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Multiple routes to interspecific territoriality in sister species of North American songbirds

A thesis submitted in partial satisfaction
of the requirements for the degree
Master of Science in Biology

by

Madeline Cowen

2018

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ABSTRACT OF THE THESIS

Multiple routes to interspecific territoriality in sister species of North American songbirds

by

Madeline Cowen

Master of Science in Biology
University of California, Los Angeles, 2018
Professor Gregory F. Grether, Chair

Behavioral interference between species can influence a wide range of ecological and evolutionary processes. For example, aggressive and reproductive interference can lead to competitive exclusion, facilitate invasions, and limit how species ranges shift in response to climate change. While empirical examples of these diverse outcomes abound, a general understanding of when these behaviors arise is necessary to improve predictions of species coexistence and patterns of biodiversity. One type of behavioral interference, interspecific territoriality, has been found to generate important ecological and evolutionary patterns across numerous taxonomic groups, yet still unknown are the ecological circumstances associated with interspecific territoriality and its likelihood to persist through time. Here I present the first comparative study of interspecific territoriality among all sister species of North American songbirds. I tested core hypotheses regarding the origins and maintenance of interspecific territoriality and evaluated the role of interspecific territoriality and hybridization in shaping species distributions and in determining the likelihood of closely related species transitioning from parapatry to sympatry. To do so, I conducted extensive literature searches to identify sister species pairs that exhibit interspecific territoriality and assessed whether ecological traits and morphological divergence predict interspecific territoriality. Among closely related North American songbirds, interspecific

territoriality is pervasive, and interspecifically territorial species pairs have more recently diverged than non-interspecifically territorial pairs. Analysis of the ecological correlates of interspecific territoriality indicates that misdirected intraspecific aggression and resource competition can each lead to interspecific territoriality. These patterns have implications for the ability of species pairs to coexist in sympatry: time since divergence between closely related songbird species does not predict breeding range overlap, nor does interspecific territoriality enable closely related species to transition from parapatric to sympatric distributions. Instead, the combination of interspecific territoriality and hybridization appears to be an unstable state associated with parapatry, whereas species that are interspecifically territorial and do not hybridize are able to achieve fine-scale and coarse-scale breeding range overlap. In sum, these results suggest that interspecific territoriality has multiple ecological origins and that interspecific territoriality and hybridization together can have striking impacts on species ranges. Our work highlights the value of comparative analyses for identifying ecological causes and evolutionary outcomes of this important interspecific behavioral interaction.

The thesis of Madeline Cowen is approved.

Michael Edward Alfaro

Thomas Bates Smith

Gregory F. Grether, Committee Chair

University of California, Los Angeles

2018

To my family for their endless love, support, patience, and more, and to the women scientists and educators in my life, especially my mother, Bertha Vazquez, and Rachel Levin, for nurturing my curiosity, inspiring my sense of justice, advocating for countless young scientists, and leading by example.

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CHAPTER 1

Multiple routes to interspecific territoriality in sister species of North American songbirds

1.1 Introduction

When populations of two closely related species come into contact, whether or not they coexist is influenced by the extent to which they compete for resources, mates, and territories. A vast body of empirical and theoretical work has outlined the ecological and evolutionary outcomes of these forms of competition. For example, if one species is a superior exploitative competitor of a shared limiting resource, it can competitively exclude the other from the area of overlap, but if the two species instead partition the resource spatially or temporally, or diverge in resource use, they may be able to coexist (MacArthur & Levins 1967; Grant 1972; Schoener 1974; Tilman 1980; Schluter 1994). Reproductive interference between species, which can include mate guarding, the formation of mixed-species pairs, and interspecific copulation, can lead to the sexual exclusion of one species, the eroding of species boundaries, or the evolution of pre-mating barriers (Gröning & Hochkirch 2008; Kishi & Nakazawa 2013). Aggressive interference between species, such as fighting or territorial defense, can also result in habitat partitioning or competitive exclusion if one species dominates aggressive interactions (Robinson & Terborgh 1995; Amarasekare 2002; Grether *et al.* 2013). Moreover, species may compete with each other through several forms of competition. For instance, traits that influence the outcome and incidence of aggressive interactions may evolve through divergent or convergent agonistic character displacement, depending on whether the species compete for resources or mates (Grether *et al.* 2009;

Drury *et al.* 2015).

Although competition and behavioral interference between species have important impacts on ecological and evolutionary patterns in biological communities, these different types of species interactions have been unevenly studied. Interspecific territoriality has been especially understudied, despite evidence of its influence on species coexistence and its close association with both ecological competition and reproductive interference (Grether *et al.* 2009, 2013, 2017; Losin *et al.* 2016). Empirical support for the role of interspecific territoriality in leading to diverse ecological and evolutionary outcomes spans numerous taxonomic groups. For example, in congeneric singing mice, the larger species *Scotinomys xerampelinus* excludes the smaller *Scotinomys teguina* from an altitudinal zone (Pasch *et al.* 2013). In response to pervasive reproductive interference, interspecific defense of mating territories persists in numerous sympatric damselfly species in the genus *Hetaerina* (Drury *et al.* 2015). Aggressive asymmetries in territorial encounters could explain character displacement among invading *Anolis* lizards in Florida (Grether *et al.* 2013), and, along with maternal effects, the ongoing replacement of mountain bluebirds by Western bluebirds (Duckworth & Badyaev 2007). Since anthropogenic habitat changes and global climate change can impact species distributions and lead to novel species interactions (Gilman *et al.* 2010; Urban *et al.* 2012), understanding how interspecific territoriality permits or prevents extensive range overlap and coexistence is timely. Despite the pervasiveness of interspecific territoriality and its clear impacts on species ecology and trait evolution, the ecological traits associated with interspecific territoriality, its interactions with other forms of competition, and its stability through time are poorly understood, preventing us from being able to predict competitive outcomes in observed and novel animal communities.

1.1.1 Hypotheses on the origin and maintenance of interspecific territoriality

The foundational hypotheses proposed to explain interspecific territoriality consider it a phenomenon that may persist, fade, or emerge depending on whether the two interacting species identify each other as competitors and are true strong competitors. The *misdirected intraspecific aggression hypothesis* states that interspecific territoriality can develop when two intraspecifically territorial species that share agonistic signals (characters used to identify competitors) but are not strong competitors encounter each other and fail to discriminate between heterospecifics and conspecifics (Murray 1981). Since territorial displays and aggressive interactions are costly, species should diverge in agonistic signals or develop enhanced discriminatory ability, and over time no longer be interspecifically territorial (Murray 1981). Thus, this hypothesis predicts that interspecific territoriality should occur between species with similar agonistic signals, and should only persist when low encounter rates and/or hybridization prevent divergence (Murray 1981).

The "resource competition hypothesis" posits that interspecific territoriality can be *adaptive when there is resource competition* because it enables competitors for a shared limiting resource to partition that resource. In this case, interspecific territoriality that existed upon secondary contact would persist as long as species remained strong ecological competitors (Grether *et al.* 2009). Alternatively, if competing species fail to recognize each other as territorial competitors upon secondary contact, agonistic signals and/or competitor recognition functions of both species may evolve to recognize the other species as a competitor, and thus interspecific territoriality evolves (Cody 1969, 1973; Grether *et al.* 2009). Orians & Willson (1964) proposed a version of the misdirected intraspecific aggression and resource competition hypotheses that states that interspecific territoriality is often maladaptive, but can persist when there is resource competition between species that are unable to diverge in resource use, which could occur when the habitat is too simple to support multiple niches or when adjacent niches are already occupied by other species.

Under the hypothesis that interspecific territoriality can be *adaptive when there is repro-*

ductive interference (henceforth, the reproductive interference hypothesis), indiscriminate male mate recognition can result in a form of local mate competition between species that makes interspecific territory defense adaptive (Payne 1980; Drury *et al.* 2015). Accordingly, this hypothesis predicts a positive association between interspecific territoriality and indices of reproductive interference (e.g., rate of cross-species mating attempts, occurrence or frequency of hybridization), even after controlling for phylogenetic history. In contrast, the misdirected intraspecific aggression hypothesis predicts that the combination of interspecific territoriality and reproductive interference is unstable and that we should only see species in that state when they rarely encounter each other. While it is likely that interspecific territoriality has arisen for different reasons in different systems, very few studies have considered multiple hypotheses in a comparative framework.

A recent study evaluated evidence for each of these hypotheses in North American representatives of the wood-warbler family Parulidae (in the order Passeriformes) (Losin *et al.* 2016). Based on the high prevalence of interspecific territoriality in this family (19 out of the 49 species that breed in North America are interspecifically territorial) and the lack of an association between interspecific territoriality and ecological niche restrictions, the authors inferred that interspecific territoriality is a more stable phenomenon than commonly assumed. They found that interspecific territoriality was positively associated with similarity in territorial signals but also with fine-scale habitat overlap (syntopy), which they interpreted as more consistent with the resource competition hypothesis than with the misdirected intraspecific aggression hypothesis. While they did not find an association between interspecific territoriality and measures of niche overlap, this might be because wood-warblers have generally high niche overlap (Lovette & Hochachka 2006). This highlights the importance of assessing ecological predictors of interspecific territoriality in a dataset with greater ecological and phylogenetic diversity.

Here, we look beyond wood-warblers to evaluate the hypotheses outlined above in sister species of songbirds (order Passeriformes) that breed in North America. Our focus on sister species allows us to accomplish three specific goals. First, we evaluate support

for each of the foundational hypotheses about interspecific territoriality across a larger breadth of ecological and life history strategies than in any previous study. More specifically, we test for predicted associations between ecological, behavioral, and phenotypic traits and interspecific territoriality (Table 1.1). All three hypotheses predict that interspecific territoriality is more likely between species that are more closely related. All three hypotheses also predict that similarity in plumage and song (common agonistic signals in passerines) should be positively associated with interspecific territoriality, but only the resource competition and reproductive interference hypotheses predict that this association will be significant after controlling for shared phylogenetic history. If the resource competition hypothesis is true, species that overlap in foraging guild and are similar in morphological traits associated with foraging, such as bill length, should be more likely to be interspecifically territorial than species that occupy different foraging guilds and differ in feeding morphology. Similarity in morphological traits such as mass may also predict territoriality between species if mass similarity is related to overlap in resource use or in species recognition, but could also be related to dominance in interspecific aggressive encounters (Martin & Ghalambor 2014; Martin *et al.* 2017). If the reproductive interference hypothesis is true, species that hybridize should be more likely to be interspecifically territorial than species that do not hybridize.

The second strength of our sister species approach is that it allows us to determine whether there are multiple origins of interspecific territoriality. This is because sister species represent relatively recent secondary contact, and thus contemporary interactions between these species are more likely to reflect their interactions upon secondary contact. Our likelihood of detecting evidence for the misdirected intraspecific aggression hypothesis is greater in a study of sister species than in a study of more distantly related species because closely related species have had less time to diverge in agonistic signals. However, closely related species are also more likely to overlap substantially in resource use and to hybridize than distantly related species, and therefore may in fact be strong competitors for resources and/or mates. While the hypotheses we evaluate have several shared

predictions, they also make contrasting predictions that could cancel each other out if interspecific territoriality has multiple origins. Thus, to distinguish between these hypotheses, we take into consideration syntopy (Rivas 1964), a fine-scale measure of breeding habitat overlap that also serves as a measure of how frequently the species are likely to encounter each other in sympatry, since the more they interact the stronger the influence of interspecific territoriality as an adaptive or maladaptive force will be. Interactions between predictor variables and syntopy thus help to distinguish between patterns of interspecific territoriality predicted by the misdirected intraspecific aggression hypothesis among species that are low in syntopy and those predicted by one of the adaptive interspecific territoriality hypotheses among species that are high in syntopy (Figure 1.1).

The third strength of our sister species approach is that it allows us to adapt two recent approaches for characterizing the relationship between co-evolution and species transitions into sympatry. Although several empirical and theoretical studies show that competition can influence invasion success or overlap in species distributions (MacArthur 1972; Diamond 1975; Price & Kirkpatrick 2009; Pigot & Tobias 2013), whether competition can yield patterns of coexistence at the level of species ranges instead of local-scale "checkerboard" patterns remains an open debate (Connor & Simberloff 1979; Gotelli *et al.* 2010). While the hypotheses we consider predict that interspecific territoriality can impact local species co-occurrence, they do not make explicit predictions about whether these impacts extend to the coarser scale of breeding range sympatry. Here, we investigate whether behavioral interference influences the likelihood of closely related species pairs achieving extensive breeding range overlap by evaluating models that include interspecific territoriality and hybridization as covariates.

Our work identifies the potential for interspecific territoriality and reproductive interference to determine breeding range overlap between closely related species, and highlights that even for species with shared phylogenetic history and limited ecological variation, the ecological circumstances associated with interspecific territoriality are diverse.

1.2 Methods

1.2.1 Species pairs identification and classification

Our dataset consists of sister species of passerine birds that breed in North America and that overlap in breeding range. We identified sister species by sampling 10^4 trees from the posterior distribution of a North American passerine phylogeny (Hackett *et al.* 2008) and selecting those that appeared as sister species in 90% or more phylogenies. Since allopatric sister species do not have the opportunity to be interspecifically territorial, for each allopatric true sister species pair, we selected the next most closely related species in the phylogeny that is sympatric with one of the allopatric species to form a pair of closely related sympatric species. We calculated patristic distance from this phylogeny using the cophenetic.phylo function in the R package ape (Paradis *et al.* 2004). Several species in the phylogeny have recently been identified as taxonomically unique species, so we could not calculate patristic distance between those recently split species. We determined patristic distance for one such pair, *Troglodytes pacificus* and *T. hiemalis*, from the literature (Toews & Irwin 2008). All other species pairs that lacked patristic distance were omitted from our analyses (2 species pairs). For most analyses, we also excluded species pairs that are allopatric in the breeding season according to 2016 and 2017 species distribution shapefiles from BirdLife International (www.birdlife.org).

We determined whether each species pair is interspecifically territorial with comprehensive literature searches using Web of Science, Birds of North America Online (Rodewald 2015), ProQuest Theses and Dissertations, and Google Scholar. We also contacted Birds of North America Online authors for additional behavioral observations. To ensure that we found all records on a species, we searched for all scientific and common names currently and historically used for that species according to Avibase (https://avibase.bsc-eoc.org/). As in Losin *et al.* (2016), we considered a study to provide enough evidence for interspecific territoriality if it contained at least two accounts of interspecific territorial aggression between unique individuals. Behaviors that qualified as

interspecific territorial aggression include aggressive displays or countersinging, fighting, or chasing of a heterospecific from a territory. We did not consider aggression over a food source or defense of a nest from a predator to be examples of interspecific territoriality. Aggressive response to playback and expansion of territory in response to removal of heterospecifics supported the classification of interspecific territoriality, but were not required since not all species pairs had been studied with these methods. If behavior of both species in a pair had been studied together and no interspecific territoriality was reported, we classified that pair as non-interspecifically territorial. We omitted from our dataset any species pairs whose behavior had not been studied in sympatry (26 pairs), with two exceptions: the *Empidonax* species *E. difficilis* and *E. occidentalis* as well as the *Troglodytes* species *T. pacificus* and *T. hiemalis* have only recently been recognized as separate species (Johnson 1980; Toews & Irwin 2008), and have been reported to have non-overlapping territories in sympatry, so we classified them as interspecifically territorial. After excluding the species pairs that had not been studied in sympatry, we excluded species pairs for which neither species in the pair was intraspecifically territorial (2 species pairs), or for which we lacked data on fine-scale breeding habitat overlap (1 species pair). A full list of species pairs can be found in Table S1. If a study in our literature search indicated whether one species initiated the interspecific territorial defense or successfully displaced the other species, we recorded that species as the "aggressor" or the "dominant" species, respectively.

To assess whether greater study effort increased the likelihood of species being reported as interspecifically territorial, we determined the number of records for each species in the Zoological Records database (Thomson Reuters, New York, NY) and compared differences in the number of records between interspecifically and non-interspecifically territorial species. In addition to categorizing species pairs as interspecifically territorial or not, we also identified hybridization between the species in each pair (disregarding hybridization in captivity) from the McCarthy (2006) compilation of hybridization studies and from additional literature searches for studies published in the years 2000 to present. We

compared differences in the number of Zoological Records between hybridizing and non-hybridizing species.

1.2.2 Breeding range overlap quantification

All data processing and statistical analyses were performed in R version 3.5.0. We used two metrics to represent breeding season range overlap and habitat use of species pairs. First, we calculated the proportion of breeding range sympatry by dividing the area of overlap between BirdLife shapefiles by the breeding range area of the species with the smallest breeding range in each pair. However, BirdLife shapefiles were missing for two species pairs. We therefore also estimated sympatry using the Breeding Bird Survey (BBS; Sauer *et al.* 2017), a dataset of transects run across North America during the breeding season since the 1960s to survey the number of birds observed. Each BBS route is run annually, with 50 stops along each route. We measured sympatry by dividing the number of routes shared by both species by the total number of routes where the species with the fewest routes was observed. To replace the missing Birdlife sympatry values with rescaled BBS sympatry estimates, we used predicted values from used a zero-intercept linear regression of the available Birdlife sympatry estimates on the BBS sympatry estimates (R^2 = 0.69, df = 85, $p < 0.0001$).

Our second measure of overlap measured syntopy, which is the extent to which species overlap in both time and space, such that species with higher syntopy are more likely to occur in the same habitat at the same time within their breeding range. We measured syntopy by identifying BBS routes where both species in a breeding season were found and dividing the number of "shared" stops (where both species were observed) by the number of stops where either species was observed. For two sympatric species pairs without BBS data (*Plectrophenax hyperboreus* and *Plectrophenax nivalis*; *Ammodramus caudacutus* and *Ammodramus nelsoni*), we used rescaled measures of syntopy from eBird records (Sullivan *et al.* 2009). Similarly to syntopy calculated from the BBS, syntopy from eBird was calculated

within years. We excluded redundant records that occurred within 70 meters of each other and any records greater than 24.5 miles from the record of the other species in the species pair, since 24.5 miles is the length of a BBS route. We defined the number of "shared" locations as the number of records within 1/4 mile of a record of the other species, corresponding to the 1/4 mile search radius at BBS stops. We used predicted values from a quadratic zero-intercept linear regression of eBird syntopy on BBS syntopy (R^2 = 0.67, $F_{2,66}$ = 68.99, $p < 0.0001$) to replace the missing BBS syntopy values. To evaluate whether the paired species are more (or less) syntopic than expected by chance, we calculated a second syntopy metric based just on the BBS data: we divided the 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 (as in Losin *et al.* (2016)). This metric equals zero if the species were never found at the same stop, one if the species were found together as often as expected by chance and greater than one if the species were found together more often than expected by chance.

1.2.3 Ecological traits quantification

To determine whether interspecific territoriality could be predicted by species traits, we collected ecomorphological traits for each species and calculated the difference between these traits for each species pair. Because male birds engaged in territorial displays and defense in all species in our dataset, we collected trait measurements for males of each species. As in Losin *et al.* (2016), we collected mass and bill length (exposed culmen length) values from the Birds of North America Online or additional references (e.g., Oberholser 1974, Dunning 2008). To account for possible geographic variation in the traits, we used measurements collected close to the location where interspecific territoriality (or a lack of interspecific territoriality) was documented for each species pair when possible. If the bill length measurement we found for a species was a measurement from the nostril to the tip of the bill instead of the exposed culmen length, we used linear regression to extrapolate the exposed culmen length (R^2 = 0.985, df = 23, $p < 0.0001$). Since mass and bill length are

significantly correlated (r = 0.41, N = 45, P = 0.005), we performed principal component analysis on the two variables (Figure A.1), resulting in one principal component that captured "size" difference and a second component that captured "bill shape" difference. We categorized foraging guild overlap between species in a species pair by calculating the number of foraging guild axes in which species overlapped. With this metric, species are categorized by food type, foraging technique, and foraging substrate according to breeding season foraging habits (Graaf *et al.* 1985), and species pairs are given a number from 0 to 3 based on the number of axes in which they overlap. We categorized the habitat complexity of each species using descriptions from the Birds of North America Online and categories from Losin *et al.* (2016), with 1 representing a simple habitat such as a grassland, marsh, or tundra, 2 representing intermediate habitat, such as chaparral or forest edge, and 3 representing complex habitat such as a deciduous forest.

1.2.4 Quantification of territorial signal similarity

To determine whether interspecific territoriality could be predicted by overlap in common territorial signals, we quantified species similarity in territorial song and plumage coloration. To assess similarity in song, we downloaded high quality sound files from xeno-canto (https://www.xeno-canto.org/) and the Cornell Macaulay library (Table S2) that matched the description in the Birds of North America of the vocalization used by each species for territorial advertisement and interactions. We categorized the size of the territorial repertoire for each species with descriptions in the Birds of North America, and determined the number of song files needed to capture repertoires of different sizes with a sensitivity analysis (Supplementary methods, Figure A.2). For species with relatively small repertoires (fewer than 4 song types), we collected 2 representative song files, and for species with relatively large repertoires (4 or more song types), we collected 4 song files. We performed noise reduction on sound files with background noise with Audacity version 2.1.3 (http://web.audacityteam.org/), using starting values of noise reduction = 12, sensitivity = 6, frequency smoothing = 0. We then normalized all sound files together.

To assess similarity in song between each species in a pair, we used two approaches. First, we calculated a measure of song dissimilarity based on numerous song parameters. We used the R package warbleR (Araya-Salas & Smith-Vidaurre 2016) to extract acoustic parameters (Table S3) and then additionally calculated the number of notes, the length of the longest note, the total note duration, the average note duration, the longest pause between notes, and the average per song. We averaged parameters for the sound files for each species and performed phylogenetic principal component analysis (pPCA; Revell 2009; Figure A.3) on these averaged parameters (since pPCA requires exactly one data point per species in the phylogeny). We then calculated the Euclidean distance across all phylogenetic principal components between each species in a pair as a measure of song dissimilarity.

Second, we used spectral cross-correlation analysis (Clark *et al.* 1987) to quantify similarity in the frequency-time structure of song files. Spectral cross-correlation incrementally time-shifts spectrograms and calculates the cross-correlation between the frequency-time matrices of the spectrograms at each increment. We used the xcor function in warbleR to perform spectral cross-correlation analysis between all song files in a species pair, and averaged the maximum cross-correlation value from those comparisons as a second metric of song similarity. These two song measures are significantly correlated but not strongly enough to be considered redundant measures ($r = -0.37$, $N = 45$, $P = 0.011$).

To quantify similarity in plumage coloration and pattern, we recruited volunteers to score images of songbirds based on how similar they appeared. We obtained digital images of each species from two field guides (Sibley 2000; Dunn & Alderfer 2006) and asked participants to rank the plumage similarity of each species pair on a 0-4 scale using those images. We partitioned the images into seven surveys that we distributed with Survey Gizmo (https://www.surveygizmo.com) through social media and birding groups. Each survey contained approximately 30 pairs of images, with images repeated across surveys and within surveys, and a test for colorblindness. We filtered out incomplete responses and responses from participants who failed the color vision test. After obtaining

at least 10 complete responses per survey, we calculated the mean similarity score for each species pair. Plumage similarity scores given to species pairs were highly correlated between field guides (ρ = 0.79, N = 14), within surveys (ρ = 0.92, N = 14), and across surveys (ρ = 0.85, N = 14).

1.2.5 Assessing ecological predictors of interspecific territoriality

We first used univariate tests to compare differences in each trait in our dataset between interspecifically territorial and non-interspecifically territorial species pairs. Because the potential to detect such differences depends on the level of variability among sister species, we calculated coefficients of variation (for traits measured on a ratio scale) and coefficients of nominal variation (for binary traits; Kvålseth 1995). In addition to comparing traits among sympatric species, we also compared sympatric species in our dataset to allopatric species in terms of phylogenetic distance and similarity in morphological and phenotypic traits.

To assess the misdirected intraspecific aggression hypothesis, the resource competition hypothesis, and the reproductive interference hypothesis, we ran a generalized linear model with interspecific territoriality as a binomial response variable and the ecological, phenotypic, and behavioral traits relevant to each hypothesis (Table 1.1) as the predictor variables. The models we used to evaluate whether a single hypothesis explained the pattern of interspecific territoriality observed included as predictors hybridization (presence or absence), syntopy, ecomorphological principal components, the number of overlapping foraging niche axes (0-3), song similarity (pPCA distance and maximum spectral cross-correlation), and plumage similarity. To evaluate whether the misdirected intraspecific aggression hypothesis and the reproductive interference hypothesis each explain a subset of the cases of interspecific territoriality, we included an interaction term between syntopy and hybridization to distinguish hybridizing species that frequently encountered each other from hybridizing species with infrequent encounters (Figure 1.1A). To test whether

the misdirected intraspecific aggression hypothesis and the resource competition hypothesis each explain a subset of the cases of interspecific territoriality, we ran two models, each with a different interaction term to distinguish between species with a trait related to resource competition that frequently encountered each other or infrequently encountered each other (Figure 1.1B). The first interaction term was between syntopy and the number of overlapping foraging guild axes as a direct measure of resource competition, and the second was between syntopy and the size principal component. For each linear model, we ran a second generalized linear model that included patristic distance as a predictor variable to control for phylogenetic non-independence in sister species.

To further assess the interaction between syntopy and the size principal component, we performed a binomial test of whether size difference corresponds to being the "aggressor" or "dominant" species in the interspecific territorial encounters observed. To test the hypothesis that interspecific territoriality is associated with simple habitats, we performed a Fisher's exact test to evaluate whether interspecific territoriality is associated with either species occurring in a simple habitat.

While the syntopy metric captures variation among species pairs in fine-scale breeding habitat overlap in sympatry, the degree to which species are sympatric across their respective ranges is also likely to influence whether interspecific territoriality persists in the zone of overlap. For example, gene flow from allopatry might swamp local adaptation in sympatry if the species are only sympatric in a small portion of their ranges. Thus, we examined whether controlling for breeding range sympatry impacted the results of each pair of phylogenetically controlled and non-phylogenetically controlled linear models examining ecological predictors of interspecific territoriality.

1.2.6 Modeling transitions to sympatry

To test the hypothesis that interspecific territoriality impacts coarse-scale distributional patterns, we ran three generalized linear models with breeding range overlap as the con-

tinuous response variable (Gaussian family) to determine whether behavioral interference predicts sympatry among closely related species. In the first model, we used only patristic distance as a predictor to test whether breeding range overlap is related to divergence time. In the second model, we used interspecific territoriality and patristic distance as predictors, and in the third model, the interaction between interspecific territoriality and hybridization as well as patristic distance as predictors of breeding range overlap.

Finally, we used two recent approaches for evaluating the role of covariates on transitioning to sympatry. These approaches assume that speciation occurs in allopatry, as is assumed for most vertebrates (Mayr 1942), and that following speciation, species transition from an allopatric phase and then a parapatric phase before coming into broadly overlapping secondary sympatry. First, we implemented a multi-state Markov modeling approach (Pigot & Tobias 2013) to assess whether interspecific territoriality increases the rates at which species pairs transition from parapatry to sympatry. We considered species with continuous breeding range overlap greater than 0% but less than 20% to be parapatric, as in Cooney *et al.* (2017). We also ran models using a cutoff of 25% to evaluate sensitivity to the threshold. We did not consider transitions from allopatry to sympatry since it is not possible for allopatric species pairs to undergo behavioral interference. We compared a Markov model with the rate of transitioning between geographic phases determined by phylogenetic distance to a model that included interspecific territoriality as a covariate. Second, we used a maximum likelihood approach modified from Shi *et al.* (2018) to fit three models in which the probability of occurring in sympatry varies according to a single parameter. In the first model, this parameter is a constant. In the second model, this parameter varies as an exponential decay function such that sympatry varies with phylogenetic distance and/or another behavioral interference covariate. In the third model, this parameter varies logistically, again with phylogenetic distance and/or a behavioral interference covariate. For covariates, we considered interspecific territoriality alone, hybridization alone, or the combination of interspecific territoriality and hybridization. We compared which models best modeled the likelihood of sympatry.

In addition to directly comparing interspecific territoriality and breeding range overlap, we also conducted univariate comparisons of allopatric species to interspecifically territorial and non-interspecifically territorial sympatric species with ANOVA tests, following significant results with post-hoc Tukey tests to make pairwise comparisons.

1.3 Results

1.3.1 Data Summary

Of 76 sympatric species pairs of closely related North American songbirds, we were able to categorize 50 species pairs as interspecifically territorial or not. Excluding species that lacked information on patristic distance or breeding range overlap, our dataset consisted of 45 sympatric species pairs. Of those, approximately 47% (21 pairs) are interspecifically territorial. There were fewer records in the Zoological Records database for the species pairs we could not classify than for species pairs that we were able to classify ($range_1$ = -4.61 – 5.2; $range_2$ = -4.61 – 4.65; $median_1$ = 1.61; $median_2$ = 2.25; Mann-Whitney test on log(x + 0.01) transformed data, n_1 = 26, n_2 = 50, P = 0.013), and there were significantly more records for species pairs classified as interspecifically territorial than for species pairs classified as non-interspecifically territorial ($range_1$ = -4.61 – 1.33; $range_2$ = 0.37 – 1.55; $median_1$ = 0.65; $median_2$ = 0.94; Mann-Whitney test on cube root transformed data, n_1 = 24, n_2 = 20, P = 0.015). Species with more records generally were also more likely to have been reported to hybridize ($range_1$ = 0.24 – 1.05; $range_2$ = -4.61 – 1.55; $median_1$ = 0.57; $median_2$ = 0.97; Mann-Whitney test on cube root transformed data, n_1 = 18, n_2 = 26, P = 0.006).

1.3.2 Assessing ecological predictors of interspecific territoriality

Interspecifically territorial species pairs are more closely related than non-interspecifically territorial pairs (t = 2.35, P = 0.012, N_1 = 24, N_2 = 21) but species pairs in these two categories do not differ significantly in other measured traits and behaviors (Tables 1.2,

1.3). In general, the species pairs in our dataset have similar plumage and song and overlap greatly in foraging guild, as reflected by low coefficients of variation in these variables (Table 1.4). The paired species differ most in morphological traits, syntopy, and sympatry. These species are highly syntopic, with most species occurring in syntopy more than would be expected by chance (range = 0–11.55, median = 1.81). In our dataset of "true" North American passerine sister species (N = 78, i.e., excluding species pairs we included because one species is the most closely related sympatric species to the other), most sister species with breeding range overlap are "sympatric" according to a standard threshold of overlap (37 pairs overlap in at least 20% of the breeding range of the species with the smallest breeding range, out of 66 true sister species with breeding range overlap). Only 12 sister species pairs are allopatric, and the remaining 29 are parapatric.

The two generalized linear models without interaction terms that we used to assess support for the three hypotheses (Table 1.1) yielded no significant predictors of interspecific territoriality and were not significantly better at predicting interspecific territoriality than a null model (Tables S4, S5). In the model with an interaction between hybridization and syntopy but without controlling for patristic distance, the interaction term emerged as significantly and negatively associated with interspecific territoriality (Figure 1.2, Table 1.5). In other words, hybridizing interspecifically territorial species are less syntopic than non-hybridizing interspecifically territorial species, with the reverse relationship between hybridization and syntopy among non-interspecifically territorial species. The main effects of syntopy and hybridization were significant and positively associated with interspecific territoriality (Table 1.5), although the main effect of hybridization was no longer significant after including patristic distance in the model (Table S6). The models with an interaction between foraging guild overlap and syntopy yielded no significant terms, and were also poor models for predicting interspecific territoriality (Tables 1.6, S7).

In the models with an interaction between the size principal component and syntopy, however, the interaction term emerged as significant and negatively associated with interspecific territoriality, and plumage dissimilarity emerged as significant and positively

associated with interspecific territoriality, regardless of phylogenetic correction (Figure 1.3, Tables 1.7, S8). Recent divergence or hybridization could drive this pattern in morphological similarity, such that interspecifically territorial species that are low in syntopy are more closely related than those that are highly syntopic, or that hybridization rates are higher among species that are low in syntopy. Thus, we qualitatively compared the interaction between the size principal component and syntopy to an interaction between patristic distance and syntopy, subsetted by hybridization (Figure 1.3). This comparison showed that the change in size difference across syntopy for non-interspecifically territorial species is similar to the change in relatedness across syntopy. In contrast, the change in patristic distance across syntopy is shallower than the change in size difference across syntopy for interspecifically territorial species. In other words, interspecifically territorial species pairs that are highly syntopic are more different in size even after controlling for the age of the species pairs. Additionally, the significant interaction between the size principal component and syntopy occurs even among hybridizing species pairs, and among extensively hybridizing species pairs (Figure S4), indicating that differences in hybridization rates do not explain the observed pattern.

For the 15 species pairs we were able to categorize (of 21 interspecifically territorial species pairs) according to aggression and dominance in interspecific territorial interactions, aggression and dominance were asymmetric in 10 pairs. For pairs in which there is asymmetry in territorial interactions, the dominant species is not significantly larger (binomial test, N = 10, p = 0.95), nor is the aggressive species consistently larger (binomial test, N = 8, p = 0.94). In contrast to the Orians & Willson (1964) prediction that interspecific territoriality could persist in simple habitats, habitat simplicity did not differ between interspecifically territorial and non-interspecifically territorial species pairs (Fisher's exact test, p = 0.15), with most interspecifically territorial species pairs (0 out of 10 pairs we could score) occurring in complex or intermediate habitats.

Controlling for sympatry in all models did not change which terms were significant or whether the model was significantly better than a null model, but the AICc score increased

for models that included sympatry.

1.3.3 Modeling transitions to sympatry

Patristic distance alone did not significantly predict extent of breeding range overlap or whether species are in sympatry or parapatry (logistic regression estimate $\pm$ SE: 0.15 $\pm$ 0.35, p = 0.68, Tables S9, S10). Including interspecific territoriality in the model did not improve the prediction of breeding range overlap, nor did the combination of interspecific territoriality and patristic distance predict the binary category of parapatry or sympatry (Tables S11, S12). There was a significant interaction between interspecific territoriality and hybridization in a logistic regression model controlling for patristic distance with breeding range overlap as the dependent variable (Figure 1.4, Table 1.8) but not with parapatry versus sympatry as the dependent variable (Table S13).

Regardless of the cutoff used to classify species as parapatric or sympatric, the best model in the multi-state Markov approach was the model that did not include any covariates (Table 1.9). Hybridization appears to reduce the waiting time to sympatry and the combination of hybridization and interspecific territoriality may increase waiting time (Figure 1.5), but neither of these models was better than a model in which only divergence time determined the rate of transitioning to sympatry.

Our maximum likelihood approach suggests that the probability of sympatry is independent of divergence time and interspecific territoriality. Including patristic distance, interspecific territoriality, hybridization, or combinations of these as covariates did not improve the fit of the models, regardless of the threshold for sympatry (Tables S14-S19).

Allopatric species are not significantly different in divergence time from non-interspecifically territorial species (Tukey Honest Significant Difference test, $p > 0.05$), nor are allopatric species significantly different in divergence time from IT species (Tukey Honest Significant Difference test, $p > 0.05$).

1.4 Discussion

Interspecific territoriality occurs in almost half of the sympatric closely related species pairs of North American songbirds, which suggests that territoriality between species should be an important consideration in studies of species interactions. While the hypotheses about interspecific territoriality have been developed through study of diverse empirical systems, ours is the first study to document the pervasiveness of interspecific territoriality across such a phylogenetically diverse group. Our analyses indicate that there is no universal driver of interspecific territoriality, but that interspecific territoriality is likely maintained due to multiple processes acting across this clade. Furthermore, we found that time since divergence does not predict whether species are in sympatry, and that the combination of territoriality and hybridization between closely related species may limit their ability to coexist in extensive sympatry.

1.4.1 Multiple routes to interspecific territoriality

Our first goal was to determine which of three hypotheses (Table 1.1) best explains the ecological circumstances and evolutionary trajectory of interspecific territoriality. To do this, we examined the ecological, phenotypic, and behavioral predictors of interspecific territoriality. Interspecifically territorial species are not less syntopic than non-interspecifically territorial species as the misdirected intraspecific aggression hypothesis predicts, nor are they more syntopic as the resource competition and reproductive interference hypotheses predict. Neither foraging guild overlap, morphological divergence, nor hybridization predict interspecific territoriality, in contrast to the predictions of the hypotheses that state that interspecific territoriality can be adaptive in certain ecological circumstances. Additionally, interspecifically territorial species are not more likely to be found in simple habitats, in contrast to one of the predictions of the hypothesis proposed by Orians & Willson (1964).

Our second goal was to identify whether interspecific territoriality has multiple origins.

We found strong evidence that the misdirected intraspecific aggression and the hypothesis that interspecific territoriality is adaptive for mediating reproductive interference (here referred to as the reproductive interference hypothesis) are unlikely to jointly explain interspecific territoriality at the tips of the Passeriformes phylogeny. In combination, these hypotheses predict that interspecifically territorial species should either be relatively low in syntopy (the misdirected aggression hypothesis) or relatively high in syntopy and hybridizing (the reproductive interference hypothesis). In contrast, we found that interspecifically territorial species pairs that hybridize are lower in syntopy than interspecifically territorial species that do not hybridize, and thus the interaction between syntopy and hybridization is in the opposite direction to what is predicted by the combination of these two hypotheses. While we find that neither the misdirected intraspecific aggression hypothesis nor the hypothesis that interspecific territoriality is adaptive for mediating resource competition (referred to here as the resource competition hypothesis) alone predicts the pattern of interspecific territoriality in our dataset, we cannot rule out the possibility that each hypothesis explains a subset of the species in our dataset. The presence of hybridizing interspecifically territorial species with low syntopy is consistent with the misdirected intraspecific aggression hypothesis, and the presence of non-hybridizing interspecifically territorial species with high syntopy is only predicted by the resource competition hypothesis. These results indicate that the combination of hybridization and interspecific territoriality in closely related species is an unstable state that can only persist when species have low encounter rates, but in the absence of hybridization, interspecific territoriality can mediate resource partitioning among highly syntopic species. In other words, interspecific territoriality may arise when closely related species that rarely encounter each other meet and hybridize, or when closely related species are resource competitors and are likely to encounter each other within the breeding sympatric zone.

In combination, the misdirected intraspecific aggression hypothesis and the resource competition hypothesis predict an interaction between foraging niche and syntopy because the former hypothesis predicts that interspecific territoriality is associated with low syntopy

while the latter predicts that interspecific territoriality is associated with both high syntopy and high foraging niche overlap. We did not find a significant interaction between foraging guild and syntopy, but this might be due to low variation in the foraging guild metric; most species pairs in our dataset overlapped in all three foraging guild axes. While not all of the highly syntopic, non-hybridizing interspecifically territorial species overlap in all three foraging axes, models of interspecific territoriality have shown that moderate levels of niche overlap can be sufficient to maintain interspecific territoriality (Grether *et al.* 2009). Perhaps more sensitive metrics of niche overlap could help clarify why some highly syntopic, non-hybridizing species are interspecifically territorial while others are not.

The interaction between the size principal component and syntopy was negatively associated with interspecific territoriality, even after controlling for patristic distance. The direction of this interaction is opposite to what is predicted by the resource competition hypothesis: interspecifically territorial species that are low in syntopy are more similar in size than interspecifically territorial species that are high in syntopy, while the reverse is true for non-interspecifically territorial species. While patristic distance or hybridization could be plausible explanations for this pattern in morphological similarity, we did not find that relatedness or hybridization accounted for the size variation in species pairs. This finding may correspond to MacArthur's theory that interspecific territoriality should only occur between species pairs when one species can "improve its lot" by engaging in the interaction (MacArthur 1972); in other words, interspecific territoriality could be adaptive for one species in the pair if being aggressive with its close relative permits coexistence.

Although MacArthur (1972) did not describe a pattern associated with dominance in interspecific territorial interactions, being larger in body size can give species an advantage in aggressive interactions between closely related species (Martin & Ghalambor 2014; Martin *et al.* 2017). Indeed, we find that, among highly syntopic species in our dataset, those that are interspecifically territorial have larger differences in size than species that are not interspecifically territorial. Unfortunately, however, we were unable to identify whether one species was consistently the aggressor and/or victor in all incidences of interspecific

territorial aggression based on our literature searches. For the 10 species pairs that we identified as being asymmetrical in aggression and dominance in interspecific territorial interactions, the direction of the size asymmetry did not predict which species initiated or won interspecific territorial interactions. However, several of the categorizations of aggression and dominance that we made were only based on two encounters, whereas other studies categorizing dominance in aggressive encounters used at least six encounters (Martin & Ghalambor 2014). Future empirical studies of interspecific territoriality are greatly needed to provide data on asymmetries in aggressiveness and in outcomes of interspecific territorial aggression. Such asymmetries could be important for predicting evolutionary and ecological outcomes of interspecific interactions, just as asymmetries in competitive ability are recognized as critical for predicting outcomes of interspecific resource competition and reproductive interference (Tilman 1980; Amarasekare 2002; Kishi & Nakazawa 2013). Even if size difference is unrelated to asymmetries in interspecific aggression among closely related North American passerines, however, it could play an important role in the emergence of interspecific territoriality as an adaptive response to resource competition that permits coexistence between closely related species. For example, large differences in size could indicate asymmetric efficiency at exploiting a common limiting resource (Persson 1985), and interspecific territoriality could provide enough of an advantage to the less efficient resource exploiter that the two species can coexist (Grether *et al.* 2013). Alternatively, the increase in size difference that we observe among interspecifically territorial species across increasing levels of syntopy could represent divergence in morphology driven by interspecific territoriality, consistent with the evolutionary trajectory predicted by the misdirected intraspecific aggression hypothesis. However, this interaction between size difference and syntopy remains significant for predicting interspecific territoriality even when extent of breeding range sympatry is included in the model. This pattern thus exists even for species pairs that have relatively low breeding range sympatry and could experience dispersal from allopatry that prevents character displacement.

Our study is similar in approach to a recent study of wood-warblers (Losin *et al.* 2016), but has quite distinct findings. Losin *et al.* (2016) inferred that interspecific territoriality is unlikely to be maladaptive in wood-warblers, but they were unable to determine whether hybridization or resource competition drives interspecific territoriality in wood-warblers. Unlike Losin *et al.* (2016), we find evidence that contradicts the predictions of the reproductive interference hypothesis. Our results instead may be consistent with the misdirected intraspecific aggression hypothesis and the resource competition hypothesis. The most likely biological explanation for this difference is the average divergence time between species in the two datasets. Because wood-warbler species pairs on average have diverged less recently than the sister species in our dataset, interspecific territoriality in wood-warblers that may have at one point been the result of misdirected intraspecific aggression could have disappeared as species evolved mechanisms to discriminate between heterospecifics and conspecifics. Secondary contact between distantly related species is also unlikely to lead to mistaken species identity since phenotypic and song characteristics are more likely to be different with increased divergence time, so interspecific territoriality may never have developed as a maladaptive phenomenon for many of the wood-warbler species pairs. By sampling across the order Passeriformes, our study includes species from non-parulid families, in which interspecific territoriality may emerge under different circumstances due to different life history strategies and ecologies. Since our sister species dataset includes relatively recently diverged species, many of which hybridize and/or are resource competitors, interspecific territoriality may yet evolve or be maintained between species that initially are territorial as a result of misdirected intraspecific aggression. Thus, a signature for adaptive interspecific territoriality may emerge over time.

The nature of sister species datasets may also limit our ability to detect patterns of interspecific territoriality. Our study shows that sister passerine species, which diverged on average 9.4 million years ago, overlap greatly in the ecological traits we measured, including those that were significant predictors of interspecific territoriality for wood-warblers, which may limit the power of sister species analyses. The low variation we

detected in plumage, song, and foraging guild suggests that detecting a significant association between these traits and interspecific territoriality could be challenging. In addition to this, the scale at which we measured traits may limit variation in those traits in our dataset. Some species may rely on only song and not visual cues to identify competitors, or a specific color and not overall similarity in plumage. Bill length may be an important trait under selection for some species in our dataset, but other bill measurements, such as bill depth, or morphological traits, such as tarsus length, may be more relevant when using morphology to assess resource competition in other species. Overlap in all three foraging axes may not indicate complete ecological competition; some species consume several food types, and we may not be able to detect competition over a true limiting resource in our measure of foraging guild. Empirical studies of the species pairs in our dataset therefore could improve the resolution of our dataset by identifying truly limiting resources as well as specific traits used for competitor recognition. Despite these limitations, however, we still detect tremendous variation in interspecific territoriality across species that vary in hybridization, syntopy, and in foraging niche overlap (Figure 1.6).

To increase the power to identify correlates of interspecific territoriality and distinguish between hypotheses about its ecological origins and evolutionary outcomes, our study should be extended to a dataset with greater diversity in divergence times between species pairs. A literature search across the North American representatives of Passeriformes, not just the most closely related species, has found that approximately 52% of North American passerines (103 of 197 species studied) are interspecifically territorial with at least one other species. As with our study and the wood-warbler study, the prevalence of interspecific territoriality across all North American passerines demonstrates that interspecific territoriality is part of many species' ecologies. An analysis of this taxonomic group would achieve the large ecological and phylogenetic variation needed in a comparative study of interspecific territoriality, and could yield information about convergence or divergence in ecological, phenotypic, and behavioral traits by using phylogenetic comparative methods as in Losin *et al.* (2016).

1.4.2 Impact of interspecific territoriality on species distributions

The third goal of our study was to identify important distributional patterns in sister songbirds and determine whether interspecific territoriality impacts the likelihood of closely related species achieving breeding sympatry. Sister species of songbirds have several noteworthy distributional patterns. Although several studies find that co-occurrence in secondary sympatry is associated with greater phylogenetic distance (Weir & Price 2011; Pigot & Tobias 2013), approximately 84% (74/88) of sister species in this dataset are broadly sympatric, with an average breeding range overlap of 43.63% of the range of the species with the smaller range. In contrast to several studies of the rate of secondary sympatry in birds (Weir & Price 2011; Pigot & Tobias 2013), we found that divergence time did not predict whether species pairs were in allopatry or sympatry, nor did it predict the extent of breeding range overlap. While divergence time is shorter for interspecifically territorial than for non-interspecifically territorial species, allopatric species are comparable to both groups in divergence time. This indicates that patristic distance alone is not a sufficient predictor of behavioral interference and likelihood of coexistence.

We find some evidence that interspecific territoriality and hybridization together lead to reduced breeding range overlap. Specifically, the combination of interspecific territoriality and hybridization primarily occurs between species with low overlap in breeding range, suggesting that this combination is an unstable state that does not permit extensive coexistence. While the hypotheses we examined do not all make specific predictions about the impact of interspecific territoriality on breeding range overlap, their predictions about persistence at fine-scale breeding habitat overlap can be extended here. The persistence of interspecific territoriality between species with low sympatry could be consistent with misdirected intraspecific aggression, which predicts that interspecific territoriality may persist only among species with rare interactions. The presence of interspecific territoriality between species with a large overlap in breeding range and relatively high syntopy suggests that interspecific territoriality in some circumstances may permit species coexistence.

The finding that, among non-interspecifically territorial species, hybridization is associated with greater breeding range overlap has two possible explanations. First, hybridization may be more likely to occur between species that have a higher likelihood of encountering each other, and more extensive breeding range overlap could lead to a greater chance of interactions between individuals of the two species. Second, hybridization can be predicted from the number of Zoological Records; the probability of detecting hybridization may similarly increase with sympatry (and syntopy) because if species have more opportunities to interact, the likelihood of detecting the species may also increase.

The finding that interspecifically territorial species pairs have more Zoological Records than those classified as non-interspecifically territorial suggests that additional research on sympatric species pairs may uncover more examples of interspecific territoriality. In our study, species pairs that lacked data were excluded from our analyses. We classified species pairs as non-interspecifically territorial if their behavior had been studied in sympatry and no evidence of interspecific territorial aggression was reported, but it is possible that additional study of these species pairs could yield observations of interspecific territorial aggression.

Despite the association we found between interspecific territoriality, hybridization, and continuous breeding range overlap, our models assessing the likelihood of transitioning to extensive breeding range overlap are not improved by the inclusion of interspecific territoriality and/or hybridization in the model. In the multi-state Markov models, the best model for characterizing the rate at which species transition from parapatry to sympatry included no behavioral interference covariates. The maximum-likelihood approach we used similarly found that a null model best describes the probability of occurring in sympatry, relative to models that include behavioral interference covariates as well as models that included divergence time. According to these models, interference interactions between species do not have an impact on broad-scale species coexistence. Surprisingly, divergence time between species is also a poor predictor of breeding range overlap. That said, if interspecific territoriality is adaptive in some circumstances and maladaptive in

others, its effect on breeding range overlap may also differ between those circumstances. Additionally, the coding of variables in these models may have contributed to the null result. In the generalized linear model, the interaction between interspecific territoriality and hybridization predicted the continuous variable of breeding range overlap, but not the binary variable of parapatry or sympatry. The Markov model and maximum likelihood approach we used both rely on binary classification of species into parapatry or sympatry categories, and thus may have lost some predictive power. Additionally, we added the combination of interspecific territoriality and hybridization into these two modeling approaches as a 1 if species were interspecifically territorial and hybridized, or a 0 for all other situations. Thus, again we lost some predictive power since this groups together non-interspecifically territorial, non-hybridizing species with species pairs that are either interspecifically territorial or hybridize.

1.4.3 Conclusions

Taken together, our findings lend some insight into the early stages of secondary contact following allopatric speciation. Our results point to a possible stage in the speciation process of secondary contact between closely related species that treat each other as competitors and mates, thus remaining in parapatry until they diverge sufficiently in competitor and mate recognition. Other closely related species, however, may be able to achieve breeding range sympatry and extensive fine-scale breeding range overlap despite being interspecifically territorial, suggesting that interspecific territorial aggression could adaptively mediate their coexistence. We found that interspecific territoriality is common among closely related species of passerine birds, but that even at the tips of the songbird phylogeny, the ecological circumstances associated with interspecific territoriality are diverse. This suggests that the evolutionary stability of interspecific territoriality may also be vary across taxa. A combination of additional empirical research and larger comparative studies could further improve our understanding of how interspecific territoriality arises and contributes to the ecologies and coexistence of animal species.

1.5 Figures and Tables

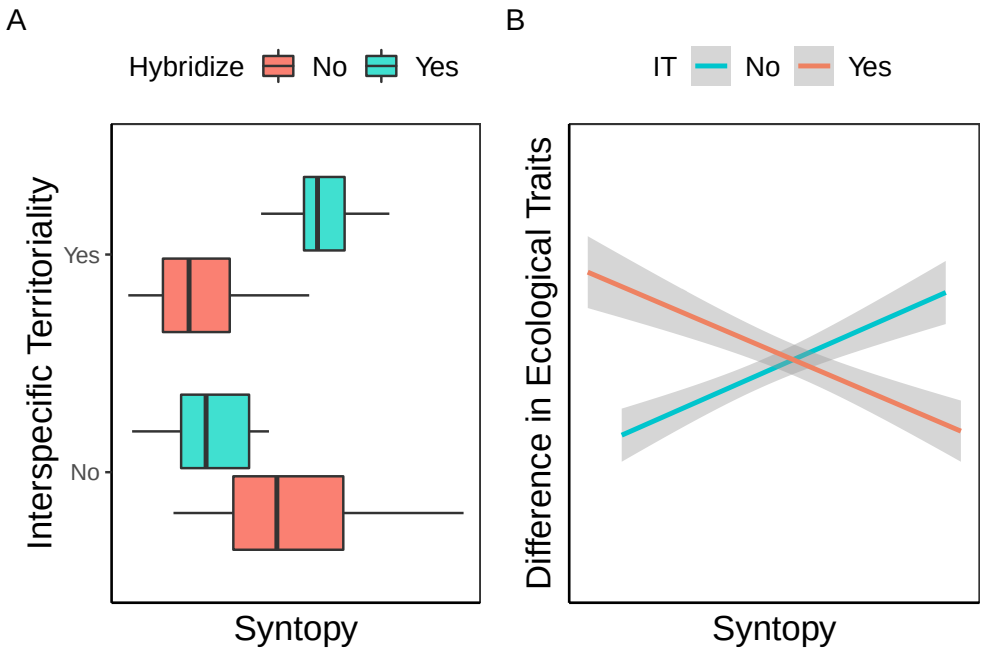

Figure 1.1: Predicted results with simulated data if more than one hypothesis explains the pattern of interspecific territoriality in closely related North American songbirds. In (A), the misdirected intraspecific aggression hypothesis and the reproductive interference hypotheses together posit that interspecific territoriality can be maladaptive for non-hybridizing species but adaptive for mediating reproductive interference when there is hybridization, and thus predict that hybridizing, interspecifically territorial species can coexist in greater syntopy. In (B), the misdirected intraspecific aggression hypothesis and the resource competition hypotheses together posit that interspecific territoriality can be maladaptive among species that are not resource competitors but adaptive for mediating reproductive interference when there is resource competition, as measured by similarity in traits related to resource use and overlap in foraging niche. These thus predict that interspecific territoriality enables strong resource competitors to coexist while being highly syntopic.

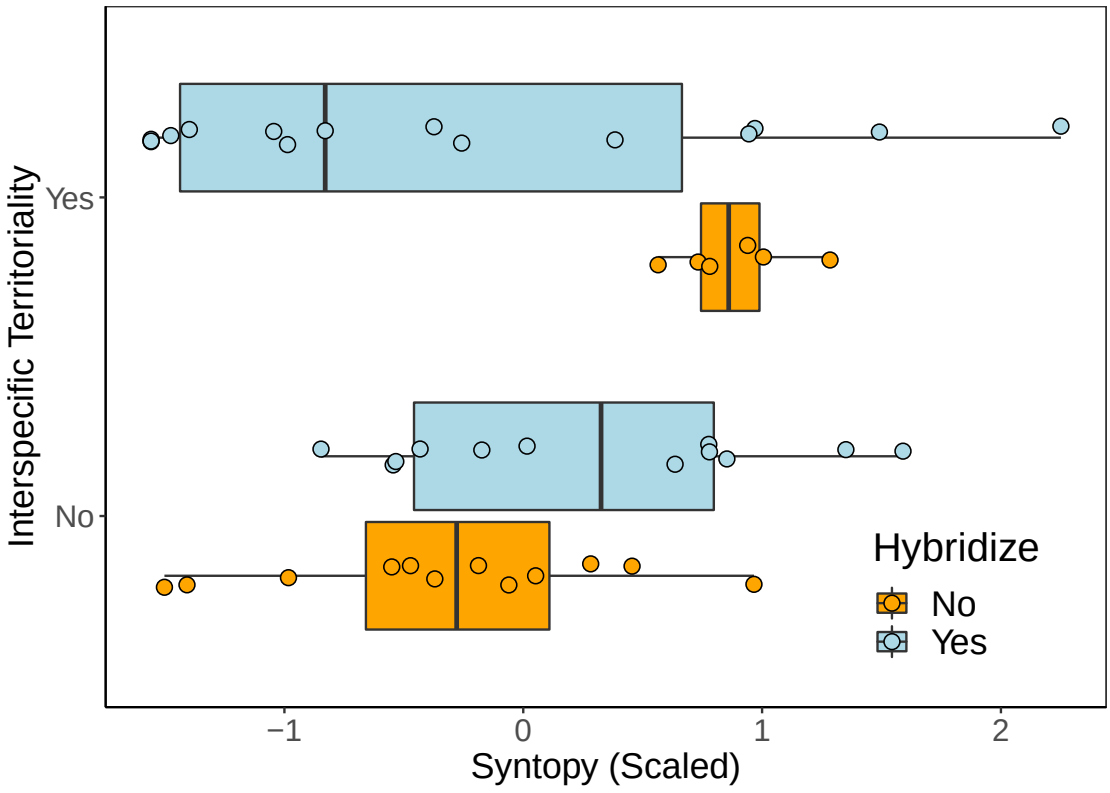

Figure 1.2: Interaction term between syntopy and hybridization. Interspecifically territorial species that hybridize are less syntopic than non-interspecifically territorial species that hybridize. Interspecifically territorial species that do not hybridize are more syntopic than non-interspecifically territorial species that do not hybridize.

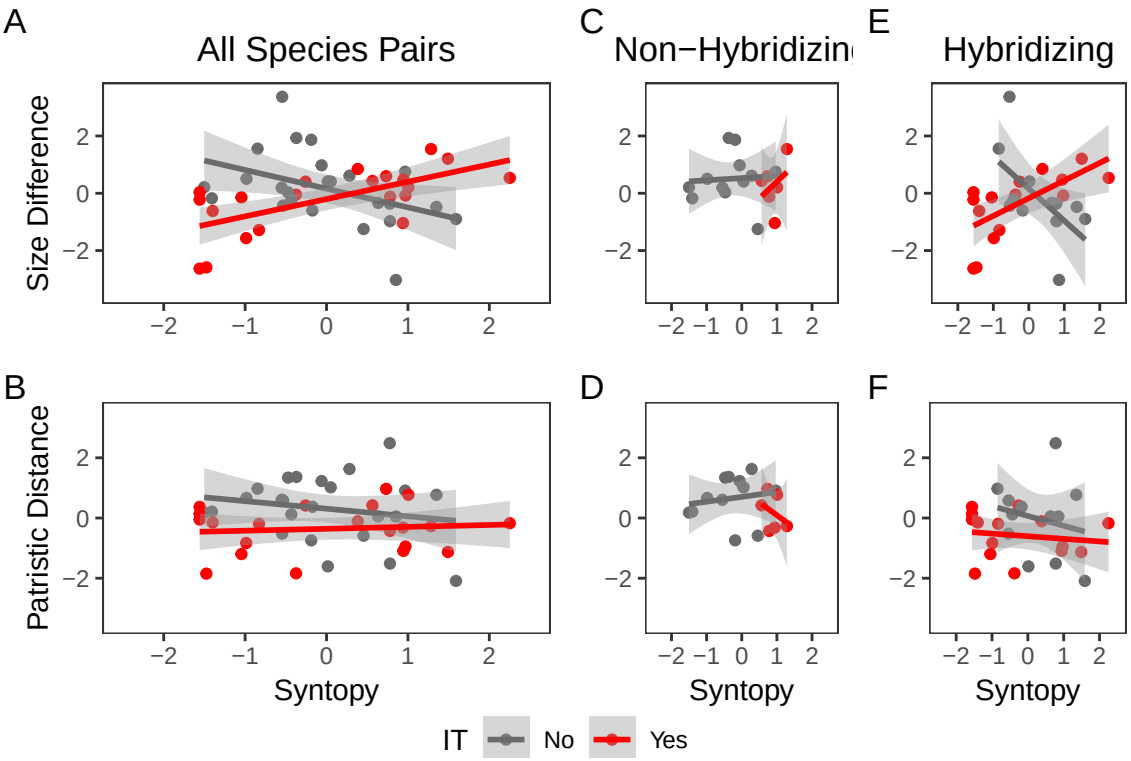

Figure 1.3: Interaction between syntopy and the size principal component (A, C, E) compared to the interaction between syntopy and patristic distance (B, D, F). Interspecifically territorial species are more similar in size when low in syntopy than when highly syntopic. The reverse is true for non-interspecifically territorial species. This pattern is true for a subset that includes only hybridizing species (E). The change in size difference across syntopy for non-interspecifically territorial species is similar to the change in relatedness across syntopy but stronger for interspecifically territorial species.

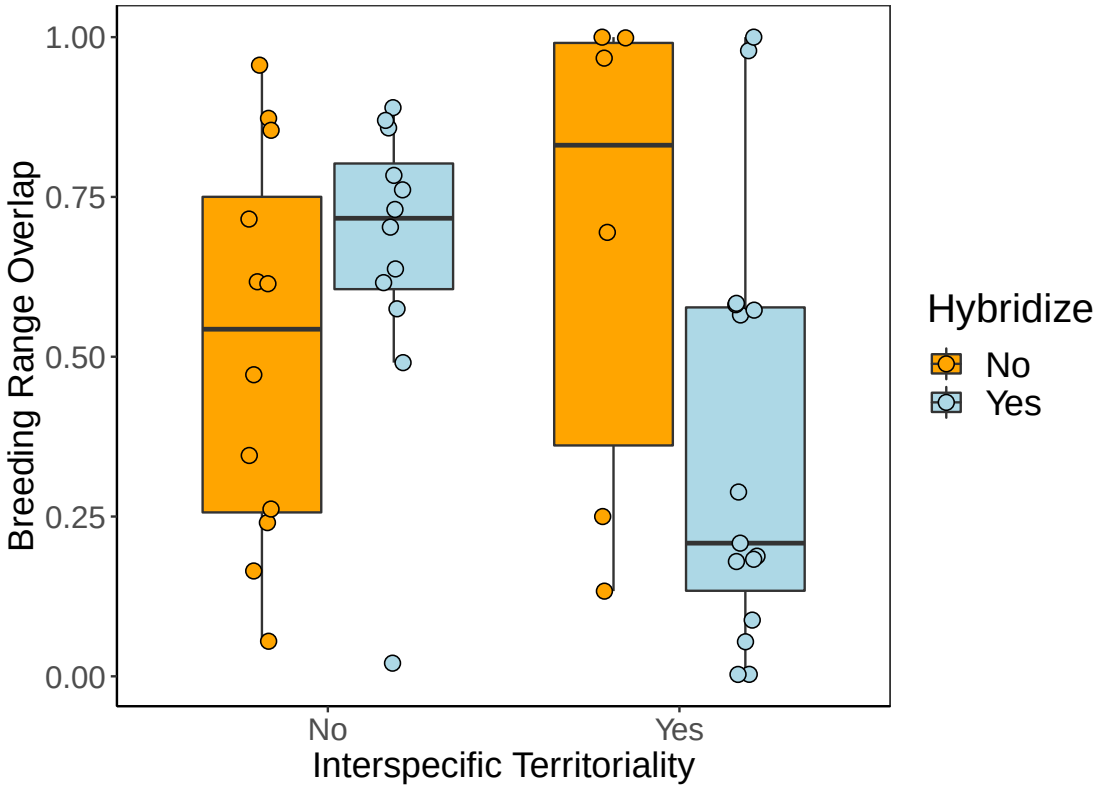

Figure 1.4: Interaction between interspecific territoriality and hybridization predicts breeding range sympatry.

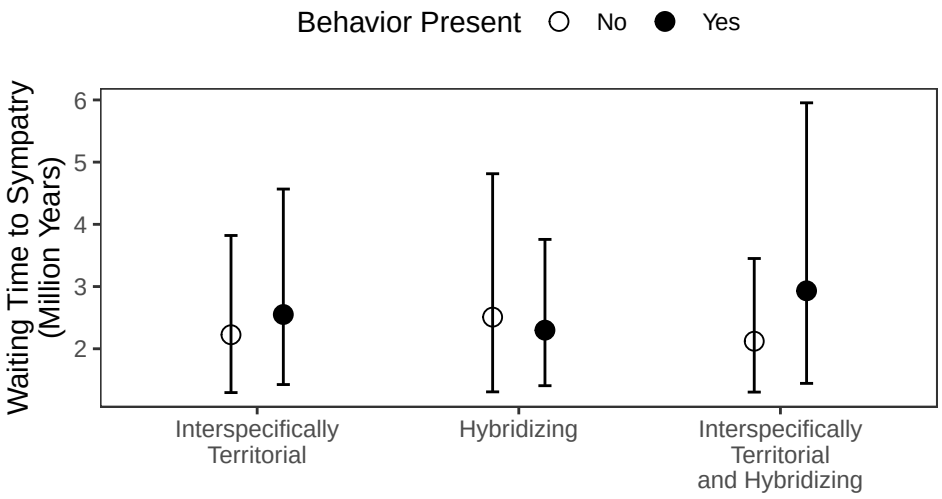

Figure 1.5: Rates of transitioning into sympatry based on multi-state Markov modeling approach.

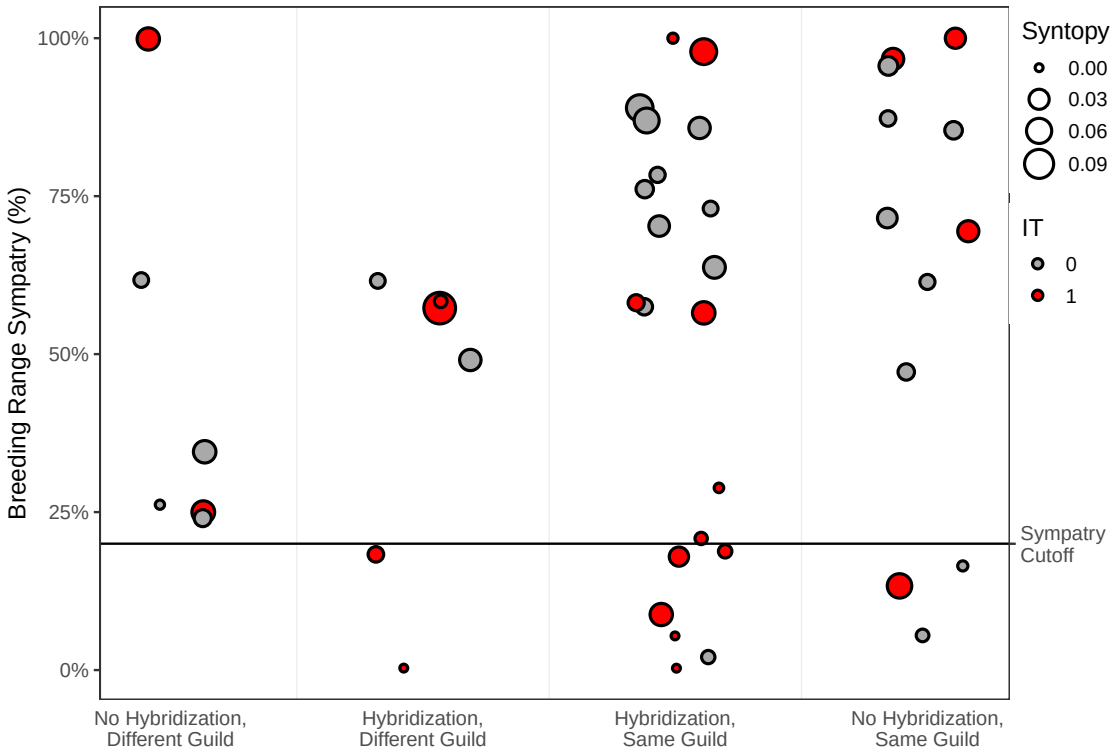

Figure 1.6: Variation in closely related species in resource overlap, hybridization, and interspecific territoriality. This variation is represented by a two-digit number in which the first digit stands for resource competition and the second for hybridization. A 0 means the species in that pair do not have that competition, and a 1 means they do. For example, 01 represents a species pair that does not overlap completely in resource use but that does hybridize. Interspecifically territorial species pairs are represented by red points, and size of points varies according to syntopy.

Table 1.1: Direction of Predictions

	Misdirected intraspecific aggression	Adaptive for resource competition	Adaptive for reproductive interference
Patristic distance	–	–	–
Plumage similarity	+/	+/+	+/+
Song similarity	+/	+/+	+/+
Foraging guild overlap		+/+	
Bill length difference		-/-	
Mass difference		-/-	
Hybridization	+/		+/+
Syntopy	–	+	+

[1] before/after phylogenetic correction

Table 1.2: Univariate comparisons between interspecifically territorial (I.T.) species pairs (N = 20) and non-interspecifically territorial (non-I.T.) species pairs (N = 25)

		Non-I.T.		I.T.			
Variable	Transformation	Mean	SE	Mean	SE	t	P
Patristic distance	log	2.10	0.04	1.44	0.04	2.35	0.012
Song similarity (SPCC)		0.34	0.01	0.40	0.01	-1.61	0.058
Song dissimilarity (pPCA)		14.52	0.19	12.44	0.27	1.37	0.089
Mass difference	log(x + 0.01)	1.16	0.07	0.69	0.08	0.89	0.189
Plumage dissimilarity		1.76	0.04	1.78	0.04	-0.09	0.535
Syntopy	log(x + 0.01)	-3.59	0.02	-3.57	0.04	-0.09	0.536

Table 1.3: Univariate comparisons between interspecifically territorial (I.T.) species pairs (N = 20) and non-interspecifically territorial (non-I.T.) species pairs (N = 25)

		Non-I.T.		I.T.		
Variable	Transformation	Range	Median	Range	Median	P
Bill difference	log (x + 0.01)	-4.61 - 2.94	0.19	-4.61 - 1.51	-0.06	0.14
Sympatry	sqrt	0.14 - 0.98	0.79	0.05 - 1	0.52	0.17
Guild overlap		1 - 3	3	0 - 3	3	0.58

Table 1.4: Coefficients of variation and of nominal variation for predictor and response variables

Variable	Coefficient of Variation	Coefficient of Nominal Variation
Mass difference	332.87	
Bill difference	159.06	
Patristic distance	117.86	
Syntopy	95.49	
Sympatry	61.93	
Plumage dissimilarity	49.85	
Song dissimilarity (pPCA)	37.9	
Song similarity (SPCC)	35.68	
Foraging guild overlap	28.88	
Interspecific territoriality		0.93
Hybridization		0.8

Table 1.5: Generalized linear model predicting interspecific territoriality with interaction between syntopy and hybridization

Selected Predictors	Estimate	Std Error	Z Value	P Value
(Intercept)	1.19	3.04	0.39	0.696
Syntopy	5.88	2.64	2.23	0.026*
Hybridization	3.63	1.78	2.04	0.042*
Plumage dissimilarity	0.20	0.44	0.46	0.647
Song dissimilarity (pPCA)	-0.70	0.58	-1.20	0.23
Song similarity (SPCC)	-0.88	0.66	-1.33	0.184
Shape PC	0.10	0.51	0.21	0.837
Size PC	0.33	0.36	0.93	0.355
Guild overlap	-1.69	1.05	-1.61	0.108
Syntopy x hybridization	-6.69	2.74	-2.44	0.015*

Table 1.6: Generalized linear model predicting interspecific territoriality with interaction between syntopy and guild overlap

Selected Predictors	Estimate	Std Error	Z Value	P Value
(Intercept)	0.02	1.59	0.01	0.989
Syntopy	2.08	1.59	1.31	0.190
Guild overlap	-0.23	0.60	-0.39	0.698
Hybridization	0.61	0.81	0.76	0.449
Plumage dissimilarity	0.06	0.35	0.16	0.870
Song dissimilarity (pPCA)	-0.71	0.47	-1.51	0.132
Song similarity (SPCC)	0.06	0.45	0.13	0.899
Size PC	0.12	0.31	0.40	0.692
Shape PC	-0.13	0.46	-0.27	0.787
Syntopy x guild overlap	-0.79	0.58	-1.37	0.172

Table 1.7: Generalized linear model predicting interspecific territoriality with interaction between syntopy and size PC

Selected Predictors	Estimate	Std Error	Z Value	P Value
(Intercept)	1.24	2.14	0.58	0.561
Syntopy	0.62	0.64	0.98	0.329
Size PC	0.48	0.98	0.49	0.625
Guild overlap	-1.05	0.85	-1.24	0.217
Hybridization	1.49	1.19	1.25	0.21
Plumage dissimilarity	1.48	0.71	2.09	0.036*
Song dissimilarity (pPCA)	-1.06	0.69	-1.54	0.124
Song similarity (SPCC)	-0.46	0.65	-0.71	0.476
Shape PC	-0.37	0.82	-0.45	0.654
Syntopy x size PC	-4.55	1.65	-2.75	0.006*

Table 1.8: Generalized linear model predicting breeding range overlap with interaction between interspecific territoriality and hybridization

Selected Predictors	Estimate	Std Error	T Value	P Value
(Intercept)	0.08	0.30	0.27	0.787
Interspecific territoriality	0.33	0.49	0.68	0.503
Hybridization	0.33	0.41	0.82	0.415
Patristic distance	-0.07	0.17	-0.45	0.655
Interspecific territoriality x hybridization	-1.30	0.61	-2.15	0.037*

Table 1.9: delta AICc values for models with indicated covariates

ParaSymp1	ParaSymp2
0.00	0.00
2.08	2.18
2.15	1.39
1.63	1.90

APPENDIX A

Appendix to "Multiple routes to interspecific territoriality in sister species of North American songbirds"

A.1 Supplementary Methods

Since songbird species vary in the size of their vocal repertoires, the number of song samples needed to capture the vocal array of a species could also vary depending on repertoire size. While there are many recordings for some species on online databases, other species have not been frequently recorded, and it can be difficult to find high quality song samples without background noise. Thus, we performed a sensitivity analysis to determine the number of song samples needed to represent species with small or large vocal repertoires. We randomly selected six species from each category of "small", "medium", and "large" repertoire size (1 – 4, 5 – 14, and 15 or more songs, respectively). For each species, we downloaded and edited six sound files from xeno-canto.org, following the methods in the main text. We chose six because it was difficult to find more than six high quality files without other birds or noises in the background for most species.

After collecting these songs, we calculated the "true" phylogenetic principal component scores for each species by averaging the acoustic parameters across the six song samples, and then performing phylogenetic principal component analysis (pPCA) with all 15 species. We then repeated this process of averaging acoustic parameters by species and calculating the pPCA score, but averaged parameters across different numbers of song samples depending on the size of the species' repertoires. First, we used two song samples

for each species regardless of repertoire size. Next, we used two samples for species with small repertoires or with medium-sized repertoires, and four samples for species with large repertoires. Next, we used two samples for species with small repertoires and four samples for species with medium or large repertoires. Finally, we averaged across two samples for species with small repertoires, four for species with medium repertoires, and six for species with large repertoires. To compare the pPCA scores calculated from these sampling schemes, we repeated the process of randomly sampling songs from the six files we downloaded, averaging acoustic parameters for those songs, and calculating the pPCA scores for each species one hundred times, and took the correlation between these pPCA scores with the "true" scores. The sampling scheme that yielded high correlations with the fewest samples needed was sampling two songs for species with small repertoires and four samples for species with medium or large repertoires (Figure A.2). Thus, for species with a repertoire size of one to four songs, we collected two songs, and for species with a repertoire of five or more songs, we collected four songs.

A.2 Supplementary Figures

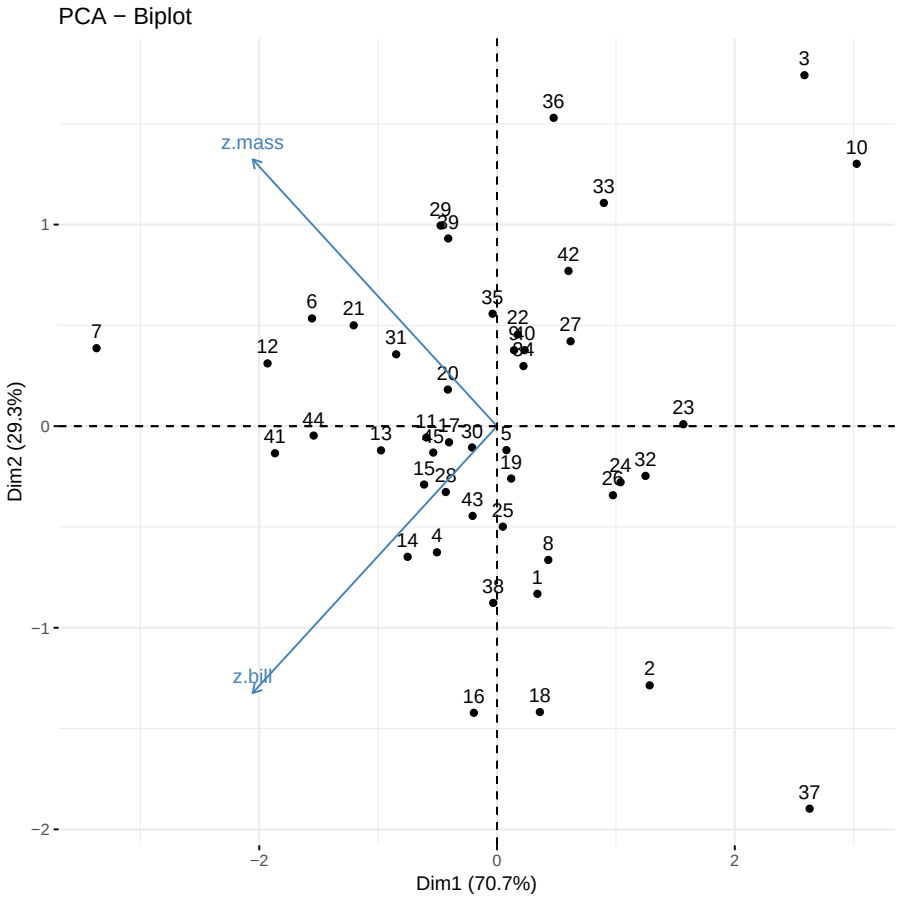

Figure A.1: Principal component loadings of ecomorphological traits

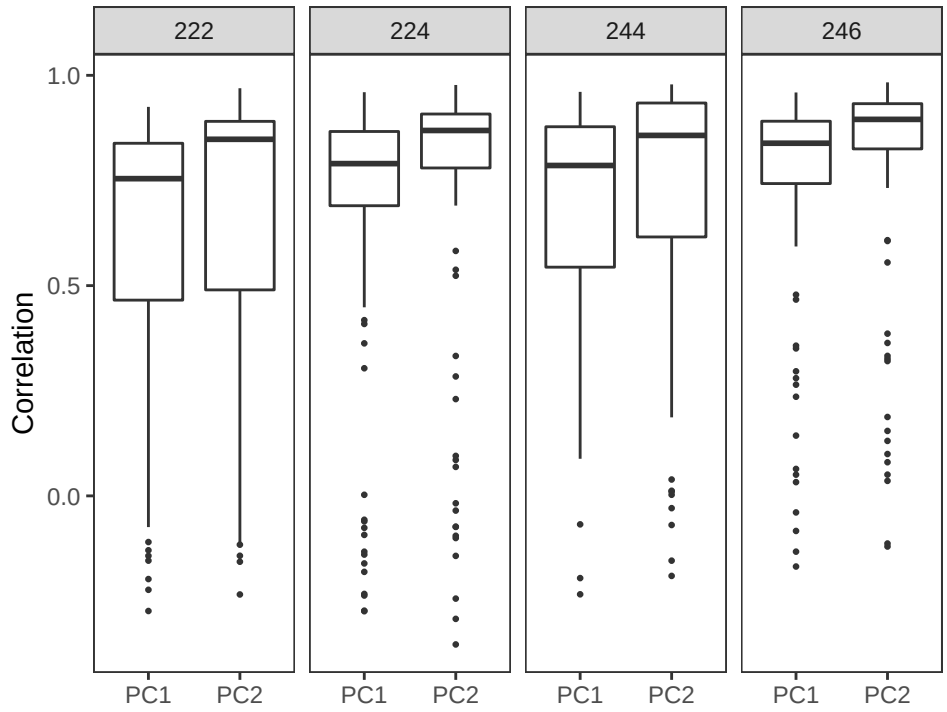

Figure A.2: Song simulation results depicting the correlation between the scores calculated from each sampling scheme and the scores calculated across six song files for each species. Each panel represents a different sampling scheme based on the size of species repertoires.

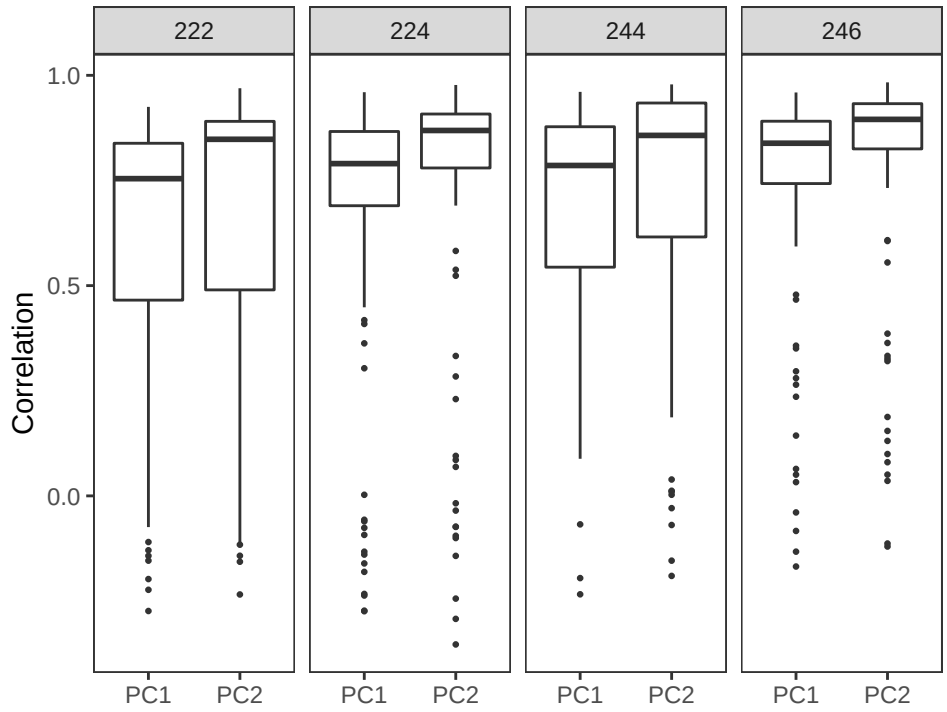

Figure A.3: Song simulation results depicting the correlation between the scores calculated from each sampling scheme and the scores calculated across six song files for each species. Each panel represents a different sampling scheme based on the size of species repertoires.

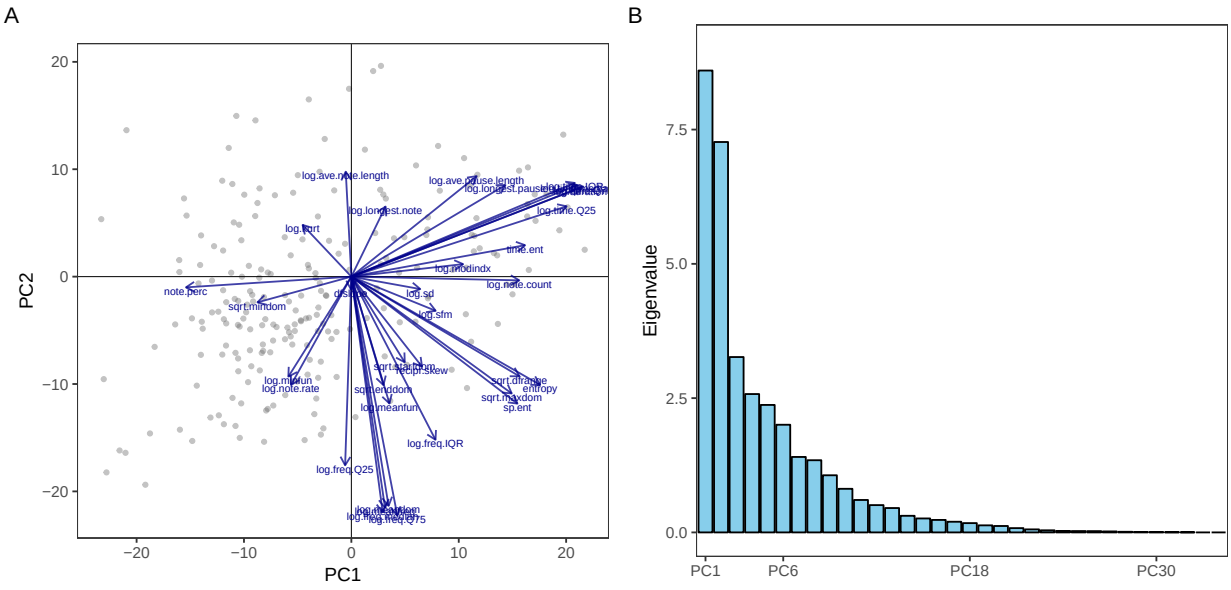

Figure A.4: Phylogenetic principal component analysis of acoustic parameters with (A) variable loadings and (B) variation captured by each principal component axis.

A.3 Supplementary Tables

Table S1 Interspecific territoriality classifications based on literature search

Species 1	Species 2	Interspecific territoriality	References
Aphelocoma insularis	Aphelocoma californica	Allopatric	
Lanius excubitor	Lanius ludovicianus	Allopatric	
Baeolophus inornatus	Baeolophus ridgwayi	Allopatric	
Sitta pygmaea	Sitta pusilla	Allopatric	
Toxostoma rufum	Toxostoma longirostre	Allopatric	
Calcarius ornatus	Calcarius pictus	Allopatric	
Setophaga virens	Setophaga chrysoparia	Allopatric	
Cardellina pusilla	Cardellina rubrifrons	Allopatric	
Melozone aberti	Melozone crissalis	Allopatric	
Ammodramus henslowii	Ammodramus bairdii	Allopatric	
Junco phaeonotus	Junco hyemalis	Allopatric	
Peucaea aestivalis	Peucaea cassinii	Allopatric	
Empidonax traillii	Empidonax alnorum	Yes	Prescott 1987; Hechtenthal 2007; Gorski 1969
Tyrannus forficatus	Tyrannus verticalis	Yes	Sutton 1967
Baeolophus atricristatus	Baeolophus bicolor	Yes	Curry & Patten 2016
Tachycineta thalassina	Tachycineta bicolor	Yes	Winkler 2011
Polioptila californica	Polioptila melanura	Yes	Atwood 1988
Sialia currucoides	Sialia mexicana	Yes	Herlugson 1980; Duckworth 2013; Pinkowski 1979; Duckworth and Badyaev 2007
Spinus lawrencei	Spinus psaltria	Yes	Coutlee 1968; Linsdale 1957
Plectrophenax hyperboreus	Plectrophenax nivalis	Yes	Winker et al 2002; Maley & Winker 2010; Johnson et al. 2013; Sealy 1969

(continued)

Species 1	Species 2	Interspecific territoriality	References
Vermivora cyanoptera	Vermivora chrysoptera	Yes	Ficken and Ficken 1968; Confer and Larkin 1998; Confer and Knapp 1977; Will 1986; Confer et al. 2003
Setophaga petechia	Setophaga pensylvanica	Yes	Morse 1966
Setophaga townsendi	Setophaga occidentalis	Yes	Pearson 2000, Pearson and Manuwal 2000, Pearson and Rohwer 2000
Icterus bullockii	Icterus galbula	Yes	Edinger 1985
Agelaius tricolor	Agelaius phoeniceus	Yes	Payne 1969
Quiscalus major	Quiscalus mexicanus	Yes	Selander & Giller 1961; Pratt 1973
Sturnella magna	Sturnella neglecta	Yes	Lanyon 1957; Wiens 1969; Lanyon 1956b; Elbert 2010; Rohwer 1973
Pheucticus melanocephalus	Pheucticus ludovicianus	Yes	Kroodsma 1974
Piranga ludoviciana	Piranga olivacea	Yes	Peterson 1995
Aphelocoma woodhouseii	Aphelocoma californica	Yes	Correspondance with John McCormack
Peucaea botterii	Peucaea cassinii	Yes	Tramontano 1971
Myiarchus tyrannulus	Myiarchus cinerascens	Yes	Brush 1983
Ammodramus caudacutus	Ammodramus maritimus	Yes	Woolfenden 1956; BNA
Empidonax occidentalis	Empidonax difficilis	Yes (recent split)	Johnson 1980; Correspondance with Peter Lowther
Troglodytes pacificus	Troglodytes hiemalis	Yes (recent split)	Toews and Irwin 2008
Empidonax hammondii	Empidonax oberholseri	No	
Tyrannus vociferans	Tyrannus tyrannus	No	
Cyanocitta cristata	Cyanocitta stelleri	No	

(continued)

Species 1	Species 2	Interspecific territoriality	References
Corvus cryptoleucus	Corvus corax	No	
Poecile gambeli	Poecile atricapillus	No	
Petrochelidon fulva	Petrochelidon pyrrhonota	No	
Progne subis	Stelgidopteryx serripennis	No	
Thryomanes bewickii	Thryothorus ludovicianus	No	
Cistothorus platensis	Cistothorus palustris	No	
Catherpes mexicanus	Salpinctes obsoletus	No	
Toxostoma crissale	Toxostoma lecontei	No	
Bombycilla cedrorum	Bombycilla garrulus	No	
Regulus calendula	Regulus satrapa	No	
Acanthis hornemanni	Acanthis flammea	No	
Parkesia noveboracensis	Parkesia motacilla	No	
Setophaga graciae	Setophaga nigrescens	No	
Euphagus cyanocephalus	Euphagus carolinus	No	
Melospiza georgiana	Melospiza lincolnii	No	
Ammodramus caudacutus	Ammodramus nelsoni	No	
Zonotrichia atricapilla	Zonotrichia leucophrys	No	
Cardinalis sinuatus	Cardinalis cardinalis	No	
Sitta pygmaea	Sitta canadensis	No	
Toxostoma curvirostre	Toxostoma longirostre	No	
Geothlypis philadelphia	Oporornis agilis	No	
Molothrus aeneus	Molothrus ater	No	
Melozone aberti	Melozone fusca	No	
Piranga ludoviciana	Piranga flava	No	
Sayornis phoebe	Sayornis nigricans	No data	
Contopus virens	Contopus sordidulus	No data	
Myiarchus crinitus	Myiarchus cinerascens	No data	
Pica nuttalli	Pica hudsonia	No data	
Corvus caurinus	Corvus brachyrhynchos	No data	
Vireo plumbeus	Vireo cassinii	No data	
Vireo gilvus	Vireo philadelphicus	No data	
Oreoscoptes montanus	Mimus polyglottos	No data	
Catharus fuscescens	Catharus minimus	No data	

(continued)

Species 1	Species 2	Interspecific territoriality	References
Haemorhous purpureus	Haemorhous cassinii	No data	
Loxia leucoptera	Loxia curvirostra	No data	
Geothlypis philadelphia	Geothlypis tolmiei	No data	
Oreothlypis luciae	Oreothlypis virginiae	No data	
Setophaga striata	Setophaga castanea	No data	
Icterus parisorum	Icterus graduacauda	No data	
Icterus spurius	Icterus cucullatus	No data	
Dolichonyx oryzivorus	Xanthocephalus xanthocephalus	No data	
Chondestes grammacus	Calamospiza melanocorys	No data	
Pipilo erythrophthalmus	Pipilo maculatus	No data	
Spizella breweri	Spizella pusilla	No data	
Spizella pallida	Spizella passerina	No data	
Ammodramus savannarum	Arremonops rufivirgatus	No data	
Passerina caerulea	Passerina amoena	No data	
Passerina ciris	Passerina versicolor	No data	
Artemisiospiza nevadensis	Artemisiospiza belli	No data	
Catharus fuscescens	Catharus bicknelli	No data	
Cardellina pusilla	Cardellina canadensis	No data	

A.3.1 References used to classify species pairs in Table S1

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Table S2 Sound files downloaded from xeno-canto to characterize song similarity between species pairs.

Recording_ID	Species	Recordist	Url
316236	Sayornis phoebe	Antonio Xeira	https://www.xeno-canto.org/316236
132866	Sayornis phoebe	Jonathon Jongsma	https://www.xeno-canto.org/132866
318152	Sayornis nigricans	Bobby Wilcox	https://www.xeno-canto.org/318152
192057	Sayornis nigricans	Paul Marvin	https://www.xeno-canto.org/192057
110655	Sayornis nigricans	Lauren Harter	https://www.xeno-canto.org/110655
237806	Sayornis nigricans	Jarrod Swackhamer	https://www.xeno-canto.org/237806
72079	Sayornis nigricans	Richard E Webster	https://www.xeno-canto.org/72079
313072	Sayornis nigricans	Ted Floyd	https://www.xeno-canto.org/313072
18694	Contopus virens	David Bradley	https://www.xeno-canto.org/18694
158909	Contopus virens	Ian Cruickshank	https://www.xeno-canto.org/158909
141880	Contopus sordidulus	Patrick Turgeon	https://www.xeno-canto.org/141880
190093	Contopus sordidulus	Richard E. Webster	https://www.xeno-canto.org/190093
161658	Empidonax hammondii	Ian Cruickshank	https://www.xeno-canto.org/161658
196460	Empidonax hammondii	Richard E. Webster	https://www.xeno-canto.org/196460
14293	Empidonax oberholseri	Andrew Spencer	https://www.xeno-canto.org/14293
161661	Empidonax oberholseri	Ian Cruickshank	https://www.xeno-canto.org/161661
196032	Empidonax traillii	Richard E. Webster	https://www.xeno-canto.org/196032
6757	Empidonax traillii	Darrell L. Peterson	https://www.xeno-canto.org/6757
302253	Empidonax alnorum	James Bradley	https://www.xeno-canto.org/302253
376468	Empidonax alnorum	Michael Harrison	https://www.xeno-canto.org/376468
254619	Empidonax occidentalis	Jonathon Jongsma	https://www.xeno-canto.org/254619
253552	Empidonax occidentalis	Eric DeFonso	https://www.xeno-canto.org/253552
330648	Empidonax difficilis	Ken Chamberlain	https://www.xeno-canto.org/330648
181813	Empidonax difficilis	Skip Russell	https://www.xeno-canto.org/181813
334630	Empidonax difficilis	Scott Gravette	https://www.xeno-canto.org/334630
225903	Myiarchus crinitus	Peter Boesman	https://www.xeno-canto.org/225903
312459	Myiarchus crinitus	Paul Marvin	https://www.xeno-canto.org/312459
132678	Myiarchus cinerascens	Dan Lane	https://www.xeno-canto.org/132678
348126	Myiarchus cinerascens	Richard E. Webster	https://www.xeno-canto.org/348126
376756	Tyrannus vociferans	Manuel Grosselet	https://www.xeno-canto.org/376756
172942	Tyrannus vociferans	Eric DeFonso	https://www.xeno-canto.org/172942
140649	Tyrannus tyrannus	Paul Driver	https://www.xeno-canto.org/140649
132630	Tyrannus tyrannus	Dan Lane	https://www.xeno-canto.org/132630

(continued)

Recording_ID	Species	Recordist	Url
82743	Tyrannus tyrannus	Ryan P. O'Donnell	https://www.xeno-canto.org/82743
134875	Tyrannus tyrannus	Jonathon Jongsma	https://www.xeno-canto.org/134875
132677	Tyrannus forficatus	Dan Lane	https://www.xeno-canto.org/132677
147499	Tyrannus forficatus	Paul Marvin	https://www.xeno-canto.org/147499
316205	Tyrannus verticalis	Bobby Wilcox	https://www.xeno-canto.org/316205
184924	Tyrannus verticalis	Richard E. Webster	https://www.xeno-canto.org/184924
154313	Psilorhinus morio	bernard Fort	https://www.xeno-canto.org/154313
351151	Psilorhinus morio	Frank Lambert	https://www.xeno-canto.org/351151
368411	Cyanocorax luxuosus	Dan Lane	https://www.xeno-canto.org/368411
278387	Cyanocorax luxuosus	Paul Marvin	https://www.xeno-canto.org/278387
116374	Cyanocitta cristata	Ryan O'Donnell	https://www.xeno-canto.org/116374
234669	Cyanocitta cristata	Danny Zapata-Henao	https://www.xeno-canto.org/234669
361830	Cyanocitta stelleri	Frank Lambert	https://www.xeno-canto.org/361830
14433	Cyanocitta stelleri	Andrew Spencer	https://www.xeno-canto.org/14433
22007	Cyanocitta stelleri	Chris Parrish	https://www.xeno-canto.org/22007
355087	Cyanocitta stelleri	Thomas Magarian	https://www.xeno-canto.org/355087
362511	Cyanocitta stelleri	Frank Lambert	https://www.xeno-canto.org/362511
41245	Cyanocitta stelleri	Scott Olmstead	https://www.xeno-canto.org/41245
360668	Pica nuttalli	Paul Marvin	https://www.xeno-canto.org/360668
297461	Pica nuttalli	Ross Gallardy	https://www.xeno-canto.org/297461
254491	Pica hudsonia	Jonathon Jongsma	https://www.xeno-canto.org/254491
321397	Pica hudsonia	Nick Komar	https://www.xeno-canto.org/321397
109766	Corvus caurinus	Andrew Spencer	https://www.xeno-canto.org/109766
160058	Corvus caurinus	Ian Cruickshank	https://www.xeno-canto.org/160058
124432	Corvus brachyrhynchos	GABRIEL LEITE	https://www.xeno-canto.org/124432
316302	Corvus brachyrhynchos	Sue Riffe	https://www.xeno-canto.org/316302
322466	Corvus cryptoleucus	Richard E. Webster	https://www.xeno-canto.org/322466
136206	Corvus cryptoleucus	Dan Lane	https://www.xeno-canto.org/136206
325124	Corvus corax	Sue Riffe	https://www.xeno-canto.org/325124
213233	Corvus corax	Richard Hoyer	https://www.xeno-canto.org/213233
213233	Corvus corax	Richard Hoyer	https://www.xeno-canto.org/213233
91967	Lanius excubitor	Andrew Spencer	https://www.xeno-canto.org/91967
44982	Lanius excubitor	Todd Wilson	https://www.xeno-canto.org/44982
319815	Lanius excubitor	Bruce Lagerquist	https://www.xeno-canto.org/319815

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Recording_ID	Species	Recordist	Url
91968	Lanius excubitor	Andrew Spencer	https://www.xeno-canto.org/91968
44981	Lanius excubitor	Todd Wilson	https://www.xeno-canto.org/44981
44982	Lanius excubitor	Todd Wilson	https://www.xeno-canto.org/44982
307003	Lanius ludovicianus	Ted Floyd	https://www.xeno-canto.org/307003
76966	Lanius ludovicianus	Andrew Spencer	https://www.xeno-canto.org/76966
76963	Lanius ludovicianus	Andrew Spencer	https://www.xeno-canto.org/76963
76964	Lanius ludovicianus	Andrew Spencer	https://www.xeno-canto.org/76964
318011	Lanius ludovicianus	Nick Komar	https://www.xeno-canto.org/318011
367268	Lanius ludovicianus	Vicki Dern	https://www.xeno-canto.org/367268
374109	Vireo plumbeus	Matt Wistrand	https://www.xeno-canto.org/374109
170091	Vireo plumbeus	Micah Riegner	https://www.xeno-canto.org/170091
323415	Vireo plumbeus	Richard E. Webster	https://www.xeno-canto.org/323415
323431	Vireo plumbeus	Richard E. Webster	https://www.xeno-canto.org/323431
323424	Vireo plumbeus	Richard E. Webster	https://www.xeno-canto.org/323424
14274	Vireo plumbeus	Chris Parrish	https://www.xeno-canto.org/14274
76908	Vireo cassinii	Stuart Fisher	https://www.xeno-canto.org/76908
136030	Vireo cassinii	Brian Sullivan	https://www.xeno-canto.org/136030
378430	Vireo cassinii	Jeremy Minns	https://www.xeno-canto.org/378430
135027	Vireo cassinii	Tom Forwood Jr.	https://www.xeno-canto.org/135027
102950	Vireo cassinii	Eric DeFonso	https://www.xeno-canto.org/102950
379329	Vireo cassinii	Lance A. M. Benner	https://www.xeno-canto.org/379329
376564	Vireo gilvus	Michael Harrison	https://www.xeno-canto.org/376564
14276	Vireo gilvus	Chris Parrish	https://www.xeno-canto.org/14276
297175	Vireo gilvus	Paul Marvin	https://www.xeno-canto.org/297175
297175	Vireo gilvus	Paul Marvin	https://www.xeno-canto.org/297175
102968	Vireo gilvus	Jonathon Jongsma	https://www.xeno-canto.org/102968
325352	Setophaga aestiva	Sue Riffe	https://www.xeno-canto.org/325352
137608	Vireo philadelphicus	Randy Dzenkiw	https://www.xeno-canto.org/137608
317596	Vireo philadelphicus	Matt Wistrand	https://www.xeno-canto.org/317596
180710	Vireo philadelphicus	Ian Cruickshank	https://www.xeno-canto.org/180710
189440	Vireo philadelphicus	Andrew Spencer	https://www.xeno-canto.org/189440
298975	Vireo philadelphicus	Martin St-Michel	https://www.xeno-canto.org/298975
317596	Vireo philadelphicus	Matt Wistrand	https://www.xeno-canto.org/317596
160849	Poecile gambeli	Ian Cruickshank	https://www.xeno-canto.org/160849

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Recording_ID	Species	Recordist	Url
240242	Poecile gambeli	Carrie Branch	https://www.xeno-canto.org/240242
352827	Poecile atricapillus	Ted Floyd	https://www.xeno-canto.org/352827
335759	Poecile atricapillus	Thomas Magarian	https://www.xeno-canto.org/335759
34320	Baeolophus atricristatus	Andrew Spencer	https://www.xeno-canto.org/34320
147279	Baeolophus atricristatus	Paul Marvin	https://www.xeno-canto.org/147279
21965	Baeolophus atricristatus	Chris Parrish	https://www.xeno-canto.org/21965
77331	Baeolophus atricristatus	Chris Harrison	https://www.xeno-canto.org/77331
33596	Baeolophus bicolor	Andrew Spencer	https://www.xeno-canto.org/33596
233656	Baeolophus bicolor	David Sarkozi	https://www.xeno-canto.org/233656
370491	Baeolophus bicolor	Eric DeFonso	https://www.xeno-canto.org/370491
33585	Baeolophus bicolor	Andrew Spencer	https://www.xeno-canto.org/33585
360933	Baeolophus bicolor	Matt Brady	https://www.xeno-canto.org/360933
97374	Baeolophus bicolor	Daniel Lane	https://www.xeno-canto.org/97374
350982	Baeolophus inornatus	Richard E. Webster	https://www.xeno-canto.org/350982
350922	Baeolophus inornatus	Richard E. Webster	https://www.xeno-canto.org/350922
350941	Baeolophus inornatus	Richard E. Webster	https://www.xeno-canto.org/350941
350943	Baeolophus inornatus	Richard E. Webster	https://www.xeno-canto.org/350943
350899	Baeolophus ridgwayi	Richard E. Webster	https://www.xeno-canto.org/350899
350901	Baeolophus ridgwayi	Richard E. Webster	https://www.xeno-canto.org/350901
350899	Baeolophus ridgwayi	Richard E. Webster	https://www.xeno-canto.org/350899
350902	Baeolophus ridgwayi	Richard E. Webster	https://www.xeno-canto.org/350902
361256	Alauda arvensis	Elias A. Ryberg	https://www.xeno-canto.org/361256
302578	Alauda arvensis	James Bradley	https://www.xeno-canto.org/302578
361649	Alauda arvensis	Krzysztof Deoniziak	https://www.xeno-canto.org/361649
285581	Alauda arvensis	david m	https://www.xeno-canto.org/285581
34861	Eremophila alpestris	Tayler Brooks	https://www.xeno-canto.org/34861
345553	Eremophila alpestris	Thomas Magarian	https://www.xeno-canto.org/345553
277952	Eremophila alpestris	Paul Marvin	https://www.xeno-canto.org/277952
378584	Eremophila alpestris	Rachel Hudson	https://www.xeno-canto.org/378584
113685	Phylloscopus examinandus	Adria Sole	https://www.xeno-canto.org/113685
340441	Phylloscopus borealis	Tom Wulf	https://www.xeno-canto.org/340441
40211	Phylloscopus examinandus	Klaas Felix Jachmann	https://www.xeno-canto.org/40211
140994	Phylloscopus borealis	Andrew Spencer	https://www.xeno-canto.org/140994
215758	Psaltriparus minimus	Ted Floyd	https://www.xeno-canto.org/215758

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Recording_ID	Species	Recordist	Url
358701	Psaltriparus minimus	Ted Floyd	https://www.xeno-canto.org/358701
34112	Petrochelidon fulva	Andrew Spencer	https://www.xeno-canto.org/34112
34112	Petrochelidon fulva	Andrew Spencer	https://www.xeno-canto.org/34112
203606	Petrochelidon pyrrhonota	Andrew Spencer	https://www.xeno-canto.org/203606
317115	Petrochelidon pyrrhonota	Hal Mitchell	https://www.xeno-canto.org/317115
140266	Tachycineta thalassina	Paul Driver	https://www.xeno-canto.org/140266
105332	Tachycineta thalassina	Andrew Spencer	https://www.xeno-canto.org/105332
22009	Tachycineta thalassina	Chris Parrish	https://www.xeno-canto.org/22009
105332	Tachycineta thalassina	Andrew Spencer	https://www.xeno-canto.org/105332
163176	Tachycineta bicolor	Paul Marvin	https://www.xeno-canto.org/163176
313481	Tachycineta bicolor	Matt Wistrand	https://www.xeno-canto.org/313481
299635	Tachycineta bicolor	Paul Marvin	https://www.xeno-canto.org/299635
322861	Tachycineta bicolor	Peter Boesman	https://www.xeno-canto.org/322861
33563	Progne subis	Andrew Spencer	https://www.xeno-canto.org/33563
278201	Progne subis	Patrick Turgeon	https://www.xeno-canto.org/278201
302415	Stelgidopteryx serripennis	James Bradley	https://www.xeno-canto.org/302415
123367	Stelgidopteryx serripennis	Chris Harrison	https://www.xeno-canto.org/123367
122453	Thryomanes bewickii	Chris Harrison	https://www.xeno-canto.org/122453
141351	Thryomanes bewickii	Mike Nelson	https://www.xeno-canto.org/141351
217813	Thryomanes bewickii	Paul Marvin	https://www.xeno-canto.org/217813
70970	Thryomanes bewickii	Mary Beth Stowe	https://www.xeno-canto.org/70970
124068	Thryothorus ludovicianus	Chris Harrison	https://www.xeno-canto.org/124068
122452	Thryothorus ludovicianus	Chris Harrison	https://www.xeno-canto.org/122452
70982	Thryothorus ludovicianus	Mary Beth Stowe	https://www.xeno-canto.org/70982
236014	Thryothorus ludovicianus	Danny Zapata-Henao	https://www.xeno-canto.org/236014
137656	Cistothorus stellaris	Patrick Turgeon	https://www.xeno-canto.org/137656
151605	Cistothorus stellaris	Randy Dzenkiw	https://www.xeno-canto.org/151605
137656	Cistothorus stellaris	Patrick Turgeon	https://www.xeno-canto.org/137656
137656	Cistothorus stellaris	Patrick Turgeon	https://www.xeno-canto.org/137656
230753	Cistothorus stellaris	Paul Marvin	https://www.xeno-canto.org/230753
230753	Cistothorus stellaris	Paul Marvin	https://www.xeno-canto.org/230753

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Recording_ID	Species	Recordist	Url
153248	Cistothorus palustris	Bird Studies Canada - Prairie and Parkland Marsh Monitoring Program (PPMMP)	https://www.xeno-canto.org/153248
110106	Cistothorus palustris	Andrew Spencer	https://www.xeno-canto.org/110106
153248	Cistothorus palustris	Bird Studies Canada - Prairie and Parkland Marsh Monitoring Program (PPMMP)	https://www.xeno-canto.org/153248
153248	Cistothorus palustris	Bird Studies Canada - Prairie and Parkland Marsh Monitoring Program (PPMMP)	https://www.xeno-canto.org/153248
110106	Cistothorus palustris	Andrew Spencer	https://www.xeno-canto.org/110106
14863	Cistothorus palustris	Andrew Spencer	https://www.xeno-canto.org/14863
279681	Catherpes mexicanus	Paul Marvin	https://www.xeno-canto.org/279681
297532	Catherpes mexicanus	Ross Gallardy	https://www.xeno-canto.org/297532
373820	Salpinctes obsoletus	Jeff Dyck	https://www.xeno-canto.org/373820
325011	Salpinctes obsoletus	Jim Holmes	https://www.xeno-canto.org/325011
325011	Salpinctes obsoletus	Jim Holmes	https://www.xeno-canto.org/325011
229185	Salpinctes obsoletus	Peter Boesman	https://www.xeno-canto.org/229185
147295	Polioptila californica	Paul Marvin	https://www.xeno-canto.org/147295
203741	Polioptila californica	Andrew Spencer	https://www.xeno-canto.org/203741
71907	Polioptila melanura	Richard E Webster	https://www.xeno-canto.org/71907
361932	Polioptila melanura	Paul Marvin	https://www.xeno-canto.org/361932
348158	Polioptila melanura	Richard E. Webster	https://www.xeno-canto.org/348158
361929	Polioptila melanura	Paul Marvin	https://www.xeno-canto.org/361929
303354	Sitta pygmaea	Ted Floyd	https://www.xeno-canto.org/303354
343422	Sitta pygmaea	Bruce Lagerquist	https://www.xeno-canto.org/343422
161393	Sitta pygmaea	Paul Marvin	https://www.xeno-canto.org/161393
363167	Sitta pygmaea	Frank Lambert	https://www.xeno-canto.org/363167
192108	Sitta pusilla	Paul Marvin	https://www.xeno-canto.org/192108
138619	Sitta pusilla	Paul Marvin	https://www.xeno-canto.org/138619
33523	Sitta pusilla	Andrew Spencer	https://www.xeno-canto.org/33523
152170	Sitta pusilla	Dan Lane	https://www.xeno-canto.org/152170

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Recording_ID	Species	Recordist	Url
75118	Oreoscoptes montanus	Ryan P. O'Donnell	https://www.xeno-canto.org/75118
12118	Oreoscoptes montanus	Nathan Pieplow	https://www.xeno-canto.org/12118
320563	Oreoscoptes montanus	Ted Floyd	https://www.xeno-canto.org/320563
13841	Oreoscoptes montanus	Andrew Spencer	https://www.xeno-canto.org/13841
321942	Mimus polyglottos	Richard E. Webster	https://www.xeno-canto.org/321942
321923	Mimus polyglottos	Richard E. Webster	https://www.xeno-canto.org/321923
172494	Mimus polyglottos	Eric DeFonso	https://www.xeno-canto.org/172494
21733	Mimus polyglottos	Chris Parrish	https://www.xeno-canto.org/21733
255629	Toxostoma crissale	Richard E. Webster	https://www.xeno-canto.org/255629
231467	Toxostoma crissale	Peter Boesman	https://www.xeno-canto.org/231467
255759	Toxostoma crissale	Richard E. Webster	https://www.xeno-canto.org/255759
301084	Toxostoma crissale	Ed Pandolfino	https://www.xeno-canto.org/301084
17826	Toxostoma lecontei	Nathan Pieplow	https://www.xeno-canto.org/17826
28253	Toxostoma lecontei	Andrew Spencer	https://www.xeno-canto.org/28253
141432	Toxostoma lecontei	Paul Marvin	https://www.xeno-canto.org/141432
141433	Toxostoma lecontei	Paul Marvin	https://www.xeno-canto.org/141433
269473	Toxostoma rufum	Paul Marvin	https://www.xeno-canto.org/269473
231517	Toxostoma rufum	Peter Boesman	https://www.xeno-canto.org/231517
104665	Toxostoma rufum	Andrew Spencer	https://www.xeno-canto.org/104665
13184	Toxostoma rufum	Andrew Spencer	https://www.xeno-canto.org/13184
21656	Toxostoma longirostre	Chris Parrish	https://www.xeno-canto.org/21656
5077	Toxostoma longirostre	Nathan Pieplow	https://www.xeno-canto.org/5077
368455	Toxostoma longirostre	Dan Lane	https://www.xeno-canto.org/368455
176252	Toxostoma longirostre	Ted Floyd	https://www.xeno-canto.org/176252
205426	Sialia currucoides	Eric DeFonso	https://www.xeno-canto.org/205426
100904	Sialia currucoides	Andrew Spencer	https://www.xeno-canto.org/100904
71747	Sialia mexicana	Richard E Webster	https://www.xeno-canto.org/71747
33308	Sialia mexicana	Andrew Spencer	https://www.xeno-canto.org/33308
184465	Catharus fuscescens	Martin St-Michel	https://www.xeno-canto.org/184465
318447	Catharus fuscescens	Jim Berry	https://www.xeno-canto.org/318447
356192	Catharus minimus	Frank Lambert	https://www.xeno-canto.org/356192
65822	Catharus minimus	Ian Cruickshank	https://www.xeno-canto.org/65822
370820	Calliope calliope	Vladimir Shkurov	https://www.xeno-canto.org/370820
329588	Calliope calliope	Masato Nagai (Japan)	https://www.xeno-canto.org/329588

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Recording_ID	Species	Recordist	Url
326518	Calliope calliope	Alex Thomas	https://www.xeno-canto.org/326518
329588	Calliope calliope	Masato Nagai (Japan)	https://www.xeno-canto.org/329588
376525	Calliope calliope	Lars Edenius	https://www.xeno-canto.org/376525
326518	Calliope calliope	Alex Thomas	https://www.xeno-canto.org/326518
139593	Oenanthe oenanthe	Andrew Spencer	https://www.xeno-canto.org/139593
354835	Oenanthe oenanthe	Frank Lambert	https://www.xeno-canto.org/354835
203610	Oenanthe oenanthe	Andrew Spencer	https://www.xeno-canto.org/203610
203610	Oenanthe oenanthe	Andrew Spencer	https://www.xeno-canto.org/203610
294071	Bombycilla cedrorum	Lance A. M. Benner	https://www.xeno-canto.org/294071
375862	Bombycilla cedrorum	Jeremy Welch	https://www.xeno-canto.org/375862
319175	Bombycilla garrulus	Martin St-Michel	https://www.xeno-canto.org/319175
18968	Bombycilla garrulus	Andrew Spencer	https://www.xeno-canto.org/18968
340719	Regulus calendula	Bruce Lagerquist	https://www.xeno-canto.org/340719
371123	Regulus calendula	Jeff Dyck	https://www.xeno-canto.org/371123
65850	Regulus calendula	Ian Cruickshank	https://www.xeno-canto.org/65850
192500	Regulus calendula	Richard E. Webster	https://www.xeno-canto.org/192500
189416	Regulus satrapa	Andrew Spencer	https://www.xeno-canto.org/189416
269231	Regulus satrapa	Frank Lambert	https://www.xeno-canto.org/269231
252878	Regulus satrapa	Iain	https://www.xeno-canto.org/252878
104683	Regulus satrapa	Andrew Spencer	https://www.xeno-canto.org/104683
302647	Haemorhous purpureus	James Bradley	https://www.xeno-canto.org/302647
195203	Haemorhous purpureus	Richard E. Webster	https://www.xeno-canto.org/195203
76419	Haemorhous purpureus	Andrew Spencer	https://www.xeno-canto.org/76419
376618	Haemorhous purpureus	Bruce Lagerquist	https://www.xeno-canto.org/376618
302193	Haemorhous cassinii	James Bradley	https://www.xeno-canto.org/302193
365853	Haemorhous cassinii	Bruce Lagerquist	https://www.xeno-canto.org/365853
340366	Haemorhous cassinii	Bruce Lagerquist	https://www.xeno-canto.org/340366
365853	Haemorhous cassinii	Bruce Lagerquist	https://www.xeno-canto.org/365853
161313	Spinus lawrencei	Paul Marvin	https://www.xeno-canto.org/161313
328992	Spinus lawrencei	Lance A. M. Benner	https://www.xeno-canto.org/328992
161308	Spinus lawrencei	Paul Marvin	https://www.xeno-canto.org/161308
71938	Spinus lawrencei	Richard E Webster	https://www.xeno-canto.org/71938
144129	Spinus psaltria	Lauren Harter	https://www.xeno-canto.org/144129
374080	Spinus psaltria	Matt Wistrand	https://www.xeno-canto.org/374080

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Recording_ID	Species	Recordist	Url
71954	Spinus psaltria	Richard E Webster	https://www.xeno-canto.org/71954
324033	Spinus psaltria	Paul Marvin	https://www.xeno-canto.org/324033
140679	Acanthis hornemanni	Andrew Spencer	https://www.xeno-canto.org/140679
142535	Acanthis hornemanni	Andrew Spencer	https://www.xeno-canto.org/142535
142565	Acanthis hornemanni	Andrew Spencer	https://www.xeno-canto.org/142565
140678	Acanthis hornemanni	Andrew Spencer	https://www.xeno-canto.org/140678
141708	Acanthis flammea	Andrew Spencer	https://www.xeno-canto.org/141708
216985	Acanthis flammea	Janne Bruun	https://www.xeno-canto.org/216985
141708	Acanthis flammea	Andrew Spencer	https://www.xeno-canto.org/141708
132609	Acanthis flammea	Jarek Matusiak	https://www.xeno-canto.org/132609
192152	Loxia leucoptera	Martin St-Michel	https://www.xeno-canto.org/192152
15165	Loxia leucoptera	Andrew Spencer	https://www.xeno-canto.org/15165
323021	Loxia leucoptera	Peter Boesman	https://www.xeno-canto.org/323021
165652	Loxia leucoptera	Davyd Betchkal	https://www.xeno-canto.org/165652
327483	Loxia curvirostra	Bruce Lagerquist	https://www.xeno-canto.org/327483
76432	Loxia curvirostra	Andrew Spencer	https://www.xeno-canto.org/76432
143212	Loxia curvirostra	Andrew Spencer	https://www.xeno-canto.org/143212
143214	Loxia curvirostra	Andrew Spencer	https://www.xeno-canto.org/143214
293744	Calcarius ornatus	Paul Marvin	https://www.xeno-canto.org/293744
161063	Calcarius ornatus	Paul Marvin	https://www.xeno-canto.org/161063
70076	Calcarius pictus	Paul Driver	https://www.xeno-canto.org/70076
141001	Calcarius pictus	Andrew Spencer	https://www.xeno-canto.org/141001
331841	Plectrophenax hyperboreus	John Puschock	https://www.xeno-canto.org/331841
331842	Plectrophenax hyperboreus	John Puschock	https://www.xeno-canto.org/331842
352930	Plectrophenax nivalis	Frank Lambert	https://www.xeno-canto.org/352930
104581	Plectrophenax nivalis	Ryan P. O'Donnell	https://www.xeno-canto.org/104581
375266	Parkesia noveboracensis	Susan Hochgraf	https://www.xeno-canto.org/375266
30791	Parkesia noveboracensis	Andrew Spencer	https://www.xeno-canto.org/30791
55023	Parkesia noveboracensis	Andrew Spencer	https://www.xeno-canto.org/55023
176656	Parkesia motacilla	David Swain	https://www.xeno-canto.org/176656
175483	Parkesia motacilla	Peter Wilton	https://www.xeno-canto.org/175483
253571	Geothlypis philadelphia	Martin St-Michel	https://www.xeno-canto.org/253571
142746	Geothlypis philadelphia	Martin St-Michel	https://www.xeno-canto.org/142746
79659	Geothlypis tolmiei	Ian Cruickshank	https://www.xeno-canto.org/79659

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Recording_ID	Species	Recordist	Url
379004	Geothlypis tolmiei	James Bradley	https://www.xeno-canto.org/379004
78891	Vermivora cyanoptera	Jonathon Jongsma	https://www.xeno-canto.org/78891
320488	Vermivora cyanoptera	Jonathon Jongsma	https://www.xeno-canto.org/320488
103849	Vermivora chrysoptera	Todd Wilson	https://www.xeno-canto.org/103849
103587	Vermivora chrysoptera	Andrew Spencer	https://www.xeno-canto.org/103587
323617	Leiothlypis luciae	Richard E. Webster	https://www.xeno-canto.org/323617
323622	Leiothlypis luciae	Richard E. Webster	https://www.xeno-canto.org/323622
175370	Leiothlypis virginiae	Micah Riegner	https://www.xeno-canto.org/175370
133180	Leiothlypis virginiae	Micah Riegner	https://www.xeno-canto.org/133180
79502	Setophaga striata	Andrew Spencer	https://www.xeno-canto.org/79502
330578	Setophaga striata	Martin St-Michel	https://www.xeno-canto.org/330578
324946	Setophaga striata	Martin St-Michel	https://www.xeno-canto.org/324946
219836	Bucco capensis	Peter Boesman	https://www.xeno-canto.org/219836
78900	Setophaga castanea	Andrew Spencer	https://www.xeno-canto.org/78900
137479	Setophaga castanea	Martin St-Michel	https://www.xeno-canto.org/137479
133258	Setophaga castanea	Fernand DEROUSSEN	https://www.xeno-canto.org/133258
253753	Setophaga castanea	Martin St-Michel	https://www.xeno-canto.org/253753
50445	Setophaga aestiva	Ian Davies	https://www.xeno-canto.org/50445
316039	Setophaga aestiva	John Baur	https://www.xeno-canto.org/316039
243422	Setophaga aestiva	Maxime Aubert	https://www.xeno-canto.org/243422
292262	Setophaga aestiva	Martin St-Michel	https://www.xeno-canto.org/292262
330193	Setophaga pensylvanica	Martin St-Michel	https://www.xeno-canto.org/330193
78815	Setophaga pensylvanica	Andrew Spencer	https://www.xeno-canto.org/78815
83530	Setophaga pensylvanica	Jelmer Poelstra	https://www.xeno-canto.org/83530
52446	Setophaga pensylvanica	Andrew Spencer	https://www.xeno-canto.org/52446
13586	Setophaga americana	Chris Parrish	https://www.xeno-canto.org/13586
187645	Setophaga americana	Paul Driver	https://www.xeno-canto.org/187645
134971	Setophaga americana	L G Price	https://www.xeno-canto.org/134971
171645	Setophaga americana	Dan Lane	https://www.xeno-canto.org/171645
29780	Setophaga pitiayumi	Daniel Lane	https://www.xeno-canto.org/29780
147503	Setophaga pitiayumi	Paul Marvin	https://www.xeno-canto.org/147503
100178	Setophaga pitiayumi	Chris Benesh	https://www.xeno-canto.org/100178
29781	Setophaga pitiayumi	Daniel Lane	https://www.xeno-canto.org/29781

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Recording_ID	Species	Recordist	Url
30785	Setophaga virens	Andrew Spencer	https://www.xeno-canto.org/30785
59121	Setophaga virens	Tayler Brooks	https://www.xeno-canto.org/59121
138633	Setophaga virens	Jonathon Jongsma	https://www.xeno-canto.org/138633
237743	Setophaga virens	Dan Lane	https://www.xeno-canto.org/237743
64462	Setophaga chrysoparia	Chris Warren	https://www.xeno-canto.org/64462
34946	Setophaga chrysoparia	Andrew Spencer	https://www.xeno-canto.org/34946
171977	Setophaga chrysoparia	Ronnie Kramer	https://www.xeno-canto.org/171977
297557	Setophaga chrysoparia	Ross Gallardy	https://www.xeno-canto.org/297557
269030	Setophaga townsendi	Frank Lambert	https://www.xeno-canto.org/269030
76413	Setophaga townsendi	Andrew Spencer	https://www.xeno-canto.org/76413
36563	Setophaga townsendi	Tayler Brooks	https://www.xeno-canto.org/36563
134887	Setophaga townsendi	Tom Forwood Jr.	https://www.xeno-canto.org/134887
143150	Setophaga occidentalis	Andrew Spencer	https://www.xeno-canto.org/143150
143037	Setophaga occidentalis	Andrew Spencer	https://www.xeno-canto.org/143037
143147	Setophaga occidentalis	Andrew Spencer	https://www.xeno-canto.org/143147
104725	Setophaga occidentalis	Walter Szeliga	https://www.xeno-canto.org/104725
34652	Setophaga graciae	Andrew Spencer	https://www.xeno-canto.org/34652
333564	Setophaga graciae	Richard E. Webster	https://www.xeno-canto.org/333564
153516	Setophaga graciae	Paul Marvin	https://www.xeno-canto.org/153516
235007	Setophaga graciae	Garrett MacDonald	https://www.xeno-canto.org/235007
56222	Setophaga nigrescens	Scott Olmstead	https://www.xeno-canto.org/56222
293949	Setophaga nigrescens	Patrick Turgeon	https://www.xeno-canto.org/293949
175373	Setophaga nigrescens	Micah Riegner	https://www.xeno-canto.org/175373
364282	Setophaga nigrescens	Ken Blankenship	https://www.xeno-canto.org/364282
79605	Cardellina pusilla	Andrew Spencer	https://www.xeno-canto.org/79605
55017	Cardellina pusilla	Andrew Spencer	https://www.xeno-canto.org/55017
102395	Cardellina rubrifrons	Scott Olmstead	https://www.xeno-canto.org/102395
34328	Cardellina rubrifrons	Andrew Spencer	https://www.xeno-canto.org/34328
299339	Cardellina rubrifrons	Lauren Harter	https://www.xeno-canto.org/299339
324538	Cardellina rubrifrons	Richard E. Webster	https://www.xeno-canto.org/324538
342584	Icterus bullockii	Bruce Lagerquist	https://www.xeno-canto.org/342584
34869	Icterus bullockii	Tayler Brooks	https://www.xeno-canto.org/34869
185570	Icterus galbula	Richard E. Webster	https://www.xeno-canto.org/185570
185570	Icterus galbula	Richard E. Webster	https://www.xeno-canto.org/185570

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Recording_ID	Species	Recordist	Url
178046	Icterus galbula	Jonathon Jongsma	https://www.xeno-canto.org/178046
134872	Icterus galbula	Jonathon Jongsma	https://www.xeno-canto.org/134872
278197	Sonus naturalis	Patrick Turgeon	https://www.xeno-canto.org/278197
160813	Icterus galbula	Ian Cruickshank	https://www.xeno-canto.org/160813
71058	Icterus parisorum	Mary Beth Stowe	https://www.xeno-canto.org/71058
34323	Icterus parisorum	Andrew Spencer	https://www.xeno-canto.org/34323
71057	Icterus parisorum	Mary Beth Stowe	https://www.xeno-canto.org/71057
71057	Icterus parisorum	Mary Beth Stowe	https://www.xeno-canto.org/71057
224636	Icterus parisorum	Peter Boesman	https://www.xeno-canto.org/224636
224638	Icterus parisorum	Peter Boesman	https://www.xeno-canto.org/224638
358991	Icterus graduacauda	Paul Marvin	https://www.xeno-canto.org/358991
330587	Icterus graduacauda	Andrew Spencer	https://www.xeno-canto.org/330587
330605	Icterus graduacauda	Andrew Spencer	https://www.xeno-canto.org/330605
224599	Icterus graduacauda	Peter Boesman	https://www.xeno-canto.org/224599
360193	Icterus graduacauda	Paul Marvin	https://www.xeno-canto.org/360193
190409	Icterus graduacauda	Andrew Spencer	https://www.xeno-canto.org/190409
286430	Icterus spurius	Paul Marvin	https://www.xeno-canto.org/286430
173791	Icterus spurius	Paul Marvin	https://www.xeno-canto.org/173791
173791	Icterus spurius	Paul Marvin	https://www.xeno-canto.org/173791
173791	Icterus spurius	Paul Marvin	https://www.xeno-canto.org/173791
56323	Icterus spurius	Chuck Davis	https://www.xeno-canto.org/56323
56323	Icterus spurius	Chuck Davis	https://www.xeno-canto.org/56323
371807	Icterus cucullatus	Manuel Grosselet	https://www.xeno-canto.org/371807
371807	Icterus cucullatus	Manuel Grosselet	https://www.xeno-canto.org/371807
299105	Icterus cucullatus	Paul Marvin	https://www.xeno-canto.org/299105
299105	Icterus cucullatus	Paul Marvin	https://www.xeno-canto.org/299105
313460	Icterus cucullatus	Manuel Grosselet	https://www.xeno-canto.org/313460
371807	Icterus cucullatus	Manuel Grosselet	https://www.xeno-canto.org/371807
275165	Molothrus bonariensis	Robert S. Ridgely	https://www.xeno-canto.org/275165
364743	Molothrus bonariensis	Paul Marvin	https://www.xeno-canto.org/364743
315047	Molothrus bonariensis	Paul Marvin	https://www.xeno-canto.org/315047
197319	Molothrus bonariensis	Paul Marvin	https://www.xeno-canto.org/197319
131566	Molothrus ater	Eric DeFonso	https://www.xeno-canto.org/131566
160985	Molothrus ater	Paul Marvin	https://www.xeno-canto.org/160985

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Recording_ID	Species	Recordist	Url
197272	Molothrus ater	Paul Marvin	https://www.xeno-canto.org/197272
160987	Molothrus ater	Paul Marvin	https://www.xeno-canto.org/160987
358848	Agelaius tricolor	Jim Holmes	https://www.xeno-canto.org/358848
162048	Agelaius tricolor	Paul Marvin	https://www.xeno-canto.org/162048
191985	Agelaius phoeniceus	Patrick Turgeon	https://www.xeno-canto.org/191985
167989	Agelaius phoeniceus	Ian Cruickshank	https://www.xeno-canto.org/167989
164257	Agelaius phoeniceus	Ian Cruickshank	https://www.xeno-canto.org/164257
125253	Agelaius phoeniceus	Thomas G. Graves	https://www.xeno-canto.org/125253
307865	Agelaius phoeniceus	Thomas G. Graves	https://www.xeno-canto.org/307865
363449	Agelaius phoeniceus	Thomas G. Graves	https://www.xeno-canto.org/363449
64532	Quiscalus major	Mike Nelson	https://www.xeno-canto.org/64532
317042	Quiscalus major	Jim Holmes	https://www.xeno-canto.org/317042
317165	Quiscalus major	Dan Lane	https://www.xeno-canto.org/317165
254941	Quiscalus major	Nick Komar	https://www.xeno-canto.org/254941
176148	Quiscalus mexicanus	Ted Floyd	https://www.xeno-canto.org/176148
163159	Quiscalus mexicanus	Paul Marvin	https://www.xeno-canto.org/163159
163159	Quiscalus mexicanus	Paul Marvin	https://www.xeno-canto.org/163159
163159	Quiscalus mexicanus	Paul Marvin	https://www.xeno-canto.org/163159
378600	Euphagus cyanocephalus	Thomas Magarian	https://www.xeno-canto.org/378600
352025	Euphagus cyanocephalus	Bruce Lagerquist	https://www.xeno-canto.org/352025
286407	Euphagus carolinus	Bobby Wilcox	https://www.xeno-canto.org/286407
65829	Euphagus carolinus	Ian Cruickshank	https://www.xeno-canto.org/65829
333314	Dolichonyx oryzivorus	Nathan Hentze	https://www.xeno-canto.org/333314
185815	Dolichonyx oryzivorus	Richard E. Webster	https://www.xeno-canto.org/185815
110084	Xanthocephalus xanthocephalus	Andrew Spencer	https://www.xeno-canto.org/110084
302568	Xanthocephalus xanthocephalus	James Bradley	https://www.xeno-canto.org/302568
320486	Sturnella magna	Jonathon Jongsma	https://www.xeno-canto.org/320486
320478	Sturnella magna	Jonathon Jongsma	https://www.xeno-canto.org/320478
320478	Sturnella magna	Jonathon Jongsma	https://www.xeno-canto.org/320478
373464	Sturnella magna	Bobby Wilcox	https://www.xeno-canto.org/373464
313791	Sturnella magna	Matt Wistrand	https://www.xeno-canto.org/313791
321630	Sturnella magna	Tom Behnfield	https://www.xeno-canto.org/321630
76505	Sturnella neglecta	Jonathon Jongsma	https://www.xeno-canto.org/76505
55149	Sturnella neglecta	Todd Wilson	https://www.xeno-canto.org/55149

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Recording_ID	Species	Recordist	Url
14290	Sturnella neglecta	Andrew Spencer	https://www.xeno-canto.org/14290
104524	Sturnella neglecta	Jonathon Jongsma	https://www.xeno-canto.org/104524
179850	Chondestes grammacus	Ted Floyd	https://www.xeno-canto.org/179850
76967	Chondestes grammacus	Andrew Spencer	https://www.xeno-canto.org/76967
76967	Chondestes grammacus	Andrew Spencer	https://www.xeno-canto.org/76967
184978	Chondestes grammacus	Richard E. Webster	https://www.xeno-canto.org/184978
14299	Calamospiza melanocorys	Chris Parrish	https://www.xeno-canto.org/14299
192321	Calamospiza melanocorys	Paul Marvin	https://www.xeno-canto.org/192321
185132	Calamospiza melanocorys	Richard E. Webster	https://www.xeno-canto.org/185132
13604	Calamospiza melanocorys	Andrew Spencer	https://www.xeno-canto.org/13604
297494	Melozone aberti	Ross Gallardy	https://www.xeno-canto.org/297494
111857	Melozone aberti	Richard E Webster	https://www.xeno-canto.org/111857
297494	Melozone aberti	Ross Gallardy	https://www.xeno-canto.org/297494
79661	Melozone aberti	Scott Olmstead	https://www.xeno-canto.org/79661
376023	Melozone aberti	Antonio Xeira	https://www.xeno-canto.org/376023
247614	Melozone aberti	Patrick Turgeon	https://www.xeno-canto.org/247614
297483	Melozone crissalis	Ross Gallardy	https://www.xeno-canto.org/297483
126358	Melozone crissalis	Richard E. Webster	https://www.xeno-canto.org/126358
370508	Pipilo erythrophthalmus	Eric DeFonso	https://www.xeno-canto.org/370508
254338	Pipilo erythrophthalmus	Bryan Calk	https://www.xeno-canto.org/254338
228170	Pipilo erythrophthalmus	Peter Boesman	https://www.xeno-canto.org/228170
78874	Pipilo erythrophthalmus	Jonathon Jongsma	https://www.xeno-canto.org/78874
213439	Pipilo maculatus	Oscar Ballesteors	https://www.xeno-canto.org/213439
54425	Pipilo maculatus	Mike Nelson	https://www.xeno-canto.org/54425
104527	Pipilo maculatus	Jonathon Jongsma	https://www.xeno-canto.org/104527
373799	Pipilo maculatus	Patrick Turgeon	https://www.xeno-canto.org/373799
320479	Ammodramus henslowii	Jonathon Jongsma	https://www.xeno-canto.org/320479
302528	Ammodramus henslowii	Lauren Harter	https://www.xeno-canto.org/302528
6758	Ammodramus bairdii	Darrell L. Peterson	https://www.xeno-canto.org/6758
103658	Ammodramus bairdii	Andrew Spencer	https://www.xeno-canto.org/103658
185576	Ammodramus bairdii	Richard E. Webster	https://www.xeno-canto.org/185576
321046	Melospiza georgiana	Michael Harrison	https://www.xeno-canto.org/321046
294004	Melospiza georgiana	Martin St-Michel	https://www.xeno-canto.org/294004
256458	Melospiza lincolnii	Ian Cruickshank	https://www.xeno-canto.org/256458

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Recording_ID	Species	Recordist	Url
302413	Melospiza lincolnii	James Bradley	https://www.xeno-canto.org/302413
55559	Ammodramus caudacutus	Andrew Spencer	https://www.xeno-canto.org/55559
59191	Ammodramus caudacutus	Tayler Brooks	https://www.xeno-canto.org/59191
55204	Ammodramus nelsoni	Andrew Spencer	https://www.xeno-canto.org/55204
110145	Ammodramus nelsoni	Andrew Spencer	https://www.xeno-canto.org/110145
373914	Junco phaeonotus	Scott Olmstead	https://www.xeno-canto.org/373914
253912	Junco phaeonotus	Bobby Wilcox	https://www.xeno-canto.org/253912
241177	Junco phaeonotus	Jarrod Swackhamer	https://www.xeno-canto.org/241177
253909	Junco phaeonotus	Bobby Wilcox	https://www.xeno-canto.org/253909
321752	Junco phaeonotus	Richard E. Webster	https://www.xeno-canto.org/321752
321764	Junco phaeonotus	Richard E. Webster	https://www.xeno-canto.org/321764
76622	Junco hyemalis	Andrew Spencer	https://www.xeno-canto.org/76622
314047	Junco hyemalis	Ken Blankenship	https://www.xeno-canto.org/314047
111224	Junco hyemalis	Richard E Webster	https://www.xeno-canto.org/111224
111225	Junco hyemalis	Richard E Webster	https://www.xeno-canto.org/111225
111225	Junco hyemalis	Richard E Webster	https://www.xeno-canto.org/111225
169518	Junco hyemalis	Micah Riegner	https://www.xeno-canto.org/169518
354817	Zonotrichia atricapilla	Frank Lambert	https://www.xeno-canto.org/354817
322859	Zonotrichia atricapilla	Peter Boesman	https://www.xeno-canto.org/322859
322889	Zonotrichia leucophrys	Peter Boesman	https://www.xeno-canto.org/322889
353498	Zonotrichia leucophrys	Frank Lambert	https://www.xeno-canto.org/353498
322623	Amphispiza bilineata	Richard E. Webster	https://www.xeno-canto.org/322623
111338	Amphispiza bilineata	Richard E Webster	https://www.xeno-canto.org/111338
297533	Amphispiza bilineata	Ross Gallardy	https://www.xeno-canto.org/297533
322635	Amphispiza bilineata	Richard E. Webster	https://www.xeno-canto.org/322635
34419	Amphispiza quinquestriata	Andrew Spencer	https://www.xeno-canto.org/34419
87005	Amphispiza quinquestriata	Daniel Lane	https://www.xeno-canto.org/87005
41239	Amphispiza quinquestriata	Scott Olmstead	https://www.xeno-canto.org/41239
234106	Amphispiza quinquestriata	James and David Bradley	https://www.xeno-canto.org/234106
186399	Spizella breweri	Richard E. Webster	https://www.xeno-canto.org/186399
341518	Spizella breweri	Thomas Magarian	https://www.xeno-canto.org/341518
142631	Spizella pusilla	Jonathon Jongsma	https://www.xeno-canto.org/142631
1379	Spizella pusilla	Robin Carter	https://www.xeno-canto.org/1379

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Recording_ID	Species	Recordist	Url
160801	Spizella pallida	Ian Cruickshank	https://www.xeno-canto.org/160801
186813	Spizella pallida	Richard E. Webster	https://www.xeno-canto.org/186813
14415	Spizella passerina	Chris Parrish	https://www.xeno-canto.org/14415
188094	Spizella passerina	Richard E. Webster	https://www.xeno-canto.org/188094
13646	Spizella passerina	Chris Parrish	https://www.xeno-canto.org/13646
189062	Spizella passerina	Richard E. Webster	https://www.xeno-canto.org/189062
195836	Spizella passerina	Richard E. Webster	https://www.xeno-canto.org/195836
138703	Spizella passerina	Garrett MacDonald	https://www.xeno-canto.org/138703
83720	Ammodramus savannarum	James Morgan	https://www.xeno-canto.org/83720
246800	Ammodramus savannarum	Eric DeFonso	https://www.xeno-canto.org/246800
176151	Arremonops rufivirgatus	Ted Floyd	https://www.xeno-canto.org/176151
164249	Arremonops rufivirgatus	Paul Marvin	https://www.xeno-canto.org/164249
33516	Peucaea aestivalis	Andrew Spencer	https://www.xeno-canto.org/33516
33781	Peucaea aestivalis	Andrew Spencer	https://www.xeno-canto.org/33781
152127	Peucaea aestivalis	Dan Lane	https://www.xeno-canto.org/152127
135133	Peucaea aestivalis	Dan Lane	https://www.xeno-canto.org/135133
111468	Peucaea cassinii	Richard E Webster	https://www.xeno-canto.org/111468
360791	Peucaea cassinii	Antonio Xeira	https://www.xeno-canto.org/360791
111468	Peucaea cassinii	Richard E Webster	https://www.xeno-canto.org/111468
123897	Peucaea cassinii	Chris Harrison	https://www.xeno-canto.org/123897
13594	Peucaea cassinii	Andrew Spencer	https://www.xeno-canto.org/13594
172649	Peucaea cassinii	Eric DeFonso	https://www.xeno-canto.org/172649
14960	Passerina caerulea	Andrew Spencer	https://www.xeno-canto.org/14960
191550	Passerina caerulea	Phoenix Birder	https://www.xeno-canto.org/191550
375861	Passerina amoena	Jeremy Welch	https://www.xeno-canto.org/375861
206004	Passerina amoena	Eric DeFonso	https://www.xeno-canto.org/206004
277012	Passerina ciris	Paul Marvin	https://www.xeno-canto.org/277012
371810	Passerina ciris	Manuel Grosselet	https://www.xeno-canto.org/371810
266317	Passerina versicolor	Richard E. Webster	https://www.xeno-canto.org/266317
34436	Passerina versicolor	Andrew Spencer	https://www.xeno-canto.org/34436
382102	Passerina versicolor	Manuel Grosselet	https://www.xeno-canto.org/382102
6658	Passerina versicolor	Manuel Grosselet	https://www.xeno-canto.org/6658
369969	Pheucticus melanocephalus	Eric DeFonso	https://www.xeno-canto.org/369969
172821	Pheucticus melanocephalus	Eric DeFonso	https://www.xeno-canto.org/172821

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Recording_ID	Species	Recordist	Url
109305	Pheucticus melanocephalus	Andrew Spencer	https://www.xeno-canto.org/109305
254456	Pheucticus melanocephalus	Jonathon Jongsma	https://www.xeno-canto.org/254456
315288	Pheucticus ludovicianus	Antonio Xeira	https://www.xeno-canto.org/315288
134880	Pheucticus ludovicianus	Jonathon Jongsma	https://www.xeno-canto.org/134880
373511	Pheucticus ludovicianus	Bobby Wilcox	https://www.xeno-canto.org/373511
181480	Piranga ludoviciana	Randy Dzenkiw	https://www.xeno-canto.org/181480
190053	Piranga ludoviciana	Richard E. Webster	https://www.xeno-canto.org/190053
192752	Piranga ludoviciana	Paul Marvin	https://www.xeno-canto.org/192752
302200	Piranga ludoviciana	James Bradley	https://www.xeno-canto.org/302200
144033	Piranga olivacea	Laura Gooch	https://www.xeno-canto.org/144033
179639	Piranga olivacea	Martin St-Michel	https://www.xeno-canto.org/179639
291932	Piranga olivacea	Martin St-Michel	https://www.xeno-canto.org/291932
17153	Piranga olivacea	Allen T. Chartier	https://www.xeno-canto.org/17153
244067	Piranga olivacea	Maxime Aubert	https://www.xeno-canto.org/244067
17152	Piranga olivacea	Allen T. Chartier	https://www.xeno-canto.org/17152
368457	Cardinalis sinuatus	Dan Lane	https://www.xeno-canto.org/368457
322450	Cardinalis sinuatus	Richard E. Webster	https://www.xeno-canto.org/322450
382035	Cardinalis sinuatus	Manuel Grosselet	https://www.xeno-canto.org/382035
322440	Cardinalis sinuatus	Richard E. Webster	https://www.xeno-canto.org/322440
235432	Cardinalis cardinalis	Danny Zapata-Henao	https://www.xeno-canto.org/235432
291402	Cardinalis cardinalis	Eric Hough	https://www.xeno-canto.org/291402
297495	Cardinalis cardinalis	Ross Gallardy	https://www.xeno-canto.org/297495
285316	Cardinalis cardinalis	Paul Marvin	https://www.xeno-canto.org/285316
26684	Anthus cervinus	Patrik Åberg	https://www.xeno-canto.org/26684
105855	Cinnyris solaris	Colin Trainor	https://www.xeno-canto.org/105855
26684	Anthus cervinus	Patrik Åberg	https://www.xeno-canto.org/26684
382130	Anthus cervinus	Jens Kirkeby	https://www.xeno-canto.org/382130
203607	Anthus rubescens	Andrew Spencer	https://www.xeno-canto.org/203607
203608	Anthus rubescens	Andrew Spencer	https://www.xeno-canto.org/203608
62832	Motacilla flava	Holger Schielzeth	https://www.xeno-canto.org/62832
362774	Motacilla flava	Dimitri	https://www.xeno-canto.org/362774
345893	Motacilla alba	Tero Linjama	https://www.xeno-canto.org/345893
374719	Motacilla alba	Frank A. Roos	https://www.xeno-canto.org/374719
215457	Aphelocoma woodhouseii	Kristie Nelson	https://www.xeno-canto.org/215457

(continued)

Recording_ID	Species	Recordist	Url
290279	Aphelocoma woodhouseii	Manuel Grosselet	https://www.xeno-canto.org/290279
215457	Aphelocoma woodhouseii	Kristie Nelson	https://www.xeno-canto.org/215457
360967	Aphelocoma californica	Paul Marvin	https://www.xeno-canto.org/360967
297455	Aphelocoma californica	Ross Gallardy	https://www.xeno-canto.org/297455
349731	Aphelocoma californica	Paul Marvin	https://www.xeno-canto.org/349731
352935	Troglodytes pacificus	Frank Lambert	https://www.xeno-canto.org/352935
195801	Troglodytes pacificus	Richard E. Webster	https://www.xeno-canto.org/195801
193225	Troglodytes pacificus	Richard E. Webster	https://www.xeno-canto.org/193225
195054	Troglodytes pacificus	Richard E. Webster	https://www.xeno-canto.org/195054
193993	Troglodytes pacificus	Richard E. Webster	https://www.xeno-canto.org/193993
195801	Troglodytes pacificus	Richard E. Webster	https://www.xeno-canto.org/195801
351174	Troglodytes hiemalis	Richard E. Webster	https://www.xeno-canto.org/351174
103884	Troglodytes hiemalis	Todd Wilson	https://www.xeno-canto.org/103884
103884	Troglodytes hiemalis	Todd Wilson	https://www.xeno-canto.org/103884
188933	Troglodytes hiemalis	Richard E. Webster	https://www.xeno-canto.org/188933
377372	Troglodytes hiemalis	Michael Harrison	https://www.xeno-canto.org/377372
188931	Troglodytes hiemalis	Richard E. Webster	https://www.xeno-canto.org/188931
262814	Artemisiospiza nevadensis	Lance A. M. Benner	https://www.xeno-canto.org/262814
364570	Artemisiospiza nevadensis	Jim Holmes	https://www.xeno-canto.org/364570
368296	Artemisiospiza belli	Jim Holmes	https://www.xeno-canto.org/368296
309039	Artemisiospiza belli	Shannon Skalos	https://www.xeno-canto.org/309039
303354	Sitta pygmaea	Ted Floyd	https://www.xeno-canto.org/303354
343422	Sitta pygmaea	Bruce Lagerquist	https://www.xeno-canto.org/343422
161393	Sitta pygmaea	Paul Marvin	https://www.xeno-canto.org/161393
363167	Sitta pygmaea	Frank Lambert	https://www.xeno-canto.org/363167
362017	Sitta canadensis	Frank Lambert	https://www.xeno-canto.org/362017
269235	Sitta canadensis	Frank Lambert	https://www.xeno-canto.org/269235
269235	Sitta canadensis	Frank Lambert	https://www.xeno-canto.org/269235
172414	Sitta canadensis	Eric DeFonso	https://www.xeno-canto.org/172414
255797	Toxostoma curvirostre	Richard E. Webster	https://www.xeno-canto.org/255797
309812	Toxostoma curvirostre	Manuel Grosselet	https://www.xeno-canto.org/309812
368460	Toxostoma curvirostre	Dan Lane	https://www.xeno-canto.org/368460
371093	Toxostoma curvirostre	Manuel Grosselet	https://www.xeno-canto.org/371093
21656	Toxostoma longirostre	Chris Parrish	https://www.xeno-canto.org/21656

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Recording_ID	Species	Recordist	Url
5077	Toxostoma longirostre	Nathan Pieplow	https://www.xeno-canto.org/5077
368455	Toxostoma longirostre	Dan Lane	https://www.xeno-canto.org/368455
176252	Toxostoma longirostre	Ted Floyd	https://www.xeno-canto.org/176252
253571	Geothlypis philadelphia	Martin St-Michel	https://www.xeno-canto.org/253571
142746	Geothlypis philadelphia	Martin St-Michel	https://www.xeno-canto.org/142746
252951	Oporornis agilis	Nancy Hetrick	https://www.xeno-canto.org/252951
181481	Oporornis agilis	Randy Dzenkiw	https://www.xeno-canto.org/181481
244475	Molothrus aeneus	Bobby Wilcox	https://www.xeno-canto.org/244475
246087	Molothrus aeneus	Scott Olmstead	https://www.xeno-canto.org/246087
333844	Molothrus aeneus	Richard E. Webster	https://www.xeno-canto.org/333844
246087	Molothrus aeneus	Scott Olmstead	https://www.xeno-canto.org/246087
131566	Molothrus ater	Eric DeFonso	https://www.xeno-canto.org/131566
160985	Molothrus ater	Paul Marvin	https://www.xeno-canto.org/160985
197272	Molothrus ater	Paul Marvin	https://www.xeno-canto.org/197272
160987	Molothrus ater	Paul Marvin	https://www.xeno-canto.org/160987
297494	Melozone aberti	Ross Gallardy	https://www.xeno-canto.org/297494
111857	Melozone aberti	Richard E Webster	https://www.xeno-canto.org/111857
297494	Melozone aberti	Ross Gallardy	https://www.xeno-canto.org/297494
79661	Melozone aberti	Scott Olmstead	https://www.xeno-canto.org/79661
376023	Melozone aberti	Antonio Xeira	https://www.xeno-canto.org/376023
247614	Melozone aberti	Patrick Turgeon	https://www.xeno-canto.org/247614
323281	Melozone fusca	Richard E. Webster	https://www.xeno-canto.org/323281
257200	Melozone fusca	Scott Olmstead	https://www.xeno-canto.org/257200
323281	Melozone fusca	Richard E. Webster	https://www.xeno-canto.org/323281
18127	Melozone fusca	Andrew Spencer	https://www.xeno-canto.org/18127
297491	Peucaea botterii	Ross Gallardy	https://www.xeno-canto.org/297491
196552	Peucaea botterii	Dan Lane	https://www.xeno-canto.org/196552
111468	Peucaea cassinii	Richard E Webster	https://www.xeno-canto.org/111468
360791	Peucaea cassinii	Antonio Xeira	https://www.xeno-canto.org/360791
268679	Myiarchus tyrannulus	Richard E. Webster	https://www.xeno-canto.org/268679
35375	Myiarchus tyrannulus	Andrew Spencer	https://www.xeno-canto.org/35375
122918	Myiarchus cinerascens	Richard E. Webster	https://www.xeno-canto.org/122918
318523	Myiarchus cinerascens	Jarrod Swackhamer	https://www.xeno-canto.org/318523
184465	Catharus fuscescens	Martin St-Michel	https://www.xeno-canto.org/184465

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Recording_ID	Species	Recordist	Url
318447	Catharus fuscescens	Jim Berry	https://www.xeno-canto.org/318447
30771	Catharus fuscescens	Andrew Spencer	https://www.xeno-canto.org/30771
30771	Catharus fuscescens	Andrew Spencer	https://www.xeno-canto.org/30771
293438	Catharus fuscescens	Martin St-Michel	https://www.xeno-canto.org/293438
142745	Catharus fuscescens	Martin St-Michel	https://www.xeno-canto.org/142745
54830	Catharus bicknelli	Andrew Spencer	https://www.xeno-canto.org/54830
160919	Catharus bicknelli	Paul Marvin	https://www.xeno-canto.org/160919
79605	Cardellina pusilla	Andrew Spencer	https://www.xeno-canto.org/79605
55017	Cardellina pusilla	Andrew Spencer	https://www.xeno-canto.org/55017
79614	Cardellina canadensis	Andrew Spencer	https://www.xeno-canto.org/79614
186311	Cardellina canadensis	Martin St-Michel	https://www.xeno-canto.org/186311
296170	Cardellina canadensis	Paul Marvin	https://www.xeno-canto.org/296170
318455	Cardellina canadensis	Jim Berry	https://www.xeno-canto.org/318455
55559	Ammodramus caudacutus	Andrew Spencer	https://www.xeno-canto.org/55559
59191	Ammodramus caudacutus	Tayler Brooks	https://www.xeno-canto.org/59191
59157	Ammodramus maritimus	Tayler Brooks	https://www.xeno-canto.org/59157
359417	Ammodramus maritimus	Linda Stehlik	https://www.xeno-canto.org/359417
319003	Piranga ludoviciana	Ted Floyd	https://www.xeno-canto.org/319003
323204	Piranga ludoviciana	Richard E. Webster	https://www.xeno-canto.org/323204
1252	Piranga ludoviciana	Don Jones	https://www.xeno-canto.org/1252
14092	Piranga ludoviciana	Andrew Spencer	https://www.xeno-canto.org/14092
293628	Piranga hepatica	Paul Marvin	https://www.xeno-canto.org/293628
35383	Piranga hepatica	Andrew Spencer	https://www.xeno-canto.org/35383
35383	Piranga hepatica	Andrew Spencer	https://www.xeno-canto.org/35383
21764	Piranga hepatica	Chris Parrish	https://www.xeno-canto.org/21764
65375	Pooecetes gramineus	Eric DeFonso	https://www.xeno-canto.org/65375
366656	Pooecetes gramineus	Frank Lambert	https://www.xeno-canto.org/366656
125749	Pooecetes gramineus	Richard E. Webster	https://www.xeno-canto.org/125749
377801	Pooecetes gramineus	Bobby Wilcox	https://www.xeno-canto.org/377801
368296	Artemisiospiza belli	Jim Holmes	https://www.xeno-canto.org/368296
309039	Artemisiospiza belli	Shannon Skalos	https://www.xeno-canto.org/309039
356271	Spizelloides arborea	Frank Lambert	https://www.xeno-canto.org/356271
203711	Spizelloides arborea	Andrew Spencer	https://www.xeno-canto.org/203711
353480	Passerella iliaca	Frank Lambert	https://www.xeno-canto.org/353480

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Recording_ID	Species	Recordist	Url
322857	Passerella iliaca	Peter Boesman	https://www.xeno-canto.org/322857
209847	Zonotrichia querula	Terry Davis	https://www.xeno-canto.org/209847
142845	Zonotrichia querula	Ian Cruickshank	https://www.xeno-canto.org/142845
329881	Zonotrichia albicollis	John Patterson	https://www.xeno-canto.org/329881
329835	Zonotrichia albicollis	John Patterson	https://www.xeno-canto.org/329835
143941	Leucosticte tephrocotis	Andrew Spencer	https://www.xeno-canto.org/143941
143944	Leucosticte tephrocotis	Andrew Spencer	https://www.xeno-canto.org/143944
107919	Leucosticte tephrocotis	Jelmer Poelstra	https://www.xeno-canto.org/107919
344692	Leucosticte tephrocotis	Thomas Magarian	https://www.xeno-canto.org/344692
284845	Leucosticte atrata	Paul Marvin	https://www.xeno-canto.org/284845
143900	Leucosticte atrata	Andrew Spencer	https://www.xeno-canto.org/143900
143749	Leucosticte atrata	Andrew Spencer	https://www.xeno-canto.org/143749
284240	Leucosticte atrata	Paul Marvin	https://www.xeno-canto.org/284240
284544	Leucosticte atrata	Paul Marvin	https://www.xeno-canto.org/284544
143901	Leucosticte atrata	Andrew Spencer	https://www.xeno-canto.org/143901
322979	Poecile hudsonicus	Peter Boesman	https://www.xeno-canto.org/322979
46489	Poecile hudsonicus	Andrew Spencer	https://www.xeno-canto.org/46489
269229	Poecile rufescens	Frank Lambert	https://www.xeno-canto.org/269229
92190	Poecile rufescens	Nathan Pieplow	https://www.xeno-canto.org/92190
360934	Poecile carolinensis	Matt Brady	https://www.xeno-canto.org/360934
309927	Poecile carolinensis	J.R. Rigby	https://www.xeno-canto.org/309927
169225	Poecile sclateri	Paul Marvin	https://www.xeno-canto.org/169225
255743	Poecile sclateri	Frank Lambert	https://www.xeno-canto.org/255743
34325	Poecile sclateri	Andrew Spencer	https://www.xeno-canto.org/34325
317973	Poecile sclateri	Jim Holmes	https://www.xeno-canto.org/317973
103759	Limnothlypis swainsonii	Mike Nelson	https://www.xeno-canto.org/103759
59134	Limnothlypis swainsonii	Tayler Brooks	https://www.xeno-canto.org/59134
33466	Protonotaria citrea	Andrew Spencer	https://www.xeno-canto.org/33466
316226	Protonotaria citrea	Bates Estabrooks	https://www.xeno-canto.org/316226
59145	Geothlypis formosa	Tayler Brooks	https://www.xeno-canto.org/59145
20433	Geothlypis formosa	Chris Parrish	https://www.xeno-canto.org/20433
316231	Geothlypis trichas	Antonio Xeira	https://www.xeno-canto.org/316231
362478	Geothlypis trichas	Scott Gravette	https://www.xeno-canto.org/362478
78803	Setophaga ruticilla	Andrew Spencer	https://www.xeno-canto.org/78803

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Recording_ID	Species	Recordist	Url
293435	Setophaga ruticilla	Martin St-Michel	https://www.xeno-canto.org/293435
179305	Setophaga ruticilla	Martin St-Michel	https://www.xeno-canto.org/179305
247312	Setophaga ruticilla	Iain	https://www.xeno-canto.org/247312
59119	Setophaga caerulescens	Tayler Brooks	https://www.xeno-canto.org/59119
49874	Setophaga caerulescens	Andrew Spencer	https://www.xeno-canto.org/49874
133250	Setophaga caerulescens	Fernand DEROUSSEN	https://www.xeno-canto.org/133250
186365	Setophaga caerulescens	Martin St-Michel	https://www.xeno-canto.org/186365
13586	Setophaga americana	Chris Parrish	https://www.xeno-canto.org/13586
187645	Setophaga americana	Paul Driver	https://www.xeno-canto.org/187645
134971	Setophaga americana	L G Price	https://www.xeno-canto.org/134971
171645	Setophaga americana	Dan Lane	https://www.xeno-canto.org/171645
83553	Setophaga tigrina	Jelmer Poelstra	https://www.xeno-canto.org/83553
134506	Setophaga tigrina	Martin St-Michel	https://www.xeno-canto.org/134506
365856	Setophaga dominica	Matt Wistrand	https://www.xeno-canto.org/365856
372014	Setophaga dominica	Eric DeFonso	https://www.xeno-canto.org/372014
316232	Setophaga dominica	Antonio Xeira	https://www.xeno-canto.org/316232
312741	Setophaga dominica	Aidan Place	https://www.xeno-canto.org/312741
81084	Setophaga pinus	Mike Nelson	https://www.xeno-canto.org/81084
87973	Setophaga pinus	Mike Nelson	https://www.xeno-canto.org/87973
316727	Setophaga pinus	Matt Wistrand	https://www.xeno-canto.org/316727
356277	Setophaga pinus	Scott Gravette	https://www.xeno-canto.org/356277
299197	Turdus obscurus	Albert Lastukhin & Vadim Ivushkin	https://www.xeno-canto.org/299197
299196	Turdus obscurus	Albert Lastukhin & Vadim Ivushkin	https://www.xeno-canto.org/299196
113696	Turdus obscurus	Adria Sole	https://www.xeno-canto.org/113696
299196	Turdus obscurus	Albert Lastukhin & Vadim Ivushkin	https://www.xeno-canto.org/299196
351863	Turdus migratorius	Richard E. Webster	https://www.xeno-canto.org/351863
322822	Turdus migratorius	Peter Boesman	https://www.xeno-canto.org/322822
322797	Turdus migratorius	Peter Boesman	https://www.xeno-canto.org/322797
353500	Turdus migratorius	Frank Lambert	https://www.xeno-canto.org/353500
327514	Turdus rufopalliatus	Manuel Grosselet	https://www.xeno-canto.org/327514

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Recording_ID	Species	Recordist	Url
314225	Turdus rufopalliatus	Manuel Grosselet	https://www.xeno-canto.org/314225
317533	Turdus rufopalliatus	Manuel Grosselet	https://www.xeno-canto.org/317533
6243	Turdus rufopalliatus	Manuel Grosselet	https://www.xeno-canto.org/6243
277327	Turdus grayi	Paul Marvin	https://www.xeno-canto.org/277327
277034	Turdus grayi	Paul Marvin	https://www.xeno-canto.org/277034
330611	Turdus grayi	Andrew Spencer	https://www.xeno-canto.org/330611
147307	Turdus grayi	Paul Marvin	https://www.xeno-canto.org/147307
103087	Empidonax wrightii	Eric DeFonso	https://www.xeno-canto.org/103087
14088	Empidonax wrightii	Chris Parrish	https://www.xeno-canto.org/14088
35909	Empidonax minimus	Tayler Brooks	https://www.xeno-canto.org/35909
248003	Empidonax minimus	Ryan P. O'Donnell	https://www.xeno-canto.org/248003
359298	Tyrannus melancholicus	Kent Livezey	https://www.xeno-canto.org/359298
308701	Tyrannus melancholicus	Mario Trejo	https://www.xeno-canto.org/308701
133304	Tyrannus couchii	Andrew Spencer	https://www.xeno-canto.org/133304
305522	Tyrannus couchii	Paul Marvin	https://www.xeno-canto.org/305522
306945	Vireo huttoni	Scott Olmstead	https://www.xeno-canto.org/306945
323411	Vireo huttoni	Richard E. Webster	https://www.xeno-canto.org/323411
235061	Vireo huttoni	Garrett MacDonald	https://www.xeno-canto.org/235061
235062	Vireo huttoni	Garrett MacDonald	https://www.xeno-canto.org/235062
279009	Vireo huttoni	Nick Komar	https://www.xeno-canto.org/279009
297530	Vireo huttoni	Ross Gallardy	https://www.xeno-canto.org/297530
80612	Vireo vicinior	Scott Olmstead	https://www.xeno-canto.org/80612
179357	Vireo vicinior	Tim Marquardt	https://www.xeno-canto.org/179357
282205	Vireo vicinior	Paul Marvin	https://www.xeno-canto.org/282205
282192	Vireo vicinior	Paul Marvin	https://www.xeno-canto.org/282192
282184	Vireo vicinior	Paul Marvin	https://www.xeno-canto.org/282184
334409	Vireo vicinior	Scott Gravette	https://www.xeno-canto.org/334409
34881	Vireo bellii	Andrew Spencer	https://www.xeno-canto.org/34881
109424	Vireo bellii	Paul Marvin	https://www.xeno-canto.org/109424
34881	Vireo bellii	Andrew Spencer	https://www.xeno-canto.org/34881
34315	Vireo bellii	Andrew Spencer	https://www.xeno-canto.org/34315
160976	Vireo atricapilla	Paul Marvin	https://www.xeno-canto.org/160976
152882	Vireo atricapilla	Andrew Spencer	https://www.xeno-canto.org/152882
34844	Vireo atricapilla	Andrew Spencer	https://www.xeno-canto.org/34844

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Recording_ID	Species	Recordist	Url
21738	Vireo atricapilla	Chris Parrish	https://www.xeno-canto.org/21738
133059	Vireo atricapilla	Andrew Spencer	https://www.xeno-canto.org/133059
105703	Vireo atricapilla	Nathan Pieplow	https://www.xeno-canto.org/105703
145771	Vireo altiloquus	Paul Marvin	https://www.xeno-canto.org/145771
173666	Vireo altiloquus	Eric DeFonso	https://www.xeno-canto.org/173666
104635	Vireo altiloquus	Andrew Spencer	https://www.xeno-canto.org/104635
308673	Vireo altiloquus	Ross Gallardy	https://www.xeno-canto.org/308673
196029	Vireo altiloquus	Paul Marvin	https://www.xeno-canto.org/196029
213218	Vireo altiloquus	Albert Lastukhin & Max Lastukhin	https://www.xeno-canto.org/213218
252426	Vireo flavoviridis	Dan Lane	https://www.xeno-canto.org/252426
334255	Vireo flavoviridis	Jeff Norris	https://www.xeno-canto.org/334255
28547	Vireo flavoviridis	Daniel Lane	https://www.xeno-canto.org/28547
252424	Vireo flavoviridis	Dan Lane	https://www.xeno-canto.org/252424
359505	Aphelocoma insularis	Paul Marvin	https://www.xeno-canto.org/359505
358426	Aphelocoma insularis	Paul Marvin	https://www.xeno-canto.org/358426
360967	Aphelocoma californica	Paul Marvin	https://www.xeno-canto.org/360967
297455	Aphelocoma californica	Ross Gallardy	https://www.xeno-canto.org/297455
349731	Aphelocoma californica	Paul Marvin	https://www.xeno-canto.org/349731

Table S3 Acoustic parameters extracted using the R package warbleR or calculated with R. Most variables were transformed prior to phylogenetic principal component analysis to be approximately normally distributed.

Acoustic Parameters	Transformations
Duration	log(x + 0.01)
Mean frequency	log(x + 0.01)
Standard deviation of frequency	log(x + 0.01)
Median frequency	log(x + 0.01)
First quartile frequency	log(x + 0.01)
Third quartile frequency	log(x + 0.01)
Frequency interquartile range	log(x + 0.01)
Median time (time at which the signal is divided in two time intervals of equal energy)	log(x + 0.01)
First quartile time	log(x + 0.01)
Third quartile time	log(x + 0.01)
Time interquartile range	log(x + 0.01)
Spectral skewness	reciprocal
Spectral kurtosis (peakedness)	log(x + 0.01)
Spectral entropy (energy distribution of the frequency spectrum)	
Time entropy (energy distribution on the time envelope)	
Product of time and spectral entropy	
Spectral flatness	log(x + 0.01)
Average of fundamental frequency	log(x + 0.01)
Minimum fundamental frequency	log(x + 0.01)
Average dominant frequency	log(x + 0.01)
Maximum of dominant frequency	sqrt
Minimum dominant frequency	sqrt
Range of dominant frequency measured across the acoustic signal	sqrt
Modulation index	log(x + 0.01)
Dominant frequency measurement at the start of the signal	sqrt
Dominant frequency measurement at the end of the signal	sqrt
Slope of the change in dominant frequency through time	
Number of notes	log(x + 0.01)
Note rate	log(x + 0.01)
Length of longest note	log(x + 0.01)
Percentage of the song consisting of notes	
Average note length	log(x + 0.01)

Average pause length	log(x + 0.01)
Length of longest pause	log(x + 0.01)

Table S4 Generalized linear model of ecological predictors of interspecific territoriality.

Selected Predictors	Estimate	Std Error	Z Value	P Value
(Intercept)	0.34	1.45	0.23	0.816
Syntopy	0.08	0.33	0.24	0.811
Hybridization	0.80	0.76	1.06	0.288
Plumage dissimilarity	0.12	0.34	0.34	0.734
Song dissimilarity (pPCA)	-0.37	0.39	-0.96	0.336
Song similarity (SPCC)	0.14	0.44	0.32	0.749
Shape PC	-0.17	0.45	-0.38	0.705
Size PC	0.15	0.30	0.50	0.617
Guild overlap	-0.37	0.54	-0.69	0.490

Table S5 Generalized linear model of ecological predictors of interspecific territoriality, controlling for patristic distance.

Selected Predictors	Estimate	Std Error	Z Value	P Value
(Intercept)	-0.07	1.54	-0.04	0.965
Syntopy	0.02	0.34	0.06	0.954
Hybridization	0.55	0.81	0.68	0.499
Patristic distance	-0.76	0.46	-1.65	0.098
Plumage dissimilarity	0.29	0.36	0.82	0.413
Song dissimilarity (pPCA)	-0.08	0.43	-0.20	0.842
Song similarity (SPCC)	0.16	0.45	0.36	0.721
Shape PC	-0.49	0.51	-0.97	0.334
Size PC	0.08	0.30	0.27	0.785
Guild overlap	-0.15	0.58	-0.26	0.791

Table S6 Generalized linear model predicting interspecific territoriality, with an interaction between hybridization and syntopy, and controlling for patristic distance.

Selected Predictors	Estimate	Std Error	Z Value	P Value
(Intercept)	-0.84	4.00	-0.21	0.833
Syntopy	5.71	2.87	1.99	0.047*
Hybridization	3.52	2.06	1.71	0.088
Patristic distance	-0.99	0.64	-1.55	0.121
Plumage dissimilarity	0.62	0.55	1.13	0.26
Song dissimilarity (pPCA)	-0.02	0.75	-0.02	0.983
Song similarity (SPCC)	-0.81	0.69	-1.17	0.242
Shape PC	-0.40	0.66	-0.61	0.544
Size PC	0.12	0.40	0.31	0.756
Guild overlap	-0.89	1.18	-0.75	0.455
Syntopy x hybridization	-6.63	2.96	-2.24	0.025*

Table S7 Generalized linear model predicting interspecific territoriality, with an interaction between foraging guild and syntopy, and controlling for patristic distance.

Selected Predictors	Estimate	Std Error	Z Value	P Value
(Intercept)	-0.26	1.70	-0.15	0.878
Syntopy	2.03	1.70	1.19	0.234
Guild overlap	-0.04	0.64	-0.07	0.947
Hybridization	0.30	0.88	0.35	0.730
Patristic distance	-0.73	0.47	-1.56	0.119
Plumage dissimilarity	0.22	0.37	0.59	0.559
Song dissimilarity (pPCA)	-0.40	0.51	-0.80	0.425
Song similarity (SPCC)	0.12	0.46	0.25	0.802
Size PC	0.04	0.32	0.12	0.904
Shape PC	-0.40	0.52	-0.77	0.441
Syntopy x guild overlap	-0.79	0.62	-1.28	0.201

Table S8 Generalized linear model predicting interspecific territoriality, with an interaction between the size principal component and syntopy, and controlling for patristic distance.

Selected Predictors	Estimate	Std Error	Z Value	P Value
(Intercept)	1.59	2.46	0.65	0.516
Syntopy	0.70	0.68	1.03	0.304
Size PC	0.64	0.93	0.68	0.494
Guild overlap	-0.93	0.93	-0.99	0.322
Hybridization	0.81	1.34	0.60	0.547
Patristic distance	-1.36	0.87	-1.55	0.12
Plumage dissimilarity	1.87	0.83	2.25	0.024*
Song dissimilarity (pPCA)	-0.37	0.90	-0.41	0.685
Song similarity (SPCC)	-0.49	0.76	-0.65	0.517
Shape PC	-0.30	1.02	-0.29	0.772
Syntopy x size PC	-5.47	1.99	-2.75	0.006*

Table S9 Generalized linear model predicting continuous breeding range overlap, with patristic distance as the predictor variable.

Selected Predictors	Estimate	Std Error	T Value	P Value
(Intercept)	0.00	0.15	0.00	1.000
Patristic distance	0.06	0.15	0.38	0.706

Table S10 Generalized linear model predicting the binary variable of sympatry or parapatry, with patristic distance as the predictor variable.

Selected Predictors	Estimate	Std Error	T Value	P Value
(Intercept)	0.76	0.07	11.55	0*
Patristic distance	0.03	0.07	0.41	0.684

Table S11 Generalized linear model predicting continuous breeding range overlap, with interspecific territoriality and patristic distance as the predictor variables.

Selected Predictors	Estimate	Std Error	T Value	P Value
(Intercept)	0.23	0.21	1.12	0.269
Interspecific territoriality	-0.50	0.32	-1.59	0.119
Patristic distance	-0.03	0.16	-0.17	0.863

Table S12 Generalized linear model predicting the binary variable of sympatry or parapatry, with interspecific territoriality and patristic distance as the predictor variables.

Selected Predictors	Estimate	Std Error	T Value	P Value
(Intercept)	0.88	0.09	9.88	0*
Interspecific territoriality	-0.27	0.13	-1.99	0.053
Patristic distance	-0.02	0.07	-0.27	0.785

Table S13 Generalized linear model predicting the binary variable of sympatry or parapatry, with an interaction between interspecific territoriality and hybridization as the predictor variables and controlling for patristic distance.

Selected Predictors	Estimate	Std Error	T Value	P Value
(Intercept)	0.86	0.13	6.59	0*
Interspecific territoriality	-0.02	0.21	-0.09	0.93
Hybridization	0.06	0.18	0.31	0.757
Patristic distance	-0.04	0.07	-0.56	0.578
Interspecific territoriality x hybridization	-0.39	0.27	-1.45	0.154

Table S14 Model Comparison where Covariate = IT and parapatry assignment is 20%

	m1_null	m1_cov	m2_null	m2_cov	m3_null	m3_cov
ln.L	-25.03	-23.00	-25.03	-22.97	-25.03	-22.95
AICc	52.15	50.28	54.34	54.94	56.64	60.10
n_0	45.00	24.00	45.00	24.00	45.00	24.00
n_1	NA	21.00	NA	21.00	NA	21.00
theta_0	0.76	0.87	NA	NA	NA	NA
theta_1	NA	0.62	NA	NA	NA	NA
a_0	NA	NA	0.76	0.87	0.76	0.88
a_1	NA	NA	NA	0.63	NA	0.63
k_0	NA	NA	33.32	46.09	59.92	39.02
k_1	NA	NA	NA	4.70	NA	10.90
w_0	NA	NA	NA	NA	0.08	0.00
w_1	NA	NA	NA	NA	NA	0.36
conv	0.00	0.00	0.00	0.00	0.00	0.00
chi_stat	NA	4.06	0.00	4.12	0.00	4.16
p_chi	NA	0.00	1.00	0.04	1.00	0.12

Table S15 Model Comparison where Covariate = Hybrid and parapatry assignment is 20%

	m1_null	m1_cov	m2_null	m2_cov	m3_null	m3_cov
ln.L	-25.03	-24.52	-25.03	-24.52	-25.03	-23.87
AICc	52.15	53.32	54.34	58.04	56.64	61.95
n_0	45.00	18.00	45.00	18.00	45.00	18.00
n_1	NA	27.00	NA	27.00	NA	27.00
theta_0	0.76	0.83	NA	NA	NA	NA
theta_1	NA	0.70	NA	NA	NA	NA
a_0	NA	NA	0.76	0.83	0.76	1.00
a_1	NA	NA	NA	0.70	NA	0.70
k_0	NA	NA	33.32	12.27	59.92	0.31
k_1	NA	NA	NA	43.22	NA	48.08
w_0	NA	NA	NA	NA	0.08	0.00
w_1	NA	NA	NA	NA	NA	0.00
conv	0.00	0.00	0.00	0.00	0.00	0.00
chi_stat	NA	1.02	0.00	1.02	0.00	2.32
p_chi	NA	0.00	1.00	0.31	1.00	0.31

Table S16 Model Comparison where Covariate = IT*Hybrid and parapatry assignment is 20%

	m1_null	m1_cov	m2_null	m2_cov	m3_null	m3_cov
ln.L	-25.03	-22.14	-25.03	-22.14	-25.03	-22.14
AICc	52.15	48.57	54.34	53.29	56.64	58.50
n_0	45.00	30.00	45.00	30.00	45.00	30.00
n_1	NA	15.00	NA	15.00	NA	15.00
theta_0	0.76	0.87	NA	NA	NA	NA
theta_1	NA	0.53	NA	NA	NA	NA
a_0	NA	NA	0.76	0.87	0.76	0.87
a_1	NA	NA	NA	0.53	NA	0.54
k_0	NA	NA	33.32	35.46	59.92	60.90
k_1	NA	NA	NA	38.05	NA	11.01
w_0	NA	NA	NA	NA	0.08	0.02
w_1	NA	NA	NA	NA	NA	0.21
conv	0.00	0.00	0.00	0.00	0.00	0.00
chi_stat	NA	5.77	0.00	5.77	0.00	5.77
p_chi	NA	0.00	1.00	0.02	1.00	0.06

Table S17 Model Comparison where Covariate = IT and parapatry assignment is 25%

	m1_null	m1_cov	m2_null	m2_cov	m3_null	m3_cov
ln.L	-27.05	-25.15	-27.05	-25.10	-27.05	-25.09
AICc	56.20	54.59	58.39	59.20	60.69	64.40
n_0	45.00	24.00	45.00	24.00	45.00	24.00
n_1	NA	21.00	NA	21.00	NA	21.00
theta_0	0.71	0.83	NA	NA	NA	NA
theta_1	NA	0.57	NA	NA	NA	NA
a_0	NA	NA	0.71	0.83	0.71	0.83
a_1	NA	NA	NA	0.59	NA	0.59
k_0	NA	NA	42.27	38.22	300.70	55.36
k_1	NA	NA	NA	3.04	NA	3.01
w_0	NA	NA	NA	NA	0.00	0.01
w_1	NA	NA	NA	NA	NA	0.08
conv	0.00	0.00	0.00	0.00	0.00	0.00
chi_stat	NA	3.79	0.00	3.90	0.00	3.91
p_chi	NA	0.00	1.00	0.05	1.00	0.14

Table S18 Model Comparison where Covariate = Hybrid and parapatry assignment is 25%

	m1_null	m1_cov	m2_null	m2_cov	m3_null	m3_cov
ln.L	-27.05	-26.72	-27.05	-26.72	-27.05	-26.72
AICc	56.20	57.73	58.39	62.44	60.69	67.65
n_0	45.00	18.00	45.00	18.00	45.00	18.00
n_1	NA	27.00	NA	27.00	NA	27.00
theta_0	0.71	0.78	NA	NA	NA	NA
theta_1	NA	0.67	NA	NA	NA	NA
a_0	NA	NA	0.71	0.78	0.71	0.78
a_1	NA	NA	NA	0.67	NA	0.67
k_0	NA	NA	42.27	19.72	300.70	12.75
k_1	NA	NA	NA	112.78	NA	41.06
w_0	NA	NA	NA	NA	0.00	0.04
w_1	NA	NA	NA	NA	NA	0.00
conv	0.00	0.00	0.00	0.00	0.00	0.00
chi_stat	NA	0.66	0.00	0.66	0.00	0.66
p_chi	NA	0.00	1.00	0.42	1.00	0.72

Table S19 Model Comparison where Covariate = IT*Hybrid and parapatry assignment is 25%

	m1_null	m1_cov	m2_null	m2_cov	m3_null	m3_cov
ln.L	-27.05	-23.88	-27.05	-23.88	-27.05	-23.88
AICc	56.20	52.05	58.39	56.76	60.69	61.97
n_0	45.00	30.00	45.00	30.00	45.00	30.00
n_1	NA	15.00	NA	15.00	NA	15.00
theta_0	0.71	0.83	NA	NA	NA	NA
theta_1	NA	0.47	NA	NA	NA	NA
a_0	NA	NA	0.71	0.83	0.71	0.83
a_1	NA	NA	NA	0.47	NA	0.47
k_0	NA	NA	42.27	51.67	300.70	43.11
k_1	NA	NA	NA	33.58	NA	36.06
w_0	NA	NA	NA	NA	0.00	0.01
w_1	NA	NA	NA	NA	NA	0.00
conv	0.00	0.00	0.00	0.00	0.00	0.00
chi_stat	NA	6.34	0.00	6.34	0.00	6.34
p_chi	NA	0.00	1.00	0.01	1.00	0.04

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