1 **The ecological and evolutionary stability of interspecific territoriality**

2 Neil Losin[1], Jonathan P. Drury[1,2], Kathryn S. Peiman[1,3], Chaya Storch[1], Gregory F. Grether[1*]

3

4 [1]Department of Ecology and Evolutionary Biology, 621 Charles E. Young Drive South,

5 University of California, Los Angeles, CA 90095-1606, USA

6 **[2]**Current address: Institut de Biologie de l'ENS, 46 Rue d'Ulm, 75005 Paris, France

7 **[3]**Current address: Department of Biology, Carleton University, Ottawa, Canada K1S 5B6

8 *Correspondence to: ggrether@ucla.edu, telephone (310-794-9769), fax (310-206-3987)

9

20

21

22

23   **Abstract**

24   Interspecific territoriality may play an important role in structuring ecological communities, but

25   the causes of this widespread form of interference competition remain poorly understood. Here

26   we investigate the phenotypic, ecological and phylogenetic correlates of interspecific

27   territoriality in wood-warblers (Parulidae). Interspecifically territorial species have more recent

28   common ancestors and are more similar phenotypically, and are more likely to hybridize, than

29   sympatric, non-interspecifically territorial species. After phylogenetic corrections, however,

30   similarity in plumage and territorial song are the only significant predictors of interspecific

31   territoriality besides syntopy (fine-scale geographic overlap). Our results do not support the

32   longstanding hypothesis that interspecific territoriality occurs only under circumstances in which

33   niche divergence is restricted, which combined with the high incidence of interspecific

34   territoriality in wood-warblers (39% of species), suggests that this interspecific interaction is

35   more stable, ecologically and evolutionarily, than commonly assumed.

36

INTRODUCTION

Territoriality is a widespread behavioral tactic for partitioning space and defending food sources, mates, and other resources (Maher & Lott 2000). Territorial signals, such as scent marks, vocalizations, visual displays and distinctive colors, enable animals to identify potential rivals, communicate about territory boundaries from a distance, and avoid unnecessary and costly fights (Logue *et al.* 2010). When formerly allopatric species with similar territorial signals first come into contact, interspecific territoriality, i.e., defense of space against individuals of other species, can arise as a non-adaptive byproduct of intraspecific territoriality (Orians & Willson 1964; Murray 1981). But territorial aggression is costly and thus selection is expected to favor divergence in territorial signals and refinements in competitor recognition (i.e., divergent agonistic character displacement) until interspecific territoriality is eliminated, unless the benefits of excluding heterospecifics exceed the costs for at least one of the species (Orians & Willson 1964; Grether *et al.* 2009).

Whether the conditions under which interspecific territoriality is evolutionarily stable are common or rare is a longstanding, unresolved issue. Orians & Willson (1964) reasoned that interspecific territoriality ought to persist only between species that compete for resources that cannot be partitioned, because otherwise the species would be expected to diverge in ways that reduce resource overlap (i.e., ecological character displacement), making interspecific territory defense unprofitable. But interspecific territoriality itself is a mechanism of spatial habitat partitioning that may pre-empt ecological character displacement and enable species with similar ecological requirements to coexist (Robinson & Terborgh 1995; Grether *et al.* 2013). Interspecific territoriality may also be adaptive when closely related species interfere with each other reproductively, and are, in effect, competing for mates (Drury *et al.* 2015). If selection can

60   maintain interspecific territoriality in cases of secondary contact between species that (still)

61   recognize each other as competitors, it should also be possible for interspecific territoriality to

62   evolve *de novo*, or be reinforced, through changes in competitor recognition functions or

63   convergence in territorial signals (Cody 1973; Grether *et al.* 2009; Tobias & Seddon 2009; Drury

64   *et al.* 2015; Reif *et al.* 2015).

65   Murray (1981) argued that nearly all putative cases of adaptive interspecific territoriality

66   could be better explained as misdirected intraspecific territoriality between species that rarely

67   encounter each other, that only recently came into contact, or that coexist only in narrow contact

68   zones, and variants of this hypothesis have been invoked to explain interspecific aggression in

69   numerous taxa (Grether *et al.* 2009; Peiman & Robinson 2010; Ord *et al.* 2011). The crux of

70   Murray's (1981) argument is that species that overlap sufficiently in resource use for

71   interspecific territoriality to be adaptive would not be able to coexist. However, models of

72   interspecific territoriality have shown that high levels of niche overlap are not required for

73   interspecific territoriality to be adaptive (Cody 1973; Grether *et al.* 2009).

74   The key ecological question, then, is whether interspecific territoriality mediates stable

75   competitive interactions between species, potentially increasing species richness by allowing

76   species with similar requirements to coexist (Robinson & Terborgh 1995), or instead is merely a

77   temporary byproduct of recent secondary contact (Murray 1981). Here we take an empirical

78   approach to the problem and ask which factors best predict interspecific territoriality in an avian

79   clade with a well-resolved phylogeny.

80   The wood-warblers (Parulidae) represent a recent radiation with extensive post-speciation

81   range overlap (Lovette & Hochachka 2006; Lovette *et al.* 2010). Unlike *Anolis* lizards and other

82   taxa that show rapid niche differentiation (Glor *et al.* 2003), the wood-warblers exhibit

4

83   phylogenetic niche conservatism and sympatric species often occupy very similar ecological

84   niches (Lovette & Hochachka 2006). Despite early reports of fine-scale niche partitioning in

85   wood-warblers (MacArthur 1958), this does not appear to be common; the species composition

86   of local communities varies considerably, and seasonal migration and low natal philopatry may

87   prevent foraging niches from evolving to match local species assemblages (Lovette &

88   Hochachka 2006). The combination of high levels of sympatry and variable levels of niche

89   overlap make the wood-warblers a suitable group for testing alternative models of interspecific

90   territoriality.

91   Based on the hypothesis that interspecific territoriality evolves or persists under

92   ecological circumstances in which niche partitioning is constrained, Orians & Willson (1964)

93   predicted that it should primarily be found in birds that breed in structurally simple habitats, such

94   as marshes or grasslands, or among species with highly specialized feeding niches, such as

95   nectarivory. To test these predictions, and the more general prediction that interspecific

96   territoriality is related to niche overlap, we gathered data from the literature on habitat

97   complexity, body size, bill length, and foraging guild, and we used the North American Breeding

98   Bird Survey (Sauer et al. 2012) to measure the degree to which species are syntopic (i.e., occur

99   in the same habitats and localities; Rivas 1964). The hypothesis that interspecific territoriality

100   evolves in response to resource competition through convergence in territorial signals (Cody

101   1973) and the alternative hypothesis that interspecific territoriality is a non-adaptive byproduct of

102   overlap in territorial signals (Murray 1981) both predict that interspecifically territorial species

103   pairs should overlap more in territorial signals than non-interspecifically territorial species pairs,

104   but only the convergence hypothesis predicts that this should remain so after controlling for

105   phylogenetic relationships. To test these predictions, we measured species differences in male

106   plumage coloration and territorial song. To test the hypothesis that reproductive interference

107   promotes interspecific territoriality (Drury *et al.* 2015), we examined whether interspecific

108   territoriality is associated with hybridization.

109   Under all hypotheses above, interspecifically territorial species are predicted to be more

110   closely related, on average, than sympatric non-interspecifically territorial species, because

111   closely related species have had less time to diverge in traits that affect resource use, competitor

112   recognition, and mate recognition. However, if interspecific territoriality evolves or persists

113   because of resource competition, similarity in traits that affect resource exploitation (e.g., body

114   size, bill length, foraging guild, habitat use) should be a better predictor of interspecific

115   territoriality than phylogenetic distance (Orians & Willson 1964; Cody 1973). By contrast, if

116   interspecific territoriality is a non-adaptive byproduct of overlap in territorial signals (Murray

117   1981) or an adaptive response to reproductive interference (Drury *et al.* 2015), interspecifically

118   territorial species pairs are predicted to be no more similar in such ecological traits than are non-

119   interspecifically territorial species pairs, after controlling for phylogenetic relationships. Thus, by

120   taking phylogenetic relationships into account, we address a longstanding debate about the

121   adaptive significance of interspecific territoriality.

122   To our knowledge, this is the first phylogenetically based analysis of the distribution of

123   interspecific territoriality in any clade. We found that interspecific territoriality is quite common

124   and does not just occur under restricted ecological circumstances. Moreover, this study provides

125   the first phylogenetic evidence that similarity in territorial signals is linked to interspecific

126   territoriality.

127

128   **METHODS**

129

General approach

Even in North American birds, it cannot be assumed that all cases of interspecific territoriality

have been reported. To make the best use of the information available, our approach was to

compare known interspecifically territorial (IT) species pairs to other sympatric species pairs that

can confidently be classified as non-interspecifically territorial (non-IT). Below we explain in

detail how we made these determinations.

136

IT species pairs

We searched for reports of interspecific territorial aggression involving wood-warblers using the

Birds of North America Online (BNA; Poole 2005), Web of Science, BIOSIS and Zoological

Record databases (Thomson Reuters, New York, NY). We considered chases, attacks, aggressive

displays and songs directed at heterospecifics to be interspecific territorial aggression, unless

they occurred exclusively in the immediate vicinity of food or nests. We did not consider nest

defense and dominance interactions in foraging aggregations to be territorial aggression. Some

authors restrict the term interspecific territoriality to cases in which the species defend exclusive,

non-overlapping territories. In this paper, we consider territorial aggression between species to

be interspecific territoriality, whether it results in exclusive space use or not. Our threshold for

classifying a species pair as interspecifically territorial is that multiple occurrences of territorial

aggression were reported in a single study. In many cases, additional supporting evidence is

available from playback experiments, removal experiments, and territory mapping studies (see

Table S1). However, because these additional types of evidence were not available for all species

pairs, we did not use them as criteria for inclusion or exclusion.

152   To evaluate whether it is likely that there are many unreported cases of interspecific

153   territoriality in North American wood-warblers, we carried out a simple research effort analysis

154   by tallying up the total number of published papers on each species. We searched Zoological

155   Record using each species' current and previous scientific names and used logistic regression to

156   assess whether the probability of a species being reported to be interspecifically territorial

157   increases with the number of studies.

158

159   **Non-IT species pairs**

160   Because most cases of interspecific territoriality involving wood-warblers are between two

161   species of wood-warblers (see Table S1 in Supporting Information), including a taxonomically

162   wider range of non-IT species pairs in the analysis would not be informative. We therefore

163   limited all of our analyses to comparisons between sympatric species within this monophyletic

164   group (Lovette *et al.* 2010). To ensure that only truly non-IT species pairs were included, we

165   further restricted the analysis to species pairs that include one of the IT species and which occur

166   in the area where interspecific territoriality was reported. The logic behind this criterion is that

167   other cases of interspecific territoriality involving the same species in the same area would likely

168   have been reported, but it would not be reasonable to assume that all cases of interspecific

169   territoriality among wood-warblers in the same area (or elsewhere) have been reported. Based on

170   these criteria, we identified 286 non-IT species pairs.

171   To create the list of non-IT species pairs, we used the North American Breeding Bird

172   Survey (BBS; Sauer et al. 2012). At each location where interspecific territoriality was reported,

173   we found the 20 closest BBS routes that were run within ±5 years of the conclusion of the study.

174   Within these BBS routes and years, we restricted our search to routes on which both focal

8

175   species were found and used up to three of the routes closest to the study location to generate a

176   list of sympatric wood-warbler species.

177

178   **Other data collected from the literature**

179   We also used the BBS to measure the degree to which each species pair is syntopic

180   (Rivas 1964) in the region where interspecific territoriality was reported. To measure the degree

181   of syntopy, we found all BBS routes within a 250 km radius of the relevant study location(s).

182   One BBS count route comprises 50 stops (a standardized 3-minute point count is performed at

183   each stop). Within each route, we tallied the number of stops occupied by species 1, by species 2,

184   and by both species. To obtain a regional measure of syntopy, we divided the observed number

185   of stops where both species were found by the expected number of stops where both species

186   would be found if their distributions were independent (e.g., if species 1 and 2 are found at

187   proportions p and q, respectively, out of n possible stops, then the expected number of stops with

188   both species is npq). This metric equals 0 if the species were never found together at the same

189   stop, 1 if the species were found together as often as expected by chance, and >1 if the species

190   were found together more often than expected by chance.

191   Data on hybridization in parulids were obtained from McCarthy (2006) and we also

192   searched for reports of hybridization since 2004 (we disregarded hybridization in captivity and

193   anecdotal reports of hybridization in the wild that McCarthy (2006) classified as doubtful). We

194   used the BNA habitat descriptions to assign each species a habitat complexity score on a three-

195   point scale: 1, simple, such as tundra or grassland; 2, intermediate, such as chaparral or forest

196   edge; and 3, complex, such as coniferous and deciduous forest. The main rationale for this

197   habitat classification is that forests offer more opportunities for vertical stratification of niches,

198   which has long been considered to be relevant for birds (MacArthur 1958; Orians & Willson

199   1964). We based foraging guilds on de Graaf et *al*.'s (1985) classification of North American

200   birds on three niche axes: food type, feeding substrate, and method of food collection. We

201   measured foraging guild overlap for a given species pair as the number of axes on which the

202   species were classified in the same way, and we also categorized species pairs according to

203   whether they overlapped on all three axes or not. We obtained mass and bill length (exposed

204   culmen length) data from the BNA (Poole 2005), CRC handbook (Dunning 2008), and primary

205   sources. When possible, we used only measurements of breeding season males from within the

206   polygon delimited by the locations where interspecific territoriality was reported; if multiple

207   sources were available, we calculated sample-size weighted averages.

208   We calculated patristic distance (the total branch length separating two species in a

209   phylogeny) between the species pairs included in our study using the cophenetic.phylo function

210   in ape (Paradis *et al.* 2004) and Lovette et al.'s (2010) ultrametric molecular phylogeny of

211   Parulidae, which is based on mitochondrial and nuclear sequence data.

212

213   **Plumage and song data**

214   To obtain a measure of species differences in plumage, we recruited volunteer observers to

215   compare images of species pairs from field guides in a manner similar to other recent studies

216   (Martin *et al.* 2015). Although human vision is an imperfect proxy for bird vision, human

217   assessments of plumage differences have been shown to be highly correlated with differences

218   calculated from reflectance spectra (Armenta *et al.* 2008; Seddon *et al.* 2010) and are now

219   widely used in studies of avian coloration. We obtained digital scans of color illustrations of

220   males of the species in our study from two field guides (Sibley 2000; Dunn & Alderfer 2006)

221   and compiled the images into 21 sets with ~49 species comparisons per set using QuestionPro

222   (http://www.questionpro.com/). Observers were presented with pairs of images from the same

223   field guide and asked to rate the overall difference in plumage on a 0-4 scale (see Table S2). The

224   presentation order of the image pairs was randomized for each person. At least five different

225   people completed each set (158 observers in total). For each species pair, we calculated the mean

226   difference score across all observers within field guides and then across field guides. Observers

227   were not informed about the objectives of the study.

228   We used two methods to quantify species differences in territorial song, one based on

229   human hearing and the other based on the spectrogram cross-correlation (SPCC) method (Clark

230   *et al.* 1987). Both methods have merits and are widely used in comparative studies of bird song.

231   The SPCC method is not limited or biased by human perception but may fail to reveal song

232   pattern similarities that humans can detect (Bioacoustics Research Program 2011). We obtained

233   two song exemplars for each species recorded within the polygon delimited by the locations

234   where interspecific territoriality was reported (or as close to the polygon as possible) from xeno-

235   canto.org. We removed background noise (noise reduction = 22 dB, sensitivity = -7.97 dB,

236   frequency smoothing = 260 Hz, attack/decay time = 0.01 secs), cut out all parts of the recordings

237   except for two bouts of singing, separated by a few seconds of silence, and then normalized the

238   edited song files using the default settings in Audacity (http://web.audacityteam.org/).

239   For the human-based song comparison method, we compiled the songs into 37 sets with

240   ~20 species comparisons per set. Listeners were presented with a pair of songs and asked to rate

241   the overall dissimilarity of the songs on a 0-4 scale (Table S2). The presentation order of the

242   song comparisons was randomized for each person. At least five different people completed each

243   set (278 listeners in total). For each species pair, we calculated the mean dissimilarity score

244   across all listeners and then across song exemplars.

245   To assess the repeatability of the mean plumage and song dissimilarity scores, we

246   calculated Spearman correlations between the means of different groups of observers that rated

247   the same species pairs (a randomly selected subset of species pairs was repeated across sets

248   expressly for this purpose). Repeatability was high for both plumage ($\rho = 0.72$, $N = 21$) and song

249   ($\rho = 0.80$, $N = 37$).

250   The SPCC method involves sliding two spectrograms relative to each other and using the

251   maximum cross-correlation value as a measure of song similarity (Clark *et al.* 1987). We used

252   the default settings for SPCC (biased normalized spectrogram correlation, no filter) in RavenPro

253   v. 1.4 (Bioacoustics Research Program 2011). The mean SPCC for a given species pair across

254   song exemplars was used in data analyses.

255   The SPCC song similarity and human-based song dissimilarity measures were

256   significantly correlated but not so strongly that they can be considered to be redundant measures

257   ($r = -0.40$, $N = 305$ species pairs, $P < 0.0001$).

258

259   **Statistical analyses**

260   The design of this study differs from most other species pair-based comparative studies in

261   that not all pairwise combinations of species are relevant to include in the analysis. Statistical

262   methods for analyzing incomplete species pair matrices are still largely untested; we therefore

263   used two different methods and compared the results. Our first approach was to fit a standard

264   multiple logistic regression (MLR) model and then use evolutionary simulations to compute

265   phylogenetically corrected confidence intervals for the test statistics (for similar approaches, see

266 Garland et al. 1993; Mahler et al. 2013; Drury et al. 2015). Specifically, we constructed a general

267 linear model with interspecific territoriality as a binary outcome variable and the following

268 species-pair predictor variables: body mass difference, bill length difference, plumage

269 dissimilarity, foraging guild overlap (0 or 1), human song dissimilarity, SPCC song similarity,

270 hybridization (0 or 1), and syntopy. We then simulated the evolution of traits representing the

271 predictor variables along the phylogeny (see Appendix S1 and Table S3), calculated the relevant

272 species-pair comparisons, recalculated the MLR model using the simulated data, and repeated

273 these steps 5000 times to generate a null distribution for the z values of the model coefficients. If

274 an observed z value lies outside the confidence limits of the corresponding null distribution, the

275 model coefficient is considered to be statistically significant with a phylogenetic correction

276 (Drury et al. 2015). We had directional predictions for each variable, and thus to obtain 1-tailed

277 tests, we used 90% confidence intervals. We made phylogenetic corrections for species

278 differences in body mass and bill length, foraging guild overlap, and the measures of plumage

279 dissimilarity and song similarity/dissimilarity. Syntopy was included in the model as a covariate.

280 As explained in Appendix S1, we used Brownian motion (BM) models to simulate the evolution

281 of body mass and bill length and both BM and Ornstein-Uhlenbeck (OU) models to simulate the

282 evolution of plumage and song. We report results for the full MLR model, with all predictor

283 variables included, and a reduced MLR model. The reduced model was obtained by backward

284 step-wise elimination; after AIC was minimized, we continued removing terms until any further

285 model simplification increased AIC by >2 (Burnham & Anderson 2002).

286   Our second approach was to fit a phylogenetic linear mixed model (PLMM), which

287 accounts for the effect of shared ancestry on trait divergence by fitting a phylogenetic variance-

288 covariance matrix, constructed from the phylogeny, as a random effect (Hadfield & Nakagawa

289   2010; Tobias et al. 2014a). This is a mathematically different approach than the evolutionary

290   simulations described above and the comparative reliability (i.e., type I and type II error rates) of

291   two approaches has yet to be established. We fitted a logistic PLMM in MCMCglmm (Hadfield

292   2010) to the same dataset as used in the MLR using the "categorical" model, with random effects

293   specifying the phylogeny, the focal species and the species to which the focal species is

294   compared, and an inverse gamma prior distribution. We included species in the 'focal' and

295   'comparison' categories an equal number of times where possible. To account for variation in the

296   time since divergence, we also included patristic distance in the model. Adding interactions

297   between patristic distance and the other predictor variables did not improve the overall fit of the

298   model as measured by DIC. We ran each model for 20E6 iterations, discarding the first 1E6 runs

299   as burn-in and sampling every 1E4 iterations, and assessed model convergence using graphic

300   diagnostics.

301   To visualize the relationships between interspecific territoriality, phylogenetic distance

302   and the key predictor variables, we constructed heat map diagrams based on bivariate logistic

303   regression models (see figure captions for further details).

304

305   **RESULTS**

306   Of the 49 wood-warbler species that breed regularly in North America (American Ornithologists'

307   Union Checklist http://checklist.aou.org/), 19 species have been reported to exhibit interspecific

308   territoriality with one or more species of wood-warbler (excluding *Vermivora bachmanii* which

309   may have been interspecifically territorial with *Setophaga discolor* but is probably extinct; Table

310   S1). Two of the 19 species have also been reported to be interspecifically territorial with

311   *Empidonax minimus* and one has been reported to be interspecifically territorial with

14

312   *Regulus satrapa* (Table S1). However, as explained above (*Non-IT species pairs* section), we did

313   not include non-wood-warbler species (or species pairs) in our statistical analyses. While some

314   cases of interspecific territoriality in wood-warblers may remain unreported, it seems unlikely

315   that there are many unreported cases because the probability of species being reported to be

316   interspecifically territorial does not increase significantly with the total number of published

317   studies of the species (logistic regression estimate $\pm$ se: 0.007 ± 0.005, $P = 0.14$, $n = 49$ species).

318   Most parulids (42 of 49 species) are found in habitats with high structural complexity,

319   and there is no significant association between habitat complexity and interspecific territoriality

320   (Table S4; Fisher's exact test, $P = 0.8$). IT species pairs do not overlap more in their foraging

321   guild classifications than non-IT species pairs (range: 0-3; median: 2; Mann-Whitney test, $n_1 =$

322   19, $n_2 = 286$, $P = 0.13$), nor are IT species pairs more likely to be members of the same foraging

323   guild than are non-IT species pairs (10 of 19 IT species pairs versus 95 of 286 non-IT species

324   pairs; Fisher's exact test, $P = 0.07$).

325   On the average, IT species pairs are more closely related, more syntopic, more similar in

326   all of the measured phenotypic characteristics, and also more likely to hybridize, than are non-IT

327   species pairs (Table 1, Figures 1 and 2). Hybridization in the wild has been reported in 5 of 19 IT

328   species pairs versus 23 of 286 non-IT species pairs (Fisher's exact test, $P = 0.02$). Extensive

329   hybridization in the wild has been reported in 3 of 19 IT species pairs versus 0 of 286 non-IT

330   species pairs (Fisher's exact test, $P < 0.0001$).

331   In MLR analyses without a phylogenetic correction, body mass, plumage dissimilarity,

332   song SPCC and syntopy emerged as significant predictors of interspecific territoriality (Table 2).

333   Song SPCC and plumage dissimilarity remained significant predictors of interspecific

334   territoriality after the OU phylogenetic correction but not after the BM phylogenetic correction

15

335 (Tables 2 and S5). The PLMM results closely resemble the MLR-OU results (Tables 2, 3 and

336 S5), although the *P*-value for song SPCC was marginal ($P = 0.05$). Body mass difference was not

337 a significant predictor of interspecific territoriality in any of the phylogenetically corrected

338 models (Tables 2, 3 and S5). Syntopy was a significant predictor of interspecific territoriality in

339 all of the models, with or without a phylogenetic correction (Tables 2, 3 and S5).

340

341 **DISCUSSION**

342 Our literature survey revealed that 39% of wood-warblers that breed in North America are

343 interspecifically territorial with one or more species in some part of their geographic range

344 (Table S1). We found no evidence that interspecific territoriality is restricted to simple habitats

345 or to species with highly specialized foraging niches. Most wood-warblers breed in complex

346 habitats, such as coniferous and deciduous forests, and the incidence of interspecific territoriality

347 is unrelated to habitat complexity (Table S4). All wood-warbler species are insectivorous, and

348 insects are not a highly stratified food source. Thus, our results do not support Orians and

349 Willson's (1964) predictions about the community ecological context of interspecific

350 territoriality; we are not aware of any prior attempts to test these predictions. The high incidence

351 of interspecific territoriality in wood-warblers and the lack of evidence that it only occurs in

352 restricted ecological circumstances suggest that it is more stable, ecologically and evolutionarily,

353 than many authors have assumed.

354　　Interspecifically territorial species tend to be phenotypically more similar to each other

355 than non-interspecifically territorial species (Table 1), but our multivariate phylogenetic analyses

356 showed that most of these phenotypic similarities can be explained by shared ancestry (Tables 2

357 and 3). We did not find specific support for the prediction, based on the niche overlap hypothesis

16

358   (Orians & Willson 1964), that ecological similarity is a better predictor of interspecific

359   territoriality than phylogenetic distance. Nevertheless, it would be premature to conclude that

360   interspecific territoriality is unrelated to resource competition. Wood-warblers exhibit

361   phylogenetic niche conservatism (Lovette & Hochachka 2006), and thus phylogenetic distance

362   may be a better index of overall ecological similarity (i.e., niche overlap) than the ecologically

363   important traits included in our study (body mass, bill length, foraging guild). Perhaps many

364   wood-warbler species are sufficiently ecologically similar for interspecific territoriality to be

365   adaptive, but only species that encounter each other frequently have evolved to recognize each

366   other as competitors. Consistent with this explanation, our syntopy metric was a highly

367   significant predictor of interspecific territoriality (Tables 1-4). Syntopy itself can be viewed as a

368   measure of ecological similarity (Lovette & Hochachka 2006), or more precisely in this case, as

369   a measure of the degree to which species use the same breeding habitats. Thus, our finding that

370   interspecific territoriality in wood-warblers occurs primarily between closely related species that

371   are highly syntopic is consistent with the hypothesis that interspecific territoriality evolved (or

372   persists) because of resource competition. By contrast, under the hypothesis that interspecific

373   territoriality is maladaptive, it is only predicted to persist in narrow zones of contact between

374   species (Murray 1981).

375   Evidence for widespread song convergence (or slowing of song divergence) has recently

376   been found in sympatric lineages of ovenbirds and woodcreepers (Furnariidae), many of which

377   may be interspecifically territorial (Tobias *et al.* 2014a). Similarly, a recent analysis of dawn

378   choruses in the Amazon showed a pattern of temporal convergence in song among congeneric

379   birds (Tobias *et al.* 2014b). To our knowledge, however, our study is the first to directly test for a

380   relationship between similarity in territorial signals and interspecific territoriality. Two of the

381   three phylogenetic statistical models that we employed indicate that interspecifically territorial

382   species are convergent in song and plumage (Tables 2, 3). The disagreement between models

383   was not between the MLR and PLMM approaches but instead between the MLR with a

384   Brownian motion (BM) simulation of trait evolution and the other two models (Tables 2, 3). We

385   are unable to determine whether our plumage and song data are fitted better by a BM or

386   Ornstein-Uhlenbeck (OU) process (Appendix S1), but studies assessing the fit of models of trait

387   evolution for plumage and song have generally found that OU models fit better than BM models

388   (Seddon *et al.* 2013; Shultz & Burns 2013; Tobias *et al.* 2014a; Dale *et al.* 2015). Our results

389   therefore offer at least tentative support for the hypothesis that interspecifically territorial species

390   have converged in territorial signals (Cody 1973; Grether *et al.* 2009; Tobias *et al.* 2014a).

391   Signal convergence could result from adaptation to a common visual or acoustic

392   environment (Boncoraglio & Saino 2007), but all species pairs in our study are sympatric and we

393   controlled for variation in syntopy. Thus, adaptation to the signaling environment is not a

394   plausible explanation for our results. Another possible explanation is that convergence results

395   from genetic introgression (Secondi *et al.* 2011). We did find higher rates of hybridization in IT

396   species pairs than in non-IT species pairs (Table 1), but genetic introgression would also be

397   expected to affect morphological traits, and we found no evidence for convergence in body mass

398   or bill length in IT species pairs (Tables 2 and 3).

399   Hybridization and other forms of reproductive interference can result in mate competition

400   between species (Reitz & Trumble 2002). When males of different species compete for mates,

401   interspecific territoriality can be adaptive even in the absence of resource overlap (Drury *et al.*

402   2015). Although hybridization was not a significant predictor of interspecific territoriality in our

403   multivariate models (Tables 2, 3), it may still be a contributing factor. Wood-warbler species

404   with more similar territorial songs are more likely to hybridize (Willis *et al.* 2014). Three of the

405   four wood-warbler species pairs that hybridize extensively in the wild (Willis *et al.* 2014) are

406   interspecifically territorial, and two of those three IT species pairs are the most similar in song

407   out of all 305 species pairs in our dataset (upper left points in Figure 2). Thus, territorial song,

408   plumage, hybridization, interspecific territoriality and phylogenetic relatedness are closely

409   entwined in wood-warblers – perhaps too much so to sort out causal relationships between these

410   variables statistically.

411   Interspecific territoriality, and indeed interference competition in general, is a complex

412   and neglected subject (Grether *et al.* 2013). Our results suggest that interspecific territoriality is

413   an important selective force acting over evolutionary timescales, rather than simply a transient or

414   accidental byproduct of intraspecific territoriality. With a larger dataset, encompassing greater

415   phylogenetic and ecological diversity, it may be possible to evaluate the relative influence of

416   resource overlap and reproductive interference on the evolution of interspecific territoriality.

417

424

425

426 **References**

427

428 1.Armenta, J.K., Dunn, P.O. & Whittingham, L.A. (2008). Quantifying avian sexual
429 dichromatism: a comparison of methods. *J. Exp. Biol.*, 211, 2423–2430.

430

431 2.Bioacoustics Research Program. (2011). Raven Pro: Interactive sound analysis software.

432

433 3.Boncoraglio, G. & Saino, N. (2007). Habitat structure and the evolution of bird song: A meta-
434 analysis of the evidence for the acoustic adaptation hypothesis. *Funct. Ecol.*, 21, 134–142.

435

436 4.Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A*
437 *Practical Information-Theoretic Approach*. 2nd edn. Springer-Verlag, New York.

438

439 5.Clark, C., Marler, P. & Beeman, K. (1987). Quantitative analysis of animal vocal phonology:
440 an application to swamp sparrow song. *Ethology*, 76, 101–115.

441

442 6.Cody, M.L. (1973). Character convergence. *Annu. Rev. Ecol. Syst.*, 4, 189–211.

443

444 7.Dale, J., Dey, C., Delhey, K., Kempenaers, B. & Valcu, M. (2015). The effects of life-history
445 and social selection on male and female plumage coloration. *Nature*, doi:10.1038/nature15509

446

447 8.Drury, J.P., Okamoto, K.W., Anderson, C.N. & Grether, G.F. (2015). Reproductive
448 interference explains persistence of aggression between species. *Proc. R. Soc. B*, 282, 20142256.

449

450 9.Dunn, J.L. & Alderfer, J. (Eds.). (2006). *National Geographic Guide to the Birds of North*
451 *America*. 5th edn. National Geographic, Washington, D.C.

452

453 10.Dunning, J. B., Jr. (Ed.). (2008). *CRC Handbook of Avian Body Masses*. 2nd edn. CRC Press,
454 Boca Raton, Florida.

455

456 11.Garland, T., Dickerman, A., Janis, C. & Jones, J. (1993). Phylogenetic analysis of covariance
457 by computer simulation. *Syst. Biol.*, 42, 265–292.

458

459   12.Glor, R.E., Kolbe, J.J., Powell, R., Larson, A. & Losos, J.B. (2003). Phylogenetic analysis of
460   ecological and morphological diversification in Hispaniolan trunk-ground anoles (*Anolis cybotes*
461   group). *Evolution*, 57, 2383–2397.

463   13.de Graaf, R.M., Tilghman, N.G. & Anderson, S.H. (1985). Foraging guilds of North
464   American birds. *Environ. Manage.*, 9, 493–536.

466   14.Grether, G.F., Anderson, C.N., Drury, J.P., Kirschel, A.N.G., Losin, N., Okamoto, K., *et al.*
467   (2013). The evolutionary consequences of interspecific aggression. *Ann. N. Y. Acad. Sci.*, 1289,
468   48–68.

470   15.Grether, G.F., Losin, N., Anderson, C.N. & Okamoto, K. (2009). The role of interspecific
471   interference competition in character displacement and the evolution of competitor recognition.
472   *Biol. Rev.*, 84, 617–635.

474   16.Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models:
475   The MCMCglmm R package. *J. Stat. Softw.*, 33, 1–22.

477   17.Hadfield, J.D. & Nakagawa, S. (2010). General quantitative genetic methods for comparative
478   biology: phylogenies, taxonomies and multi-trait models for continuous and categorical
479   characters. *J. Evol. Biol.*, 23, 494–508.

481   18.Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scand. J. Stat.*, 6,
482   65–70.

484   19.Logue, D.M., Abiola, I.O., Rains, D., Bailey, N.W., Zuk, M. & Cade, W.H. (2010). Does
485   signalling mitigate the cost of agonistic interactions? A test in a cricket that has lost its song.
486   *Proc. R. Soc. B*, 277, 2571–2575.

488   20.Lovette, I.J. & Hochachka, W.M. (2006). Simultaneous effects of phylogenetic niche
489   conservatism and competition on avian community structure. *Ecology*, 87, 14–28.

491   21.Lovette, I.J., Pérez-Emán, J.L., Sullivan, J.P., Banks, R.C., Fiorentino, I., Córdoba-Córdoba,
492   S., *et al.* (2010). A comprehensive multilocus phylogeny for the wood-warblers and a revised
493   classification of the Parulidae (Aves). *Mol. Phylogenet. Evol.*, 57, 753–770.

494

495   22.MacArthur, R.H. (1958). Population ecology of some warblers of northeastern coniferous

496   forests. *Ecology*, 39, 599–619.

497

498   23.Maher, C.R. & Lott, D.F. (2000). A review of ecological determinants of territoriality within

499   vertebrate species. *Am. Midl. Nat.*, 143, 1–29.

500

501   24.Mahler, D.L., Ingram, T., Revell, L.J. & Losos, J.B. (2013). Exceptional convergence on the

502   macroevolutionary landscape in island lizard radiations. *Science*, 341, 292–295.

503

504   25.Martin, P.R., Montgomerie, R. & Lougheed, S.C. (2015). Color patterns of closely related

505   bird species are more divergent at intermediate levels of breeding-range sympatry. *Am. Nat.*, 185,

506   443–451.

507

508   26.McCarthy, E.M. (2006). *Handbook of Avian Hybrids of the World*. Oxford University Press,

509   New York, NY.

510

511   27.Murray, B.G. (1981). The origins of adaptive interspecific territorialism. *Biol. Rev. Camb.*

512   *Philos. Soc.*, 56, 1–22.

513

514   28.Ord, T.J., King, L. & Young, A.R. (2011). Contrasting theory with the empirical data of

515   species recognition. *Evolution*, 65, 2572–2591.

516

517   29.Orians, G.H. & Willson, M.F. (1964). Interspecific territories of birds. *Ecology*, 45, 736–745.

518

519   30.Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution

520   in R language. *Bioinformatics*, 20, 289–290.

521

522   31.Peiman, K.S. & Robinson, B.W. (2010). Ecology and evolution of resource-related

523   heterospecific aggression. *Q. Rev. Biol.*, 85, 133–158.

524

525   32.Poole, A.E. (2005). *The Birds of North America Online: http://bna.birds.cornell.edu/BNA/*.

526   Cornell Lab of Ornithology, Ithaca, New York, USA.

527

528 33.Reif, J., Jiran, M., Reifovác, R., Vokurková, J., Dolatad, P.T., Petrusek, A., *et al.* (2015).
529 Interspecific territoriality in two songbird species: potential role of song convergence in male
530 aggressive interactions. *Anim. Behav.*, 104, 131–136.

531

532 34.Reitz, S.R. & Trumble, J.T. (2002). Competitive displacement among insects and arachnids.
533 *Annu. Rev. Entomol.*, 47, 435–465.

534

535 35.Rivas, L.R. (1964). A Reinterpretation of the concepts "sympatric" and "allopatric" with
536 proposal of the additional terms "syntopic" and "allotopic." *Syst. Zool.*, 13, 42–43.

537

538 36.Robinson, S.K. & Terborgh, J. (1995). Interspecific aggression and habitat selection by
539 Amazonian birds. *J. Anim. Ecol.*, 64, 1–11.

540

541 37.Sauer, J.R., Hines, J.E., Fallon, J.E., Pardieck, K.L., Ziolkowski, D.J.J. & Link, W.A. (2012).
542 *The North American Breeding Bird Survey, Results and Analysis 1966 - 2011. Version*
543 *07.03.2013*. Laurel, MD.

544

545 38.Secondi, J., Bordas, P., Hipsley, C.A. & Bensch, S. (2011). Bilateral song convergence in a
546 passerine hybrid zone: genetics contribute in one species only. *Evol. Biol.*, 38, 441–452.

547

548 39.Seddon, N., Botero, C.A., Tobias, J.A., Dunn, P.O., Macgregor, H.E.A., Rubenstein, D.R., *et*
549 *al.* (2013). Sexual selection accelerates signal evolution during speciation in birds. *Proc. R. Soc.*
550 *B Biol. Sci.*, 280, 20131065.

551

552 40.Seddon, N., Tobias, J.A., Eaton, M., Ödeen, A. & Byers, B.E. (2010). Human vision can
553 provide a valid proxy for avian perception of sexual dichromatism. *Auk*, 127, 283–292.

554

555 41.Shultz, A.J. & Burns, K.J. (2013). Plumage evolution in relation to light environment in a
556 novel clade of Neotropical tanagers. *Mol. Phylogenet. Evol.*, 66, 112–125.

557

558 42.Sibley, D.A. (2000). *The Sibley Guide to Birds*. Knopf, New York.

559

560 43.Tobias, J.A., Cornwallis, C.K., Derryberry, E.P., Claramunt, S., Brumfield, R.T. & Seddon,
561 N. (2014a). Species coexistence and the dynamics of phenotypic evolution in adaptive radiation.
562 *Nature*, 506, 359–363.

563

564 44.Tobias, J.A., Planqué, R., Cram, D.L. & Seddon, N. (2014b). Species interactions and the
565 structure of complex communication networks. *Proc. Natl. Acad. Sci. U. S. A.*, 111, 1020–1025.

566

567 45.Tobias, J.A. & Seddon, N. (2009). Signal design and perception in *Hypocnemis* antbirds:
568 evidence for convergent evolution via social selection. *Evolution*, 63, 3168–3189.

569

570 46.Willis, P.M., Symula, R.E. & Lovette, I.J. (2014). Ecology, song similarity and phylogeny
571 predict natural hybridization in an avian family. *Evol. Ecol.*, 28, 299–322.

572

573
574
575 **SUPPORTING INFORMATION**
576
577 Additional Supporting Information may be downloaded via the online version of this article at

578 Wiley Online Library (www.ecologyletters.com).

579
580 As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such

581 materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset.

582 Technical support issues arising from supporting information (other than missing files) should be addressed to the

583 authors.

584   **Table 1.** Summary of univariate comparisons between interspecifically territorial (IT) species

585   pairs ($N = 19$) and non-interspecifically territorial (non-IT) species pairs ($N = 286$) of sympatric

586   wood-warblers. Each variable was checked for deviations from normality and unequal variances

587   (using F-tests) and transformed, if necessary, to meet *t*-test assumptions using the transformation

588   shown in the table. In the case of body mass difference, no transformation eliminated the

589   difference in variance between groups and thus the *t*-test for unequal variances was used

590   (Satterthwaite's $df = 24.6$). For all other variables, a standard *t*-test was used and $df = 303$. One-

591   tailed *P*-values are shown because the tested hypotheses make directional predictions. With a

592   sequential Bonferroni correction for multiple tests (Holm 1979), across all seven *P*-values in the

593   table, the criterion for statistical significance at $\alpha = 0.05$ is $P < 0.05$.

594

Variable	Transform	IT pairs		Non-IT pairs		*t*	*P*
		Mean	SE	Mean	SE		
Body mass difference	$\sqrt{}$	1.10	0.11	1.50	0.04	3.34	0.001
Bill length difference	$\sqrt{}$	0.78	0.09	1.04	0.03	2.31	0.01
Plumage dissimilarity		3.51	0.18	4.06	0.03	3.78	0.0001
Song dissimilarity		3.57	0.17	3.79	0.04	1.33	0.09
SPCC song similarity	$\sqrt{}$	0.38	0.02	0.29	0.01	-3.62	0.0002
Syntopy	$\log(x+0.01)$	0.32	0.16	-0.11	0.04	-2.55	0.006
Patristic distance		55.9	7.6	98.6	1.8	5.93	<0.0001

Table 2. Analysis of predictors of interspecific territoriality, using multiple logistic regression (MLR) with a phylogenetic correction. Model 1 includes all available predictor variables, besides patristic distance. Model 2 resulted from using stepwise elimination. Continuous predictor variables were transformed as shown in Table 1 and then converted to *z*-scores. Confidence intervals of the *z* statistic based on phylogenetic simulations are shown for Brownian motion (BM) and Ornstein-Uhlenbeck (OU) evolutionary models. Estimates that differ significantly from zero after phylogenetic correction are indicated in bold.

Model	Variable	Estimate	SE	z	Uncorrected P	BM 90% CI of z $\sigma^2=0.016$	OU 90% CI of z $\sigma^2=0.016$, $\alpha=0.079$
1	Body mass difference	-1.39	0.82	-1.70	0.09	-2.56, 0.67	-2.88, 0.29
AIC	Bill length difference	-0.38	0.34	-1.14	0.25	-2.58, 0.72	-2.84, 0.35
114.8	Plumage dissimilarity	-0.83	0.27	-3.04	0.002	-3.21, 0.05	**-2.10, 1.15**
	Foraging guild overlap	0.71	0.56	1.27	0.20	-0.82, 2.48	-0.53, 2.81
	Hybridization	1.06	0.74	1.44	0.15	-0.01, 2.05	-0.84, 1.71
	SPCC song similarity	1.20	0.46	2.60	0.009	-0.21, 2.84	**-1.26, 1.99**
	Human song dissimilarity	0.17	0.29	0.58	0.56	-3.24, 0.01	-2.13, 1.18
	Syntopy	0.95	0.34	2.78	0.005		
2	Body mass difference	-1.68	0.76	-2.22	0.026	-2.73, 0.47	-2.99, 0.19
AIC:	Plumage dissimilarity	-0.94	0.27	-3.45	0.0006	-3.49, 0.38	**-2.11, 1.12**
111.6	SPCC song similarity	1.14	0.42	2.70	0.007	0.31, 3.02	**-1.19 1.98**
	Syntopy	0.95	0.33	2.92	0.003		

Table 3. Analysis of predictors of interspecific territoriality, using logistic phylogenetic linear

mixed model (PLMM).

Variable	posterior mean	95% CI (lower)	95% CI (upper)	effective n	P_{MCMC}
Intercept	-2184.94	-4037.18	-693.14	1900	0.0011
Body mass difference	-256.79	-704	150.74	2249	0.15
Bill length difference	-53.29	-346.77	225.23	2286	0.71
Plumage dissimilarity	-302.37	-677.5	-35.71	1900	0.0095
Foraging guild overlap	366.99	-158.26	948.01	1900	0.12
Hybridization	-156.56	-1079.86	553.38	2065	0.72
Syntopy	462.97	131.94	938.54	1900	<0.0005
SPCC song similarity	319.75	-47.43	751.51	1900	0.051
Human song dissimilarity	130.35	-120.98	458.93	1895	0.31
Patristic distance	-438.37	-880.18	-46.65	1900	0.004

Figure 1. Plumage dissimilarity between sympatric wood-warbler species pairs plotted against phylogenetic (patristic) distance. Light blue circles identify interspecifically territorial species pairs ($N = 19$); black circles identify non-interspecifically territorial species pairs ($N = 286$). The size of the circles is proportional to log(syntopy + 0.5). Species pairs that have been reported to hybridize are marked with an X. The background color shows the predicted probability of interspecific territoriality, based on a MLR model with plumage dissimilarity and patristic distance as predictors (plumage dissimilarity: estimate $\pm$ SE = -0.48 $\pm$ 0.26, z = -1.88, P = 0.060; patristic distance: estimate $\pm$ SE = -1.16 $\pm$ 0.29, z = -3.95, P < 0.0001; residual df = 302). Phylogenetic distances are clustered due to periods of rapid cladogenesis during the diversification of wood-warblers (Lovette & Hochachka 2006).

Figure 2. Song similarity between sympatric wood-warbler species pairs plotted against phylogenetic (patristic) distance. For color and symbol key, see Figure 1. Predicted values were based on a MLR model with song similarity and patristic distance as predictor variables (song similarity: estimate $\pm$ SE = 0.88 $\pm$ 0.39, z = 2.28, P = 0.023; patristic distance: estimate $\pm$ SE = -1.16 $\pm$ 0.29, z = -3.94, P < 0.0001; residual df = 302).