

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

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14 **ABSTRACT**

15 Vocal duets occur when two individuals vocalize in temporal coordination. In birds, duet
16 participation functions to cooperatively defend shared resources, localize mates, and in some
17 species, guard the mate. Previous work indicates that duetting tends to co-evolve with a non-
18 migratory lifestyle, probably because the absence of migration facilitates greater cooperation
19 between mates. We examined the evolution of duetting and migration in New World warblers
20 (Parulidae), a group that has been largely ignored by duetting research. Of the 95 species in our
21 analysis, we found evidence of duetting in 19 (20%) species, and evidence of migration in 45
22 (47.4%) species. Ancestral character reconstruction indicated that the last common ancestor of
23 the New World warblers did not duet. Duetting evolved multiple times in this group, including

24 two early origins and several more recent origins. Migration was present in the last common
25 ancestor, and was lost several times. Both duetting and migration exhibit phylogenetic signal. A
26 phylogenetically explicit correlation analysis revealed a significant negative relationship between
27 duetting and migration, in keeping with findings from other avian taxa. This study, the first
28 description of the evolution of duetting in a large avian family with a temperate-zone origin,
29 supports the hypothesis that duetting co-evolves with a sedentary natural history in birds.

30

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

32

33 **INTRODUCTION**

34 Vocal duets are acoustic signals that occur when two individuals vocalize in temporal
35 coordination (Hall 2009, Logue and Krupp 2016). Duetting is relatively common in birds,
36 occurring in 4-18% of species (Hall 2009, Tobias et al. 2016), including an estimated 1102
37 species of songbirds (Tobias et al. 2016). Duets are often composed of coordinated male and
38 female song, but may also include vocalization types other than song (Hall 2009, Benedict
39 2010). Cooperative territory defense is the primary function of duet participation in birds,
40 however duets are also used for contact maintenance and mate guarding in some species (Hall
41 2009).

42

43 Across diverse avian taxa, duetting evolves in concert with long-term pair bonds (Hall 2004,
44 Benedict 2008, Logue and Hall 2014, Tobias et al. 2016). Pair-bond stability is thought to
45 promote cooperation, which in turn favors the evolution of signals that facilitate cooperation, like
46 duetting (Hall 2004, Benedict 2008, Logue and Hall 2014, Tobias et al. 2016). Migration can

47 limit pair bond duration, which may explain why duetting is negatively associated with migration
48 in songbirds (Ens et al. 1996, Jeschke and Kokko 2008, Benedict 2008, Logue and Hall 2014,
49 Tobias et al. 2016). This evolutionary association between sedentary life-histories and duetting
50 may drive global geographic patterns in duetting: most duetting species breed outside of north-
51 temperate latitudes, where latitudinal migration is most common (Hall 2009, Logue and Hall
52 2014).

53

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

62

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

70 duetting groups, however, this clade has a migratory ancestor that bred in the North-temperate
71 zone (Winger et al. 2012).

72

73 Several studies have demonstrated links between duetting and non-migratory life histories
74 among songbirds generally (Benedict 2008, Logue and Hall 2014, Tobias et al. 2016). A
75 previous study found no evolutionary association between female song and migration in New
76 World warblers (Najar and Benedict 2015), but duet evolution does not always parallel female
77 song evolution (Odom et al. 2015), leaving open questions about what forces promote duetting
78 behavior in this clade. New World warblers' diversity (107 species, Lovette et al. 2010) and
79 proclivity to duet (≥ 19 duetting species, this paper) suggest they would be a useful taxon for
80 duetting research. For the present study, we analyzed the evolution of duetting and migration in
81 the New World warblers (family: Parulidae). Our goals were to describe the diversity of duetting
82 and migration in extant taxa, characterize the evolutionary histories of these two traits, and test
83 for their correlated evolution.

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86

87 **METHODS**

88

89 Our analyses used a recent phylogeny that includes 107 New World warbler species (Lovette et
90 al. 2010). The phylogeny was based on mitochondrial DNA (4695-4699 continuous base pairs)
91 and nuclear DNA (six introns, totaling 4602 aligned nucleotides), and was built using maximum
92 likelihood. Outgroups were pruned from the tree prior to analysis.

93

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

99

100 Birds were scored as duetting (coded 1) if one published source (HBW, New World warblers, or
101 a peer-reviewed paper) or two different recordists (from the MacCaulay or Xeno-Canto archives)
102 indicated that the species duets. If a published source contained detailed descriptions of the
103 species’ male song (e.g., note number, note or song structure, pitch, context) with no mention of
104 duetting, the species was scored as non-duetting (coded 0). Species that could not be
105 unambiguously scored as duetting or non-duetting were labeled ‘unknown’ (12 of the 107
106 (11.2%) New World Warbler species). Species who were scored ‘unknown’ were not included in
107 the analyses. Migration was scored from the HBW. Species with subspecies that were
108 heterogeneous for migration were assigned the average of their subspecies scores and then
109 rounded to the nearest whole value (e.g., 1.0 if three of five subspecies migrate). Species that
110 only migrated altitudinally were scored as non-migratory (following Winger et al. 2012, Logue
111 and Hall 2014), based on the assumption that altitudinal migration is less likely to break up pair
112 bonds than is latitudinal migration. Scores and sources of scoring information are in the
113 electronic supplementary materials (ESM Tables S3 & S4).

114

115 We used the “threshold model” to reconstruct ancestral character states (Revell 2013). The
116 threshold model assumes discrete characters can be represented over evolutionary time by an
117 underlying continuous variable called “liability”. Each of our models allowed two character
118 states: duetting / not duetting and migratory / non-migratory. Liabilities below a fixed threshold
119 correspond to one character state, and those above the threshold correspond to the other.
120 Character states of extant species were treated as prior probabilities, and liability evolved by
121 Brownian motion. We used a Bayesian Markov Chain Monte Carlo (MCMC) to sample liability
122 values at all nodes. The result is the proportion of MCMC generations in which the liability lies
123 above the threshold for each node. This proportion can be interpreted as the likelihood that a
124 given node exhibited the character.

125

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

134

135 We used effective sample size (ESS) and Geweke’s diagnostic to assess the MCMCs. Sequential
136 samples from an MCMC are not independent, so the number of samples is not an accurate
137 measure of the independent sample size. ESS accounts for this non-independence by penalizing

138 samples according to their degree of intercorrelation. It is generally desirable to maximize the
139 ESS for all variables. Geweke's diagnostic tests the stability of the MCMC by comparing the
140 distribution of scores from the beginning of the post-burn-in period to the distribution of scores
141 from the end of the MCMC. If the MCMC has stabilized sufficiently by the end of the burn-in
142 period, the beginning of the post-burn-in and the end of the chain should appear to be from the
143 same distribution. We set alpha to 0.05. It is generally desirable to have nonsignificant results of
144 Geweke's diagnostic. In addition to these metrics, we visually inspected all MCMC traces. By
145 definition, MCMC's are never truly stable, but those with sufficient long-term stability for
146 accurate inference produce traces that look like rectangular "hairy caterpillars."

147

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

153

154 We tested for correlated evolution of duetting and migration using only species with 'known'
155 character scores. To include unknown species would have risked pseudoreplication, because
156 their scores were based on the scores of their congeners. Scores consisted of binary values, so we
157 used χ^2 tests to test for correlations between duetting and migration in extant species. We also
158 tested for a correlation between phylogenetically independent contrasts (Felsenstein 1985).
159 Contrast scores included numbers between one and zero, but did not meet the assumptions of
160 parametric tests, so we used Spearman's rank correlation.

161

162 We used the HBW to score the northern-most and southern-most breeding latitudes of all 95
163 New World warbler species used in the analyses. These points were then averaged to get the
164 central breeding latitude for each species (ESM Table S5).

165

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

173

174 **RESULTS**

175

176 Of the 107 New World warbler species, we were able to find sufficient data to score 95 (88.8%)
177 species with confidence. The remaining species were scored ‘unknown’ and dropped from the
178 analyses. We scored 19 of 95 (20%) New World warbler species as duetting and 76 (80%)
179 species as non-duetting (Table 1). We estimated duetting frequencies of 0% in the genera
180 *Cardellina*, *Helmitheros*, *Limnothlypis*, *Mniotilta*, *Oreothlypis*, *Parkesia*, *Protonotaria*, *Seiurus*,
181 *Vermivora*; 8% in *Geothlypis*; 9% in *Setophaga*; 20% in *Basileuterus*; 57% in *Myiothlypis*; and
182 75% in *Myioborus*. We scored 47 species (49.5%) as migratory and 48 species (50.5%) as non-
183 migratory. Genus-specific migration frequencies were 0% in *Basileuterus*, *Myioborus*. and

184 *Myiothlypis*; 33% in *Geothlypis*; 68% in *Setophaga*; 75% in *Cardellina* and *Oreothlypis*; and
185 100% in *Helmitheros*, *Limnothlypis*, *Mniotilta*, *Parkesia*, *Protonotaria*, *Seiurus*, and *Vermivora*.

186

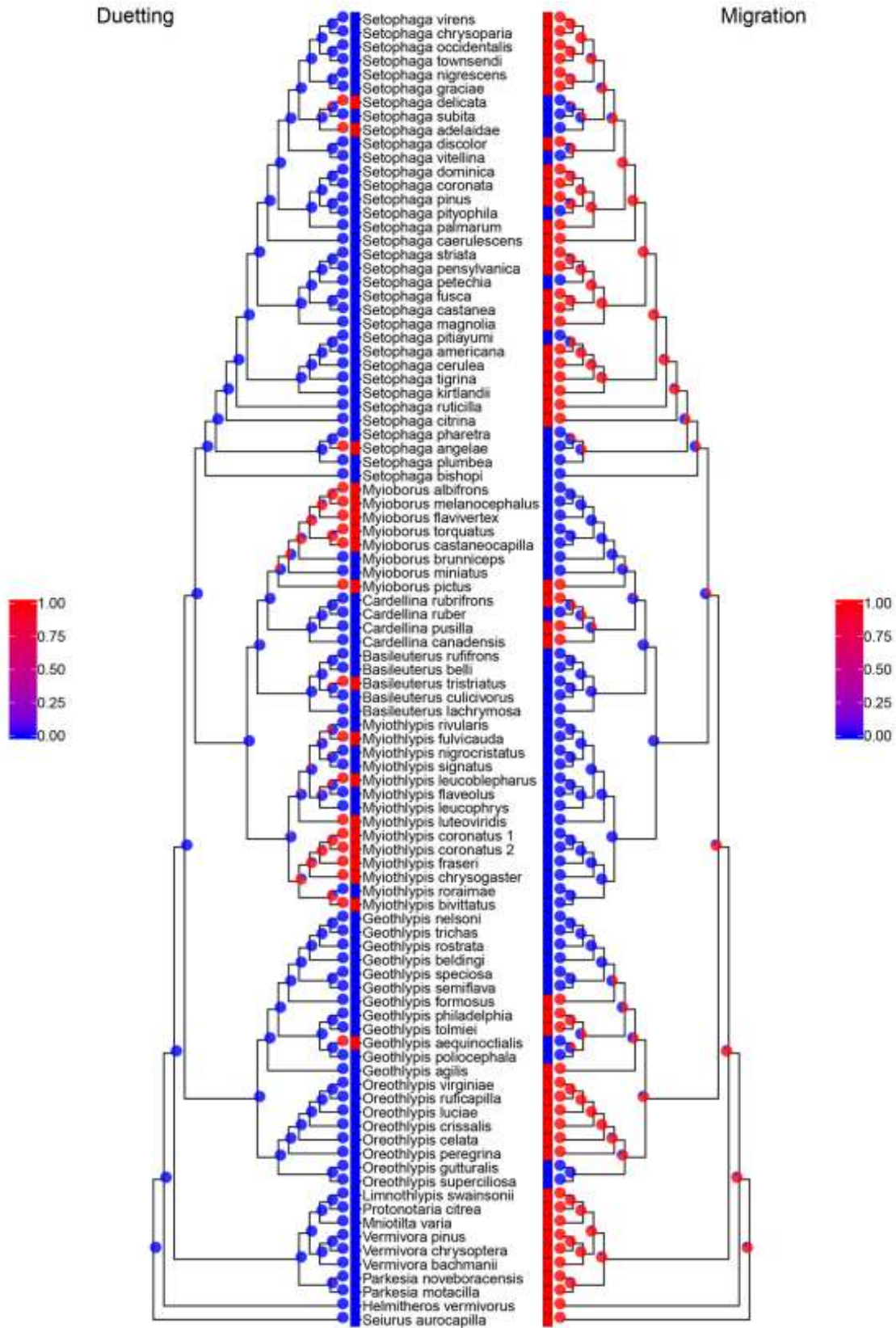
	Duetting	Non-duetting
Migratory	46	30
Non-migratory	18	1

187

188 **Table 1.**

189

190 Reconstructions of ancestral traits are shown in Figure 1. The ancestral trait reconstruction for
191 duetting was robust with 187 of 189 (99%) estimates based on ESS's >200 and 42 of 189
192 (22.2%) Geweke's diagnostic indicating stable MCMCs. The migration reconstruction was
193 similarly robust: 187 of 189 (99%) variables achieving an effective sample size >200 and 72 of
194 the 189 (38.1%) variables indicating stable MCMC's. None of the variables had both significant
195 Geweke's, and ESS < 200. All MCMC traces indicated relative stability over generational time.



196

197 **Figure 1.**

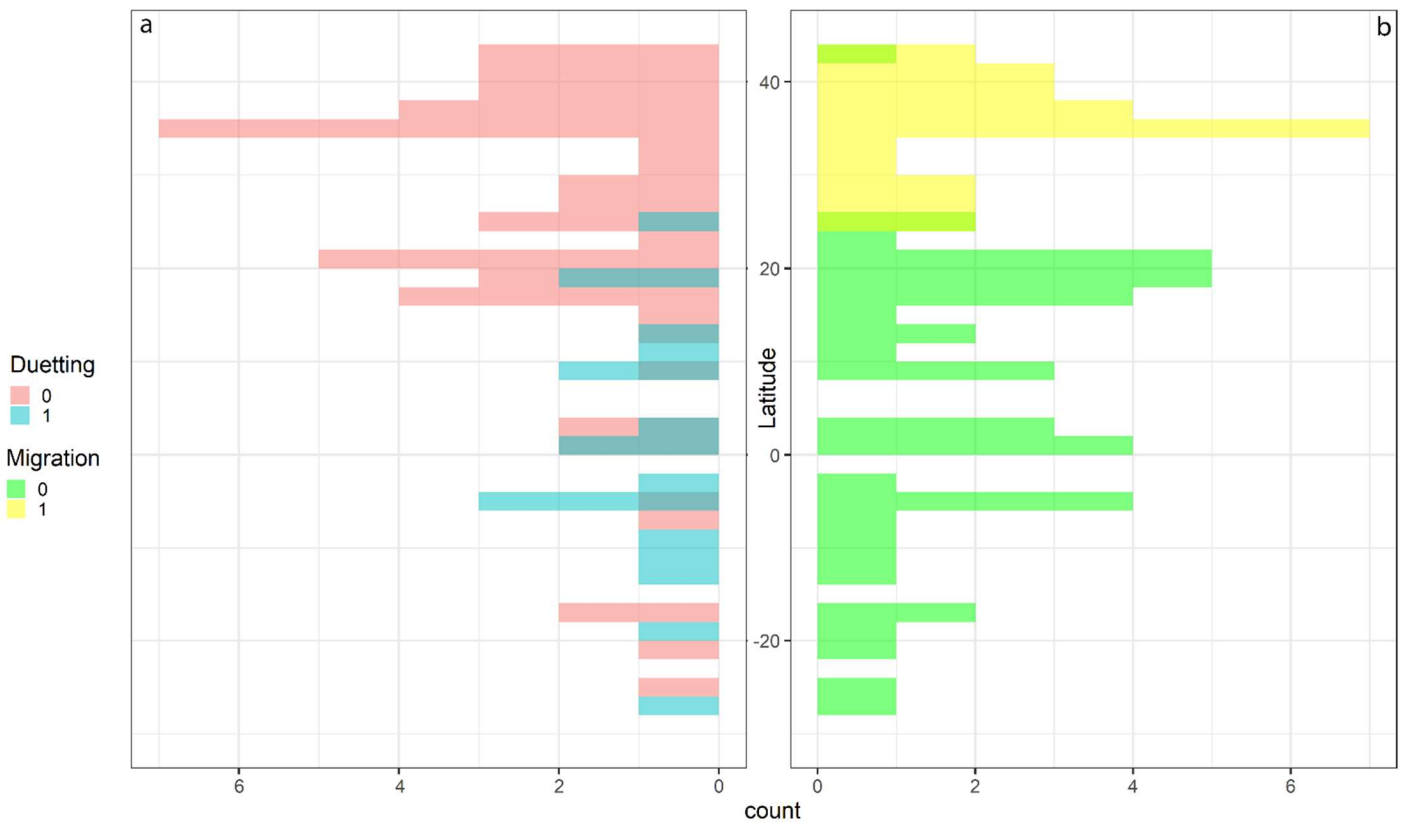
198

199 Our duetting reconstruction indicates that the last common ancestor of the New World warblers
200 did not duet (likelihood(duetting) = 0.016). We found strong evidence that duetting evolved
201 relatively early in *Myioborus* (likelihood (duetting) = 0.771), and *Myiothlypis* (likelihood
202 (duetting) = 0.765). In both groups, duetting appeared after the lineages lost migratory behavior.
203 It is unlikely that the most recent common ancestors of *Cardellina* (likelihood (duetting) =
204 0.041), *Setophaga* (likelihood (duetting) = 0.005), or *Myiothlypis* (likelihood (duetting) = 0.113)
205 duetted. The basal nodes of *Basileuterus*, *Geothlypis*, *Oreothlypis*, and the basal clade that
206 includes *Limnothlypis* and *Parkesia* show little or no evidence of duetting. The lineages leading
207 to extant duetters outside of *Myiothlypis* and *Myioborus* (e.g., in *Setophaga*) appear to have
208 evolved duetting recently.

209

210 Our migration reconstruction suggests the last common ancestor of all New World warblers
211 probably migrated (likelihood(migration) = 0.824). The last common ancestors of the genera
212 *Myioborus* (likelihood(migration) = 0.133), *Basileuterus* (likelihood(migration) = 0.050), and
213 *Myiothlypis* (likelihood(migration) = 0.0015) probably did not migrate. Reconstructions are
214 equivocal for the last common ancestors of *Cardellina* (likelihood(migration) = 0.406), and
215 *Setophaga* (likelihood(migration) = 0.436). There is stronger evidence of migration in the last
216 common ancestors of the clade comprising *Oreothlypis* and *Geothlypis* (likelihood(migration) =
217 0.773), and the basal clade that includes *Limnothlypis* and *Parkesia* (likelihood(migration) =
218 0.904). There is also some evidence of migration at the first split of *Setophaga*
219 (likelihood(migration) = 0.571) and the last common ancestor of *Geothlypis*
220 (likelihood(migration) = 0.615). Our reconstructions suggest that transitions to non-migratory

221 natural histories began early in the diversification of the New World warblers, but duetting
 222 evolved more recently.
 223
 224 The tests for phylogenetic signal were statistically significant for both duetting ($\lambda = 0.99$, $p <$
 225 0.0001) and migration ($\lambda = 0.87$, $p < 0.0001$). Without controlling for phylogeny we found a
 226 significant, negative correlation between duetting and migration among known, extant species
 227 (Chi square: $x\text{-squared} = 18.57$, $p < 0.0001$, $df = 1$). After controlling for phylogeny with the
 228 method of independent contrasts, the correlation remained significant (Spearman's rank
 229 correlation: $\rho = -0.25$, $p = 0.015$, $df = 94$). Duetting was associated with lower breeding
 230 latitudes and migration was associated with higher breeding latitudes in our sample (Fig. 2).
 231



232
 233 **Figure 2.**

234

235 **DISCUSSION**

236

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

243

244 There is strong evidence that the last common ancestor of the extant Parulidae did not duet, and
245 that duetting originated multiple times in the family. The ancestral trait reconstruction suggests
246 duetting evolved twice during the early diversification of the family: at or near the common
247 ancestor of *Myioborou* and after the first split of *Myiothlypis*. There have also been several
248 recent gains of duetting, especially in *Setophaga* and *Myiothlypis*. Duetting appears to have been
249 lost in the lineages leading to *Myioborou brunniceps* and *Myiothlypis rorimae*. Both of those
250 species, however, are poorly known to science, so further investigation may reveal that they duet.
251 We conclude that duetting has probably been gained more than it has been lost in the New World
252 warblers. The recent gains (and possible losses) of duetting are evidence that duetting can evolve
253 rapidly, while the finding of strong phylogenetic signal indicates that duetting has been
254 conserved over evolutionary time in some lineages. Similar patterns were found in the New
255 World blackbirds: the common ancestor did not duet, gains of duetting exceeded losses, and
256 duetting evolved both recently and earlier in the clade's evolutionary history (Icteridae; Odom et

257 al. 2015). The occurrence of both ancient and recent evolutionary transitions from non-duetting
258 to duetting make Parulidae and Icteridae model families for research on duet evolution. For
259 example, we might use these groups to test whether duets tend to increase in structural and
260 temporal coordination over evolutionary time.

261

262 We scored 49.4% of the New World warblers in our sample as migrating latitudinally. This is
263 similar to the results of two previous efforts to score migration in Parulidae, which arrived at
264 estimates of 45.4% and 46.7%, respectively (Winger et al. 2012, Najar and Benedict 2015). The
265 difference in estimates is largely attributable to the fact that, unlike the present study, those
266 studies scored partial migrants (as opposed to rounding them). Additionally, in the case of the
267 2015 study, altitudinal migrants were also scored as migratory. New World warblers are more
268 prone to migration than are birds in general, of which ~ 18.5% are estimated to migrate (Rolland
269 Jonathan et al. 2014). Like duetting, migration was heterogeneously distributed throughout the
270 family, and exhibited phylogenetic signal. The last common ancestor of Parulidae probably
271 migrated. This finding is reflected in the high migration rates among the basal taxa and matches
272 the conclusions of two previous studies (Winger et al. 2014, Najar and Benedict 2015). Ten
273 genera are mostly migratory, and three large genera do not migrate at all (including both of the
274 genera with the highest duetting rates). Early losses of migration occurred in the last common
275 ancestor of *Geothlypis*, and the last common ancestor of the clades *Myioborus* through
276 *Setophaga*. There was an early secondary evolution of migration in *Setophaga*. There is also
277 evidence of recent losses (*Setophaga delicata* through *S. adelaidae*, *S. vitellina*, *S. pityophila*, *S.*
278 *pitayumi*, *Geothlypis semperi*, and *Oreothlypis peregrina* through *O. superciliosa*) and gains of
279 migration (*C. rubrifrons* through *C. canadensis*, *G. formosus* through *G. tolmiei*, and *G. agilis*).

280

281 Migration is generally a labile trait in birds (Pulido 2007). Our findings largely support the idea
282 that migration is evolutionarily labile in New World warblers. We also see evidence that
283 migration status is conserved in some lineages, a finding that is supported by the significant
284 result from our test for phylogenetic signal. Our results replicate Winger et al.'s (2012) finding
285 of phylogenetic signal for migration in Parulidae. That study used different scoring and analytic
286 methods, strengthening the value of this replication. In this study we found that Pagel's λ for
287 migration and duetting were similar, but the value for duetting was slightly higher (0.95 versus
288 0.89 for migration), suggesting a stronger phylogenetic signal for duetting than for migration.
289 Some vocal traits change too rapidly to produce phylogenetic signal (Rheindt et al. 2004). Others
290 can be conserved over time, both revealing and reflecting evolutionary history (Price and Lanyon
291 2002). The results of this study suggest that duetting in New World warblers is a vocal trait that
292 evolves slowly enough to produce phylogenetic signal, but is labile enough to have evolved
293 recently in the phylogeny.

294

295 We believe our trait reconstructions for both duetting and migration are valid despite the
296 occurrence of some low ESS's and significant Geweke's diagnostics. The low ESS's occurred on
297 short branches with homogenous local environments. Those conditions generate strong
298 correlations between subsequent generations (poor mixing). We used a large number of
299 generations to increase the ESSs, but that decision also increased the number of significant
300 Geweke's diagnostics. Importantly, the significant Geweke's diagnostics were attributable to
301 high power, rather than large effects (ESM text, Figs. S1 & S2). The similarity in diagnostic
302 metrics between our two reconstructions, coupled with confirmation of the migration results

303 from other studies (Winger et al. 2012, Najar and Benedict 2015), gives us confidence in our
304 duet evolution results.

305

306 Our results support previous findings that latitudinal migration and duetting are negatively
307 correlated in birds (Benedict 2008, Logue and Hall 2014, Tobias et al. 2016). We scored all
308 duetting New World warblers as non-migratory, and a phylogenetically controlled correlation
309 showed a significant relationship between these two traits. Because the ancestral New World
310 warbler was migratory and non-duetting, this pattern necessarily results from gains of duetting in
311 lineages that also lost migration. Estimated trait values at nodes within the phylogeny (Fig. 1)
312 suggest that losses of migration typically occurred first, and then duets evolved in sedentary
313 species. A previous study linking these two traits found that the relationship between them was
314 largely driven by losses of duetting in migratory species (Logue and Hall 2014). Results
315 presented here indicate that both gains and losses of these traits may be integral in larger
316 patterns, and that changes to migration behavior may drive changes in signaling. As in previous
317 studies, we suspect pair bond duration mediates the relationship between migration and duetting,
318 and we encourage further study of the social behavior of the many species of New World
319 warblers for which pair bond duration is unknown. As in previous studies, duetting and
320 sedentariness were associated with tropical and southern hemisphere breeding (Fig. 2, Hall 2004,
321 2009; Logue and Hall 2014).

322

323 Past research suggests that there is little, if any, phylogenetic signal for female song in New
324 World warblers, and no correlation between female song and migration (Najar and Benedict
325 2015). Duetting in Parulidae does not rely on the presence of female song because some New

326 World warblers that duet lack female song (e.g., *S. adalaidae*, which duets with a *pip* call
327 (Staicer 1992) and some with female song do not duet (e.g., *S. ruticilla*). The evolutionary
328 dissociation between female song and duetting contrasts with New World blackbirds, in which
329 female song is a pre-requisite for vocal duetting (Odom et al. 2015). Although female song and
330 duetting are not perfectly correlated in New World warblers, these two traits exhibit similar
331 patterns within the group. An early New World warbler ancestor with female song occurred
332 within the genus *Myiothlypis*, and this genus showed high rates of both female song and duetting
333 (Najar and Benedict 2015). Duets are also prevalent in *Myioborus*, but it was impossible to
334 accurately score female song in most of that group because the songs of these species are poorly
335 described (Najar and Benedict 2015). In both Najar & Benedict (2015) and the present study, the
336 accuracy of analyses is limited by the available data. It is likely that we have incorrectly scored
337 some tropical duetting species as non-duetters because the vocal behavior of many tropical
338 warbler species is poorly known. Our published dataset will permit updated analyses as more is
339 learned about duetting behavior in tropical warblers.

340

341 Patterns of vocal evolution in New World warblers differ from patterns of vocal evolution in the
342 closely related and well-studied New World blackbirds (Odom et al. 2015). In that family,
343 female song is negatively correlated with non-migratory behavior, but after controlling for the
344 presence of female song, the association between sedentariness and duetting is not significant
345 (Odom et al. 2015). Odom et al. (2015) argue that, in blackbirds, female song is a prerequisite for
346 the evolution of duetting, but that different selective pressures may promote the two signal types
347 (Odom et al. 2015). An alternative hypothesis is that similar selective forces underlie female
348 song and duetting but duetting takes longer to evolve. In warblers, duets are not restricted to

349 lineages with female song, so the evolution of duetting may be less constrained than it is in
350 blackbirds. New World warblers are not unique in this regard: many duetting species do not
351 produce learned songs at all (Hall 2004, 2009). Comparisons between the Icteridae and the
352 Parulidae highlight the multiple avenues through which duets may evolve and covary with
353 migratory behavior.

354

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

362

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368

369 **Author Contributions**

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

373

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459

460 **APPENDIX**

461 **Figure captions:**

462 **Table 1.** Table depicting the co-occurrence of duetting and migratory character for 95 New
463 World warblers. Numbers indicate number of species that exhibit the characters orthogonal to
464 them.

465

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

468

469 **Figure 2.** The distribution of breeding latitudes as a function of (a) duetting and (b) migration in
470 a sample of 95 New World warbler species. Positive latitudes are in degrees north, and negative
471 latitudes are in degrees south.

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