



RESEARCH ARTICLE

The evolution of vocal duets and migration in New World warblers (Parulidae)

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ABSTRACT

Vocal duets occur when 2 individuals vocalize in temporal coordination. In birds, duet participation functions to cooperatively defend shared resources, localize mates, and in some species, guard the mate. Previous work indicates that duetting tends to co-evolve with a non-migratory lifestyle, probably because the absence of migration facilitates greater cooperation between mates. We examined the evolution of duetting and migration in New World warblers (Parulidae), a group that has been largely ignored by duetting research. Of the 95 species in our analysis, we found evidence of duetting in 19 (20%) species, and evidence of migration in 45 (47.4%) species. Ancestral character reconstruction indicated that the last common ancestor of the New World warblers did not duet. Duetting evolved multiple times in this group, including 2 early origins and several more recent origins. Migration was present in the last common ancestor and was lost several times. Both duetting and migration exhibit phylogenetic signal. A phylogenetically explicit correlation analysis revealed a significant negative relationship between duetting and migration, in keeping with findings from other avian taxa. This study, the first description of the evolution of duetting in a large avian family with a temperate-zone origin, supports the hypothesis that duetting co-evolves with a sedentary natural history in birds.

Keywords: ancestral character reconstruction, duet, migration, threshold model, warbler

Evolución de duetos vocales y migración en los Parulidae del Nuevo Mundo

RESUMEN

Los duetos vocales suceden cuando dos individuos vocalizan en coordinación temporal. En las aves, la participación en un dueto funciona para defender cooperativamente recursos compartidos, localizar parejas y, en algunas especies, para proteger a la pareja. Trabajos previos indican que el dueto tiende a co-evolucionar con un estilo de vida no migratorio, probablemente debido a que la ausencia de migración facilita una mayor cooperación en la pareja. Examinamos la evolución del dueto y de la migración en los Parulidae del Nuevo Mundo, un grupo que ha sido en gran medida ignorado por la investigación sobre duetos. De las 95 especies de nuestro análisis, encontramos evidencia de dueto en 19 (20%) especies, y evidencia de migración en 45 (47.4%) especies. Una reconstrucción del carácter ancestral indicó que el último ancestro común de los Parulidae del Nuevo Mundo no realizaba dueto. El dueto evolucionó múltiples veces en este grupo, incluyendo dos orígenes tempranos y varios orígenes recientes adicionales. La migración estuvo presente en el último ancestro común y se perdió varias veces. Tanto el dueto como la migración muestran una señal filogenética. Un análisis de correlación filogenéticamente explícito reveló una relación negativa significativa entre el dueto y la migración, de acuerdo con los resultados de otros taxa de aves. Este estudio, la primera descripción de la evolución del dueto en una gran familia de aves con origen en una zona templada, apoya la hipótesis de que el dueto co-evolucionó con una historia natural de sedentarismo en las aves.

Palabras clave: curruca, dueto, migración, modelo de umbral, reconstrucción del carácter ancestral

INTRODUCTION

Vocal duets are acoustic signals that occur when 2 individuals vocalize in temporal coordination (Hall 2009, Logue and Krupp 2016). Duetting is relatively common in birds, occurring in 4–18% of species (Hall 2009, Tobias et al. 2016), including an estimated 1,102 species of songbirds

(Tobias et al. 2016). Duets are often composed of coordinated male and female song, but may also include vocalization types other than song (Hall 2009, Benedict 2010). Cooperative territory defense is the primary function of duet participation in birds, however, duets are also used for contact maintenance and mate guarding in some species (Hall 2009).

Across diverse avian taxa, duetting evolves in concert with long-term pair bonds (Hall 2004, Benedict 2008, Logue and Hall 2014, Tobias et al. 2016). Pair-bond stability is thought to promote cooperation, which in turn favors the evolution of signals that facilitate cooperation, like duetting (Hall 2004, Benedict 2008, Logue and Hall 2014, Tobias et al. 2016). Migration can limit pair-bond duration, which may explain why duetting is negatively associated with migration in songbirds (Ens et al. 1996, Benedict 2008, Jeschke and Kokko 2008, Logue and Hall 2014, Tobias et al. 2016). This evolutionary association between sedentary life histories and duetting may drive global geographic patterns in duetting: most duetting species breed outside of north-temperate latitudes, where latitudinal migration is most common (Hall 2009, Logue and Hall 2014).

Previous studies on the evolution of avian duetting are based on taxonomically diverse samples (Hall 2004, Benedict 2008, Logue and Hall 2014, Tobias et al. 2016). Evolutionary studies that focus on specific taxa can complement taxonomically diverse studies by asking whether general patterns apply to the focal taxon (Odom et al. 2015). Consistent results in multiple clades would lend support to the general conclusion. Conversely, divergent results would demand explanation. Taxonomically restricted samples are also useful for the reconstruction of ancestral traits, because they permit detailed exploration of evolutionary history and set the stage for future taxon-specific investigations (Price 2009, Price et al. 2009, Odom et al. 2015).

Many New World warblers sing duets, but in contrast to well-studied duetting groups like wrens (Troglodytidae), antbirds (Thamnophilidae), and blackbirds (Icteridae), there is virtually no peer-reviewed research on duetting in warblers (Hall 2009). Females of many Parulidae species sing, offering the potential for male-female song duets to evolve (Najar and Benedict 2015, Matthews et al. 2017). Female warblers also produce call notes that are used in some duets (Staicer 1992). All members of this clade are socially monogamous and territorial while breeding, as is typical of species that duet (Benedict 2008, Logue and Hall 2014, Tobias et al. 2016). Atypically for duetting groups, however, this clade has a migratory ancestor that bred in the North-temperate zone (Winger et al. 2012).

Several studies have demonstrated links between duetting and non-migratory life histories among songbirds generally (Benedict 2008, Logue and Hall 2014, Tobias et al. 2016). A previous study found no evolutionary association between female song and migration in New World warblers (Najar and Benedict 2015), but duet evolution does not always parallel female song evolution (Odom et al. 2015), leaving open questions about which forces promote duetting behavior in this clade. New World warblers'

diversity (107 species, Lovette et al. 2010) and proclivity to duet (≥ 19 duetting species, this paper) suggest they would be a useful taxon for duetting research. For the present study, we analyzed the evolution of duetting and migration in the New World warblers (family: Parulidae). Our goals were to describe the diversity of duetting and migration in extant taxa, characterize the evolutionary histories of these 2 traits, and test for their correlated evolution.

METHODS

Our analyses used a recent phylogeny that includes 107 New World warbler species (Lovette et al. 2010). The phylogeny was based on mitochondrial DNA (4,695–4,699 continuous base pairs [bp]) and nuclear DNA (6 introns, totaling 4,602 aligned nucleotides), and was built using maximum likelihood. Outgroups were pruned from the tree prior to analysis.

We scored duetting from *The Handbook of the Birds of the World* (hereafter, HBW: del Hoyo et al. 2011), *New World Warblers* (Curson 1994), peer-reviewed papers, and queries of recording archives from the Macaulay Library (date: November 3, 2016; query terms: "Parulidae" and "duet"), and Xeno-Canto.org (date: November 9, 2016; query terms: "duet" or "antiphonal" in "Type" or "Remark" fields, and all current and recent Parulidae genera in the "Genus" field).

Birds were scored as duetting (coded 1) if there was 1 published source (HBW, *New World Warblers*, or a peer-reviewed paper) or 2 different recordists (from the Macaulay or Xeno-Canto archives) which indicated that the species duets. If a published source contained detailed descriptions of the species' male song (e.g., note number, note or song structure, pitch, context) with no mention of duetting, the species was scored as non-duetting (coded 0). Species that could not be unambiguously scored as duetting or non-duetting were labeled "unknown" (12 of the 107 [11.2%] New World warbler species). Species who were scored "unknown" were not included in the analyses. Migration was scored from the HBW. Species with subspecies that were heterogeneous for migration were assigned the average of their subspecies scores and then rounded to the nearest whole value (e.g., 1.0 if 3 of 5 subspecies migrate). Species that only migrated altitudinally were scored as non-migratory (following Winger et al. 2012, Logue and Hall 2014), based on the assumption that altitudinal migration is less likely to break up pair bonds than is latitudinal migration. Scores and sources of scoring information are in the electronic Supplementary Materials (Supplementary Material Tables S1 and S2; Duet scoring list).

We used the "threshold model" to reconstruct ancestral character states (Revell 2013). The threshold model assumes discrete characters can be represented over

evolutionary time by an underlying continuous variable called “liability.” Each of our models allowed 2 character states: duetting/not duetting and migratory/non-migratory. Liabilities below a fixed threshold correspond to 1 character state, and those above the threshold correspond to the other. Character states of extant species were treated as prior probabilities, and liability evolved by Brownian motion. We used a Bayesian Markov Chain Monte Carlo (MCMC) to sample liability values at all nodes. The result is the proportion of MCMC generations in which the liability lies above the threshold for each node. This proportion can be interpreted as the likelihood that a given node exhibited the character.

We created a long MCMC (50 million generations) because we were running many variables simultaneously ($n = 189$ variables, corresponding to the number of tips and internal nodes). Relative to short MCMCs, long MCMCs offer more generational time for variables to stabilize. Burn-in periods vary depending on the size of the chain, and the rate of stabilization among the variables. Some of our variables were slow to stabilize, so we programmed a 20% burn-in time, rather than the conventional 10% (Gordon et al. 2015, Lerp et al. 2016). Subsampling generations eases the computational burden of running large MCMCs. We took 1 sample every 100 generations.

We used effective sample size (ESS) and Geweke’s diagnostic to assess the MCMCs. Sequential samples from an MCMC are not independent, so the number of samples is not an accurate measure of the independent sample size. ESS accounts for this non-independence by penalizing samples according to their degree of intercorrelation. It is generally desirable to maximize the ESS for all variables. Geweke’s diagnostic tests the stability of the MCMC by comparing the distribution of scores from the beginning of the post-burn-in period with the distribution of scores from the end of the MCMC. If the MCMC has stabilized sufficiently by the end of the burn-in period, the beginning of the post-burn-in and the end of the chain should appear to be from the same distribution. We set alpha (α) to 0.05. It is generally desirable to have nonsignificant results of Geweke’s diagnostic. In addition to these metrics, we visually inspected all MCMC traces. By definition, MCMCs are never truly stable, but those with sufficient long-term stability for accurate inference produce traces that look like rectangular “hairy caterpillars.”

Phylogenetic signal (or phylogenetic inertia) is the tendency for related taxa to be more similar to each other than they are to more distantly related taxa. We used Pagel’s lambda to test for phylogenetic signal among species with known characters. This test uses a likelihood ratio to compare the hypothesized tree to a null tree with no phylogenetic signal (Lovette et al. 2010). The null hypothesis is that there is no phylogenetic signal.

We tested for correlated evolution of duetting and migration using only species with “known” character scores. To include unknown species would have risked pseudoreplication, because their scores were based on the scores of their congeners. Scores consisted of binary values, so we used chi-square (χ^2) tests to test for correlations between duetting and migration in extant species. We also tested for a correlation between phylogenetically independent contrasts (Felsenstein 1985). Contrast scores included numbers between 1 and 0, but did not meet the assumptions of parametric tests, so we used Spearman’s rank correlation.

We used the HBW to score the northern-most and southern-most breeding latitudes of all 95 New World warbler species used in the analyses. These points were then averaged to get the central breeding latitude for each species (Supplementary Material Table S3).

All analyses were run in R (R Core Team 2013). Ancestral trait reconstructions used the packages ape (Paradis et al. 2004) and phytools (Revell 2012). The test for phylogenetic signal also used phytools. MCMC diagnostic tools were from the coda package (Plummer et al. 2006). The correlation and phylogenetically independent correlation tests were performed using functions from the psych (Revelle 2018) and phytools packages. The tree diagram was created using the ggtree package (Yu et al. 2017). The latitude diagram was created using the ggplot2 package (Wickham 2016). Data and R code are available in the online Supplementary Materials (r8stree.tre).

RESULTS

Of the 107 New World warbler species, we were able to find sufficient data to score 95 (88.8%) species with confidence. The remaining species were scored “unknown” and dropped from the analyses. We scored 19 of 95 (20%) New World warbler species as duetting and 76 (80%) species as non-duetting (Table 1). We estimated duetting frequencies of 0% in the genera *Cardellina*, *Helmitheros*, *Limnothlypis*, *Mniotilta*, *Oreothlypis*, *Parkesia*, *Protonotaria*, *Seiurus*, and *Vermivora*; 8% in *Geothlypis*; 9% in *Setophaga*; 20% in *Basileuterus*; 57% in *Myiothlypis*; and 75% in *Myioborus*. We scored 47 species (49.5%) as migratory and 48 species (50.5%) as non-migratory. Genus-specific migration frequencies were 0% in *Basileuterus*, *Myioborus*, and *Myiothlypis*; 33% in *Geothlypis*; 68% in *Setophaga*; 75% in *Cardellina* and *Oreothlypis*; and 100% in *Helmitheros*,

TABLE 1. The co-occurrence of duetting and migratory character for 95 New World warblers. The numbers indicate the number of species that exhibit the characters orthogonal to them.

	Duetting	Non-duetting
Migratory	46	30
Non-migratory	18	1

Limnothlypis, *Mniotilta*, *Parkesia*, *Protonotaria*, *Seiurus*, and *Vermivora*.

Reconstructions of ancestral traits are shown in Figure 1. The ancestral trait reconstruction for duetting was robust with 187 of 189 (99%) estimates based on an ESS

>200 and 42 of 189 (22.2%) Geweke's diagnostic indicating stable MCMCs. The migration reconstruction was similarly robust: 187 of 189 (99%) variables achieving an ESS >200 and 72 of the 189 (38.1%) variables indicating stable MCMCs. None of the variables had both significant

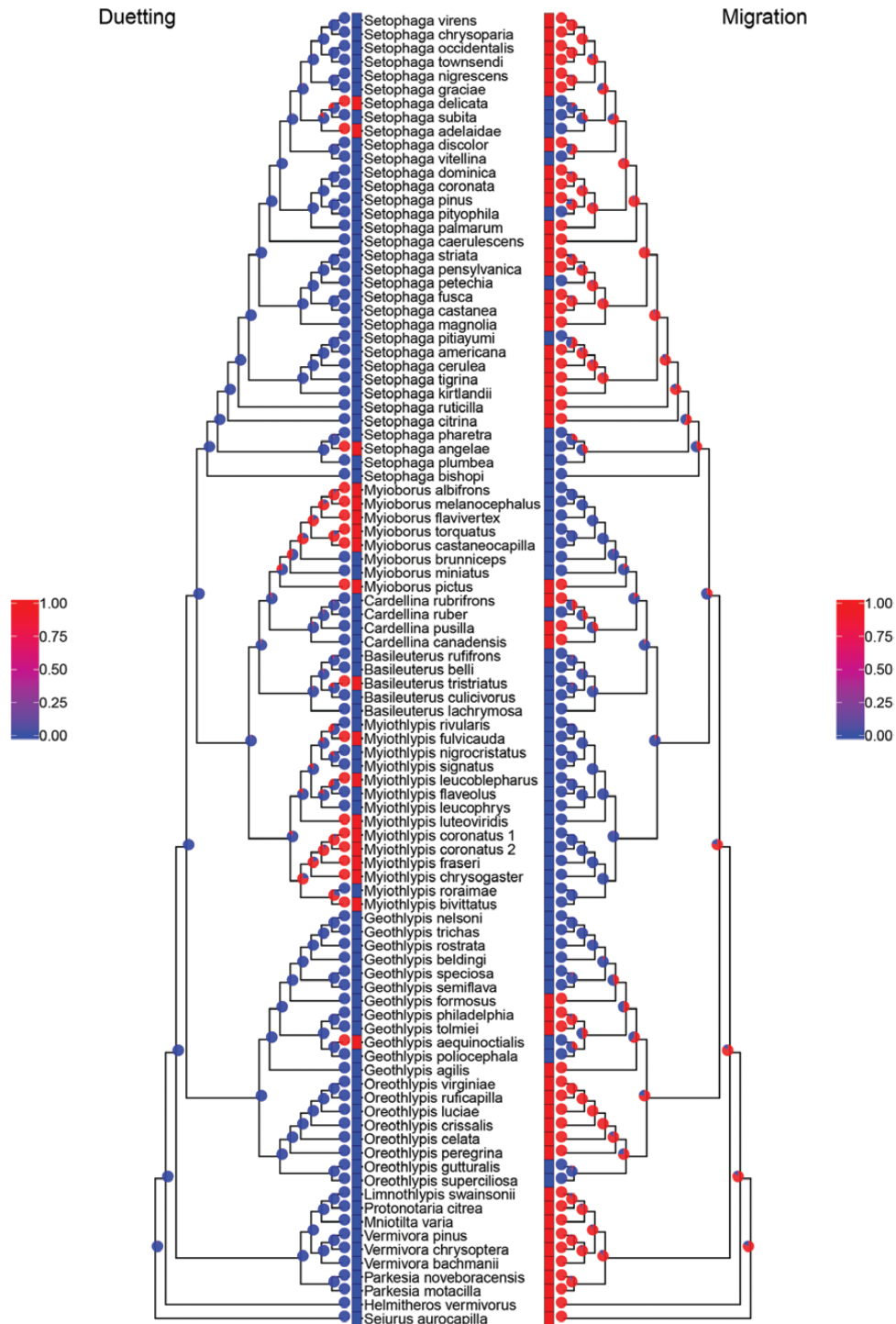


FIGURE 1. Threshold reconstruction of duetting (left tree) and migration (right tree) for 95 New World warblers. Circles at branch tips represent posterior estimates, and squares represent priors.

Geweke's and an ESS <200. All MCMC traces indicated relative stability over generational time.

Our duetting reconstruction indicates that the last common ancestor of the New World warblers did not duet (likelihood [duetting] = 0.016). We found strong evidence that duetting evolved relatively early in *Myioborus* (likelihood [duetting] = 0.771), and *Myiothlypis* (likelihood [duetting] = 0.765). In both groups, duetting appeared after the lineages lost migratory behavior. It is unlikely that the most recent common ancestors of *Cardellina* (likelihood [duetting] = 0.041), *Setophaga* (likelihood [duetting] = 0.005), or *Myiothlypis* (likelihood [duetting] = 0.113), duetted. The basal nodes of *Basileuterus*, *Geothlypis*, *Oreothlypis*, and the basal clade that includes *Limnothlypis* and *Parkesia*, show little or no evidence of duetting. The lineages leading to extant duetters outside of *Myiothlypis* and *Myioborus* (e.g., in *Setophaga*) appear to have evolved duetting recently.

Our migration reconstruction suggests the last common ancestor of all New World warblers probably migrated (likelihood [migration] = 0.824). The last common ancestors of the genera *Myioborus* (likelihood [migration] = 0.133), *Basileuterus* (likelihood [migration] = 0.050), and *Myiothlypis* (likelihood [migration] = 0.015) probably did not migrate. Reconstructions are equivocal for the last common ancestors of *Cardellina* (likelihood [migration] = 0.406) and *Setophaga* (likelihood [migration] = 0.436). There is stronger evidence of migration in the last common ancestors of the clade comprising *Oreothlypis* and *Geothlypis* (likelihood [migration] = 0.773), and the basal clade that includes *Limnothlypis* and *Parkesia* (likelihood [migration] = 0.904). There is also some evidence of

migration at the first split of *Setophaga* (likelihood [migration] = 0.571) and the last common ancestor of *Geothlypis* (likelihood [migration] = 0.615). Our reconstructions suggest that transitions to non-migratory natural histories began early in the diversification of the New World warblers, but duetting evolved more recently.

The tests for phylogenetic signal were statistically significant for both duetting ($\lambda = 0.99$, $P < 0.0001$) and migration ($\lambda = 0.87$, $P < 0.0001$). Without controlling for phylogeny we found a significant, negative correlation between duetting and migration among known, extant species ($\chi^2 = 18.57$, $df = 1$, $P < 0.0001$). After controlling for phylogeny with the method of independent contrasts, the correlation remained significant (Spearman's rank correlation: $\rho = -0.25$, $df = 94$, $P = 0.015$). Duetting was associated with lower breeding latitudes and migration was associated with higher breeding latitudes in our sample (Figure 2).

DISCUSSION

Our analysis of the prevalence of vocal duetting in extant New World warblers indicated that duetting occurs in 20% of New World warbler species we were able to score. This estimate is similar to the estimates for New World blackbirds (18%, Odom et al. 2015), songbirds (15.6%, Logue and Hall 2014), and all birds (~16%, Tobias et al. 2016). Duetting is non-randomly distributed among New World warblers, with the highest concentration in the genera *Myioborus* and *Myiothlypis*.

There is strong evidence that the last common ancestor of the extant Parulidae did not duet, and that duetting originated multiple times in the family. The ancestral

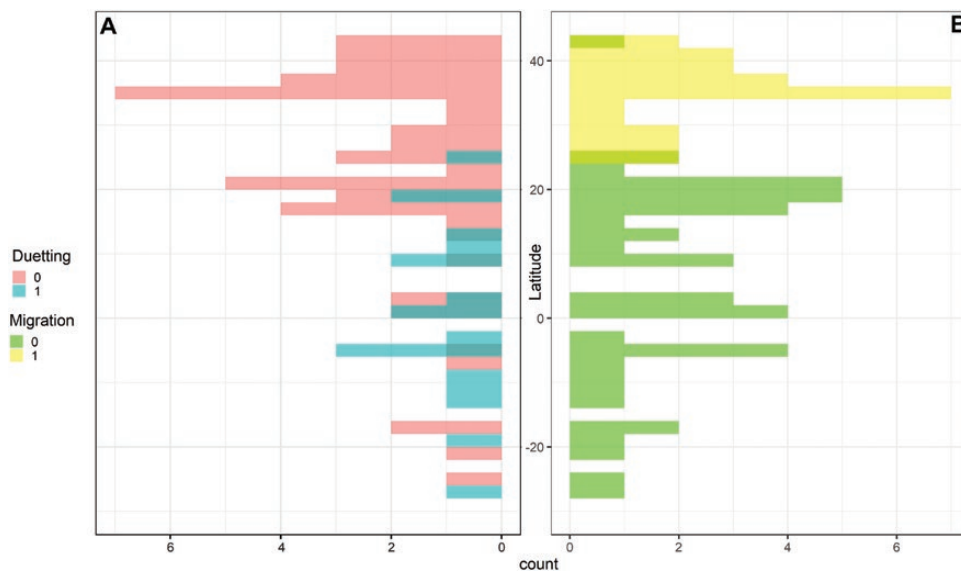


FIGURE 2. The distribution of breeding latitudes as a function of (A) duetting and (B) migration in a sample of 95 New World warbler species. Positive latitudes are in degrees north (°N), and negative latitudes are in degrees south (°S).

trait reconstruction suggests duetting evolved twice during the early diversification of the family: at or near the common ancestor of *Myioborus* and after the first split of *Myiothlypis*. There have also been several recent gains of duetting, especially in *Setophaga* and *Myiothlypis*. Duetting appears to have been lost in the lineages leading to *Myioborus brunneiceps* and *Myiothlypis rorimae*. Both of those species, however, are poorly known to science, so further investigation may reveal that they duet. We conclude that duetting has probably been gained more than it has been lost in the New World warblers. The recent gains (and possible losses) of duetting are evidence that duetting can evolve rapidly, while the finding of strong phylogenetic signal indicates that duetting has been conserved over evolutionary time in some lineages. Similar patterns were found in the New World blackbirds: the common ancestor did not duet, gains of duetting exceeded losses, and duetting evolved both recently and earlier in the clade's evolutionary history (Icteridae; Odom et al. 2015). The occurrence of both ancient and recent evolutionary transitions from non-duetting to duetting make Parulidae and Icteridae model families for research on duet evolution. For example, we might use these groups to test whether duets tend to increase in structural and temporal coordination over evolutionary time.

We scored 49.4% of the New World warblers in our sample as migrating latitudinally. This is similar to the results of 2 previous efforts to score migration in Parulidae, which arrived at estimates of 45.4% and 46.7%, respectively (Winger et al. 2012, Najar and Benedict 2015). The difference in estimates is largely attributable to the fact that, unlike the present study, those studies scored partial migrants (as opposed to rounding them). Additionally, in the case of the 2015 study, altitudinal migrants were also scored as migratory. New World warblers are more prone to migration than are birds in general, of which ~18.5% are estimated to migrate (Rolland et al. 2014). Like duetting, migration was heterogeneously distributed throughout the family, and exhibited phylogenetic signal. The last common ancestor of Parulidae probably migrated. This finding is reflected in the high migration rates among the basal taxa and matches the conclusions of 2 previous studies (Winger et al. 2014, Najar and Benedict 2015). Ten genera are mostly migratory, and 3 large genera do not migrate at all (including both of the genera with the highest duetting rates). Early losses of migration occurred in the last common ancestor of *Geothlypis*, and the last common ancestor of the clades *Myioborus* through *Setophaga*. There was an early secondary evolution of migration in *Setophaga*. There is also evidence of recent losses (*Setophaga delicata* through *S. adelaidae*, *S. vitellina*, *S. pityophila*, *S. pityayumi*, *Geothlypis semperi*, and *Oreothlypis peregrina* through *O. superciliosa*) and gains of migration (*C. rubrifrons*

through *C. canadensis*, *G. formosus* through *G. tolmiei* and *G. agilis*).

Migration is generally a labile trait in birds (Pulido 2007). Our findings largely support the idea that migration is evolutionarily labile in New World warblers. We also see evidence that migration status is conserved in some lineages, a finding that is supported by the significant result from our test for phylogenetic signal. Our results replicate Winger et al.'s (2012) finding of phylogenetic signal for migration in Parulidae. That study used different scoring and analytic methods, strengthening the value of this replication. In this study we found that Pagel's λ for migration and duetting were similar, but the value for duetting was slightly higher (0.95 vs. 0.89 for migration), suggesting a stronger phylogenetic signal for duetting than for migration. Some vocal traits change too rapidly to produce phylogenetic signal (Rheindt et al. 2004). Others can be conserved over time, both revealing and reflecting evolutionary history (Price and Lanyon 2002). The results of this study suggest that duetting in New World warblers is a vocal trait that evolves slowly enough to produce phylogenetic signal, but is labile enough to have evolved recently in the phylogeny.

We believe our trait reconstructions for both duetting and migration are valid despite the occurrence of some low ESSs and significant Geweke's diagnostics. The low ESSs occurred on short branches with homogenous local environments. Those conditions generate strong correlations between subsequent generations (poor mixing). We used a large number of generations to increase the ESSs, but that decision also increased the number of significant Geweke's diagnostics. Importantly, the significant Geweke's diagnostics were attributable to high power, rather than large effects (Supplementary Material text, Figures S1 and S2). The similarity in diagnostic metrics between our 2 reconstructions, coupled with confirmation of the migration results from other studies (Winger et al. 2012, Najar and Benedict 2015), gives us confidence in our duet evolution results.

Our results support previous findings that latitudinal migration and duetting are negatively correlated in birds (Benedict 2008, Logue and Hall 2014, Tobias et al. 2016). We scored all duetting New World warblers as non-migratory, and a phylogenetically controlled correlation showed a significant relationship between these 2 traits. Because the ancestral New World warbler was migratory and non-duetting, this pattern necessarily results from gains of duetting in lineages that also lost migration. Estimated trait values at nodes within the phylogeny (Figure 1) suggest that losses of migration typically occurred first, and then duets evolved in sedentary species. A previous study linking these 2 traits found that the relationship between them was largely driven by losses of duetting in migratory species (Logue and Hall 2014). Results presented here indicate

that both gains and losses of these traits may be integral in larger patterns, and that changes to migration behavior may drive changes in signaling. As in previous studies, we suspect pair-bond duration mediates the relationship between migration and duetting, and we encourage further study of the social behavior of the many species of New World warblers for which pair-bond duration is unknown. As in previous studies, duetting and sedentariness were associated with tropical and southern hemisphere breeding (Figure 2; Hall 2004, 2009, Logue and Hall 2014).

Past research suggests that there is little, if any, phylogenetic signal for female song in New World warblers, and no correlation between female song and migration (Najar and Benedict 2015). Duetting in Parulidae does not rely on the presence of female song because some New World warblers that duet lack female song (e.g., *S. adelaidae*, which duets with a pip call; Staicer 1992), and some with female song do not duet (e.g., *S. ruticilla*). The evolutionary dissociation between female song and duetting contrasts with New World blackbirds, in which female song is a prerequisite for vocal duetting (Odom et al. 2015). Although female song and duetting are not perfectly correlated in New World warblers, these 2 traits exhibit similar patterns within the group. An early New World warbler ancestor with female song occurred within the genus *Myiothlypis*, and this genus showed high rates of both female song and duetting (Najar and Benedict 2015). Duets are also prevalent in *Myioborus*, but it was impossible to accurately score female song in most of that group because the songs of these species are poorly described (Najar and Benedict 2015). In both Najar and Benedict (2015) and the present study, the accuracy of analyses is limited by the available data. It is likely that we have incorrectly scored some tropical duetting species as non-duetters because the vocal behavior of many tropical warbler species is poorly known. Our published dataset will permit updated analyses as more is learned about duetting behavior in tropical warblers.

Patterns of vocal evolution in New World warblers differ from patterns of vocal evolution in the closely related and well-studied New World blackbirds (Odom et al. 2015). In that family, female song is negatively correlated with non-migratory behavior, but after controlling for the presence of female song, the association between sedentariness and duetting is not significant (Odom et al. 2015). Odom et al. (2015) argue that, in blackbirds, female song is a prerequisite for the evolution of duetting, but that different selective pressures may promote the 2 signal types (Odom et al. 2015). An alternative hypothesis is that similar selective forces underlie female song and duetting but duetting takes longer to evolve. In warblers, duets are not restricted to lineages with female song, so the evolution of duetting may be less constrained than it is in blackbirds. New World warblers are not unique in this regard: many

duetting species do not produce learned songs at all (Hall 2004, 2009). Comparisons between the Icteridae and the Parulidae highlight the multiple avenues through which duets may evolve and covary with migratory behavior.

To summarize, our results describe a hypothesized evolutionary history of duetting and migration in New World warblers. There were sufficient character transitions in both duetting and migration to robustly establish the evolutionary relationship between these 2 traits. We found support for the inverse evolutionary link between duetting and migration, adding to the evidence for the generality of this pattern across multiple groups with varied traits. These findings provide a point of comparison with related taxa, and a foundation for future research on the evolution of duetting and migration in New World warblers.

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Ethics statement: Animal care is not relevant to this study, because we did not collect data from living birds.

Author contributions: D.M.L. conceived of the idea and design; L.R.M., N.N. and J.C. collected data; L.R.M., D.M.L., L.B. and N.N. wrote or substantially edited the paper; L.R.M. and D.M.L. designed and developed methods; L.R.M. and J.C. analyzed the data; and L.R.M. and D.M.L. contributed resources and funding.

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