delta, are more likely to be tied to conditions on the breeding grounds. As the date of snowmelt and temperatures on the breeding grounds can vary widely between years (Niehaus and Ydenberg 2006, Kwon 2016), there would be a benefit to moving quickly northward until the local stopover environment provided information about breeding ground conditions.

## Ecological and Environmental Drivers of Migratory Progression

Kwon (2016) showed that Western Sandpipers in Nome, Alaska, delayed nest initiation by 4.3 days between the time periods of 1993–1996 and 2010–2014, corresponding to a 3.6°C decrease in the mean prelaying temperature between the same periods. If southern signals are cueing earlier initiation of migration, while the northern or breeding signal is to delay arrival, this would be expected to result in the pattern that we observed. Our post hoc analysis supports the contention that migrants are cueing into different signals depending on latitude. The southern sites showed little impact of temperature on peak passage dates, but the northern sites showed that peak passage dates became earlier in warmer years.

While the available data suggest that peak passage dates are influenced by temperatures at northern sites, we were unable to examine the influence of food availability or predation. Predation may influence the timing of movement within a flyway. Lank et al. (2003) posited that southward migration strategies of Western Sandpipers and Dunlins may be driven by the migration of Peregrine Falcons (*Falco peregrinus*). Taylor et al. (2007) modeled northward movement by Western Sandpipers and found that, as predator danger increased along the flyway, migrants were heavier when they departed their nonbreeding areas, allowing them to stop for shorter periods at sites farther along the flyway. Clark and Butler (1999) found that wind conditions strongly affected northward movements, but also that a latitudinal gradient in predator abundance kept migrants from moving northward earlier. If such a gradient has shifted as Peregrine Falcon populations have increased across the western hemisphere (Cade et al. 1988), this could present an alternative reason for an earlier shift northward. Predation pressure could cause arrival on the breeding grounds to occur later if synchrony is more important than selection for a specific date (Harts et al. 2016). Under a scenario of increasing predation on the breeding and nonbreeding grounds, Harts et al. (2016) predicted a pattern of early initiation of migration and delayed departure from sites closest to the breeding grounds.

While the timing of arrival on the breeding grounds is related to the timing of food availability (Both et al. 2010, Jones and Cresswell 2010, McKinnon et al. 2012, Senner et al. 2017), the impact of food availability on the timing of northward migratory progression has not been well explored in shorebirds. Nonetheless, Taylor et al. (2007) found that a reduction in food availability along the flyway led to birds initiating migration later and reducing usage at subsequent sites along the migration route. Geese appear to base departure rules from stopovers in part on plant phenology (Duriez et al. 2009), with the suggestion that they follow a 'green wave' northward (van der Graaf et al. 2006). If there were strong seasonal trends in the timing of food abundance along the flyway, we would expect birds to quickly adjust their migratory timing to take advantage of this change, but we know of no such trend or changes in food distribution along the Pacific Flyway of North America.

## Context and Comparison of Detected Shifts in Migratory Timing

Our approach attempted to ascertain the extent of changes in migratory timing across the flyway, rather than estimating the trend at any given site. Even so, our conclusions rely heavily on the patterns in timing observed at Roberts Bank and Kachemak Bay, the sites with the greatest survey effort and strongest interannual trends. However, the inclusion of all available count data along the flyway attempted to ensure that observed effects were not driven solely by these 2 sites and that within-site trends were not widely skewed by small sample sizes. Our post hoc analysis showed that our measures of peak passage date were related to climatic variables, suggesting that seasonal variation in timing may be tied to local conditions.

Our model, which accounted for the role of local temperature, indicated that the timing of peak passage for Western Sandpipers at Roberts Bank has shifted since 1991 (when surveys began at the site) to occur ~2.9 days earlier, while at Kachemak Bay it has shifted to occur later by ~1.9 days. While a shift of 2 to 4 days may seem inconsequential in relation to the annual cycle of these species, such a shift represents a major change in the progression across a portion of the migratory flyway. Tracking studies have suggested that individual Western Sandpipers can complete their migration to the Copper River delta within 8 days (7.7 ± 0.8 days, though the shortest travel time was only 42 hr) after departure from San Francisco Bay (Iverson et al. 1996). A lengthening of migration duration by almost 50% across a portion of this flyway represents a strong shift in what is a short, but vital, part of their annual cycle. European passerines have shown shifts in migration dates of 0.1–0.2 days $\text{year}^{-1}$ earlier (Knudsen et al. 2011). Shifts of similar magnitude (0.25 days $\text{year}^{-1}$ earlier) have been found for some northbound passerines on the Pacific Flyway (Barton and Sandercock 2018). Our observed temporal shifts of 0.09 and 0.08 days $\text{year}^{-1}$ at Kennedy Creek and Roberts Bank are slightly smaller.

Based in part on a power analysis, we believe that our observed trends are unlikely to have been driven by a survey or sampling bias. The best supported pattern remains that Western Sandpipers at Roberts Bank have shifted the timing of their peak date of passage to occur about twice as early as that at Kachemak Bay occurs later. For Western Sandpipers, Roberts Bank has been the stopover site most consistently surveyed across the time period that we examined and has not had an apparent change in usage. The stopover sites other than Roberts Bank and Kachemak Bay (Kennedy Creek, Tofino Flats, Hartney Bay, and Copper River Delta) ensure that our modeling results are more representative of the flyway than showing only the sites with the best data coverage. Our pooled estimates of peak passage dates suggest that Western Sandpiper migration progressed northward at an estimated rate of 199 km $\text{day}^{-1}$ in 1991 and 153 km $\text{day}^{-1}$ in 2016, which is slower than that observed in individual tracking studies of Western Sandpipers along the flyway (Iverson et al. 1996, Bishop et al. 2004), but within the range of migration speeds observed across species (Schmaljohann and Both 2017).

## Dunlins: Impact of Wintering Populations

The observed patterns of migratory progression for Dunlins may have been shaped by changes in the nonbreeding season prior to migration. Dunlins use the most southerly study sites (Kennedy Creek and Roberts Bank) during both the nonbreeding and migration periods (Buchanan 1988, Butler 1994). It is at these 2 sites that we saw earlier peak passage dates occurring. With the overwintering population simulations, we demonstrated that the combination of migration timing and proportion of the population spending the nonbreeding period at a stopover site strongly affected the peak passage date estimate. If a range-wide shift northward in the nonbreeding population (e.g., resulting from milder winters) led to an increased number of birds at the southern sites at the initiation of surveys, this could explain the observed shift to earlier peak passage dates. Alternatively, the earlier peak passage dates could indicate a northward shift in the population within the nonbreeding period prior to the initiation of a breeding migration as early springs become milder at more northerly nonbreeding sites (Rainio et al. 2006, Swanson and Palmer 2009), although such a shift was not evident in Christmas Bird Count data in Washington and Oregon, USA (Fernández et al. 2010).

There is some support outside our peak passage date estimates for a shift in nonbreeding Dunlin distribution. While the fitting of the truncated normal distribution failed for Kennedy Creek in many later years, the date of last observation of at least 100 Dunlins at the site has shifted earlier by ~10 days since 2001 (J. B. Buchanan personal observation), suggesting an earlier shift northward for overwintering birds. Dunlins have been shown to be increasingly aggregated in years of high population abundance and also as Peregrine Falcon populations have increased (Ydenberg et al. 2017). This shift in aggregation could influence winter usage by Dunlins of large sites, such as Roberts Bank, thereby shaping the number of birds at the start of surveys and, therefore, the peak passage date estimates for these sites. The reliability of our approach for measuring migratory progression is uncertain for sites where counts are composed of high proportions of winter-resident birds.

## Conclusion

In conclusion, we suggest that changes in the migratory progression of Western Sandpipers are consistent with a scenario of lengthened duration of spring migration in the northern portion of the migration flyway. Based on the available data and our simulation analyses, we believe that the most likely scenario to explain the observed trends in earlier peak passage dates of Western Sandpipers results from a shift to initiate migration earlier and spend longer at a northern stopover site such as the Copper River delta. Passage timing at the sites closer to the breeding grounds seems to be partially driven by temperature, suggesting that in warmer years migrants depart onward toward the breeding grounds after shorter stay lengths than in colder years. Any behavioral shift could occur through individual plasticity or through changes in the composition of migration strategies within the population (Van Buskirk et al. 2012, Gill et al. 2014). The changes in the timing of migration of Dunlins are suggestive of nonbreeding populations aggregating more heavily at larger sites or shifting northward in some years.

Overall, our novel use of migratory shorebird counts highlights a potential alternative use for count data. Our methodology and analysis show the benefit of utilizing migratory counts across the flyway as opposed to surveying and analyzing each site individually. Although our dataset included 2 of the most important stopover sites along the northern portion of the flyway, counts were nonetheless limited in their scope due to incomplete coverage and would benefit from the addition of counts farther south on the flyway and at intermediate sites such as the Stikine River delta. Long-term monitoring of all important stopover sites within this or other flyways is an essential tool for assessing the health and behavior of migratory populations. Projects such as the Migratory Shorebird Project (Point Blue Conservation Science 2014) are vital to standardizing protocols across a flyway and ensuring that data from sites across a flyway can be brought together for more comprehensive analyses.

We feel that our methodology for assessing peak passage date is more robust than the commonly used mean or median capture date. We recommend exploring existing datasets using our methodology as a quick and low-cost way of detecting changes in migratory timing in other systems. Finally, this study adds to the literature showing the importance of the Copper River delta to Western Sandpipers (Iverson et al. 1996, Warnock and Bishop 1998, Clark and Butler 1999, Bishop et al. 2000). If, as we predict, sandpipers are spending longer at this site, it is important to get updated lengths of stay and census counts to assess population status. Without both, an increase in the length of stay could be masking a population decline at the site.

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**Author contributions:** M.C.D. and D.D.H. conceived the project idea and developed analytical methodology. D.D.H. developed the migration simulation with input from others. D.D.H. performed analysis of data and ran model analysis. J.B.B. collected data at Kennedy Creek. M.J.F.L. and M.C.D. collected data at Roberts Bank. M.C.D. and M.J.F.L. collected data at Tofino Mudflats and M.C.D. developed the interpolation models used for Hartney Bay and Copper River delta counts. M.A.B. collected data at Copper River Delta and the early data from Hartney Bay. G.M. and The Kachemak Bay Birders collected data at Kachemak Bay. D.D.H. wrote the paper with supervision and substantial edits from M.C.D. J.B.B., M.A.B., G.M., and M.J.F.L. contributed substantial edits to the manuscript.

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