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# Seasonally migratory songbirds have different historic population size characteristics than resident relatives

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**eLife Assessment**

This is a **valuable** study of the role that life history differences might play in determining population size and demography. While concerns about generation times and population structure leave the evidence for the claims in parts **incomplete**, the work is of considerable interest to anyone who tries to understand evolutionary consequences of life history changes.

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## Abstract

Modern genomic methods enable estimation of a lineage's long-term effective population sizes back to its origins. This ability allows unprecedented opportunities to determine how adoption of a major life-history trait affects lineages' populations relative to those without the trait. We used this novel approach to study the population effects of the life-history trait of seasonal migration across evolutionary time. Seasonal migration is a common life-history strategy, but its effects on long-term population sizes relative to lineages that don't migrate are largely unknown. Using whole-genome data, we estimated effective population sizes over millions of years in closely related seasonally migratory and resident lineages in a group of songbirds. Our main predictions were borne out: Seasonal migration is associated with larger effective population sizes ($N_e$), greater long-term variation in $N_e$, and a greater degree of initial population growth than among resident lineages. Initial growth periods were remarkably long (0.63-4.29 Myr), paralleling the expansion and adaptation phases of taxon cycles, a framework of lineage expansion and eventual contraction over time encompassing biogeography and evolutionary ecology. Heterogeneity among lineages is noteworthy, despite geographic proximity (including overlap) and close relatedness. Seasonal migration imbues these lineages with fundamentally different population size attributes through evolutionary time compared to closely related resident lineages.

## Introduction

Modern genomic methods enable estimation of a lineage's long-term effective population sizes back to its origins (Li & Durbin, 2011; Mazet et al., 2015; Nadachowska-Brzyska et al., 2015). This ability allows unprecedented opportunities to study the populational effects of past evolutionary and climatic phenomena on organismal lineages, and this new area of paleodemographics is likely to grow rapidly (Nadachowska-Brzyska et al. 2021, Germain et al. 2023a,b). We use this approach in a novel way to test hypotheses about how adoption of a major life-history trait affected lineages' populations relative to those without the trait.

Seasonal migration is a common life-history strategy among the world's birds, but its effects on long-term population sizes relative to lineages that don't have this trait are largely unknown (Newton, 2008; Rappole, 2013). Demographic differences between seasonally migratory and resident lineages have been studied for decades, but, thus far, ecological, behavioral, and genetic approaches have necessarily been focused on recent and microevolutionary phenomena (e.g., Greenberg, 1980; Pérez-Tris et al., 2004; Sandercock & Jaramillo, 2002). Here we look much deeper, contrasting changes in effective population sizes through millions of years between closely related migratory and resident lineages.

Thrushes in the genus *Catharus* and this group's sister *Hylocichla mustelina* (Aves: Turdidae) are a model songbird system for studying the evolutionary effects of seasonal migration. This group has both migratory and resident lineages (**Fig. 1**), and it has been important in the study of seasonal migration, divergence, and speciation (e.g., Blain et al., 2024; Delmore et al., 2015, 2016; Everson et al., 2019; Justen et al., 2024; Outlaw et al., 2003; Ruegg et al., 2014; Termignoni-Garcia et al., 2022; Voelker et al., 2013; Winker, 2000, 2010; Winker and Pruett, 2006). These animals are relatively small, omnivorous or insectivorous, forest-related birds with lineages that are long-distance seasonal migrants in North America and others that are resident in tropical North and South America (Collar, 2005). The current breeding grounds of the migratory lineages span the Russian Far East, Alaska, northern Canada, and the United States, and their wintering ranges include Mexico, the Caribbean, Central America, and tropical South America. In contrast, the resident lineages occupy Mexico, Central America, and northwestern South America (Collar, 2005; Fig. S1).

We made three predictions about effective population sizes ($N_e$) in seasonally migratory versus resident lineages of these thrushes. First, we can think of North America roughly as an inverted triangle, with substantially more geographic space in the north than in the south. Among these thrushes, the migratory lineages breed in that northern, on average, larger space. The resident lineages instead currently occupy, on average, smaller geographic ranges, even in South America, where they are largely montane (Fig. S1). Thus, larger breeding ranges among migrants, on average, should yield higher population sizes ($N_e$).

Second, climatic variability is also higher with increased latitude, often temporarily rendering vast swaths of northern North America unoccupiable to many long-distance migrant species (e.g., Colinvaux et al., 2000; Pielou, 1991). Thus, higher-latitude breeding occupancy should cause larger fluctuations in population size, meaning that variation in $N_e$ will on average be higher among seasonal migrants. Finally, seasonal migration is likely to cause enhanced ecological (and in this case also geographic) release (i.e., in the occupancy of new niche space) in relation to resident relatives.

Thus, as migratory lineages' mobility enabled them to take advantage of seasonal resource blooms in ecosystems at higher latitudes and expand their breeding ranges (geographic and ecological expansion), their populations should, on average, have grown proportionally more and at a faster

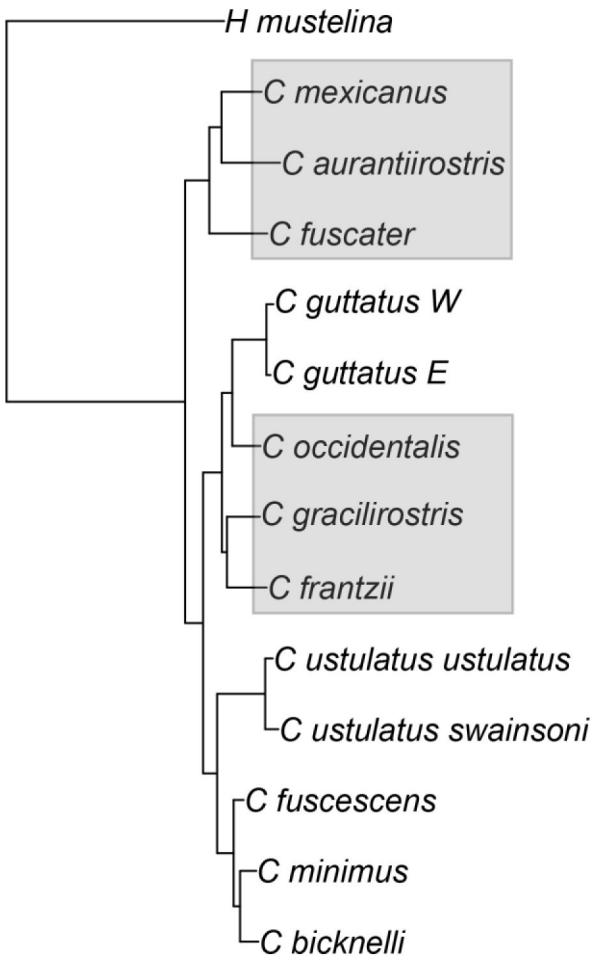



**Figure 1.**

The phylogenetic tree of the songbird lineages in this study, from the genera *Catharus* and *Hylocichla*. Neotropical residents are shaded in gray.

rate than sedentary lineages, thus achieving the first prediction.

Here we test these predictions by reconstructing effective population sizes of these thrush lineages through time using whole-genome data and the pairwise sequentially Markovian coalescent (PSMC; Li & Durbin, 2011).

## Results

The focal variables of our hypotheses all lacked phylogenetic signal. Mean effective population sizes and their variation were both higher among migratory lineages, as predicted (**Table 1**; $U$ = 7 and 10, $p < 0.05$ for both; one-tailed Mann-Whitney $U$-test). The degree of early population growth was also proportionally higher among migrants, as predicted (**Table 1**; $U = 9$, $p < 0.05$; one-tailed Mann-Whitney $U$-test), but the rate of this early growth was not different between the two groups (**Table 1**; $U = 21.5$, $p > 0.05$).

To examine why the degree of initial migrant population growth was higher but the rate of growth was not, we considered that this might be because that growth extended over a longer period of time. To our surprise, we found that these growth periods were remarkably long, ranging from 0.63-4.29 My and averaging 2.51 My (**Table 1**, **Fig. 2**). Migratory lineages did have a longer initial period of growth (migrants mean *deltaT* = 3.10 My vs. resident mean *deltaT* = 1.72 My; **Table 1**; $U = 9$, $p < 0.05$).

In addition to testing our hypotheses, our results reveal other important attributes of these songbirds. First, they appear to show few of the general population declines at the beginning of the last glacial period (LGP, ~115 Kya) that Nadachowska-Brzyska et al. (2016) found among a global sampling of birds (**Figs. 3**, S3). Secondly, and more importantly, there is a general lack of temporal synchrony in historic population size changes (**Figs. 3**, S3), despite considerable geographic proximity and overlap of ranges (especially during the nonbreeding season). Finally, a pattern widely shared in the group is that most of the recent populations are below each lineage's historic peak, and this trend predates the arrival of humans in the New World (**Figs. 3**, S3). A striking exception is *C. ustulatus swainsoni*, which has had remarkable long-term growth (Fig. S3).

## Discussion

To our knowledge, this is the first study to contrast long-term effective population size changes among closely related species to test *a priori* hypotheses about the population effects of a major life-history trait; here we focused on seasonal migration. This perspective offers several new insights into migrant demographics and evolutionary ecology. Migratory thrush lineages showed higher effective population sizes, greater population size variation, and proportionally larger initial population growth than resident relatives. A migratory life-history strategy thus imbues these lineages with population size characteristics that are fundamentally different, on average, from those of resident relatives.

Although migratory thrush lineages showed higher proportional initial growth than resident relatives, this was not achieved through rapid adaptation to new geographic and ecological opportunities as we predicted. Population growth in migrants and residents was positive early in the lineages' histories (*deltaT*) in all cases but one (*C. aurantiirostris*), and it occurred over fairly long periods of time (**Table 1**, **Fig. 2**). That this process initially (on average) involves millions of years of population growth in this group, apparently extended by a migratory life-history strategy that provided access to higher latitudes (**Tables 1**, S2), is an insight from our study that should be examined in future work from a broader taxonomic perspective. While actual, census

## Table 1.

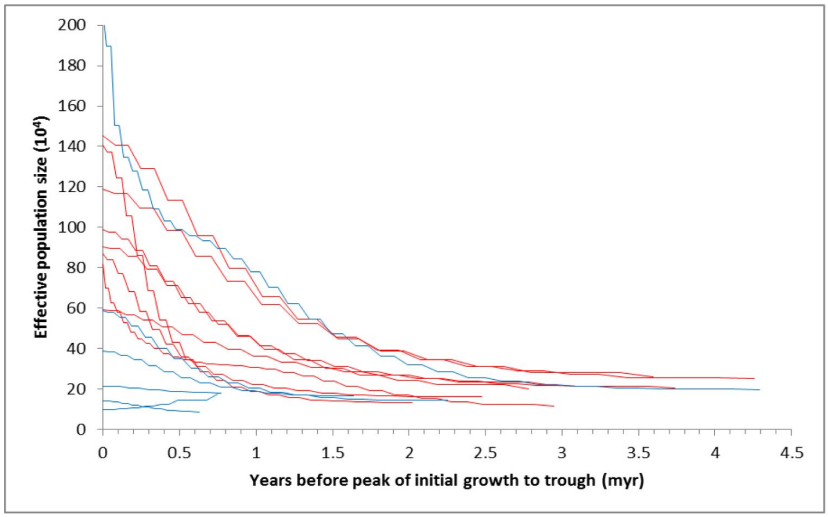
Data from pairwise sequentially Markovian coalescent (PSMC) analyses reflecting effective population sizes ($N_e \times 10^4$) through history at depths > 50 Kyr and the five variables derived and analyzed from that output. Taxa shaded in gray are Neotropical residents.

| Taxon | Mean $N_e$ (± SD) | SD/mean | Degree of early growth 1 - ($N_{trough}/N_{peak}$) | Rate of early growth degree/deltaT | deltaT |
|---|---|---|---|---|---|
| *Hylocichla mustelina* | 35.63 (± 20.11) | 0.56 | 0.86 | 2.92E-07 | 2,946,862 |
| *Catharus fuscescens* | 95.59 (± 50.99) | 0.53 | 0.83 | 1.93E-07 | 4,284,020 |
| *C. guttatus E* | 75.34 (± 65.69) | 0.87 | 0.90 | 4.48E-07 | 2,021,768 |
| *C. guttatus W* | 39.72 (± 24.20) | 0.61 | 0.81 | 3.28E-07 | 2,477,684 |
| *C. minimus* | 63.71 (± 28.83) | 0.45 | 0.78 | 2.17E-07 | 3,594,914 |
| *C. ustulatus swainsoni* | 76.61 (± 66.61) | 0.87 | 0.79 | 2.12E-07 | 3,740,764 |
| *C. ustulatus ustulatus* | 39.56 (± 12.15) | 0.31 | 0.63 | 2.14E-07 | 2,943,763 |
| *C. bicknelli* | 46.90 (± 24.12) | 0.51 | 0.78 | 2.79E-07 | 2,781,554 |
| *C. aurantiirostris* | 12.38 (± 2.83) | 0.23 | -0.75 | -1.00E-06 | 747,451 |
| *C. fuscater* | 11.38 (± 1.66) | 0.15 | 0.39 | 6.18E-07 | 627,449 |
| *C. frantzii* | 24.71 (± 8.41) | 0.34 | 0.17 | 2.20E-07 | 774,024 |
| *C. gracilirostris* | 29.98 (± 9.28) | 0.31 | 0.58 | 3.52E-07 | 1,637,663 |
| *C. mexicanus* | 37.10 (± 16.18) | 0.44 | 0.75 | 3.34E-07 | 2,250,295 |
| *C. occidentalis* | 76.40 (± 53.14) | 0.70 | 0.91 | 2.11E-07 | 4,292,405 |
| **Means (± SD)** | | | | | |
| migrants | 59.34 (± 35.70)* | 0.57 (± 0.20)* | 0.798 (± 0.08)* | 2.73E-7 (± 0.85E-7) | 3,098,906 (± 732,563)* |
| residents | 31.99 (± 15.25) | 0.36 (± 0.19) | 0.341 (± 0.59) | 1.23E-7 (± 5.69E-7) | 1,721,547 (+ 1,409,939) |

* $p < 0.05$.

## Figure 2.

Partial historic effective population size curves from all lineages in this study, based on pairwise sequentially Markovian coalescent (PSMC) analyses. Each peak of initial growth is set to zero years to set a common framework in which to visualize the periods and magnitudes of initial growth among migrant (red) and resident (blue) lineages. See specific lineages with their bootstrapped results in Fig. S2.



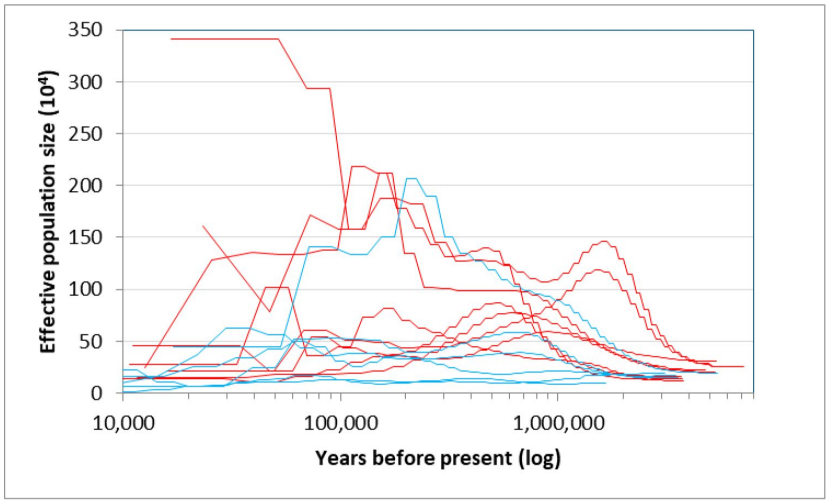



**Figure 3.**

Historic effective population size curves from all lineages, based on pairwise sequentially Markovian coalescent (PSMC) analyses. Migrant lineages are in red and resident lineages in blue. See specific lineages with their bootstrapped results in Fig. S2.

population sizes would likely have shown considerable variation across this time, especially after the glacial cycles of the Pleistocene began ~2.6 Mya, the long-term effective population sizes of migrants tended to show steady increases, achieving peaks on average almost 3 My after the lineages' PSMC inception (**Figs. 1**, S3; **Table 1**).

With *deltaT* being generally long but highly variable (**Table 1**), one can envision in this group a sort of ur-thrush trajectory in which unique, lineage-specific processes occur as each evolves, influenced by geography, ecological factors, and life-history strategy. These long periods of early growth are concordant with the initial expansion or adaptation phases of taxon cycles, a conceptual framework of lineage expansion and contraction over time through interactions between biogeography and evolutionary ecology (Pepke et al., 2019; Ricklefs & Bermingham, 2002; Ricklefs & Cox, 1972; Wilson, 1961).

Another noteworthy pattern widely shared in this group is that most recent populations are below each lineage's historic peak (**Figs. 3**, S3). This, too, is reminiscent of taxon cycles (smaller populations in later stages), and this trend both predates the arrival of humans in the New World (Fig. S3) and reflects a broader pattern of historic avian declines (Germain et al. 2023b). Yet another pattern is a general lack of temporal synchrony in historic population size changes, despite considerable geographic proximity and overlap of ranges (**Figs. 3**, S3). In their review of taxon cycles, Ricklefs & Bermingham (2002) inferred from such a lack of similarity among lineages that each is in a unique population-environment relationship, responding idiosyncratically in a coevolutionary relationship with factors such as parasites, predators, pathogens, and competitors.

We attribute the higher variation in $N_e$ among migrants to be the result of the relative instability of northern biomes compared with tropical ones through glacial-interglacial cycles (e.g., Colinvaux et al., 2000; Pielou, 1991).

## Population structure

PSMC estimates of population size can be affected by population structure: a change in structure can produce the signal of a change in size (Mazet et al., 2015, 2016; Wakeley, 1999). Some of the population size changes we observed might therefore reflect changes only in levels of population connectivity. There are well-understood differences between seasonal migrants and residents in population structure. Migrants generally have lower levels of geographic partitioning of both phenotypic (subspecies) and genetic variation (Belliure et al., 2000; Delmore et al., 2020; Mayr, 1963; Montgomery, 1896). The resident lineages we studied are more prone to this structure than the migrant lineages, with migrants having an average of 2.5 subspecies per lineage and residents having an average of 5.9 (Collar, 2005). Migratory lineages therefore come closer to meeting the assumption of PSMC analyses that populations are panmictic. Thus, in addition to our geographic and ecological scenario differing between the migrant and resident lineages we studied, we also have a pervasive effect of population structure affecting our results, likely increasingly complementing geographic expansion among seasonal migrants as lineage ages approach the recent. However, the greatest effects of inflated $N_e$ over evolutionary time would likely occur among nonmigrants, with more isolation and less mixing (Li & Durbin, 2011).

Accounting for population structure in these models to distinguish between the two phenomena is a difficult computational problem; the correlation is not simple, and it might not be tractable with data from a single individual (Mazet et al., 2016; Nadachowska-Brzyska et al., 2016, 2022). However, each individual has a genome amalgamated from the entire lineage metapopulation, including individuals and populations that have not been sampled (Mazet et al., 2015). When not focusing on relatively recent or rapid changes (e.g., in human or other bottlenecked systems, where this has been most studied), these issues are probably not as important (Mazet et al., 2016). For example, sister lineages usually show identical effective population size attributes at their origins, reflecting their shared histories (Delmore et al., 2020; Li & Durbin, 2011;

Nadachowska-Brzyska et al., 2016). Inasmuch as many of our most interesting results are in deep time, where we expect current individuals of a lineage to have the most thorough mixing or amalgamation of lineage-specific metapolulation history, the effects of population structure are likely to become less important and the results reflect (as we have necessarily interpreted) more of a lineage-wide phenomenon than a variably structured, demically biased one. However, it is clear that the latter bias becomes stronger as lineages progress toward the present, and for more recent times population structure will be an important aspect of comparing effective population size estimates and their changes between migrant and resident lineages. In this respect we were conservative in ignoring the most recent 50 Kyr.

It also important to consider the time scales involved and the sampling regime. Glacial-interglacial cycles averaged ~100 Kyr back to 0.74 Mya and then averaged ~41 Kyr from then back to 2.47 Mya; about 50-60 of these cycles occurred (Lisiecki & Raymo 2005: fig. 4). This probably caused considerable levels of structuring and mixing in these lineages. In addition, in the PSMC output from one of our lineages, *C. ustulatus swainsonii*, we find that there are 54 time segments sampled for the Pleistocene, indicating the inadequacy of this method to reflect fine-scale changes and suggesting that each estimate is generally capturing a lot of both structuring and mixing.

At present, there is no way to fully disentangle the effects of population structure and geographic space on our results, but we make two observations leading us to infer that general differences in population structure are not the main factor driving our results. First, structure will have smaller effects on the PSMC signal in the deep past than in more recent history. Second, climatic changes are known to cause coordinated shifts among codistributed taxa, e.g., in promoting the partitioning of genetic variation among glacial refugia (Hewitt, 2000). A lack of coordinated shifts in our PSMC results suggests that climate-driven shifts in population structure are not a major feature (Fig. S3).

## Geography and evolutionary ecology

Early population growth among migrant lineages is likely affected by some degree of ecological release as these birds engage with the novel environments their increased movements expose them to and they occupy new niche space. However, in this system we cannot readily decouple the expanded geographic and ecological opportunities that seasonal migration provides. The relationship between avian range size and migration is complex, but correlation with latitude is notably strong in North America (Pegan & Winger, 2020). Two aspects of our results suggest that geography operating alone is unlikely to explain the larger migrant population sizes observed (**Table 1**, Fig. S3). The first is that early population growth is positive in all but one of the lineages we studied; despite a probable lack of marked geographic expansion among residents, they, too, experienced long-term growth. The second is that these initial growth periods are quite long, extending over much longer periods than we should expect for populations responding to opportunities for geographic expansion.

PSMC analyses excel at long time frames, but initial growth in residents and migrants suggests a strong role for ecological factors. Global climate reconstruction data do not suggest that there were similar long, steady trends during these time periods to match these thrush population size changes (Lisiecki & Raymo, 2005; Fig. S3). Perhaps geographic space does make a difference, on average, between the two life-history strategies. That these growth periods are long also suggests the importance of ecological factors, though. For example, the boreal and subarctic woodland breeding habitats of most *C. ustulatus swainsoni* and *C. minimus* expanded dramatically across North America as glaciers receded since the last glacial maximum (LGM), a period of < 20 Kyr (Pielou, 1991). A spatial response of such rapidity, less than 1% of the time of the initial historic growth phases of these two lineages (> 3 Myr; **Table 1**), leads us to infer that breeding range size alone is not a satisfactory explanation for our results. This post-LGM expansion reflects census size, and not effective population size ($N_e$), but it implies that a migratory *Catharus* lineage's matching (or mapping) of $N_e$ to average long-term available geographic space is not likely to take

millions of years. In other words, their comparatively recent rapid postglacial expansion into new space suggests a sort of preadaptation that is not apparent early in the lineages' histories. Together, these aspects of our results suggest that while geographic factors are involved, ecological factors are also important. Teasing these factors apart might also explain the finding of Germain et al. (2023a) that migrants in general have had larger populations than residents during the last 0.67 my.

Identifying key **ecological mechanisms** affecting population sizes among migrants is difficult, and they will likely vary among lineages. There are numerous factors potentially involved. Biotic interactions in general show greater effects on range limits at the warmer than the cooler edges (Paquette & Hargreaves, 2021). Long-distance migrants especially, in their extensive latitudinal movements, would receive a range expansion advantage in this respect regardless of continental landmass shape—and also through higher diel food harvest rates due to longer days and shorter nights. Many additional ecological factors affect the population sizes of migrants versus residents, but the relationships between seasonal migration and predators, parasites, diseases, and competitors are extremely complex and key aspects remain poorly understood (Altizer et al., 2011; Newton, 2008).

Seasonal migration can be integrally related to predator avoidance, but among birds its effects are not understood in the full, circannual context relative to resident relatives, and they are not generalizable (Brönmark et al., 2008; McKinnon et al., 2010; Newton, 2008; Rappole, 2013). Exposure to parasites and pathogens varies both spatially and seasonally. Although breeding range diminishment of these exposures can be important in some migrants (probably not among all lineages), full annual exposure to both disease and parasite diversity is likely higher, resulting in at least some lineages showing larger immune defense organs (Bennett & Fallis, 1960; Figuerola & Green, 2000; Jenkins et al., 2011; Møller & Erritzoe, 1998; Piersma, 1997; Ricklefs et al., 2017). Exposure to higher circannual parasite and pathogen diversity might not be correlated with susceptibility, however; migration creates a geographic break that can lower transmission, causing migrants overall to be less vulnerable to population declines (Hall et al., 2014).

Presently, *C. minimus*, for example, shows an increased breeding and migratory prevalence and diversity of avian malaria, a blood parasite, but aspects of this relationship probably changed over the time scales involved (Pulgarín-R et al., 2019; Ricklefs et al., 2014). Avian migrants are more likely to be affected by blood parasites in ecological rather than evolutionary time, although the latter are also operating (Hellgren et al., 2007; Ricklefs et al., 2014). At the deeper times of avian families, seasonal migration is an important factor affecting blood parasite-host coevolution by breaking down the congruence of phylogenetic relationships between hosts and parasites, and there are also important differences among biting-fly vectors and their transmission of avian blood parasite hosts (Jenkins et al., 2011; Ricklefs et al., 2014). These issues suggest that reconstructing associations and their effects in deep time will be difficult.

Interspecific competition has long been studied between migrants and residents, but its potential role in affecting relative population sizes between the two groups is largely unknown (Rappole, 2013). As close relatives, these thrushes are likely to be each others' closest competitors, so it is conceivable that the increased relative abundance of migrants might depress realized population sizes among residents. In this group, geographic ranges overlap broadly during the nonbreeding season, but the tropical residents tend to occupy higher elevations than nonbreeding migrants (Collar, 2005). Both interspecific competition and inland, montane, and mature-forest retreats among older taxa are major factors in taxon cycles (Ricklefs & Bermingham, 2002; Ricklefs & Cox, 1972; Wilson, 1961) and might also be operating in this system.

## Conclusions

Paleodemographic analyses in a hypothesis-testing framework offer important new insights into the effects of the major life-history trait of seasonal migration on long-term effective population sizes. Our results indicate larger and more variable migrant populations relative to residents, and these populations grow in a way suggesting an important role not only for seasonal migration and geography, but also for evolutionary ecology. Although there are several plausible ecological mechanisms, their relative importance is unknown. The differences we found are between group averages, and variation among lineages includes residents that are migrant-like (*C. occidentalis*; **Table 1**, **Figs. 1**, **2**, **S3**) and vice-versa (e.g., *C. u. ustulatus*; **Table 1**, Fig. S3). Understanding why residents like *C. occidentalis* show migrant-like historic population characteristics will help us understand the mechanisms affecting these lineages. Such reasons could be as simple as realized range expansion (i.e., geographic and ecological opportunity), and this hypothesis appears to fit the deeply split eastern-western sister lineages within species in which smaller western ranges have smaller effective population sizes (*C. guttatus* and *C. ustulatus*; Fig. S3). Or the reasons might be as complex as a lineage dropping out of migration to become sedentary (*C. occidentalis* is sister to the migrant *C. guttatus*; **Fig. 1**).

It is clear that seasonally migratory lineages in this system have, on average, fundamentally different effective population size attributes through evolutionary time than closely related resident lineages. Population structure is probably not a main driver of these results. What remains unclear are the relative roles of geographic and ecological expansions in causing these differences. Both are likely important. More studies in other systems will be needed to tease these roles apart and to determine which ecological mechanisms are involved.

What other patterns will emerge across geographic, temporal, and phylogenetic space? Further sampling among other closely related groups containing mixed lineages of migrants and residents are needed, as are complementary approaches to reconstructing demographic history, using more individuals per lineage and other population genomic methods applicable to that type of sampling (e.g., Beichman et al., 2017; Delmore et al., 2020; Marchi et al., 2021). Such studies will also help determine the relative contributions of seasonal migration and its geographic and ecological expansion components in the context of what appears to be a normal tendency for early lineage growth (**Figs. 1**, S3, **Table 1**).

# Materials and methods

The thrush lineages in our study are from the genus *Catharus* and its sister, the single species in the genus *Hylocichla*. These comprise Nearctic-Neotropic seasonal migrants and Neotropical residents. Among the latter, some lineages (*C. aurantiirostris*, *occidentalis*, *frantzii*, and *mexicanus*) have some populations that exhibit some short-distance migration—likely partial migration or hard-weather movements, either in elevation or with extreme northern populations moving south (Collar, 2005). These lineages thus comprise two groups, which for simplicity we will refer to as 'seasonal migrants' and 'residents': seasonal migrants with extensive latitudinal movements, and residents that are either wholly sedentary or with some individuals moving rather limited distances within the Neotropics. The eight migrant lineages are: *Hylocichla mustelina*, *Catharus fuscescens*, *C. guttatus* E (eastern lineage), *C. guttatus* W (western lineage), *C. minimus*, *C. ustulatus swainsoni*, *C. u. ustulatus*, and *C. bicknelli*. (Note that four of these lineages represent two deeply divergent lineages each within what are currently considered two biological species, *C. guttatus* and *C. ustulatus*; Topp et al., 2013). The six resident lineages are: *Catharus aurantiirostris*, *C. fuscater*, *C. frantzii*, *C. gracilirostris*, *C. mexicanus*, and *C. occidentalis*. Over the full evolutionary history of this *Hylocichla-Catharus* clade, changes among lineages occurred in the trait of long-distance migration (Outlaw et al., 2003; Voelker et al., 2013; Winker and Pruett, 2006; **Fig.**

**1**). Our study does not assume that this trait was constant within each lineage after the speciation events when these switches occurred. Instead, we consider that for a major trait like long-distance migration, losses and gains at the full lineage level are likely to be infrequent, and that current evidence of trait distribution on a phylogeny provides a powerful comparative framework in which to elucidate the effects of that trait on other lineage attributes.

DNA was extracted from high-quality voucher specimens or blood samples for 14 thrush lineages (Table S1). Whole-genome sequencing libraries were constructed using Nextera (Illumina) DNA Flex Library Prep kits, and libraries were sequenced on a NovaSeq S4 (Illumina, San Diego, CA) using paired-end 150 bp reads. Reads were aligned to the *C. ustulatus* genome (inland subspecies, Reference bCatUst1, NCBI PRJNA613294) using bwa (mem algorithm with default settings, Li and Durbin 2009). We did not use a maskfile. Identical treatment of all lineages in these respects should provide a strong foundation for a comparative study like this among close relatives. Resulting .sam files were converted to .bam format with samtools (Li et al., 2009); picardtools was used to clean, sort and add read groups to .bam files (*http://broadinstitute.github.io/picard/*). Between 97 and 98% of reads mapped to the reference for an average read depth of 23 × (range 15.9-29.8 ×).

We analyzed whole-genomic data from the .bam files using the pairwise sequentially Markovian coalescent (PSMC) approach in the software package psmc (Li & Durbin, 2011). This analysis uses pairwise (allelic) estimates of coalescent times for each locus across the genome in a nonoverlapping manner, developing a distribution of times to most recent common ancestor (TMRCAs), and the frequency of these coalescent events is inversely proportional to effective population size (Li & Durbin, 2011; Mather et al., 2020).

We used a generation time of 2.5 yr, taken as an average among many of these species (Dellinger et al., 2020; Evans et al., 2020; Mack & Yong, 2020; Saether et al., 2005; Townsend et al., 2020; Whitaker et al., 2020), and a mutation rate of $2.3 \times 10^{-9}$ mutations per site per year (Smeds et al., 2016). Single individuals represent lineage characteristics using this approach (Li & Durbin, 2011; Mazet et al., 2015; Nadachowska-Brzyska et al., 2015). Importantly for our focal questions, variations in these parameters do not affect the shape of the curve of population sizes ($N_e$) through time, but rather the values of the time and $N_e$ estimates (Nadachowska-Brzyska et al. 2015). Being closely related and of similar size, we expect these taxa to have very similar generation times and mutation rates (e.g., Bird et al., 2020; Healy et al., 2014). However, seasonal migration can have an effect on survival and thus generation time, and Bird et al. (2020) produced modeled estimates for this group, providing an alternate approach. The basis for these modeled values is tiny, and the accuracy of the modeled results uncertain, so we use these estimates with caution. But as a check on our results, we ran all of our analyses again with the variable generation times given by Bird et al. (2020). As expected, most of the differences are time-related, and, importantly, the overall results are not different (Table S2).

Hilgers et al. (2024) recently showed that artifactual peaks can occur due to recent time parameter settings in the PSMC program (Li & Durbin 2011) that are often used as a default setting. They recommended that such recent peaks can be eliminated by breaking the first atomic time interval (typically 4) into either two (2+2) or four (1+1+1+1) smaller windows. We had four lineages that appeared to have such peaks: *H. mustelina*, *C. fuscescens*, *C. guttatus* E, and *C. gracilirostris*. For the latter three, breaking the recent period parameter into four windows (1+1+1+1) eliminated these peaks. For *H. mustelina*, smaller windows (2+2 and 1+1+1+1) made the recent peak even higher, so we have used the default setting (the most conservative result), as with the remaining taxa that did not show such peaks.

The PSMC method is not foolproof; for example, aspects of selection, inbreeding, and isolation can affect population size estimates (Mather et al., 2020). No method of genomic population demographic reconstruction is known to be consistently and reliably accurate (Marchi et al.,

2021), but uniform application of a powerful method like PSMC to genome-scale data in a closely related group of lineages can provide new insights into the evolutionary effects of major life-history strategies.

For all variables, PSMC output for times more recent than 50 Kya was ignored, because recent estimates of effective population size using this method are less reliable (Li & Durbin, 2011; Nadachowska-Brzyska et al., 2016). We consider this to be a conservative cutoff date. Our two focal variables, mean effective population size ($N_e$) and the coefficient of variation (SD/mean), were obtained from standard PSMC output. Our examination of early population growth involved deriving two additional variables from the PSMC output: degree of initial growth (1 - ($N_{trough}/N_{peak}$)), and rate of growth (degree/time period over which initial growth occurred; the latter we term *deltaT*; Fig. S2).

We note that estimates of the dates of divergence events in *Catharus* evolution vary by study, genetic marker, methodology, and parameter estimates such as generation time and mutation or substitution rates (Outlaw et al., 2003; Topp et al., 2013; Voelker et al., 2013; Winker and Pruett, 2006). Date estimates in our study that differ from previous work reflect these methodological issues, and here it is the relative values among lineages within our study that are most important.

We tested the assumption of phylogenetic independence of continuous characters obtained from the PSMC analyses using a phylogeny reconstructed using maximum likelihood from 1.5 Mb of autosomal sequence from chromosome 22 in MEGA X (Kumar et al. 2018; **Fig. 1**), which produced the expected topology given prior work (e.g., Everson et al., 2019), and, for phylogenetic independence, the Abouheif-Moran approach (Abouheif, 1999; Münkenmüller et al., 2012) as implemented in the R package adephylo (Jombart et al., 2010). For those variables not showing phylogenetic signal, we tested our hypotheses using a one-tailed Mann-Whitney *U*-test. This nonparametric test has the advantage of not requiring that particular assumptions are met (e.g., homogeneity of variance), nor precise measurements (thus accommodating uncertainty in our $N_e$ estimates; Sokal & Rohlf, 1995; Whitlock & Schluter, 2015).

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## Additional files

***Supporting Information, tables and figures***

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## Editors

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**Joint Public Review:**

Summary:

This interesting study applies the PSMC model to a set of new genome sequences for migratory and nonmigratory thrushes and seeks to describe differences in the population size history among these groups. The authors create a set of summary statistics describing the PSMC traces - mean and standard deviation of Ne, plus a set of metrics describing the shape of the oldest Ne peak - and use these to compare across migratory and resident species (taking single samples sequenced here as representative of the species). The analyses are framed as supporting or refuting aspects of a biogeographic model describing colonization dynamics from tropical to temperate North and South America.

Strengths:

* This is a creative use of PSMC to test explicit a priori hypotheses about season migration and Ne. The PSMC analyses seem well done and the authors acknowledge much of the complexity of interpretation in the discussion.

* We appreciate the test-of-hypothesis design of the study and the explicit formulation of three main expectations to test. The data analysis has been done with appropriate available tools.

Key weaknesses from the original round of review:

* Short of developing some novel theory deep in the PSMC model, I think readers would need to see simulations showing that the analyses employed in this paper are capable of

supporting or refuting their biogeographic hypothesis before viewing them as strongly supporting a specific biogeographic model. Tools like msprime and stdpopsim can be used to simulate genome-scale data with fairly complex biogeographic models. Running simulations of a thrush-like population under different biogeographic scenarios and then using PSMC to differentiate those patterns would be a more convincing argument for the biogeographic aspects of this paper. The other benefit of this approach would be to nail down a specific quantitative version of the taxon cycles model referenced in the abstract, and it would allow the authors to better study and explain the motivation behind the specific summary statistics they develop for PSMC posthoc analysis.

* The authors hypothesized that the wider realized breeding and ecological range characterising migrants versus resident lineages could be a major drive for increased effective population size and population expansion in migrants versus residents. I understand that this pattern (wider range in migrants) is a common characteristic across bird lineages and that it is viewed as a result of adapting to migration. A problem that I see in their dataset is that the breeding grounds range of the two groups are located in very different geographic areas (mainly South versus North America). The authors could have expanded their dataset to include species whose breeding grounds are from the two areas, regardless of their migratory behaviour, as a comparison to disentangle whether ecological differences of these two areas can affect the population sizes or growth rates.

* As I understand from previous literature, the time-scale to population growth and estimates of effective population sizes considered in the present paper for the resident versus migratory clades seem to widely predate the times to speciation for the same lineages, which were reported in previous work of the same authors (Everson et al 2019) and others (Termignoni-Garcia et al 2022). This piece of information makes the calculation of species-specific population size changes difficult to interpret in the light of lineages' comparison. It is unclear what the authors consider to be lineage-specific in these estimates, as the clades were likely undergoing substantial admixture during the time predating full isolation.

* Regarding the methodological difficulties in interpreting the impact of population structure on the estimates of effective population sizes with the PSMC approach, I would think that performing simulations to compare different scenarios of different degrees of structured populations would have helped substantially understand some of the outcomes.

* The authors use an average generation time for all taxa, but the citations imply generation time is known for at least some of them. Are there differences in generation time associated with migration? I am not a bird biologist, but quick googling suggests maybe this is the case? (https://doi.org/10.1111/1365-2656.13983). I think it important the authors address this, as differences in generation time I believe should affect estimates of Ne and growth.

[Editors' note: the original reviews in full are here: https://elifesciences.org/reviewed-preprints/90848/reviews. The reviewers were not available to comment on the latest version of the submission.]

https://doi.org/10.7554/eLife.90848.2.sa1

**Author response:**

The following is the authors' response to the original reviews.

> ***eLife Assessment***
>
> *This study presents valuable finding regarding the role of life history differences in determining population size and demography. The evidence for the claims is still partially*

> *incomplete, with concerns about generation times and population structure. Nonetheless, the work will be of considerable interest to biologists thinking about the evolutionary consequences of life history changes.*

Thank you. We have addressed the generation time and population structure issues in detail in our revision and hope that you, like us, find them to be of sufficiently low concern (i.e., they are not driving the results) that they do not overshadow the main findings and conclusions.

The opportunity to make in-depth revisions also helped the manuscript in two ways unanticipated by both us and the reviewers. First, KW made a mistake in the original analysis of phylogenetic signal, and catching that error simplifies that aspect of the study (there is none in our measured variables). Second, in June 2024 Hilgers et al. (2024; https://doi.org/10.1101/2024.06.17.599025) posted an important manuscript to *bioRxiv* noting the possibility of false population size peaks in PSMC analyses using the standard default settings. Our results had three of those, which we have eliminated. $N_e$ither of these issues affect the overall conclusions, but their resolution improves the work.

> ***Public Reviews:***
>
> ***Reviewer #1 (Public Review):***
>
> *Summary:*
>
> *This interesting study applies the PSMC model to a set of new genome sequences for migratory and nonmigratory thrushes and seeks to describe differences in the population size history among these groups. The authors create a set of summary statistics describing the PSMC traces - mean and standard deviation of $N_e$, plus a set of metrics describing the shape of the oldest $N_e$ peak - and use these to compare across migratory and resident species (taking single samples sequenced here as representative of the species). The analyses are framed as supporting or refuting aspects of a biogeographic model describing colonization dynamics from tropical to temperate North and South America.*
>
> *Strengths:*
>
> *At a technical level, the sequencing and analysis up through PSMC looks good and the paper is engaging and interesting to read as an introduction to some verbal biogeographic models of avian evolution in the Pleistocene.*

The core findings - higher and more variable $N_e$ in migratory species - seem robust, and the biogeographic explanation is plausible.

Thanks. We thought so as well. Our analyses go beyond being simply descriptive and test some simple hypotheses, including a biogeographic+ecological expansion opportunity gained in some lineages through the adoption of a seasonal migration life-history strategy.

> *Weaknesses:*
>
> *I did not find the analyses particularly persuasive in linking specific aspects of clade-level PSMC patterns causally to evolutionary driving forces. To their credit, the authors have anticipated my main criticism in the discussion. This is that variation in population size inferred by methods like PSMC is in "effective" terms, and the link between effective and census population size is a morass of bias introduced by population structure and selection so robustly connecting specific aspects of PSMC traces to causal evolutionary forces is somewhere between extremely difficult and impossible.*

As R1 notes, we do not attempt to link effective population sizes and census sizes (though we do discuss this), and we are also careful to discuss correlated rather than causative factors when going beyond the overarching hypotheses regarding life-history strategy.

> *Population structure is the most obvious force that can generate large $N_e$ changes mimicking the census-sizefocused patterns the authors discuss. The authors argue in the discussion that since they focus on relatively deep time (>50kya at least, with most analyses focusing on the 5mya - 500kya range) population structure is "likely to become less important", and the resident species are usually more structured today (true) which might bias the findings against the observed higher $N_e$ in migrants.*

To clarify, the patterns we discuss are entirely related to effective population size, not census size. But, yes, this is why we've given population structure its own section in the Discussion.

> *But is structure really unimportant in driving PSMC results at these specific timescales? There is no numerical analysis presented to support the claim in this paper. The biogeographic model of increased temperate-latitude land area supporting higher populations could yield high $N_e$ via high census size, but shifts in population structure (for example, from one large panmictic population to a series of isolated refugial populations as a result of glaciation-linked climate changes) could plausibly create elevated and more variable $N_e$. Is it more land area and ecological release leading to a bigger and faster initial $N_e$ bump, or is it changes in population connectivity over time at expanding range edges, or is the whole single-bump PSMC trace an artifact of the dataset size, or what? The authors have convinced me that the $N_e$ history of migratory thrushes is on average very different from nonmigrant thrushes, but beyond that it's unclear what exactly we've learned here about the underlying process.*

We do not argue that population structure is unimportant, only that it is less important as one goes into deeper time. Further, we agree with the reviewer's observation above that structure is more likely to bias nonmigrant estimates of $N_e$. In other words, following Li & Durbin's (2011) simulations, we interpret that an inflated $N_e$ due to structure should occur more often among residents. We have clarified this in the revision. We also agree that what we've learned about the underlying process is not entirely clear, but as we stated, population structure does not seem to be the main driver, and there is evidence that both biogeographic and ecological factors are involved. With this being the first time that these questions have been asked, we think we've made an important advance and that we've opened a number of avenues for future study.

It also important to consider the time scales involved and the sampling regime. Glacial-interglacial cycles averaged ~100 Kyr back to 0.74 Mya and then averaged ~41 Kyr from then back to 2.47 Mya; about 50-60 of these cycles occurred (Lisiecki & Raymo 2005: fig. 4). This probably caused a lot of population structuring and mixing in these lineages. In addition, in the PSMC output from one of our lineages, *C. ustulatus swainsonii*, we find that there are 54 time segments sampled for the Pleistocene, indicating the inadequacy of this method to reflect fine-scale changes and suggesting that each estimate is capturing a lot of both phenomena, structuring and mixing. We have added this to the revision.

> *I generally agree with the authors that "at present there is no way to fully disentangle the effects of population structure and geographic space on our results". But given that, I think there are two options - either we can fully acknowledge that oversimplified demographic models like PSMC cannot be interpreted as supporting evidence of any particular mechanistic or biogeographic hypothesis and stop trying to use them to do that, or we have to do our best to understand specifically which models can be distinguished by the analyses we're employing.*

> *Short of developing some novel theory deep in the PSMC model, I think readers would need to see simulations showing that the analyses employed in this paper are capable of supporting or refuting their biogeographic hypothesis before viewing them as strongly supporting a specific biogeographic model. Tools like msprime and stdpopsim can be used to simulate genome-scale data with fairly complex biogeographic models. Running simulations of a thrush-like population under different biogeographic scenarios and then using PSMC to differentiate those patterns would be a more convincing argument for the biogeographic aspects of this paper. The other benefit of this approach would be to nail down a specific quantitative version of the taxon cycles model referenced in the abstract, and it would allow the authors to better study and explain the motivation behind the specific summary statistics they develop for PSMC posthoc analysis.*

These could very well be fruitful pursuits for future work, but they are beyond the scope of this paper. The impossibility of reconstructing ranges through deep time makes anything other than the very general biogeographic hypothesis we've posed an uncertain pursuit. Also, a purely biogeographic approach neglects the likelihood of ecological expansion also being involved. We get at the importance of the latter in the "Geography and evolutionary ecology" section of the Discussion. Below, the editor states that discussions among reviewers indicate that simulations are not warranted at this time. We agree that the complexities involved are substantial, to the point of making direct relevance to this empirical study uncertain (especially in such an among-lineage context). Regarding taxon cycles, we merely point out that that conceptual framework seems relevant given our findings. This was not even remotely anticipated at the outset of the study, so we are reluctant to do anything more than point out its possible relevance in several aspects of the results. Finally, the motivation for the study's summary statistics were entirely driven by the hypotheses, as given in Methods, and due to an earlier error (noted above), there are no post-hoc analyses in the revision. Sorry for the needless confusion.

> ***Reviewer #2 (Public Review):***
>
> *Summary:*
>
> *Winker and Delmore present a study on the demographic consequences of migratory versus resident behavior by contrasting the evolutionary history of lineages within the same songbird group (thrushes of the genus Catharus).*
>
> *Strengths:*
>
> *I appreciate the test-of-hypothesis design of the study and the explicit formulation of three main expectations to test. The data analysis has been done with appropriate available tools.*
>
> *Weaknesses:*
>
> *The current version of the paper, with the case study chosen, the results, and the relative discussion, is not satisfying enough to support or reject the hypotheses here considered.*

Given the stated strengths, the weaknesses noted seem a little incongruous, but we understand from the comments below that the reviewer would like to see the study redesigned and expanded.

> *The authors hypothesized that the wider realized breeding and ecological range characterising migrants versus resident lineages could be a major drive for increased effective population size and population expansion in migrants versus residents. I understand that this pattern (wider range in migrants) is a common characteristic across*

> *bird lineages and that it is viewed as a result of adapting to migration. A problem that I see in their dataset is that the breeding grounds range of the two groups are located in very different geographic areas (mainly South versus North America). The authors could have expanded their dataset to include species whose breeding grounds are from the two areas, regardless of their migratory behaviour, as a comparison to disentangle whether ecological differences of these two areas can affect the population sizes or growth rates.*

Because the questions are about the migratory life history strategy and the best way to get at this is in a phylogenetic framework, we're not sure how we could effectively add species "regardless of their migratory behavior." Further, we know that migration causes lineages to experience variable ecological conditions that include breeding, migration, and wintering conditions. Obligate migrants are going to have different breeding ranges from their close relatives, and the more distantly related species are, the less likely it is that they respond to particular ecological conditions the same way. So we do not think that an approach that included miscellaneous species from northern and southern regions would strengthen this study. Here, the comparative framework of closely related lineages that possess or lack the trait of interest is a study design strength. We do agree, however, that future work is needed that does encompass more lineages (we would argue in a phylogenetic context), and that disentangling the effects of geography and ecology will also be an important future endeavor.

> *As I understand from previous literature, the time-scale to population growth and estimates of effective population sizes considered in the present paper for the resident versus migratory clades seem to widely predate the times to speciation for the same lineages, which were reported in previous work of the same authors (Everson et al 2019) and others (Termignoni-Garcia et al 2022). This piece of information makes the calculation of species-specific population size changes difficult to interpret in the light of lineages' comparison. It is unclear what the authors consider to be lineage-specific in these estimates, as the clades were likely undergoing substantial admixture during the time predating full isolation.*

We do recognize that timing estimates vary among studies. Differences among studies in important variables like markers, methods, generation time, and mutation or substitution rates create much of this uncertainty. Also, we are not confident in prior dating efforts in this group, largely because of gene flow and its effects on bringing estimates closer to the present. As we point out (line 485), differences among studies on these issues do not detract from the strengths here for within-study, among-lineage contrasts. In short, the timing could be off in an among-study context (and likely is with prior work, given gene flow), but relative performance of among-lineage $N_e$ differences is less susceptible to these factors. This was shown fairly well in Li & Durbin's initial use of the method among human populations. Regarding substantial admixture, PSMC curves often unite at their origins with sister lineages (when they were the same lineage). A good example is with the two *C. guttatus* E & W curves in Fig. S3, which still have substantial gene flow today (they are subspecies and in contact), yet they show remarkably different $N_e$ curves through their history. It is not possible to mark a cutoff point for each lineage that represents the cessation of admixture with another lineage (e.g., Everson et al. 2019 showed substantial admixture between three full species in this group); that period can be very long (Price et al. 2008), varies among lineages, and will not be available for deeper lineage divergences in the phylogeny. We therefore chose to use all of the time intervals retrievable from the genomic data in each lineage, considering that this uniform treatment is the best approach for our among-lineage comparison. And note that we were careful to label these as "the lineages' PSMC inception" (line 190).

> *Regarding the methodological difficulties in interpreting the impact of population structure on the estimates of effective population sizes with the PSMC approach, I would*

> *think that performing simulations to compare different scenarios of different degrees of structured populations would have helped substantially understand some of the outcomes.*

The complexities of such modeling in a system like this are daunting. The different degrees of structuring among all of these lineages across just a single glacial-interglacial cycle would necessitate a lot of guesswork; projecting that back across 50-60 such cycles just in the Pleistocene would probably end up being fiction. Disentangling the effects of structure versus changes in $N_e$ in a system like this would probably not be possible with that approach and these data. As noted above and below, there was agreement among reviewers and the editor that simulations in this case are not warranted for revision. We have added the nature of the glacialinterglacial cycles and the PSMC sampling time segments to help readers understand this better (see above in response to R1, and lines 272-278).

> *Additionally, I have struggled to understand if migratory behaviour in birds is considered to be acquired to relieve species competition, or as a consequence of expanded range (i.e., birds expand their range but their feeding ground is kept where speciation occurred as to exploit a ground with higher quality and abundance of seasonal local resources).*

The origins of migration have been a struggle for researchers since the subject was taken up. But how the trait was acquired among these species does not really matter for our study. Here, migratory lineages possess different biogeographic+ecological attributes than their close relatives that are sedentary. Our focus is on the presence and absence of this life-history trait.

> *The points raised above could be considered to improve the current version of the paper.*

Thank you. We appreciate the opportunity to guide our revision using your comments.

> ***Reviewer #3 (Public Review):***
>
> *Summary:*
>
> *This paper applies PSMC and genomic data to test interesting questions about how life history changes impact long-term population sizes.*
>
> *Strengths:*
>
> *This is a creative use of PSMC to test explicit a priori hypotheses about season migration and $N_e$. The PSMC analyses seem well done and the authors acknowledge much of the complexity of interpretation in the discussion.*
>
> *Weaknesses:*
>
> *The authors use an average generation time for all taxa, but the citations imply generation time is known for at least some of them. Are there differences in generation time associated with migration? I am not a bird biologist, but quick googling suggests maybe this is the case (https://doi.org/10.1111/1365-2656.13983). I think it important the authors address this, as differences in generation time I believe should affect estimates of $N_e$ and growth.*

Good point. The study cited by the reviewer encompasses a much higher degree of variation in body size and thus generation time. Differences in generation time in similarly sized close relatives, as in our study, should be small, and our approach has been to average those that are known. Unfortunately, generation times are not known for all of these species, but given their similarity in size we can have reasonable confidence in their being similar. We used

data from the life-history research available (as cited) to obtain our average; there are not appropriate data for the residents, though. However, there is thought to be a generation time cost to seasonal migration in birds, and Bird et al. (2020) included this in their estimates to provide modeled values for all of the lineages we studied. We're leery of using modeled values where good data for the nonmigrants in this group don't exist (and the basis for quantifying this cost is tiny), but we recognize that this second approach is available and could leave some doubt in our results if not pursued. So we re-did everything with the modeled generation times of Bird et al. (2020). As expected, most of the differences are time-related. Importantly, our overall results are not different. We present them as Table S2 and have added the details on this to the Methods.

> *The writing could be improved, both in the introduction for readers not familiar with the system and in the clarity and focus of the discussion.*

We have added a phylogeny (new Fig. 1) to help readers better understand the system, and we've re-worked the Discussion to make it clearer what is clarified by our results and what remains unclear.

> ***Recommendations for the authors:***
>
> ***Reviewing Editor comment:***
>
> *I note that discussion among the reviewers made clear that simulations are probably not the right answer given the complexity of the modeling required.*

We appreciate this conclusion, with which we agree.

> ***Reviewer #2 (Recommendations For The Authors):***
>
> *Apologies for the delay with the review, which came at a very busy time. I hope you will find my comments helpful.*

Thanks. Your comments are helpful, and we fully understand how reviews (and our revisions!) have to wait until more pressing needs are addressed.

> *I enjoyed reading the manuscript but I believe that the discussion sections could be heavily rewritten for better clarity. The discussion is sometimes redundant and lacks some flow/clarity. In a nutshell, I had the feeling that a bit of everything is thrown in the discussion but clear conclusions are not made.*

Yes, the Discussion has been difficult to write, because more issues arose in the Results than we anticipated at the outset. We feel that discussing them is relevant, but we agree that much remains unclear. This coupling of paleodemographics with geography and ecology is a new area, which opens some important new (and relevant) areas to consider. So clarity is not possible in some areas. We've revised to point out where we do have clarity (e.g., in migrant lineages having different paleodemographic attributes than nonmigrants) and where only further study can provide clarity (e.g., in the roles of geography versus ecology). The journal format does not seem to have secondary subheaders, but we've used bold in one place to highlight 'ecological mechanisms' to offset that section, one of the more complex. We've also added a paragraph in the conclusions to clarify where we have clear takeaways and where uncertainties remain.

> ***Reviewer #3 (Recommendations For The Authors):***
>
> *The introduction should engage the reader with biology, not the use of demographic methods or genomics (both of which have been around for more than a decade). I would drop the first paragraph and considerably expand the second. What has previous research on ecology/behavior/genetics found regarding the demographic effects of seasonal migration?*

There are two important aspects to our study: 1) using paleodemographic methods to test hypotheses about adoption of a major life-history trait—an important biological question regardless of system, and so far (surprisingly) unaddressed; and 2) using this novel approach to study the effects of one such trait, seasonal migration. At these timescales, nothing exists on this subject, so there is really nothing to expand with. If there is relevant literature that we've missed, we'd be happy to add it.

> *What is the missing bit of information or angle the current study addresses (other than just doing it larger and fancier with genomics)?*

The effects of major life-history traits on paleodemographics has not been addressed before, to our knowledge. The whole context is new, so we're not doing something "larger and fancier" with genomics. We are doing something that has not been done before: testing hypotheses about the effects of a major life-history trait on population sizes in evolutionary time. We're not sure how this can be made clearer. To us this seems like a very engaging biological question with wide applicability. We hope that this study is just the first of many to come, in a diversity of biological systems.

> *A figure showing the phylogenetic relationships of these taxa which are migratory would help the reader immensely. Although this is shown in Fig S3 I think it might be nice to have a map of the species and their ranges alongside a phylogeny as a main figure early on.*

Thank you. This is a good suggestion. We can't fit a phylogeny and all the distribution maps (Fig. S1) onto a page, but we can include a phylogeny as one of the main figures with nonmigrants highlighted. We've inserted this as a new Fig. 1.

> *If I understand correctly, the authors' arguments for why migratory species should show more growth hinge on large range size and geographic expansion. Yet they argue in the discussion that these forces are unlikely to be important (L226). I found the discussion on this confusing (e.g. L231 then says maybe it does matter). I think more clarity here would be helpful.*

Our argument and predictions are based both on geographic and ecological expansion. This was clearly stated as our third prediction "3) early population growth would be higher as seasonal migration opens novel ecological and geographic space…" We have gone back through and reiterated the coupling of these two factors. The line mentioned concludes the first paragraph in the section 'Geography and evolutionary ecology,' which focuses on the difficulty of decoupling these in this system. As the paragraph relates, geography alone does not seem to be driving our results (we do not argue that it is unimportant).

> *I also would have liked more time in the discussion addressing why variation in $N_e$ may be higher in migratory lineages.*

In addition to re-clarifying this in the Introduction, we have touched back on this now at line 221: "We attribute the higher variation in $N_e$ among migrants to be the result of the relative

instability of northern biomes compared with tropical ones through glacial-interglacial cycles (e.g., Colinvaux et al., 2000; Pielou, 1991)."

> *Minor comments:*
>
> *L 62: Presumably PSMC is limited by the coalescent depth of the genelaogy, which may be younger or older than population "origins" depending on the history of colonization, lineage splitting, gene flow, etc.*

We were careful to phrase these as "the lineages' PSMC inception" (line 190), and responded to this issue in more detail above in response to R2's public review.

> *L 338: I think a few more details on PSMC would be helpful. Was no maskfile used?*

We did not use a maskfile, choosing instead to generate data of decent coverage and aligning reads to a single closely related relative.

> *Did the consensus fasta include all species?*

No, we used a single reference high-quality fasta of *Catharus ustulatus* , as reported (lines 434-37). We have added that "Identical treatment of all lineages in these respects should provide a strong foundation for a comparative study like this among close relatives."

> *L 361: Fair to assume the authors used a weighted average of $N_e$ from the output, rather than just averaging the $N_e$ values from each time segment?*

No – we used all the values of $N_e$ produced by PSMC output. The PSMC method uses nonoverlapping portions of the genome in its analyses (which we've added to make that clear), and portions in juxtaposition will often provide data for very different periods in the time segments. Further, time segments are uneven within and among taxa, so it is not clear how a uniform and comparable weighting scheme could be implemented. We consider a uniform approach to be of primary importance, including for future comparisons among studies.

> *L 383 "delta" typo*

Thank you for catching this.

> *L 93: I'd be tempted to present the questions (how does seasonal migration affect population size trajectory, means, and variation) and rationale before presenting the hypotheses. I found myself reading the hypotheses and wondering "why?"*

We've tried this change in the revision. It makes the hypotheses a little harder to pull out (they are no longer numbered in a short sequence), but it is shorter and solves this concern.

> *L 337 read depth is usually expressed as X (e.g. "23X") rather than bp.*

Changed.

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