LETTER

The ecological and evolutionary stability of interspecific territoriality

Neil Losin, Jonathan P. Drury,[†]
Kathryn S. Peiman,[‡] Chaya Storch
and Gregory F. Grether*

Department of Ecology and Evolutionary Biology, University of California, 621 Charles E. Young Drive South, Los Angeles, CA 90095-1606, USA

[†]*Present address: Institut de Biologie de l'ENS, 46 Rue d'Ulm, 75005 Paris, France*

[‡]*Present address: Department of Biology, Carleton University, Ottawa, Canada K1S 5B6*

Correspondence: E-mail: ggrether@ucla.edu

Abstract

Interspecific territoriality may play an important role in structuring ecological communities, but the causes of this widespread form of interference competition remain poorly understood. Here, we investigate the phenotypic, ecological and phylogenetic correlates of interspecific territoriality in wood warblers (Parulidae). Interspecifically territorial species have more recent common ancestors and are more similar phenotypically, and are more likely to hybridise, than sympatric, non-interspecifically territorial species. After phylogenetic corrections, however, similarity in plumage and territorial song are the only significant predictors of interspecific territoriality besides syntopy (fine-scale geographic overlap). Our results do not support the long-standing hypothesis that interspecific territoriality occurs only under circumstances in which niche divergence is restricted, which combined with the high incidence of interspecific territoriality in wood warblers (39% of species), suggests that this interspecific interaction is more stable, ecologically and evolutionarily, than commonly assumed.

Keywords

Birds, character displacement, competitor recognition, convergence, interference competition, niche conservatism, Parulidae, phylogenetic, species recognition, syntopy.

INTRODUCTION

Territoriality is a widespread behavioural tactic for partitioning space and defending food sources, mates, and other resources (Maher & Lott 2000). Territorial signals, such as scent marks, vocalisations, visual displays and distinctive colours 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. defence 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 favour 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 long-standing, 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 defence 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 maintain interspecific territoriality in cases of secondary contact between species that (still) recognise each other as competitors, it should also be possible for interspecific territoriality to evolve *de novo*, or be reinforced, through changes in competitor recognition functions or convergence in territorial signals (Cody 1973; Grether *et al.* 2009; Tobias & Seddon 2009; Drury *et al.* 2015; Reif *et al.* 2015).

Murray (1981) argued that nearly all putative cases of adaptive interspecific territoriality could be better explained as misdirected intraspecific territoriality between species that rarely encounter each other, that only recently came into contact, or that coexist only in narrow contact zones, and variants of this hypothesis have been invoked to explain interspecific aggression in numerous taxa (Grether *et al.* 2009; Peiman & Robinson 2010; Ord *et al.* 2011). The crux of Murray's (1981) argument is that species that overlap sufficiently in resource use for interspecific territoriality to be adaptive would not be able to coexist. However, models of interspecific territoriality have shown that high levels of niche overlap are not required for interspecific territoriality to be adaptive (Cody 1973; Grether *et al.* 2009).

The key ecological question, then, is whether interspecific territoriality mediates stable competitive interactions between species, potentially increasing species richness by allowing species with similar requirements to coexist (Robinson & Terborgh 1995), or instead is merely a temporary byproduct of recent secondary contact (Murray 1981). Here, we take an empirical approach to the problem and ask which factors best predict interspecific territoriality in an avian clade with a well-resolved phylogeny.

The wood warblers (Parulidae) represent a recent radiation with extensive post-speciation range overlap (Lovette & Hochachka 2006; Lovette *et al.* 2010). Unlike *Anolis* lizards

and other taxa that show rapid niche differentiation (Glor *et al.* 2003), the wood warblers exhibit phylogenetic niche conservatism and sympatric species often occupy very similar ecological niches (Lovette & Hochachka 2006). Despite early reports of fine-scale niche partitioning in wood warblers (MacArthur 1958), this does not appear to be common; the species composition of local communities varies considerably, and seasonal migration and low natal philopatry may prevent foraging niches from evolving to match local species assemblages (Lovette & Hochachka 2006). The combination of high levels of sympatry and variable levels of niche overlap make the wood warblers a suitable group for testing alternative models of interspecific territoriality.

Based on the hypothesis that interspecific territoriality evolves or persists under ecological circumstances in which niche partitioning is constrained, Orians & Willson (1964) predicted that it should primarily be found in birds that breed in structurally simple habitats, such as marshes or grasslands, or among species with highly specialised feeding niches, such as nectarivory. To test these predictions, and the more general prediction that interspecific territoriality is related to niche overlap, we gathered data from the literature on habitat complexity, body size, bill length, and foraging guild, and we used the North American Breeding Bird Survey (Sauer *et al.* 2012) to measure the degree to which species are syntopic (i.e. occur in the same habitats and localities; Rivas 1964). The hypothesis that interspecific territoriality evolves in response to resource competition through convergence in territorial signals (Cody 1973) and the alternative hypothesis that interspecific territoriality is a non-adaptive byproduct of overlap in territorial signals (Murray 1981) both predict that interspecifically territorial species pairs should overlap more in territorial signals than non-interspecifically territorial species pairs, but only the convergence hypothesis predicts that this should remain so after controlling for phylogenetic relationships. To test these predictions, we measured species differences in male plumage colouration and territorial song. To test the hypothesis that reproductive interference promotes interspecific territoriality (Drury *et al.* 2015), we examined whether interspecific territoriality is associated with hybridisation.

Under all hypotheses above, interspecifically territorial species are predicted to be more closely related, on average, than sympatric non-interspecifically territorial species because closely related species have had less time to diverge in traits that affect resource use, competitor recognition and mate recognition. However, if interspecific territoriality evolves or persists because of resource competition, similarity in traits that affect resource exploitation (e.g. body size, bill length, foraging guild, habitat use) should be a better predictor of interspecific territoriality than phylogenetic distance (Orians & Willson 1964; Cody 1973). By contrast, if interspecific territoriality is a non-adaptive byproduct of overlap in territorial signals (Murray 1981) or an adaptive response to reproductive interference (Drury *et al.* 2015), interspecifically territorial species pairs are predicted to be no more similar in such ecological traits than are non-interspecifically territorial species pairs, after controlling for phylogenetic relationships. Thus, by taking phylogenetic relationships into account, we address a long-standing debate about the adaptive significance of interspecific territoriality.

To the best of our knowledge, this is the first phylogenetically based analysis of the distribution of interspecific territoriality in any clade. We found that interspecific territoriality is quite common and does not just occur under restricted ecological circumstances. Moreover, this study provides the first phylogenetic evidence that similarity in territorial signals is linked to interspecific territoriality.

METHODS

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.

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 defence 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 article, 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 in Supporting Information). 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.

To evaluate whether it is likely that there are many unreported cases of interspecific territoriality in North American wood warblers, we carried out a simple research effort analysis by tallying up the total number of published papers on each species. We searched Zoological Record using each species' current and previous scientific names and used logistic regression to assess whether the probability of a species being reported to be interspecifically territorial increases with the number of studies.

Non-IT species pairs

Because most cases of interspecific territoriality involving wood warblers are between two species of wood warblers (see Table S1), including a taxonomically wider range of non-IT

species pairs in the analysis would not be informative. We therefore limited all of our analyses to comparisons between sympatric species within this monophyletic group (Lovette *et al.* 2010). To ensure that only truly non-IT species pairs were included, we further restricted the analysis to species pairs that include one of the IT species and which occur in the area where interspecific territoriality was reported. The logic behind this criterion is that other cases of interspecific territoriality involving the same species in the same area would likely have been reported, but it would not be reasonable to assume that all cases of interspecific territoriality among wood warblers in the same area (or elsewhere) have been reported. Based on these criteria, we identified 286 non-IT species pairs.

To create the list of non-IT species pairs, we used the North American Breeding Bird Survey (BBS; Sauer *et al.* 2012). At each location where interspecific territoriality was reported, we found the 20 closest BBS routes that were run within ± 5 years of the conclusion of the study. Within these BBS routes and years, we restricted our search to routes on which both focal species were found and used up to three of the routes closest to the study location to generate a list of sympatric wood warbler species.

Other data collected from the literature

We also used the BBS to measure the degree to which each species pair is syntopic (Rivas 1964) in the region where interspecific territoriality was reported. To measure the degree of syntopy, we found all BBS routes within a 250-km radius of the relevant study location(s). One BBS count route comprises 50 stops (a standardised 3-minute point count is performed at each stop). Within each route, we tallied the number of stops occupied by species 1, by species 2 and by both species. To obtain a regional measure of syntopy, we divided the observed number of stops where both species were found by the expected number of stops where both species would be found if their distributions were independent (e.g. if species 1 and 2 are found at proportions p and q, respectively, out of n possible stops, then the expected number of stops with both species is npq). This metric equals 0 if the species were never found together at the same stop, 1 if the species were found together as often as expected by chance and > 1 if the species were found together more often than expected by chance.

Data on hybridisation in parulids were obtained from McCarthy (2006) and we also searched for reports of hybridisation since 2004 (we disregarded hybridisation in captivity and anecdotal reports of hybridisation in the wild that McCarthy (2006) classified as doubtful). We used the BNA habitat descriptions to assign each species a habitat complexity score on a three-point scale: 1, simple, such as tundra or grassland; 2, intermediate, such as chaparral or forest edge; and 3, complex, such as coniferous and deciduous forest. The main rationale for this habitat classification is that forests offer more opportunities for vertical stratification of niches, which has long been considered to be relevant for birds (MacArthur 1958; Orians & Willson 1964). We based foraging guilds on de Graaf *et al.*'s

(1985) classification of North American birds on three niche axes: food type, feeding substrate and method of food collection. We measured foraging guild overlap for a given species pair as the number of axes on which the species were classified in the same way, and we also categorised species pairs according to whether they overlapped on all three axes or not. We obtained mass and bill length (exposed culmen length) data from the BNA (Poole 2005), CRC handbook (Dunning 2008), and primary sources. When possible, we used only measurements of breeding season males from within the polygon delimited by the locations where interspecific territoriality was reported; if multiple sources were available, we calculated sample size-weighted averages.

We calculated patristic distance (the total branch length separating two species in a phylogeny) between the species pairs included in our study using the cophenetic.phylo function in ape (Paradis *et al.* 2004) and Lovette *et al.*'s (2010) ultrametric molecular phylogeny of Parulidae, which is based on mitochondrial and nuclear sequence data.

Plumage and song data

To obtain a measure of species differences in plumage, we recruited volunteer observers to compare images of species pairs from field guides in a manner similar to other recent studies (Martin *et al.* 2015). Although human vision is an imperfect proxy for bird vision, human assessments of plumage differences have been shown to be highly correlated with differences calculated from reflectance spectra (Armenta *et al.* 2008; Seddon *et al.* 2010) and are now widely used in studies of avian colouration. We obtained digital scans of colour illustrations of males of the species in our study from two field guides (Sibley 2000; Dunn & Alderfer 2006) and compiled the images into 21 sets with ~ 49 species comparisons per set using QuestionPro (http://www.questionpro.com/). Observers were presented with pairs of images from the same field guide and asked to rate the overall difference in plumage on a 0–4 scale (see Table S2). The presentation order of the image pairs was randomised for each person. At least five different people completed each set (158 observers in total). For each species pair, we calculated the mean difference score across all observers within field guides and then across field guides. Observers were not informed about the objectives of the study.

We used two methods to quantify species differences in territorial song, one based on human hearing and the other based on the spectrogram cross-correlation (SPCC) method (Clark *et al.* 1987). Both methods have merits and are widely used in comparative studies of bird song. The SPCC method is not limited or biased by human perception, but may fail to reveal song pattern similarities that humans can detect (Bioacoustics Research Program 2011). We obtained two song exemplars for each species recorded within the polygon delimited by the locations where interspecific territoriality was reported (or as close to the polygon as possible) from xeno-canto.org. We removed background noise (noise reduction = 22 dB, sensitivity = − 7.97 dB, frequency smoothing = 260 Hz, attack/decay time = 0.01 s), cut out all parts of the recordings except for two bouts of singing, sepa-

rated by a few seconds of silence, and then normalised the edited song files using the default settings in Audacity (http://web.audacityteam.org/).

For the human-based song comparison method, we compiled the songs into 37 sets with ~ 20 species comparisons per set. Listeners were presented with a pair of songs and asked to rate the overall dissimilarity of the songs on a 0–4 scale (Table S2). The presentation order of the song comparisons was randomised for each person. At least five different people completed each set (278 listeners in total). For each species pair, we calculated the mean dissimilarity score across all listeners and then across song exemplars.

To assess the repeatability of the mean plumage and song dissimilarity scores, we calculated Spearman correlations between the means of different groups of observers that rated the same species pairs (a randomly selected subset of species pairs was repeated across sets expressly for this purpose). Repeatability was high for both plumage ($\rho = 0.72$, $N = 21$) and song ($\rho = 0.80$, $N = 37$).

The SPCC method involves sliding two spectrograms relative to each other and using the maximum cross-correlation value as a measure of song similarity (Clark *et al.* 1987). We used the default settings for SPCC (biased normalised spectrogram correlation, no filter) in RavenPro v. 1.4 (Bioacoustics Research Program 2011). The mean SPCC for a given species pair across song exemplars was used in data analyses.

The SPCC song similarity and human-based song dissimilarity measures were significantly correlated, but not so strongly that they can be considered to be redundant measures ($r = -0.40$, $N = 305$ species pairs, $P < 0.0001$).

Statistical analyses

The design of this study differs from most other species pair-based comparative studies in that not all pairwise combinations of species are relevant to include in the analysis. Statistical methods for analysing incomplete species pair matrices are still largely untested; we therefore used two different methods and compared the results. Our first approach was to fit a standard multiple logistic regression (MLR) model and then use evolutionary simulations to compute phylogenetically corrected confidence intervals for the test statistics (for similar approaches, see Garland *et al.* 1993; Mahler *et al.* 2013; Drury *et al.* 2015). Specifically, we constructed a general linear model with interspecific territoriality as a binary outcome variable and the following species-pair predictor variables: body mass difference, bill length difference, plumage dissimilarity, foraging guild overlap (0 or 1), human song dissimilarity, SPCC song similarity, hybridisation (0 or 1) and syntopy. We then simulated the evolution of traits representing the predictor variables along the phylogeny (see Appendix S1 and Table S3), calculated the relevant species-pair comparisons, recalculated the MLR model using the simulated data, and repeated these steps 5000 times to generate a null distribution for the z values of the model coefficients. If an observed z value lies outside the confidence limits of the corresponding null distribution, the model coefficient is considered to be statistically significant with a phylogenetic correction (Drury *et al.* 2015). We had directional predictions for each variable,

and thus to obtain one-tailed tests, we used 90% confidence intervals. We made phylogenetic corrections for species differences in body mass and bill length, foraging guild overlap, and the measures of plumage dissimilarity and song similarity/dissimilarity. Syntopy was included in the model as a covariate. As explained in Appendix S1, we used the Brownian motion (BM) models to simulate the evolution of body mass and bill length and both BM and Ornstein–Uhlenbeck (OU) models to simulate the evolution of plumage and song. We report results for the full MLR model, with all predictor variables included, and a reduced MLR model. The reduced model was obtained by backward stepwise elimination; after AIC was minimised, we continued removing terms until any further model simplification increased AIC by > 2 (Burnham & Anderson 2002).

Our second approach was to fit a phylogenetic linear mixed model (PLMM), which accounts for the effect of shared ancestry on trait divergence by fitting a phylogenetic variance–covariance matrix, constructed from the phylogeny, as a random effect (Hadfield & Nakagawa 2010; Tobias *et al.* 2014a). This is a mathematically different approach than the evolutionary simulations described above and the comparative reliability (i.e. type I and type II error rates) of the two approaches has yet to be established. We fitted a logistic PLMM in MCMCglmm (Hadfield 2010) to the same dataset as used in the MLR using the 'categorical' model, with random effects specifying the phylogeny, the focal species and the species to which the focal species is compared, and an inverse gamma prior distribution. We included species in the 'focal' and 'comparison' categories an equal number of times where possible. To account for variation in the time since divergence, we also included patristic distance in the model. Adding interactions between patristic distance and the other predictor variables did not improve the overall fit of the model as measured by DIC. We ran each model for 20E6 iterations, discarding the first 1E6 runs as burn-in and sampling every 1E4 iterations, and assessed model convergence using graphic diagnostics.

To visualise the relationships between interspecific territoriality, phylogenetic distance and the key predictor variables, we constructed heat map diagrams based on bivariate logistic regression models (see figure captions for further details).

RESULTS

Of the 49 wood warbler species that breed regularly in North America (American Ornithologists' Union Checklist http://checklist.aou.org/), 19 species have been reported to exhibit interspecific territoriality with one or more species of wood warbler (excluding *Vermivora bachmanii*, which may have been interspecifically territorial with *Setophaga discolor*, but is probably extinct; Table S1). Two of the 19 species have also been reported to be interspecifically territorial with *Empidonax minimus* and one has been reported to be interspecifically territorial with *Regulus satrapa* (Table S1). However, as explained above (*Non-IT species pairs* section), we did not include non-wood warbler species (or species pairs) in our statistical analyses. While some cases of interspecific territoriality in wood warblers may remain unreported, it seems unlikely that there are many unreported cases because the probability

of species being reported to be interspecifically territorial does not increase significantly with the total number of published studies of the species (logistic regression estimate $\pm$ SE: 0.007 ± 0.005, $P = 0.14$, $n = 49$ species).

Most parulids (42 of 49 species) are found in habitats with high structural complexity, and there is no significant association between habitat complexity and interspecific territoriality (Table S4; Fisher's exact test, $P = 0.8$). IT species pairs do not overlap more in their foraging guild classification than do non-IT species pairs (range: 0–3; median: 2; Mann–Whitney test, $n_1 = 19$, $n_2 = 286$, $P = 0.13$), and IT species pairs are not more likely to be members of the same foraging guild than are non-IT species pairs (10 of 19 IT species pairs vs. 95 of 286 non-IT species pairs; Fisher's exact test, $P = 0.07$).

On the average, IT species pairs are more closely related, more syntopic, more similar in all of the measured phenotypic characteristics, and also more likely to hybridise, than are non-IT species pairs (Table 1, Figs 1 and 2). Hybridisation in the wild has been reported in 5 of 19 IT species pairs vs. 23 of 286 non-IT species pairs (Fisher's exact test, $P = 0.02$). Extensive hybridisation in the wild has been reported in 3 of 19 IT species pairs vs. 0 of 286 non-IT species pairs (Fisher's exact test, $P < 0.0001$).

In MLR analyses without a phylogenetic correction, body mass, plumage dissimilarity, song SPCC and syntopy emerged as significant predictors of interspecific territoriality (Table 2). Song SPCC and plumage dissimilarity remained significant predictors of interspecific territoriality after the OU phylogenetic correction, but not after the BM phylogenetic correction (Tables 2 and S5). The PLMM results closely resemble the MLR-OU results (Tables 2, 3 and S5), although the P-value for song SPCC was marginal ($P = 0.05$). Body mass difference was not a significant predictor of interspecific territoriality in any of the phylogenetically corrected models (Tables 2, 3 and S5). Syntopy was a significant predictor of interspecific territoriality in all of the models, with or without a phylogenetic correction (Tables 2, 3 and S5).

DISCUSSION

Our literature survey revealed that 39% of wood warblers that breed in North America are interspecifically territorial with
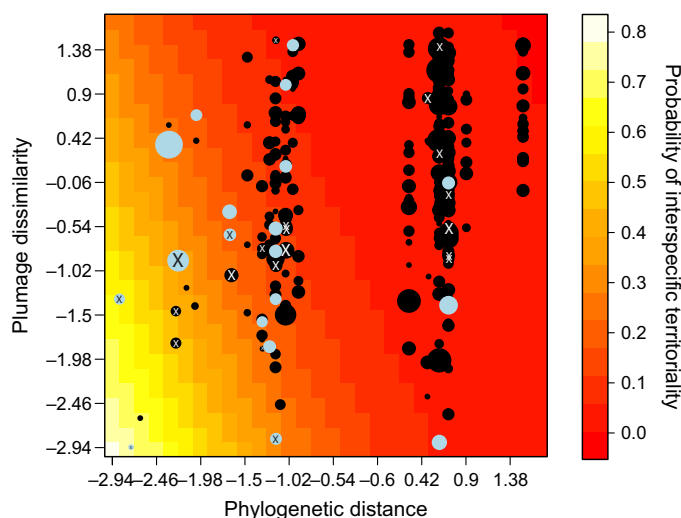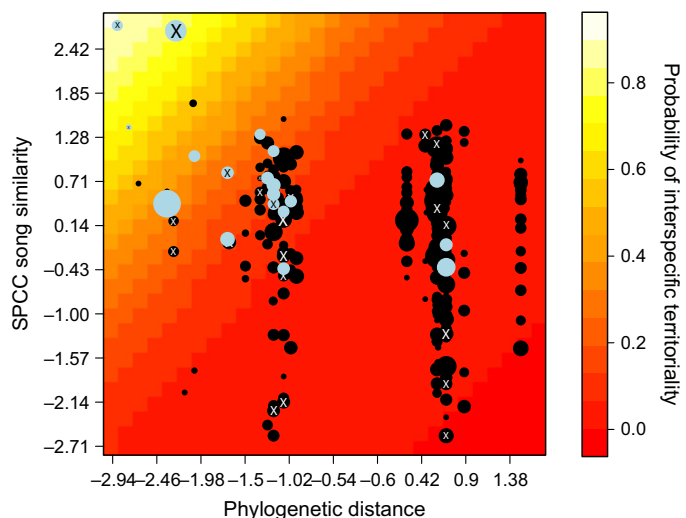

Figure 1 Plumage dissimilarity between sympatric wood warbler species pairs plotted against phylogenetic (patristic) distance. Light blue circles identify interspecifically territorial species pairs ($N = 19$); black circles identify non-interspecifically territorial species pairs ($N = 286$). The size of the circles is proportional to log(syntopy + 0.5). Species pairs that have been reported to hybridise are marked with an X. The background colour 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 ± 0.26, $z = -1.88$, $P = 0.060$; patristic distance: estimate $\pm$ SE = -1.16 ± 0.29, $z = -3.95$, $P < 0.0001$; residual d.f. = 302). Phylogenetic distances are clustered due to periods of rapid cladogenesis during the diversification of wood warblers (Lovette & Hochachka 2006). Variables were converted to z-scores prior to analysis.

one or more species in some part of their geographic range (Table S1). We found no evidence that interspecific territoriality is restricted to simple habitats or to species with highly specialised foraging niches. Most wood warblers breed in complex habitats, such as coniferous and deciduous forests, and the incidence of interspecific territoriality is unrelated to habitat complexity (Table S4). All wood warbler species are insectivorous, and insects are not a highly stratified food source. Thus, our results do not support Orians & Willson's (1964) predictions about the community ecological context of

Table 1 Summary of univariate comparisons between interspecifically territorial (IT) species pairs ($N = 19$) and non-interspecifically territorial (non-IT) species pairs ($N = 286$) of sympatric wood warblers. Each variable was checked for deviations from normality and unequal variances (using F-tests) and transformed, if necessary, to meet t-test assumptions using the transformation shown in the table. In the case of body mass difference, no transformation eliminated the difference in variance between groups and thus the t-test for unequal variances was used (Satterthwaite's d.f. = 24.6). For all other variables, a standard t-test was used and d.f. = 303. One-tailed P-values are shown because the tested hypotheses make directional predictions. With a sequential Bonferroni correction for multiple tests (Holm 1979), across all seven P-values in the table, the criterion for statistical significance at $\alpha = 0.05$ is $P < 0.05$

Variable	Transform	IT pairs		Non-IT pairs		t	P
		Mean	SE	Mean	SE		
Body mass difference	$\sqrt{}$	1.1	0.11	1.5	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

Figure 2 Song similarity between sympatric wood warbler species pairs plotted against phylogenetic (patristic) distance. For colour and symbol key, see Fig. 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 d.f. = 302). Variables were converted to z-scores prior to analysis.

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	−2184.9	−4037.2	−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
Hybridisation	−156.56	−1079.9	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

interspecific territoriality; we are not aware of any prior attempts to test these predictions. The high incidence of interspecific territoriality in wood warblers and the lack of evidence that it only occurs in restricted ecological circumstances suggest that it is more stable, ecologically and evolutionarily, than many authors have assumed.

Interspecifically territorial species tend to be phenotypically more similar to each other than non-interspecifically territorial species (Table 1), but our multivariate phylogenetic analyses showed that most of these phenotypic similarities can be explained by shared ancestry (Tables 2 and 3). We did not find specific support for the prediction, based on the niche overlap hypothesis (Orians & Willson 1964), that ecological similarity is a better predictor of interspecific territoriality than phylogenetic distance. Nevertheless, it would be premature to conclude that interspecific territoriality is unrelated to resource competition. Wood warblers exhibit phylogenetic niche conservatism (Lovette & Hochachka 2006), and thus phylogenetic distance may be a better index of overall ecological similarity (i.e. niche overlap) than the ecologically important traits included in our study (body mass, bill length, foraging guild). Perhaps many wood warbler species are sufficiently ecologically similar for interspecific territoriality to be adaptive, but only species that encounter each other frequently have evolved to recognise each other as competitors. Consistent with this explanation, our syntopy metric was a highly significant predictor of interspecific territoriality (Tables 1–3). Syntopy itself can be viewed as a measure of ecological similarity (Lovette & Hochachka 2006), or more

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 the 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 σ^2 = 0.016	OU 90% CI of z σ^2 = 0.016, α = 0.079
1. AIC: 114.8	Body mass difference	−1.39	0.82	−1.7	0.09	−2.56, 0.67	−2.88, 0.29
	Bill length difference	−0.38	0.34	−1.14	0.25	−2.58, 0.72	−2.84, 0.35
	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	0.2	−0.82, 2.48	−0.53, 2.81
	Hybridisation	1.06	0.74	1.44	0.15	−0.01, 2.05	−0.84, 1.71
	SPCC song similarity	1.2	0.46	2.6	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. AIC: 111.6	Body mass difference	−1.68	0.76	−2.22	0.026	−2.73, 0.47	−2.99, 0.19
	Plumage dissimilarity	−0.94	0.27	−3.45	0.0006	−3.49, 0.38	**−2.11, 1.12**
	SPCC song similarity	1.14	0.42	2.7	0.007	0.31, 3.02	**−1.19 1.98**
	Syntopy	0.95	0.33	2.92	0.003		

precisely in this case, as a measure of the degree to which species use the same breeding habitats. Thus, our finding that interspecific territoriality in wood warblers occurs primarily between closely related species that are highly syntopic is consistent with the hypothesis that interspecific territoriality evolved (or persists) because of resource competition. By contrast, under the hypothesis that interspecific territoriality is maladaptive, it is only predicted to persist in narrow zones of contact between species (Murray 1981).

Evidence for widespread song convergence (or slowing of song divergence) has recently been found in sympatric lineages of ovenbirds and woodcreepers (Furnariidae), many of which may be interspecifically territorial (Tobias *et al.* 2014a). Similarly, a recent analysis of dawn choruses in the Amazon showed a pattern of temporal convergence in song among congeneric birds (Tobias *et al.* 2014b). To the best of our knowledge, however, our study is the first to directly test for a relationship between similarity in territorial signals and interspecific territoriality. Two of the three phylogenetic statistical models that we employed indicate that interspecifically territorial species are convergent in song and plumage (Tables 2 and 3). The disagreement between models was not between the MLR and PLMM approaches, but instead between the MLR with a Brownian motion (BM) simulation of trait evolution and the other two models (Tables 2 and 3). We are unable to determine whether our plumage and song data are fitted better by a BM or Ornstein–Uhlenbeck (OU) process (Appendix S1), but studies assessing the fit of models of trait evolution for plumage and song have generally found that OU models fit better than BM models (Seddon *et al.* 2013; Shultz & Burns 2013; Tobias *et al.* 2014a; Dale *et al.* 2015). Our results therefore offer at least tentative support for the hypothesis that interspecifically territorial species have converged in territorial signals (Cody 1973; Grether *et al.* 2009; Tobias *et al.* 2014a).

Signal convergence could result from adaptation to a common visual or acoustic environment (Boncoraglio & Saino 2007), but all species pairs in our study are sympatric and we controlled for variation in syntopy. Thus, adaptation to the signalling environment is not a plausible explanation for our results. Another possible explanation is that convergence results from genetic introgression (Secondi *et al.* 2011). We did find higher rates of hybridisation in IT species pairs than in non-IT species pairs (Table 1), but genetic introgression would also be expected to affect morphological traits, and we found no evidence for convergence in body mass or bill length in IT species pairs (Tables 2 and 3).

Hybridisation and other forms of reproductive interference can result in mate competition between species (Reitz & Trumble 2002). When males of different species compete for mates, interspecific territoriality can be adaptive even in the absence of resource overlap (Drury *et al.* 2015). Although hybridisation was not a significant predictor of interspecific territoriality in our multivariate models (Tables 2 and 3), it may still be a contributing factor. Wood warbler species with more similar territorial songs are more likely to hybridise (Willis *et al.* 2014). Three of the four wood warbler species pairs that hybridise extensively in the wild (Willis *et al.* 2014) are interspecifically territorial, and two of those three IT species pairs are the most similar in song out of all 305 species

pairs in our dataset (upper left points in Fig. 2). Thus, territorial song, plumage, hybridisation, interspecific territoriality and phylogenetic relatedness are closely entwined in wood warblers – perhaps too much so to sort out causal relationships between these variables statistically.

Interspecific territoriality, and indeed interference competition in general, is a complex and neglected subject (Grether *et al.* 2013). Our results suggest that interspecific territoriality is an important selective force acting over evolutionary timescales, rather than simply a transient or accidental byproduct of intraspecific territoriality. With a larger dataset, encompassing greater phylogenetic and ecological diversity, it may be possible to evaluate the relative influence of resource overlap and reproductive interference on the evolution of interspecific territoriality.

REFERENCES

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

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

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

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

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

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

Dale, J., Dey, C., Delhey, K., Kempenaers, B. & Valcu, M. (2015). The effects of life-history and social selection on male and female plumage coloration. *Nature*, 527, 367–370.

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

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

Dunning, J.B., Jr. (ed.) (2008). *CRC Handbook of Avian Body Masses*, 2nd edn. CRC Press, Boca Raton, FL.

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

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

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

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

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

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

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

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

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

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

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

MacArthur, R.H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology*, 39, 599–619.

Maher, C.R. & Lott, D.F. (2000). A review of ecological determinants of territoriality within vertebrate species. *Am. Midl. Nat.*, 143, 1–29.

Mahler, D.L., Ingram, T., Revell, L.J. & Losos, J.B. (2013). Exceptional convergence on the macroevolutionary landscape in island lizard radiations. *Science*, 341, 292–295.

Martin, P.R., Montgomerie, R. & Lougheed, S.C. (2015). Color patterns of closely related bird species are more divergent at intermediate levels of breeding-range sympatry. *Am. Nat.*, 185, 443–451.

McCarthy, E.M. (2006). *Handbook of Avian Hybrids of the World*. Oxford University Press, New York, NY.

Murray, B.G. (1981). The origins of adaptive interspecific territorialism. *Biol. Rev. Camb. Philos. Soc.*, 56, 1–22.

Ord, T.J., King, L. & Young, A.R. (2011). Contrasting theory with the empirical data of species recognition. *Evolution*, 65, 2572–2591.

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

Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.

Peiman, K.S. & Robinson, B.W. (2010). Ecology and evolution of resource-related heterospecific aggression. *Q. Rev. Biol.*, 85, 133–158.

Poole, A.E. (2005). *The Birds of North America Online*: http://bna.birds.cornell.edu/BNA/. Cornell Lab of Ornithology, Ithaca, NY.

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

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

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

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

Sauer, J.R., Hines, J.E., Fallon, J.E., Pardieck, K.L., Ziolkowski, D.J.J. & Link, W.A. (2012). *The North American Breeding Bird Survey, Results and Analysis 1966–2011*. Version 07.03.2013. USGS Patuxent Wildlife Research Center, Laurel, MD.

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

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

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

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

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

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

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

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

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

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).