

Subarctic-breeding passerines exhibit phenological resilience to extreme spring conditions

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Abstract. There has been relatively little study of the capacity of subarctic passerines to adjust their phenologies to rapid changes on their breeding grounds. Here, we assess variation in passerine arrival timing in Denali National Park, Alaska, from 1995 to 2015, a period that included both the warmest and coldest recorded mean spring temperatures for the park. Using an open-population occupancy modeling approach in which arrival events are random variables, we investigated interannual variation in the arrival distribution for 10 Nearctic–Nearctic migrants, three Nearctic–Neotropical migrants, and one Palearctic migrant. Neotropical–Nearctic migrants varied in terms of the flexibility of their arrival timing, but generally showed plastic phenologies, suggesting resilience under extreme spring conditions. In comparison, Nearctic–Nearctic migrants showed similar or greater plasticity in arrival timing. A majority of species showed synchronous–asynchronous fluctuation in arrival (i.e., synchronous arrival in some years, asynchronous in others) in combination with various levels of the mean response (i.e., early, average, and late arrival), suggesting the presence of interactions between environmental conditions at multiple scales and inter-individual variation. The presence of synchronous–asynchronous fluctuation in arrival suggests that weakening of the north–south temperature gradient under continued Arctic amplification may strongly affect arrival variances. Our results also suggest that complex interactions between distributional and phenological changes may be possible. For example, the arrival distribution of Fox Sparrow (*Passerella iliaca*) became more synchronized over time, a pattern that coincided with a dramatic increase in occupancy probability through expansion of its elevational distribution. Overall, our findings suggest that monitoring of the mean–variance relationship may lead to a deeper understanding of the factors shaping phenological responses.

Key words: arrival date; climate change; intraspecific variance; long-distance migrants; occupancy model; phenotypic plasticity.

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INTRODUCTION

Advances in the breeding and migratory phenology of birds due to climate change are well documented (Parmesan and Yohe 2003, Root et al. 2003, Dunn 2004). The observed shifts are generally thought to be plastic phenotypic responses

rather than micro-evolutionary responses to selection on heritable traits (Gienapp et al. 2007, 2008, Charmantier and Gienapp 2014). Trends toward earlier arrival appear to be more widespread and of greater magnitude in short-distance migrants (e.g., Butler 2003, Mills 2005, Travers et al. 2015) compared to long-distance migrants (but see

Hüppop and Hüppop 2003, Stervander et al. 2005, Jonzén et al. 2006, Zalakevicius et al. 2006). Long-distance migrants are thought to show relatively limited plasticity in migratory timing (e.g., Pulido and Widmer 2005, Miller-Rushing et al. 2008, Both et al. 2009, McKinney et al. 2012), in part due to strong control of migratory onset by endogenous mechanisms (Berthold 1984, Gwinner 1996). On northern breeding grounds experiencing rapid warming, some long-distance migrants show insufficient adaptation of arrival timing relative to changes in the phenology of their invertebrate prey (Both and Visser 2001, Visser et al. 2004). The decoupling of arrival phenology and seasonal food availability has been linked to population declines in long-distance migrants (Both and Visser 2001, Visser et al. 2004).

While there appear to be constraints on the development of plastic migratory traits in long-distance migrants, many of these species fine-tune their migration speed in response to conditions encountered en route (Marra et al. 2005, Both 2010, Tøttrup et al. 2010) and some show variation in departure timing related to conditions on wintering grounds (Gordo et al. 2005, Saino et al. 2007, Studds and Marra 2007). Short-distance migrants, by virtue of wintering in seasonal climates, often show comparatively close tracking of spring phenology during migration and, consequently, tend to have more plastic phenologies (Alerstam and Högstedt 1980, Butler 2003). Our understanding of these relationships in passerines comes largely from studies of Palearctic migrants and from studies at North American mid-latitudes. There has been relatively little study of the potential capacity (or resilience) of passerines breeding in the subarctic to adjust their arrival phenologies to large variation in spring conditions (but see Eeva et al. 2000, Gunnarsson and Tómasson 2011, Grabowski et al. 2013, Liebezeit et al. 2014, Ward et al. 2015). In addition, studies of avian arrival phenology have focused extensively on temporal trends in first or mean arrival dates, but have largely ignored temporal patterns in the variance of the arrival distribution (but see Møller 1994b, Ptasyk et al. 2003, Møller 2008, Møller et al. 2010). Intraspecific phenotypic variation plays an integral role in ecological and evolutionary dynamics, and sole reliance on the mean trait for inference may underestimate the capacity of

species to cope with environmental change (Bolnick et al. 2011, Violle et al. 2012). Assessments of the relationship between the mean and variance of the arrival distribution may lead to a deeper understanding of the factors shaping phenological responses and the capacity of species to adapt their phenologies in response to environmental change.

The costs and benefits of early arrival are phenotype-dependent, and optimization of individual arrival timing is thought to depend on individual condition, the individual-specific costs of early arrival, and the arrival timing of competing males, which helps set the value of arriving on a given date (Møller 1994a, b, Kokko 1999). Carry-over effects often provide a mechanism for inter-individual variation in migratory and breeding timing (reviewed in Harrison et al. 2011). For example, individuals occupying poorer and/or more distant wintering habitat may arrive later on breeding grounds (e.g., Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004). Age- and sex-related differences in migration timing and stopover behavior are also well documented (Yong et al. 1998, Stewart et al. 2002, Vardanis et al. 2011, McKinnon et al. 2014). In addition to differing in their average arrival date, individuals may also differ in the capacity for phenotypic plasticity. Some individuals may show the capacity for adjustments beyond their optimal arrival date that are disproportionate to those exhibited by others. The presence of inter-individual variation in plasticity or an individual by environment interaction (Nussey et al. 2007) may be important factors underlying interannual variation in the spread of the arrival distribution (i.e., variance heterogeneity through time).

Previous studies have documented multiscale influences on arrival timing (e.g., Gordo et al. 2005, MacMynowski and Root 2007, Tøttrup et al. 2010) and the interactive effects of individual variation and environmental conditions on the arrival variance (e.g., Møller 1994b, Ptasyk et al. 2003, Møller 2008). Interactions between environmental conditions at high and mid-latitudes may affect the arrival distributions of subarctic migrants. Over recent decades, Arctic near-surface temperatures have increased at a rate almost twice that of the global average, and zonal mean temperature anomalies show larger increases with increasing latitude (Serreze and

Francis 2006, Serreze et al. 2009, Screen and Simmonds 2010). Given this weakening of the north–south temperature gradient or Arctic amplification, understanding the underlying interactions between high- and mid-latitude environments within migration systems is critical for predicting the possible effects on passerine communities.

Migratory birds are under strong directional selection for earlier breeding (Both and Visser 2001, Dingemanse et al. 2004, Visser et al. 2004, Verhulst and Nilsson 2008). Competition for territories (e.g., Kokko 1999), seasonal variation in food availability (e.g., Both and Visser 2001), predation (e.g., Lank and Ydenberg 2003), and mortality risk during the early spring transition period (Newton 2007) all exert strong selective pressure on arrival and breeding timing. These pressures are likely to be particularly acute in Arctic and subarctic breeders due to heightened mortality risk during the spring arrival period and to the time demands of producing a brood, molting, and preparing for fall migration within a highly compressed breeding season (Eeva et al. 2000). Thus, understanding the potential capacity of passerines breeding in the subarctic to adjust their arrival timing in response to large interannual variation in spring conditions is of critical importance.

In this study, we investigated interannual variation in passerine arrival timing in Denali National Park, Alaska (hereafter, Denali), from 1995 to 2015. Our sampling period included both the warmest (1995) and coldest (2013) mean spring (April–May) temperatures recorded in Denali (1926–2015; Fig. 1), providing the opportunity to assess the effects of a range of spring conditions on the arrival process. We used an open-occupancy modeling approach in which arrival events are random variables. Our objectives were to (1) assess patterns of interannual variation in the mean and variance of the arrival distribution of individual species and (2) compare and contrast the observed patterns between short- and long-distance migrants. We predicted that long-distance migrants would show limited variation in mean arrival, relatively homogenous variance across time, and compressed arrival distributions overall, because long-distance migrants generally exhibit smaller passage variances than short-distance migrants (Mills 2005, Van Buskirk et al. 2009, La Sorte et al. 2013) and high repeatability in arrival (e.g., Conklin and Battley

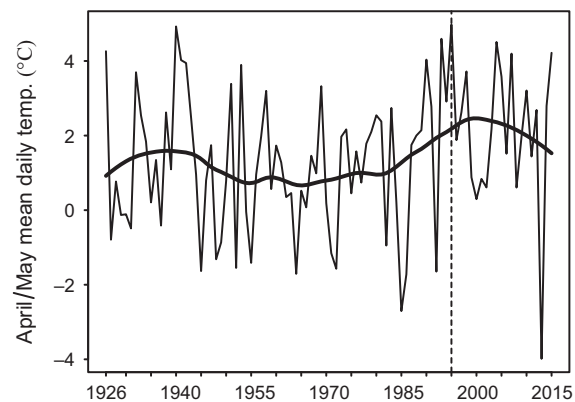


Fig. 1. Average April–May temperature (°C) from a weather station at Denali National Park Headquarters, 1926–2015. The fitted (loess) curve is shown as a solid line. The dotted vertical line indicates the first year of our study.

2011, Vardanis et al. 2011, Stanley et al. 2012). In contrast, we expected that short-distance migrants would show greater variation in the mean response and pronounced variance heterogeneity across time.

METHODS

Data collection

We conducted passerine surveys along the easternmost 118 km of the 144-km Denali Park Road (DPR), a narrow, unpaved road transecting upland forest, treeline, shrubline, and open alpine habitats in the northeastern portion of Denali (63°35.8' N, 149°38.2' W; Fig. 2). We established three roadside survey routes each comprising 50 points with 0.8 km spacing. Trained observers conducted repeated surveys from mid-April to early July during 12 years (1995–1998, 2006, and 2009–2015), and routes were surveyed 2–18 times in each year (mean = 6.5 visits/year). Standard three-minute point count surveys were conducted during favorable weather from 0.5 hours before sunrise to approximately 6 hours thereafter (Bystrack 1981). All birds seen or heard within ~400 m during the count period were recorded (Bystrack 1981), but only detections of singing males were used for our analyses. The same routes were generally surveyed by multiple observers in each year, and some observers conducted surveys in multiple years (Schmidt et al. 2013, Mizel et al.

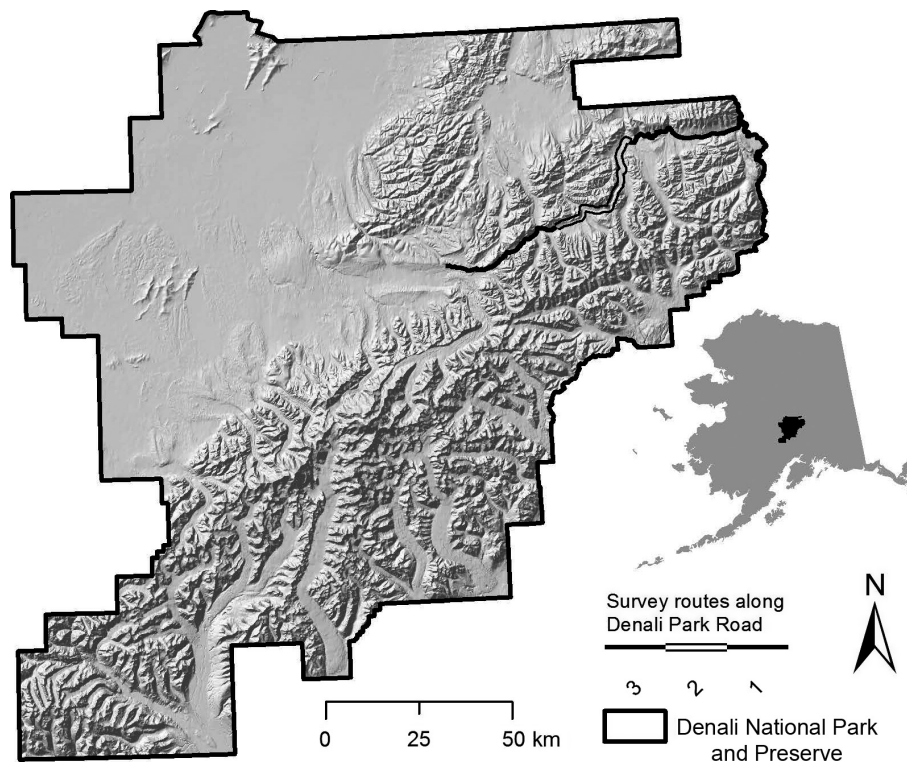


Fig. 2. Survey routes 1–3 along the park road in Denali National Park and Preserve (Denali), Alaska (modified from Mizel et al. 2016).

2016). For additional detailed descriptions of the study area and sampling scheme, see Schmidt et al. (2013) and Mizel et al. (2016).

Analyses

We restricted analysis to species detected at >10% of sites in most years to provide sufficient data to adequately model arrival, observation, and occupancy processes. We also excluded Lincoln's Sparrow (*Melospiza lincolnii*) which had detection probability <0.2 in all years, making it difficult to separate the arrival and observation processes. Our final data set included 14 species, namely 10 Nearctic–Nearctic migrants, three Nearctic–Neotropical migrants, and one Palearctic migrant (Appendix S1). We classified species as short- or long-distance migrants if their wintering grounds lie primarily north or south of the Tropic of Cancer, respectively (Rappole et al. 1983).

We used the open-population occupancy modeling approach of Roth et al. (2014) to estimate arrival events. In this approach, arrival dates are random variables conditional on detection

probability and the true occupancy state. In our data structure, the y_{ijt} observations corresponded to detection/non-detection of a given species at each point $i = 1, 2, \dots, I$, during each repeat survey $j = 1, 2, \dots, J$, in each year $t = 1, 2, \dots, T$. The true occupancy states z_{it} were Bernoulli random variables with occupancy probability ψ_{it} :

$$z_{it} \sim \text{Bernoulli}(\psi_{i,t})$$

Based on the results of Mizel et al. (2016), we assumed ψ_{it} was a linear function of year, elevation (linear and quadratic), two interaction terms, and random site-level adjustments α_i around μ :

$$\text{logit}(\psi_{it}) = \mu + \alpha_i + \alpha_1 \text{year}_t + \alpha_2 \text{elev}_i + \alpha_3 \text{elev}_i^2 + \alpha_4 \text{year}_t \times \text{elev}_i + \alpha_5 \text{year}_t \times \text{elev}_i^2$$

Roth et al. (2014) treated arrival dates as overdispersed Poisson random variables. Given severe time constraints on breeding in the subarctic, we did not expect a need for accommodating

additional variation in the right tail of the arrival distribution. In addition, given the relatively extreme interannual variation in spring conditions that occurred during our study period, we thought it necessary to account for variance heterogeneity across time. Therefore, we described arrival dates a_{it} as normal random variables with a year-specific variance and a random mean that varied by year:

$$a_{it} \sim \text{Normal}(\mu_t, \sigma_t^2)$$

We specified an arrival indicator variable I_{ijt} as an outcome of the relation of a_{it} to the survey date (i.e., date_{ijt}):

$$I_{ijt} = \begin{cases} 1 & \text{when } a_{it} \leq \text{date}_{ijt} \\ 0 & \text{when } a_{it} > \text{date}_{ijt} \end{cases}$$

The y_{ijt} observations were considered to be Bernoulli random variables with success probability specified such that detection probability p_{ijt} was conditional on the true occupancy state z_{it} and the arrival indicator I_{ijt} :

$$y_{ijt} \sim \text{Bernoulli}(z_{it} \times p_{ijt} \times I_{ijt})$$

Based on the findings of Mizel et al. (2016), we assumed detection probability was a linear function of date_{ijt} and time after sunrise, time_{ijt} :

$$\text{logit}(p_{ijt}) = \beta_0 + \beta_1 \text{date}_{ijt} + \beta_2 \text{date}_{ijt}^2 + \beta_3 \text{time}_{ijt} + \beta_4 \text{time}_{ijt}^2$$

We included the linear and quadratic effects of survey timing (relative to sunrise) to account for variation in the probability of availability or diurnal patterns of singing frequency. We included the linear and quadratic effects of survey date to account for variation in availability due to seasonal variation in singing frequency (Schmidt et al. 2013). See Roth et al. (2014) for additional details on model structure.

We were unable to estimate arrival in the years 1997 and 1998 because each of the three survey routes received ≤ 2 visits. However, we did not exclude data from these years as they contained detection and occupancy information. Instead, the arrival variance term for these years was fixed at 25, which corresponded to a mean standard

deviation of 5 d in many species, and the year-specific random mean was set equal to the overall mean of this distribution. The surveys that did occur in these years were conducted in early June (between Julian dates 154–160), that is, after all arrival events were expected to occur for all short-distance migrants and most long-distance migrants. Thus, fixing arrival at reasonable values would be expected to have minimal effect on estimates of other parameters. However, we performed a series of sensitivity analyses on all long-distance migrants in which the arrival variance was set equal to 100 instead of 25. The effect was negligible in all cases.

We fit models using OpenBUGS (Lunn et al. 2009) via the R2OpenBUGS package (Sturtz et al. 2005) in program R 3.2.2 (R Core Development Team 2015). We used diffuse priors on all occupancy and detection parameters (i.e., uniform distributions from 0 to 100 for the standard deviations of the random effects; uniform distributions -10 to 10 for all fixed occupancy and detection covariates). We used diffuse priors for all arrival parameters including uniform distributions from 0 to 30 for all standard deviations and normal distributions with mean 0 and precision 0.01 for the overall mean. Summaries of the posterior distribution were calculated from two independent Markov chains run for 60,000 iterations with a 10,000 iteration burn-in and thinning every four draws. We used the Gelman-Rubin diagnostic (Brooks and Gelman 1998) to assess convergence and scaled continuous covariates (mean = 0, SD = 1) to improve convergence properties. From posterior distributions for arrival dates at occupied sites, we calculated posterior distributions for the proportion of sites with an arrival event on or prior to each date within the survey season (i.e., cumulative arrival proportions). We also calculated the dates at which 5%, 50%, and 95% of occupied sites first showed an arrival event. This allowed us to assess the synchronicity of the arrival process (i.e., the interval between the arrival of the first and last 5% of individuals), as well as the timing of the bulk of the arrivals (i.e., arrival of 50% of the individuals). Estimates for the year-specific mean arrival dates μ_t were nearly equivalent to the 50 percentile estimates (i.e., the median) for all species. For clarity, we refer to the 50 percentile estimates as mean arrival. All estimates are presented as

posterior means with 95% Bayesian credible intervals. We considered arrival to be synchronous in a particular year if the ratio of its standard deviation to the mean standard deviation for that species was <0.5 . Arrival was considered asynchronous if this ratio was >2.0 .

Lastly, we did not include weather covariates on arrival because our approach was to estimate the latent arrival events for each site in each year and a weather covariate would be expected to affect parts of this distribution differently often with minimal effect on later arrival events. However, we accounted for interannual variation in weather by describing arrival in terms of a random mean and variance that varied by year. We also conducted a post hoc linear regression of the annual arrival shift as a function of the average April–May temperature. The annual arrival shift for species i in year j was the mean arrival date for species i in year j minus the multiyear median for species j . We excluded Arctic Warbler (*Phylloscopus borealis*), a Palearctic migrant, from this analysis because this species did not appear to respond to spring temperatures (see *Results*).

RESULTS

Long-distance migrants varied in terms of flexibility in arrival timing. Among Neotropical–Nearctic migrants, Orange-crowned Warbler (*Oreothlypis celata*) and Wilson’s Warbler (*Wilsonia pusilla*) showed interannual variation in mean arrival that was comparable to that exhibited by short-distance migrants; that is, estimates for their year-specific mean arrival dates spanned 13 and 17 days, respectively (Fig. 3a). The remaining Neotropical–Nearctic migrant, Swainson’s Thrush (*Catharus ustulatus*), showed limited variation in mean arrival except for a relatively large advance in 2011 (Fig. 3a). However, contrary to theoretical predictions, all Neotropical–Nearctic migrants exhibited large interannual variation in arrival of the 5 percentile cohort, with year-specific estimates spanning 19–27 days for the three species (Fig. 3b). In addition, all Neotropical–Nearctic migrants showed unexpected and pronounced variance heterogeneity across time (Fig. 4), the result of synchronous–asynchronous fluctuation in arrival (i.e., synchronous arrival in some years, asynchronous in others; Fig. 5a–c). Across these species, we observed asynchronous

arrival and synchronous arrival in combination with all levels of the mean response (i.e., early, average, and late arrival; Fig. 5a–c). In contrast, Arctic Warbler, a Palearctic migrant, showed almost no interannual and intrapopulation variation in its arrival timing (Fig. 5d).

As predicted, short-distance migrants exhibited modest to large interannual variation in mean arrival and arrival of the 5 percentile cohort. Across the 10 short-distance migrants that we considered, interannual variations in mean arrival and arrival of the 5 percentile cohort spanned 13–26 and 14–32 days, respectively (Fig. 3). Short-distance migrants exhibited individualistic patterns of interannual variation in the dispersion of arrival dates (Fig. 4). Some species had small variances that were relatively homogenous across time and others showed pronounced variance heterogeneity across time (Fig. 4), the result of synchronous–asynchronous fluctuation in arrival (Figs. 6c–d and 7b, e). The arrival of Fox Sparrow (*Passerella iliaca*) became more synchronized over time (Fig. 7a) in concert with dramatic expansion of its elevational distribution at both low and high elevations (Mizel et al. 2016).

Arrival timing of Nearctic–Nearctic and Neotropical–Nearctic migrants showed an apparent relationship with local temperature (Appendix S2). Correspondingly, the extremely late spring of 2013 synchronized the arrival of the entire community. With the exception of Savannah Sparrow (*Passerculus sandwichensis*) and Arctic Warbler, mean arrival dates spanned only three and five days for long- and short-distance migrants, respectively (Fig. 3a). During the early spring of 1995, most species had advanced mean arrival, but the effect tended to be greatest in the 5 percentile cohort with advances (relative to each species’ multiyear median) of 15, 18, and 20 days in Orange-crowned Warbler, Fox Sparrow, and Wilson’s Warbler, respectively (Fig. 3b).

DISCUSSION

Long-distance migrants are expected to have relatively inflexible phenologies, making them susceptible to trophic mismatches and corresponding population declines under climate change (e.g., Both and Visser 2001, Both et al. 2009). However, we found that two Neotropical–Nearctic migrants,

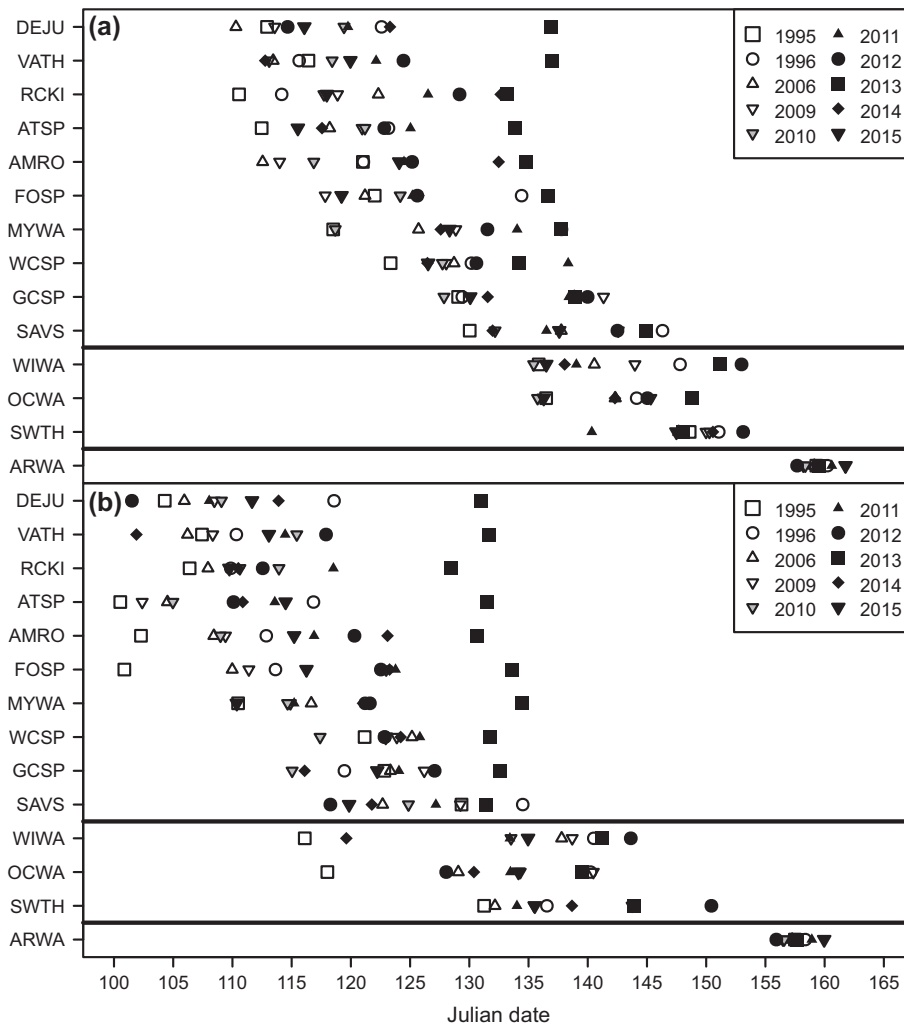


Fig. 3. Year-specific, posterior means for the Julian date on which (a) 50% and (b) 5% of occupied sites had shown an arrival event. Thick black lines separate short-distance migrants (top), Neotropical–Nearctic migrants (middle), and a Palearctic migrant (bottom). Within migration groups, species were ordered according to their average arrival date. The symbols for 1995 (open squares) and 2013 (filled squares) were enlarged for emphasis. See Appendix S1 for species names and codes.

Orange-crowned and Wilson’s warblers, showed unexpectedly plastic phenologies, suggesting resilience under extreme spring conditions. Swainson’s Thrush, the remaining Neotropical–Nearctic migrant, showed limited interannual variation in mean arrival, but greater variation in the arrival of the 5 percentile cohort, suggesting the capacity for plastic adjustments in arrival timing. Short-distance migrants showed similar or greater plasticity in arrival timing, indicating an ability to closely track the emergence of spring along their migration routes. Overall, our findings suggest

that both Neotropical–Nearctic and Nearctic–Nearctic migrants breeding in interior Alaska are able to adjust arrival in response to relatively large interannual variation in spring conditions.

The onset of spring in Denali is rapid and unpredictable in its timing. Further, it comprises large temperature variation and is often interrupted by periods of cold weather and snow, thereby representing substantial risk for early-arriving individuals. Thus, all but the latest arriving species in our study area may have undergone selection for plasticity in arrival.

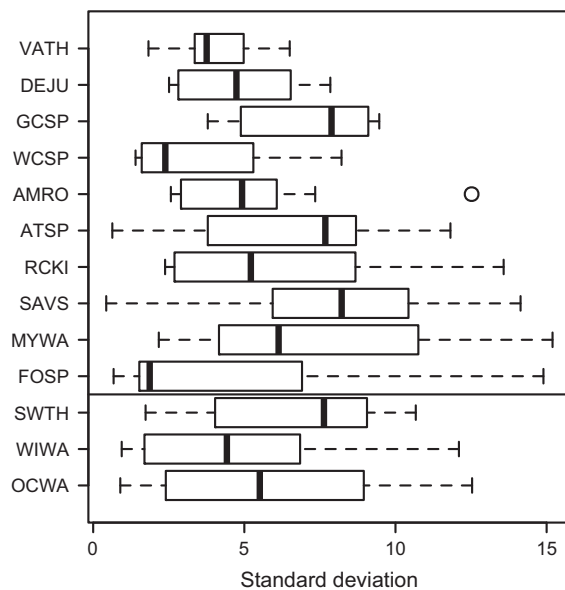


Fig. 4. Boxplot of year-specific standard deviations for migrants breeding in Denali National Park, Alaska (1995–2015). The thick black line separates short-distance from long-distance migrants (bottom). Within migration groups, species were ordered according to the standard deviation of the year-specific standard deviations. Arctic Warbler is not shown because of a lack of variability in arrival dates.

All Neotropical–Nearctic and several Nearctic–Nearctic migrants showed variance heterogeneity across time, the result of synchronous–asynchronous fluctuation in arrival. With the notable exception of Fox Sparrow, the degree of synchronicity in arrival did not appear to be strongly associated with annual occupancy, suggesting little support for interannual variation in density-dependent competition driving fluctuation in arrival variances. Instead, many species exhibited temporal trends in occupancy (Mizel et al. 2016), indicating the presence of temporal correlation in annual density amidst random interannual fluctuations in the arrival variance. Thus, the fact that we observed synchronous and asynchronous arrival in combination with various levels of the mean response (i.e., early, average, and late arrival) suggests the presence of interactions between environmental conditions at multiple scales and inter-individual variation in average arrival and, potentially, in phenotypic plasticity. That is, these interactions were likely

involved in order for the variance to be large or small, irrespective of the mean response.

This may be conceptualized by decomposing the migration systems of high-latitude breeders into three basic environments: the wintering ground environment (E_W), the migration route or mid-latitude environment (E_R), and the near-breeding ground environment (E_B). Given its potential severity, the high-latitude environment (E_B) often mediates the conflated effect of the wintering ground–migration route environment ($E_W E_R$) on arrival timing. Early-asynchronous arrival may result when conditions on the $E_W E_R$ are near average, but an unusually favorable E_B releases the vanguard cohort to show a disproportionately large advance relative to the rest of the population. For example, in 1995, Wilson’s and Orange-crowned warblers showed early arrival overall, but the shift in the 5 percentile cohort was disproportionate to that exhibited by the rest of their respective populations, resulting in early-asynchronous arrival.

Early-synchronous arrival may arise when a favorable $E_W E_R$ (e.g., mid-latitude conditions) relaxes the costs of early arrival sufficiently to induce early passage of most individuals and E_B conditions also align favorably. In 2010 and 2015, Wilson’s and Orange-crowned warblers exhibited early arrival overall, but the 5 percentile cohort did not realize a disproportionate response, resulting in early-synchronous arrival. The frequency dependence of migratory timing may also underlie early-synchronous arrival (Kokko 1999). Arrival timing is thought to be optimized on the basis of individual-specific costs and benefits which themselves are a function of individual condition and the arrival timing of other males in the population (Møller 1994a, Kokko 1999). Thus, when spring conditions are ameliorated and risk is reduced to a certain degree, average and lower-quality males may anticipate the early arrival of competing males, possibly through assessment along the migration route, triggering them to advance their arrival beyond their particular “cost-minimizing date” (Kokko 1999) or optimal migratory timing, leading to early-synchronous arrival.

Because we lack data on individuals, our understanding of inter-individual variation in phenotypic plasticity in these populations is limited and further complicated by multiscale environmental

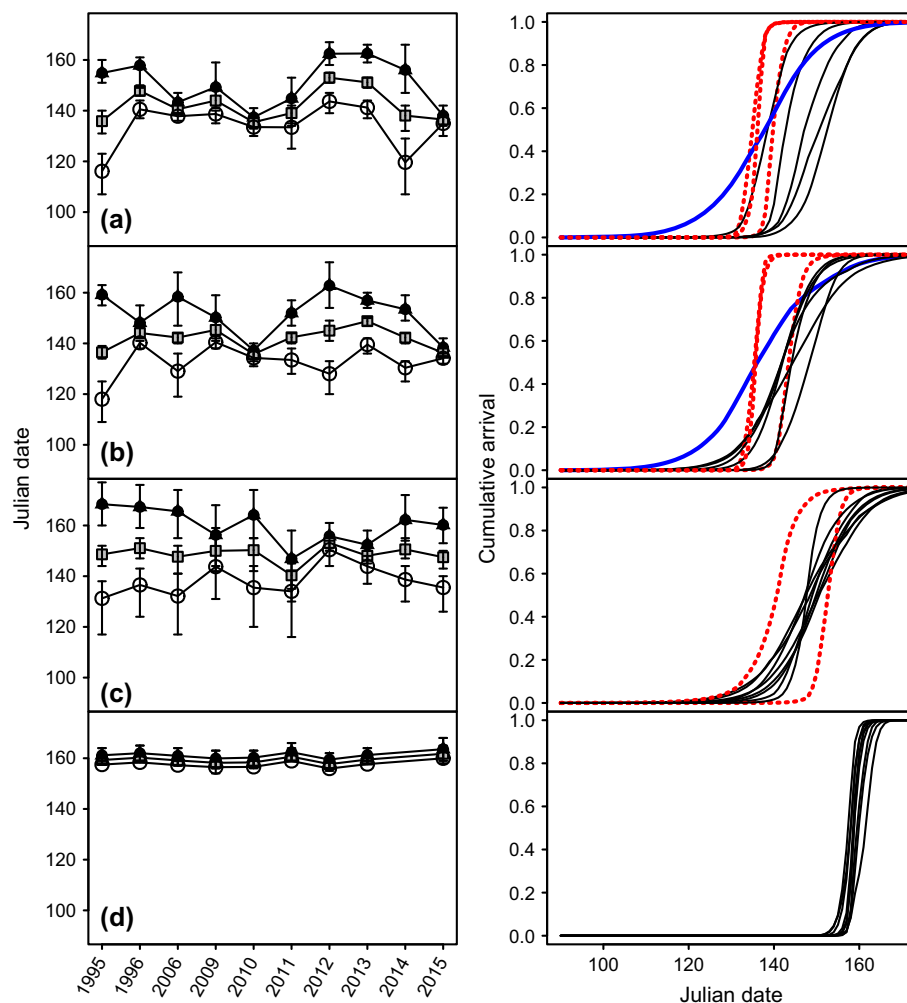


Fig. 5. Arrival distributions of long-distance migrants in Denali National Park, Alaska (1995–2015). Only years in which sampling occurred and arrival was estimable are shown. Right panels show cumulative arrival curves, and left panels show species-specific posterior means for the Julian dates in which 5% (open circles), 50% (gray squares), and 95% of occupied sites had shown an arrival event. Bayesian 95% credible intervals are also shown. Species include (a) Wilson's Warbler, (b) Orange-crowned Warbler, (c) Swainson's Thrush, and (d) Arctic Warbler. We considered arrival to be synchronous (dashed red lines) if the ratio of the standard deviation of that year to the average standard deviation was <0.5 . Arrival was considered asynchronous (blue lines) if this ratio was >2.0 .

interactions, the role of stochastic influences (e.g., wind patterns), and potential non-linear responses to environmental variation. However, the fact that we observed interannual changes in the mean–variance relationship including instances of early-synchronous and early-asynchronous arrival suggests the presence of an individual by environment interaction ($I \times E_W E_R \times E_B$), or inter-individual variation in phenotypic plasticity (Nussey et al. 2007). That is, in response to environmental variation, some males may make

adjustments from their average arrival timing that are disproportionate to those made by other males. The shape of the arrival distribution may then depend on which individuals (e.g., high or average quality) make these adjustments and in which environment(s) they are made, $E_W E_R$ and/or E_B . At a minimum, the observed pattern suggests a population-level capacity in these species to adjust their arrival timing to large variation in spring conditions. If, hypothetically, the potential for a phenological mismatch exists in these

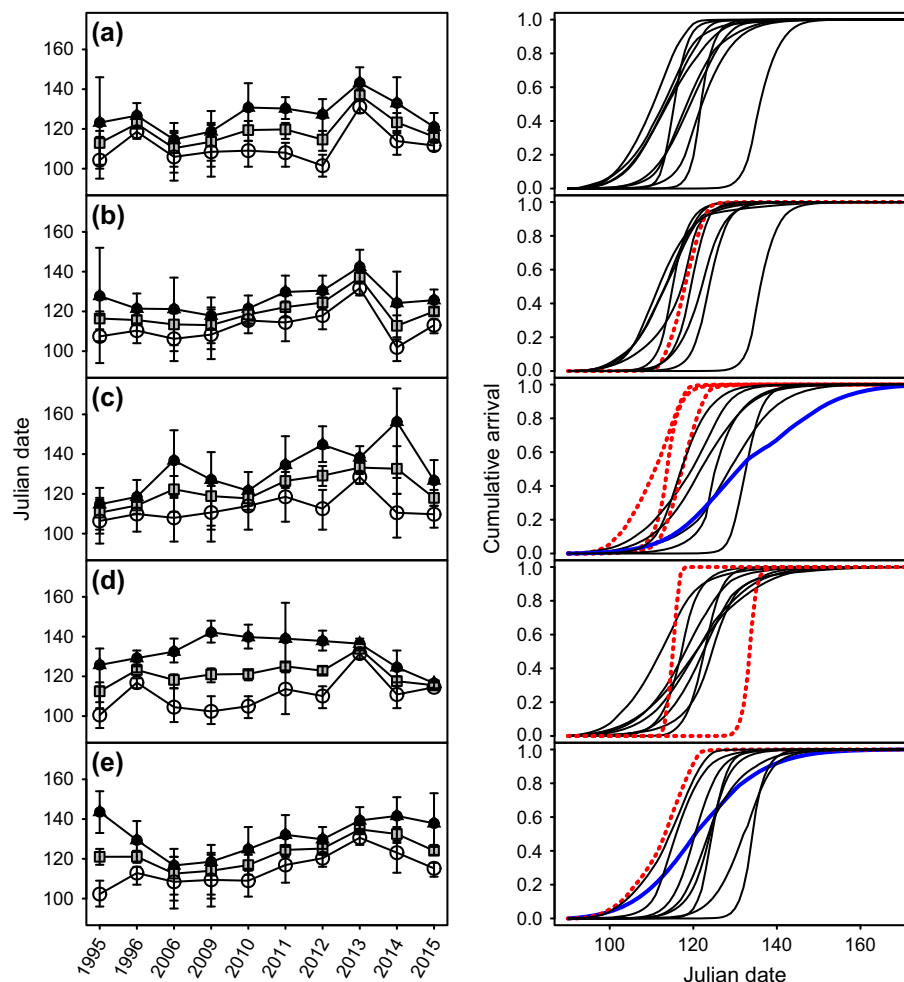


Fig. 6. Arrival distributions of short-distance migrants in Denali National Park, Alaska (1995–2015). Only years in which sampling occurred and arrival was estimable are shown. Right panels show cumulative arrival curves, and left panels show species-specific posterior means for the Julian dates in which 5% (open circles), 50% (gray squares), and 95% of occupied sites had shown an arrival event. Bayesian 95% credible intervals are also shown. Species include (a) Dark-eyed Junco, (b) Varied Thrush, (c) Ruby-crowned Kinglet, (d) American Tree Sparrow, and (e) American Robin. We considered arrival to be synchronous (dashed red lines) if the ratio of the standard deviation of that year to the average standard deviation was <0.5 . Arrival was considered asynchronous (blue lines) if this ratio was >2.0 .

species, then the affected segment of the migrant population could vary considerably on an annual basis given the observed variation in the mean–variance relationship.

In general, the arrival variances of short-distance migrants were not larger than those of Neotropical–Nearctic migrants. This was in contrast to studies conducted at North American mid-latitudes showing larger passage variances for short-distance migrants compared to Neotropical–Nearctic

migrants (Mills 2005, Van Buskirk et al. 2009, La Sorte et al. 2013), potentially indicating that interactions between high and mid-latitude environments may alter the shape of arrival distributions (Møller 2008). However, the arrival distributions of short-distance migrants were also individualistic. Several short-distance migrants showed pronounced variance heterogeneity across time or synchronous–asynchronous fluctuation. In contrast, a subset of short-distance migrants showed

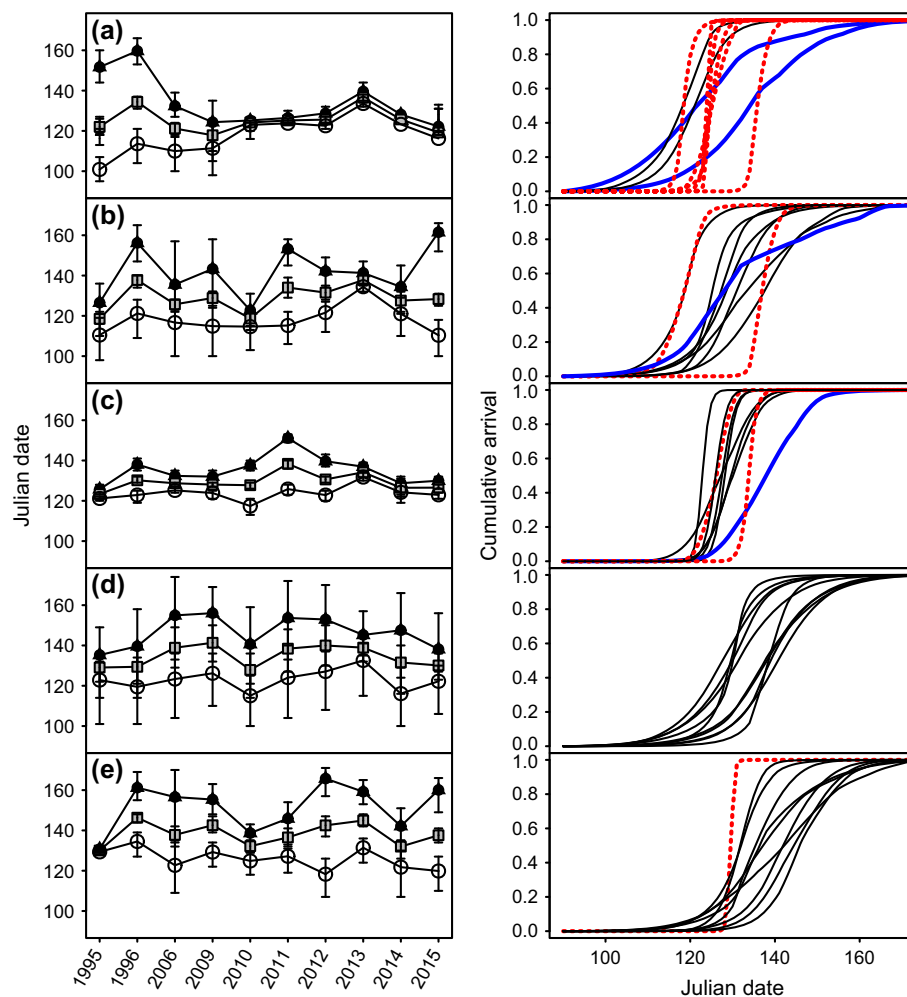


Fig. 7. Arrival distributions of short-distance migrants in Denali National Park, Alaska (1995–2015). Only years in which sampling occurred and arrival was estimable are shown. Right panels show cumulative arrival curves, and left panels show species-specific posterior means for the Julian dates in which 5% (open circles), 50% (gray squares), and 95% of occupied sites had shown an arrival event. Bayesian 95% credible intervals are also shown. Species include (a) Fox Sparrow, (b) Yellow-rumped (Myrtle) Warbler, (c) White-crowned Sparrow, (d) Golden-crowned Sparrow, and (e) Savannah Sparrow. We considered arrival to be synchronous (dashed red lines) if the ratio of the standard deviation of that year to the average standard deviation was <0.5 . Arrival was considered asynchronous (blue lines) if this ratio was >2.0 .

weak variance heterogeneity and relatively compressed arrival distributions. The latter pattern could be indicative of limited inter-individual variation in plasticity which would synchronize arrival (Kokko 1999). However, many other factors likely underlie interspecific variation in the behavior of the arrival variance, including the intensity of competition for territories (Kokko 1999, Jonzén et al. 2007), the breadth of a species' foraging niche, the temporal variance of resource

availability (Jonzén et al. 2007), variation between migration routes in spatio-temporal patterns of vegetation phenology (La Sorte et al. 2013), the distance of the migratory journey, and species-specific flight strategies including the degree of selectivity for favorable winds in timing migration flights (Karlsson et al. 2011, Nilsson et al. 2014).

Fox Sparrow, a short-distance migrant, was unique in that its arrival distribution became more synchronized over time. This pattern coincided

with a 250% increase in its abundance within the study area (Schmidt et al. 2013) and dramatic expansion of its elevational distribution (Mizel et al. 2016). Synchronization of its arrival phenology could have been driven by density-dependent intensification of competition for territories (Kokko 1999) although other explanations are possible. This unique pattern emphasizes the importance of considering other factors, such as changes in population size, when assessing variation in phenology to avoid possibly erroneous conclusions (Tryjanowski and Sparks 2001, Miller-Rushing et al. 2008).

In contrast to the rest of the species that we considered, Arctic Warbler, a Palearctic long-distance migrant, showed little plasticity in arrival timing. The entire local population arrived within a few days of June 6 each year, thereby circumventing variation in spring onset entirely but creating a highly compressed breeding season. Such inflexibility in their phenology would theoretically make them susceptible to tropic mismatches. However, the degree of specialization in their diet and the temporal breadth of peak prey availability are unknown in our study area, limiting our ability to make predictions about the potential for a phenological mismatch.

With the exception of Arctic Warbler, the arrival phenologies of the subarctic migrants that we considered appear to be relatively flexible. However, they were subject to synchronous-asynchronous fluctuation, suggesting that arrival variances may respond strongly to weakening of the north-south temperature gradient. We found that extremes in local spring temperatures have the potential to synchronize arrival across the bird community (as in the late spring of 2013) and to induce substantial advances in arrival among both long- and short-distance migrants (as in the early spring of 1995). Although the ultimate effects of climate warming on bird populations are unknown, our findings suggest that some Neotropical migrants breeding in the subarctic may have greater capacity for plastic arrival timing than was previously expected.

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