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

Kevin Winker[a,1] and Kira Delmore[b,c]

[a] University of Alaska Museum and Department of Biology and Wildlife, Fairbanks, Alaska, USA 99775. kevin.winker@alaska.edu

[b] Department of Biology, Texas A&M University, College Station, Texas, USA 77843. kdelmore@bio.tamu.edu

[c] Ecology, Evolution, and Environmental Biology, Columbia University, New York, New York USA 10027.

[1] To whom correspondence may be addressed.
Kevin Winker
University of Alaska Museum
907 Yukon Drive
Fairbanks, AK 99775
907-474-7027; fax 907-474-1987
Email: kevin.winker@alaska.edu

ORCID IDs:

Kevin Winker: https://orcid.org/0000-0002-8985-8104
Kira Delmore: https://orcid.org/0000-0003-4108-9729

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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.

KEYWORDS *Catharus*, effective population size, North America, PSMC, South America, taxon cycles, thrushes, Turdidae.

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

88 migrants in North America and others that are resident in tropical North and South America (Collar,
89 2005). The current breeding grounds of the migratory lineages span the Russian Far East, Alaska,
90 northern Canada, and the United States, and their wintering ranges include Mexico, the Caribbean,
91 Central America, and tropical South America. In contrast, the resident lineages occupy Mexico,
92 Central America, and northwestern South America (Collar, 2005; Fig. S1).

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

100 Second, climatic variability is also higher with increased latitude, often temporarily rendering
101 vast swaths of northern North America unoccupiable to many long-distance migrant species (e.g.,
102 Colinvaux et al., 2000; Pielou, 1991). Thus, higher-latitude breeding occupancy should cause larger
103 fluctuations in population size, meaning that variation in N_e will on average be higher among
104 seasonal migrants. Finally, seasonal migration is likely to cause enhanced ecological (and in this case
105 also geographic) release (i.e., in the occupancy of new niche space) in relation to resident relatives.
106 Thus, as migratory lineages' mobility enabled them to take advantage of seasonal resource blooms in
107 ecosystems at higher latitudes and expand their breeding ranges (geographic and ecological
108 expansion), their populations should, on average, have grown proportionally more and at a faster
109 rate than sedentary lineages, thus achieving the first prediction.

110 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

134 this trend predates the arrival of humans in the New World (Figs. 3, S3). A striking exception is *C.*
135 *ustulatus swainsoni*, which has had remarkable long-term growth (Fig. S3).
136
137 **DISCUSSION**
138 To our knowledge, this is the first study to contrast long-term effective population size
139 changes among closely related species to test *a priori* hypotheses about the population effects of a
140 major life-history trait; here we focused on seasonal migration. This perspective offers several new
141 insights into migrant demographics and evolutionary ecology. Migratory thrush lineages showed
142 higher effective population sizes, greater population size variation, and proportionally larger initial
143 population growth than resident relatives. A migratory life-history strategy thus imbues these
144 lineages with population size characteristics that are fundamentally different, on average, from those
145 of resident relatives.
146 Although migratory thrush lineages showed higher proportional initial growth than resident
147 relatives, this was not achieved through rapid adaptation to new geographic and ecological
148 opportunities as we predicted. Population growth in migrants and residents was positive early in the
149 lineages' histories (*deltaT*) in all cases but one (*C. aurantiirostris*), and it occurred over fairly long
150 periods of time (Table 1, Fig. 2). That this process initially (on average) involves millions of years of
151 population growth in this group, apparently extended by a migratory life-history strategy that
152 provided access to higher latitudes (Tables 1, S2), is an insight from our study that should be
153 examined in future work from a broader taxonomic perspective. While actual, census population
154 sizes would likely have shown considerable variation across this time, especially after the glacial
155 cycles of the Pleistocene began ~2.6 Mya, the long-term effective population sizes of migrants
156 tended to show steady increases, achieving peaks on average almost 3 My after the lineages' PSMC

157 inception (Figs. 1, S3; Table 1).

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

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

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

177

178 **Population structure**

179 PSMC estimates of population size can be affected by population structure: a change in

180 structure can produce the signal of a change in size (Mazet et al., 2015, 2016; Wakeley, 1999). Some
181 of the population size changes we observed might therefore reflect changes only in levels of
182 population connectivity. There are well-understood differences between seasonal migrants and
183 residents in population structure. Migrants generally have lower levels of geographic partitioning of
184 both phenotypic (subspecies) and genetic variation (Belliure et al., 2000; Delmore et al., 2020; Mayr,
185 1963; Montgomery, 1896). The resident lineages we studied are more prone to this structure than
186 the migrant lineages, with migrants having an average of 2.5 subspecies per lineage and residents
187 having an average of 5.9 (Collar, 2005). Migratory lineages therefore come closer to meeting the
188 assumption of PSMC analyses that populations are panmictic. Thus, in addition to our geographic
189 and ecological scenario differing between the migrant and resident lineages we studied, we also have
190 a pervasive effect of population structure affecting our results, likely increasingly complementing
191 geographic expansion among seasonal migrants as lineage ages approach the recent. However, the
192 greatest effects of inflated N_e over evolutionary time would likely occur among nonmigrants, with
193 more isolation and less mixing (Li & Durbin, 2011).

194 Accounting for population structure in these models to distinguish between the two
195 phenomena is a difficult computational problem; the correlation is not simple, and it might not be
196 tractable with data from a single individual (Mazet et al., 2016; Nadachowska-Brzyska et al., 2016,
197 2022). However, each individual has a genome amalgamated from the entire lineage metapopulation,
198 including individuals and populations that have not been sampled (Mazet et al., 2015). When not
199 focusing on relatively recent or rapid changes (e.g., in human or other bottlenecked systems, where
200 this has been most studied), these issues are probably not as important (Mazet et al., 2016). For
201 example, sister lineages usually show identical effective population size attributes at their origins,
202 reflecting their shared histories (Delmore et al., 2020; Li & Durbin, 2011; Nadachowska-Brzyska et

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

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

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

226 feature (Fig. S3).

227

228 **Geography and evolutionary ecology**

229 Early population growth among migrant lineages is likely affected by some degree of
230 ecological release as these birds engage with the novel environments their increased movements
231 expose them to and they occupy new niche space. However, in this system we cannot readily
232 decouple the expanded geographic and ecological opportunities that seasonal migration provides.
233 The relationship between avian range size and migration is complex, but correlation with latitude is
234 notably strong in North America (Pegan & Winger, 2020). Two aspects of our results suggest that
235 geography operating alone is unlikely to explain the larger migrant population sizes observed (Table
236 1, Fig. S3). The first is that early population growth is positive in all but one of the lineages we
237 studied; despite a probable lack of marked geographic expansion among residents, they, too,
238 experienced long-term growth. The second is that these initial growth periods are quite long,
239 extending over much longer periods than we should expect for populations responding to
240 opportunities for geographic expansion.

241 PSMC analyses excel at long time frames, but initial growth in residents and migrants
242 suggests a strong role for ecological factors. Global climate reconstruction data do not suggest that
243 there were similar long, steady trends during these time periods to match these thrush population
244 size changes (Lisiecki & Raymo, 2005; Fig. S3). Perhaps geographic space does make a difference, on
245 average, between the two life-history strategies. That these growth periods are long also suggests
246 the importance of ecological factors, though. For example, the boreal and subarctic woodland
247 breeding habitats of most *C. ustulatus swainsoni* and *C. minimus* expanded dramatically across North
248 America as glaciers receded since the last glacial maximum (LGM), a period of < 20 Kyr (Pielou,

249 1991). A spatial response of such rapidity, less than 1% of the time of the initial historic growth
250 phases of these two lineages (> 3 Myr; Table 1), leads us to infer that breeding range size alone is
251 not a satisfactory explanation for our results. This post-LGM expansion reflects census size, and not
252 effective population size (N_e), but it implies that a migratory *Catharus* lineage's matching (or
253 mapping) of N_e to average long-term available geographic space is not likely to take millions of years.
254 In other words, their comparatively recent rapid postglacial expansion into new space suggests a sort
255 of preadaptation that is not apparent early in the lineages' histories. Together, these aspects of our
256 results suggest that while geographic factors are involved, ecological factors are also important.
257 Teasing these factors apart might also explain the finding of Germain et al. (2023a) that migrants in
258 general have had larger populations than residents during the last 0.67 my.

259 Identifying key **ecological mechanisms** affecting population sizes among migrants is
260 difficult, and they will likely vary among lineages. There are numerous factors potentially involved.
261 Biotic interactions in general show greater effects on range limits at the warmer than the cooler
262 edges (Paquette & Hargreaves, 2021). Long-distance migrants especially, in their extensive latitudinal
263 movements, would receive a range expansion advantage in this respect regardless of continental
264 landmass shape—and also through higher diel food harvest rates due to longer days and shorter
265 nights. Many additional ecological factors affect the population sizes of migrants versus residents,
266 but the relationships between seasonal migration and predators, parasites, diseases, and competitors
267 are extremely complex and key aspects remain poorly understood (Altizer et al., 2011; Newton,
268 2008).

269 Seasonal migration can be integrally related to predator avoidance, but among birds its
270 effects are not understood in the full, circannual context relative to resident relatives, and they are
271 not generalizable (Brönmark et al., 2008; McKinnon et al., 2010; Newton, 2008; Rappole, 2013).

272 Exposure to parasites and pathogens varies both spatially and seasonally. Although breeding range
273 diminishment of these exposures can be important in some migrants (probably not among all
274 lineages), full annual exposure to both disease and parasite diversity is likely higher, resulting in at
275 least some lineages showing larger immune defense organs (Bennett & Fallis, 1960; Figuerola &
276 Green, 2000; Jenkins et al., 2011; Møller & Erritzoe, 1998; Piersma, 1997; Ricklefs et al., 2017).
277 Exposure to higher circannual parasite and pathogen diversity might not be correlated with
278 susceptibility, however; migration creates a geographic break that can lower transmission, causing
279 migrants overall to be less vulnerable to population declines (Hall et al., 2014).

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

290 Interspecific competition has long been studied between migrants and residents, but its
291 potential role in affecting relative population sizes between the two groups is largely unknown
292 (Rappole, 2013). As close relatives, these thrushes are likely to be each others' closest competitors,
293 so it is conceivable that the increased relative abundance of migrants might depress realized
294 population sizes among residents. In this group, geographic ranges overlap broadly during the

295 nonbreeding season, but the tropical residents tend to occupy higher elevations than nonbreeding
296 migrants (Collar, 2005). Both interspecific competition and inland, montane, and mature-forest
297 retreats among older taxa are major factors in taxon cycles (Ricklefs & Bermingham, 2002; Ricklefs
298 & Cox, 1972; Wilson, 1961) and might also be operating in this system.
299

300 **Conclusions**

301 Paleodemographic analyses in a hypothesis-testing framework offer important new insights
302 into the effects of the major life-history trait of seasonal migration on long-term effective population
303 sizes. Our results indicate larger and more variable migrant populations relative to residents, and
304 these populations grow in a way suggesting an important role not only for seasonal migration and
305 geography, but also for evolutionary ecology. Although there are several plausible ecological
306 mechanisms, their relative importance is unknown. The differences we found are between group
307 averages, and variation among lineages includes residents that are migrant-like (*C. occidentalis*; Table 1,
308 Figs. 1, 2, S3) and vice-versa (e.g., *C. u. ustulatus*; Table 1, Fig. S3). Understanding why residents like
309 *C. occidentalis* show migrant-like historic population characteristics will help us understand the
310 mechanisms affecting these lineages. Such reasons could be as simple as realized range expansion
311 (i.e., geographic and ecological opportunity), and this hypothesis appears to fit the deeply split
312 eastern-western sister lineages within species in which smaller western ranges have smaller effective
313 population sizes (*C. guttatus* and *C. ustulatus*; Fig. S3). Or the reasons might be as complex as a lineage
314 dropping out of migration to become sedentary (*C. occidentalis* is sister to the migrant *C. guttatus*; Fig.
315 1).

316 It is clear that seasonally migratory lineages in this system have, on average, fundamentally
317 different effective population size attributes through evolutionary time than closely related resident

318 lineages. Population structure is probably not a main driver of these results. What remains unclear
319 are the relative roles of geographic and ecological expansions in causing these differences. Both are
320 likely important. More studies in other systems will be needed to tease these roles apart and to
321 determine which ecological mechanisms are involved.

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

330

331 **MATERIALS AND METHODS**

332 The thrush lineages in our study are from the genus *Catharus* and its sister, the single species
333 in the genus *Hylocichla*. These comprise Nearctic-Neotropic seasonal migrants and Neotropical
334 residents. Among the latter, some lineages (*C. aurantiirostris*, *occidentalis*, *frantzii*, and *mexicanus*) have
335 some populations that exhibit some short-distance migration—likely partial migration or hard-
336 weather movements, either in elevation or with extreme northern populations moving south (Collar,
337 2005). These lineages thus comprise two groups, which for simplicity we will refer to as 'seasonal
338 migrants' and 'residents': seasonal migrants with extensive latitudinal movements, and residents that
339 are either wholly sedentary or with some individuals moving rather limited distances within the
340 Neotropics. The eight migrant lineages are: *Hylocichla mustelina*, *Catharus fuscescens*, *C. guttatus* E

341 (eastern lineage), *C. guttatus* W (western lineage), *C. minimus*, *C. ustulatus swainsoni*, *C. u. ustulatus*, and
342 *C. bicknelli*. (Note that four of these lineages represent two deeply divergent lineages each within
343 what are currently considered two biological species, *C. guttatus* and *C. ustulatus*; Topp et al., 2013).
344 The six resident lineages are: *Catharus aurantiirostris*, *C. fuscater*, *C. frantzii*, *C. gracilirostris*, *C. mexicanus*,
345 and *C. occidentalis*. Over the full evolutionary history of this *Hylocichla-Catharus* clade, changes among
346 lineages occurred in the trait of long-distance migration (Outlaw et al., 2003; Voelker et al., 2013;
347 Winker and Pruett, 2006; Fig. 1). Our study does not assume that this trait was constant within each
348 lineage after the speciation events when these switches occurred. Instead, we consider that for a
349 major trait like long-distance migration, losses and gains at the full lineage level are likely to be
350 infrequent, and that current evidence of trait distribution on a phylogeny provides a powerful
351 comparative framework in which to elucidate the effects of that trait on other lineage attributes.
352 DNA was extracted from high-quality voucher specimens or blood samples for 14 thrush
353 lineages (Table S1). Whole-genome sequencing libraries were constructed using Nextera (Illumina)
354 DNA Flex Library Prep kits, and libraries were sequenced on a NovaSeq S4 (Illumina, San Diego,
355 CA) using paired-end 150 bp reads. Reads were aligned to the *C. ustulatus* genome (inland subspecies,
356 Reference bCatUst1, NCBI PRJNA613294) using bwa (mem algorithm with default settings, Li and
357 Durbin 2009). We did not use a maskfile. Identical treatment of all lineages in these respects should
358 provide a strong foundation for a comparative study like this among close relatives. Resulting .sam
359 files were converted to .bam format with samtools (Li et al., 2009); picardtools was used to clean,
360 sort and add read groups to .bam files (http://broadinstitute.github.io/picard/). Between 97 and
361 98% of reads mapped to the reference for an average read depth of 23 × (range 15.9-29.8 ×).
362 We analyzed whole-genomic data from the .bam files using the pairwise sequentially
363 Markovian coalescent (PSMC) approach in the software package psmc (Li & Durbin, 2011). This

364 analysis uses pairwise (allelic) estimates of coalescent times for each locus across the genome in a
365 nonoverlapping manner, developing a distribution of times to most recent common ancestor
366 (TMRCAs), and the frequency of these coalescent events is inversely proportional to effective
367 population size (Li & Durbin, 2011; Mather et al., 2020).

368 We used a generation time of 2.5 yr, taken as an average among many of these species
369 (Dellinger et al., 2020; Evans et al., 2020; Mack & Yong, 2020; Saether et al., 2005; Townsend et al.,
370 2020; Whitaker et al., 2020), and a mutation rate of 2.3×10^{-9} mutations per site per year (Smeds et
371 al., 2016). Single individuals represent lineage characteristics using this approach (Li & Durbin, 2011;
372 Mazet et al., 2015; Nadachowska-Brzyska et al., 2015). Importantly for our focal questions,
373 variations in these parameters do not affect the shape of the curve of population sizes (N_e) through
374 time, but rather the values of the time and N_e estimates (Nadachowska-Brzyska et al. 2015). Being
375 closely related and of similar size, we expect these taxa to have very similar generation times and
376 mutation rates (e.g., Bird et al., 2020; Healy et al., 2014). However, seasonal migration can have an
377 effect on survival and thus generation time, and Bird et al. (2020) produced modeled estimates for
378 this group, providing an alternate approach. The basis for these modeled values is tiny, and the
379 accuracy of the modeled results uncertain, so we use these estimates with caution. But as a check on
380 our results, we ran all of our analyses again with the variable generation times given by Bird et al.
381 (2020). As expected, most of the differences are time-related, and, importantly, the overall results are
382 not different (Table S2).

383 Hilgers et al. (2024) recently showed that artifactual peaks can occur due to recent time
384 parameter settings in the PSMC program (Li & Durbin 2011) that are often used as a default setting.
385 They recommended that such recent peaks can be eliminated by breaking the first atomic time
386 interval (typically 4) into either two (2+2) or four (1+1+1+1) smaller windows. We had four lineages

387 that appeared to have such peaks: *H. mustelina*, *C. fuscescens*, *C. guttatus* E, and *C. gracilirostris*. For the
388 latter three, breaking the recent period parameter into four windows (1+1+1+1) eliminated these
389 peaks. For *H. mustelina*, smaller windows (2+2 and 1+1+1+1) made the recent peak even higher, so
390 we have used the default setting (the most conservative result), as with the remaining taxa that did
391 not show such peaks.

392 The PSMC method is not foolproof; for example, aspects of selection, inbreeding, and
393 isolation can affect population size estimates (Mather et al., 2020). No method of genomic
394 population demographic reconstruction is known to be consistently and reliably accurate (Marchi et
395 al., 2021), but uniform application of a powerful method like PSMC to genome-scale data in a
396 closely related group of lineages can provide new insights into the evolutionary effects of major life-
397 history strategies.

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

406 We note that estimates of the dates of divergence events in *Catharus* evolution vary by study,
407 genetic marker, methodology, and parameter estimates such as generation time and mutation or
408 substitution rates (Outlaw et al., 2003; Topp et al., 2013; Voelker et al., 2013; Winker and Pruett,
409 2006). Date estimates in our study that differ from previous work reflect these methodological

410 issues, and here it is the relative values among lineages within our study that are most important.

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

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Tables and Figures

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.

Figure 1. The phylogenetic tree of the songbird lineages in this study, from the genera *Catharus* and *Hylocichla*. Neotropical residents are shaded in gray.

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.

Supplementary Information

Table S1. Specimen data and NCBI-SRA numbers. Vouchered specimens are housed in the following institutions: UAM (University of Alaska Museum), MSB (Museum of Southwestern Biology, University of New Mexico), LSUMNS (Louisiana State University Museum of Natural Science), and FMNH (Field Museum of Natural History).

Table S2. 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, using variable generation times from Bird et al. (2020) for the analyses. Taxa shaded in gray are Neotropical residents.

Figure S1. Distribution maps of the thrush taxa in this study. Among seasonal migrants, green indicates breeding range and yellow is wintering range. Among sedentary lineages (those shaded in gray), purple indicates year-round range. Data are from BirdLife International and the Handbook of the Birds of the World (2021), Bird species distribution maps of the world. Version 2021.1. Available at http://datazone.birdlife.org/species/requestdis.

Figure S2. Graphic presentation of the *Catharus minimus* PSMC dataset, showing effective population size ($N_e \times 10^4$) from 50 kyr back in time to the lineages' origins as estimated from genomic data. The variables in our analyses are the mean and SD of the effective population size (N_e) values, *deltaT* of initial growth ($time_{trough} - time_{peak}$), the degree of that growth ($1 - [N_{trough}/N_{peak}]$), and the rate of that growth (degree/*deltaT*).

Figure S3. Montage of the historic effective population size curves of all lineages analyzed in this study, with each lineage in a separate panel (based on pairwise sequentially Markovian coalescent, or

735 PSMC, analyses). Sedentary lineages are highlighted in gray. Note that scales on both axes vary
736 among panels, and that the X axis is on a log scale. Bold red lines are the main curves from the
737 original data, and pink lines reflect 100 replicates from bootstrapped sequences. Bold red curves are
738 all overlaid on common axes in the single panel of Fig. 2.
739

740 Table 1. Data from pairwise sequentially Markovian coalescent (PSMC) analyses reflecting effective
741 population sizes ($N_e \times 10^4$) through history at depths > 50 Kyr and the five variables derived and
742 analyzed from that output. Taxa shaded in gray are Neotropical residents.
743

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)

* $p < 0.05$.

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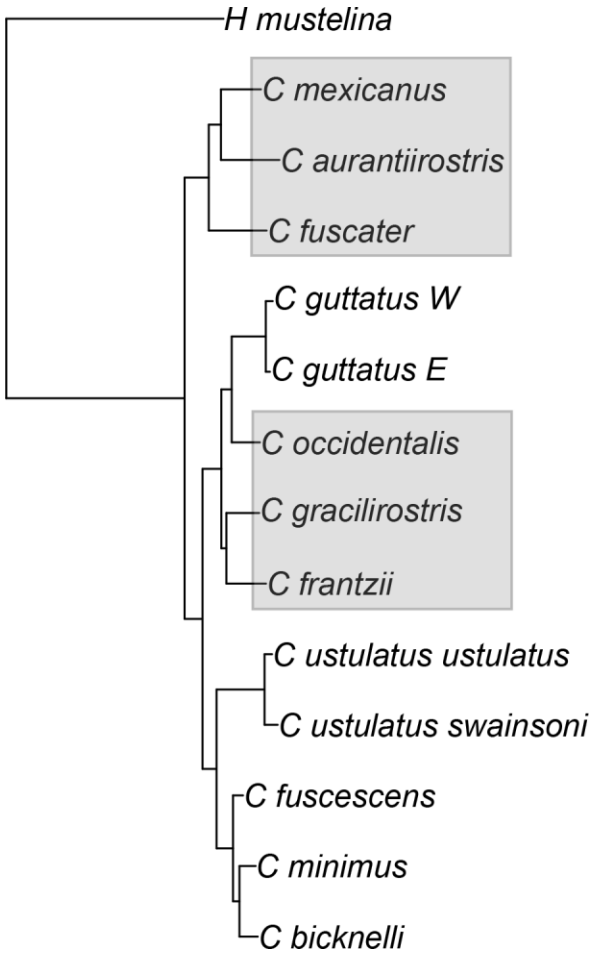
Figure 1. The phylogenetic tree of the songbird lineages in this study, from the genera *Catharus* and *Hylocichla*. Neotropical residents are shaded in gray.



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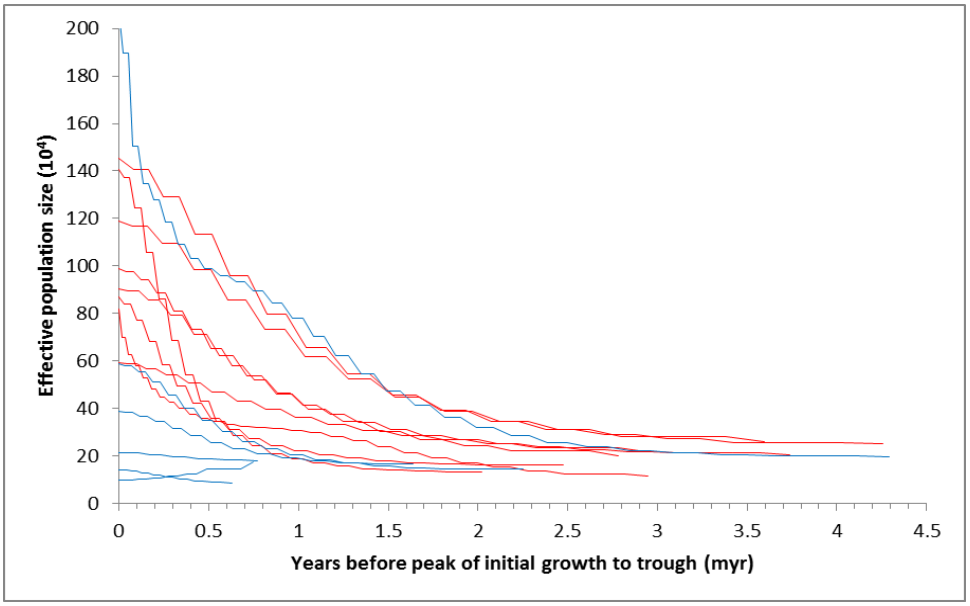

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757 Figure 2. Partial historic effective population size curves from all lineages in this study, based on
758 pairwise sequentially Markovian coalescent (PSMC) analyses. Each peak of initial growth is set to
759 zero years to set a common framework in which to visualize the periods and magnitudes of initial
760 growth among migrant (red) and resident (blue) lineages. See specific lineages with their
761 bootstrapped results in Fig. S2.
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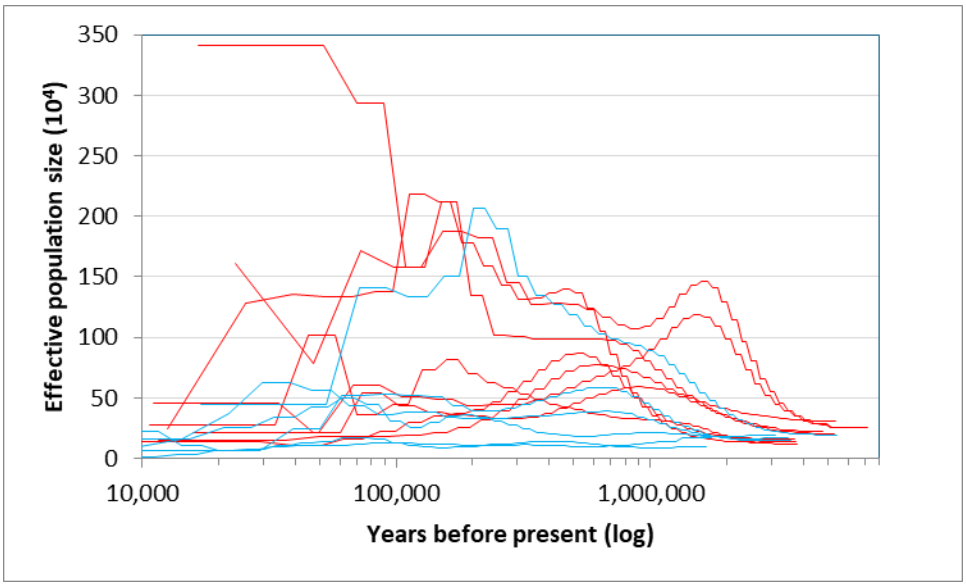

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765
766 Figure 3. Historic effective population size curves from all lineages, based on pairwise sequentially
767 Markovian coalescent (PSMC) analyses. Migrant lineages are in red and resident lineages in blue. See
768 specific lineages with their bootstrapped results in Fig. S2.