



Short Communication

When birds sing at the same pitch, they avoid singing at the same time

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Birds singing in choruses must contend with the possibility of interfering with each other's songs, but not all species will interfere with each other to the same extent due to signal partitioning. Some evidence suggests that singing birds will avoid temporal overlap only in cases where there is overlap in the frequencies their songs occupy, but the extent to which this behaviour varies according to level of frequency overlap is not yet well understood. We investigated the hypothesis that birds will increasingly avoid heterospecific temporal overlap as their frequency overlap increases by testing for a linear correlation between frequency overlap and temporal avoidance across a community of temperate eastern North American birds. We found that there was a significant correlation across the whole community and within 12 of 15 commonly occurring individual species, which supports our hypothesis and adds to the growing body of evidence that birds adjust the timing of their songs in response to frequency overlap.

Keywords: acoustic competition, signal partitioning, temporal avoidance.

Acoustic signalling is common among animals, and birds are well known for their complex vocal communications. The song is a specific vocal signal that many birds use to attract potential mates and repel rivals (Brenowitz *et al.* 1997). Singing activity in birds tends to be most concentrated in the morning, especially during a phenomenon known as the dawn chorus (Gil & Lluisa 2020). This period of highly concentrated acoustic communication creates crowded conditions that may make it challenging for targeted receivers to hear a signal. However, crowded conditions do not necessarily

mean targeted receivers will be unable to perceive a signal, as birds appear to be able to pay selective attention to different sounds in their vicinity (i.e. 'Cocktail-party Effect'), and differentiating the characteristics of an acoustic signal from the background makes perception of it simpler (Brumm & Slabbekoorn 2005). Thus, birds have evolved ways of differentiating their acoustic signals from the crowd to increase their likelihood of being heard (Brumm & Naguib 2009).

One way that birds increase their likelihood of being heard is by partitioning their signals in acoustic space. This signal partitioning can occur in a variety of ways including by different species signalling during different distinct time periods (Luther 2008), signalling from different physical locations across the landscape (Chitnis *et al.* 2020), producing signals with a different structure or pattern (Luther 2009), or producing signals which occupy different frequency ranges (i.e. 'pitch') (Nelson 1989). The ways that birds engage in signal partitioning will depend on numerous factors including other acoustically signalling organisms in the community (Hart *et al.* 2015) as well as physical constraints on the signaler (Mason & Burns 2015).

Many ways that birds may engage in signal partitioning are long-term and evolved (e.g. a bird's typical frequency range) but individuals may also employ behavioural strategies over short timescales depending on current acoustic conditions (Brumm & Slabbekoorn 2005). For instance, birds may shift the timing of their individual songs to avoid any one song overlapping in time with the individual songs of another bird. This active avoidance of temporal overlap has been demonstrated in at least a dozen bird species, with numerous playback experiments and observational studies showing that birds avoid singing during both conspecific (Knapton 1987, Maynard *et al.* 2012, Wilson *et al.* 2016, Araya-Salas *et al.* 2017) and heterospecific song (Ficken *et al.* 1974, Bremond 1978, Popp *et al.* 1985, Popp & Ficken 1987, Brumm 2006, Suzuki & Cody 2019).

Birds with songs that are sufficiently different in their acoustic characteristics will not necessarily interfere with one another even if they overlap in time. As such, the likelihood that birds will avoid temporal overlap should vary with similarity in these characteristics (Planqué & Slabbekoorn 2008). Some evidence does support variability in temporal avoidance behaviour as it pertains to frequency range. For instance, in one tropical community, birds which sang in the same frequency band as cicadas were shown to sing less often during cicada choruses (Hart *et al.* 2015), and in another tropical community, birds which sang in crowded frequency bands avoided temporal overlap with other birds within their own frequency band (Planqué & Slabbekoorn 2008). Other studies have found similar evidence that supports the idea that temporal avoidance tends to be stronger with greater frequency overlap (Malavasi & Farina 2013, Hart *et al.* 2021).

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To date, a small but growing number of studies have been published which have tackled the question of how or to what degree birds modify their behaviour on a short timescale in response to other types of signal partitioning (Planqué & Slabbekoorn 2008, Malavasi & Farina 2013, Hart *et al.* 2015, 2021). Here, we present a case study which adds to this body of literature in that it is undertaken in a temperate forest community, whereas most of the existing literature has involved tropical communities. We used 370 min of audio recording spanning both the dawn chorus and early morning from 4 days at a site in eastern North America to investigate the hypothesis that birds will increase their short-term heterospecific temporal avoidance with increasing overlap in frequency.

METHODS

Audio recording and annotation

Audio recordings were collected at Powdermill Nature Reserve, Rector, PA, USA ($40^{\circ}09'N$, $79^{\circ}16'W$) in 2018 on 27 April, 05:32 h EDT for 180 min (R1), 8 May, 05:32 h EDT for 70 min (R2), 28 May, 05:17 h EDT for 5 min (R3) and 16 July, 06:19 h EDT for 130 min (R4). R1, R2 and R3 all encompass some dawn chorus (Gil & Lluisa 2020). These recordings were collected by AudioMoth autonomous acoustic recorders (Hill *et al.* 2019), which sampled continuously at 32 kHz. The recording site was composed primarily of eastern deciduous forest surrounded by agricultural land with some small open fields and ponds approximately 300 m away. Audio recordings in this set were each split into 5-min clips. These clips were annotated using Raven software (Charif *et al.* 2010). Annotation of each vocalization recorded was performed using cursor placement on a spectrogram to extract the time and frequency interval associated with it, and the species which produced it was identified. Final annotations were determined from a consensus by three annotators. This dataset was created prior to the conceptualization of the present study. See Chronister *et al.* (2021) for further details on its creation. We excluded the first three clips (15 min) from R1 because fewer than two species vocalized during this time period, leaving 74 clips (370 min).

Estimating temporal avoidance

Previously developed methods for estimating temporal avoidance between birds have typically involved creating a simulated song performance by holding steady either the song order or the inter-song interval order while shuffling the other, or by shuffling both (e.g. Masco *et al.* 2016). Such methods use data in which individuals' vocalizations are differentiated from one another. The Chronister *et al.* (2021) dataset consists of

soundscape recordings in which individuals of the same species cannot be confidently separated from one another, and in which conspecific temporal overlaps are frequent. Eliminating the potentially confounding factor of unknown numbers of individuals that sing with their own inter-song intervals and that may temporally overlap with one another but not with themselves necessitates a variation on this simulation procedure that holds both song order and inter-song interval order steady while varying the relative timing between pairs of species. Temporal avoidance estimates were performed using Python 3.8.0 (Van Rossum & Drake 2010; Supporting Information Appendix S1).

To estimate the level of temporal avoidance among bird species, first, we separated these data into species pairs within 5-min clips ('pair-clip combinations') because varying the relative timing between species makes sense over relatively short timescales (of the order of minutes) but not over relatively long timescales (of the order of hours) during which species may join or leave the dawn chorus for reasons unrelated to short-term temporal avoidance of one another. Secondly, we simulated random relative timing within pair-clip combinations by shifting the start of each vocalization of one species in the pair by the same random amount per simulation, allowing vocalizations to loop back to the start of the clip when shifts pushed them beyond 5 min. We created 10 000 of these simulations per pair-clip combination, with each simulation shifted by a different random value. Thirdly, we calculated a temporal overlap score from the fraction of simulations per pair-clip combination that had less or the same amount of temporal overlap (in seconds) than the original clip. A temporal overlap score between 0 and 0.5 indicates that a pair-clip combination tends temporally to overlap less than expected, and a score between 0.5 and 1 that a pair-clip combination tends temporally to overlap more than expected.

Estimating frequency overlap

To estimate to what extent two birds may interfere with one another in frequency requires careful consideration not only of the total range of frequencies each bird's vocalization occupies, but also how to account for variation in how loud a vocalization is at various frequencies and across the course of the vocalization. For instance, the song of the Common Yellowthroat *Geothlypis trichas* consists of many notes that rise and fall in an undulating pattern over an approximately 2-s song (Fig. 1a). Proportionately more of its song occupies frequencies between 4 and 5 kHz, around the centre of its frequency range, than around the periphery of its frequency range. Furthermore, parts of its song are louder than others. Consequently, louder and more concentrated parts of its song pose the greatest risk of

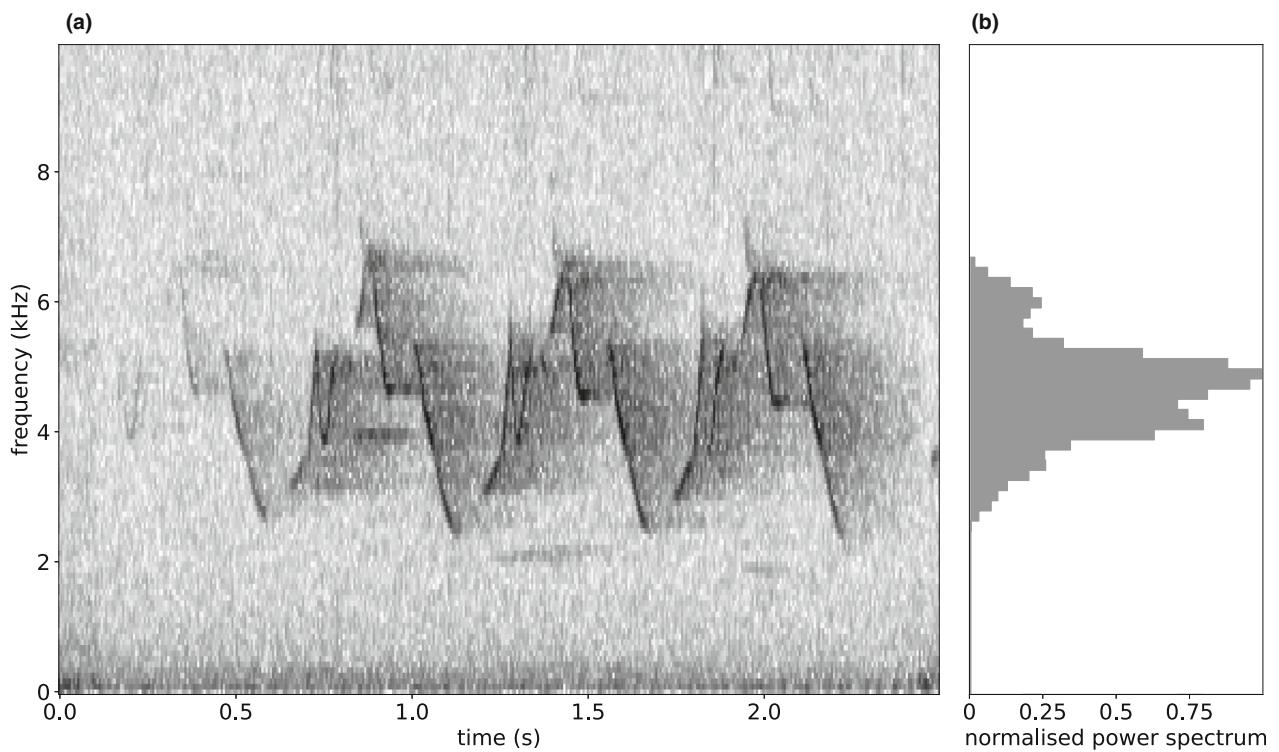


Figure 1. (a) Example spectrogram of Common Yellowthroat song along with (b) the normalized power spectrum generated for this particular vocalization.

interfering with the songs of other birds. Accounting for this, we used the power spectral density of each species' songs to score the interference between two species' vocalizations, which we describe below. Frequency overlap estimates were performed using Python 3.8.0 (Van Rossum & Drake 2010; Appendix S1).

To parallel temporal overlap scores for pair-clip combinations, we generated frequency overlap scores for the same pair-clip combinations. To do so, we first found the power spectral density (Welch's) of each song using audio clips that were shortened and band-passed to the annotated timing and frequency of songs (Fig. 1b). We excluded from this calculation any vocalizations that were more than 90% overlapped by other vocalizations. Secondly, we created a final averaged power spectrum from all vocalizations of a species in a clip and normalized it to a maximum value of one. Thirdly, we found the overlap between the power spectra of each species in a pair-clip combination from the area overlapped by both power spectra divided by the area that both power spectra occupy.

Testing association between frequency overlap and temporal avoidance

To test for an association between our frequency and temporal overlap scores, we first disqualified certain

pair-clip combinations from our analysis using three criteria. The first was that a species had to be detected for enough time within a clip to yield a meaningful temporal overlap score. We chose 5 s as the threshold. The second criterion was that both members of a pair-clip combination had to be represented by at least one vocalization that was less than 10% overlapped by other vocalizations so that a frequency overlap score could be generated. The third criterion was that species had to be permanent members of the community, not flying over. The Canada Goose *Branta canadensis* was the only species present in the dataset which was not a permanent member of the community, and we removed all five pair-clip combinations in which it was present. In all, 1917 pair-clip combinations were dropped from the analysis due to disqualification using these three criteria, leaving 1317 pair-clip combinations for analysis. Secondly, we performed two-tailed permutation tests using Pearson's correlation coefficient to evaluate whether the frequency and temporal overlap scores were significantly linearly correlated. These permutation tests involved randomly permuting the temporal overlap scores and calculating the correlation coefficient over 10 000 simulations (similar to a Mantel test). *P*-values were calculated as the proportion of simulations in which the empirical test statistic was as extreme or more extreme

than that of the real data. We chose to evaluate the correlation using a non-parametric permutation test because we cannot be certain of the shape of the null distribution of a dataset in which each piece of data within the set is not necessarily independent of every other. Thirdly, we performed two analyses using this permutation test. The first analysis tested for a significant correlation between frequency and temporal overlap scores across the whole community using all qualifying pair-clip combinations. The second tested for a significant correlation between frequency and temporal overlap scores within each commonly occurring species using only qualifying pair-clip combinations that included the species. A species was considered commonly occurring only if it appeared in at least 50 pair-clip combinations (but see Supporting Information Table S1 for all single-species permutation tests that were not considered to be commonly occurring). A Bonferroni correction was applied to adjust α for multiple comparisons among permutation tests involving individual species.

RESULTS

Thirty species were included in at least one qualifying pair-clip combination and 15 species were represented by at least 50 pair-clip combinations. The number of times a species appeared in pair-clip combinations varied greatly, with Blue-winged Warbler *Vermivora cyanoptera* appearing in only four pair-clip combinations and Eastern Towhee *Pipilo erythrophthalmus* appearing in 364 pair-clip combinations (28%), 142 more times than the second most abundant species among pair-clip combinations, the Black-throated Green Warbler *Setophaga virens*. These data included species which varied markedly in their characteristic frequency ranges. Of the 1317 pair-clip combinations, 214 (16%) had frequency overlap scores of zero, indicating that the particular pair of species vocalizing in that clip did not substantially interfere with one another. The median frequency overlap score was 0.10 and frequency overlap scores did not exceed 0.73.

There was a significant negative correlation between frequency overlap score and temporal overlap score in the community-wide permutation test ($r = -0.359$, $P < 0.0001$, $n = 1317$, $\alpha = 0.05$; see Fig. 2). In the permutation tests involving individual species, in 12 of 15 species there was a significant negative correlation between frequency overlap score and temporal overlap score (Bonferroni-adjusted $\alpha = 0.0033$; see Table 1, Supporting Information Fig. S1).

DISCUSSION

We found a significant correlation between frequency overlap and temporal avoidance across the community

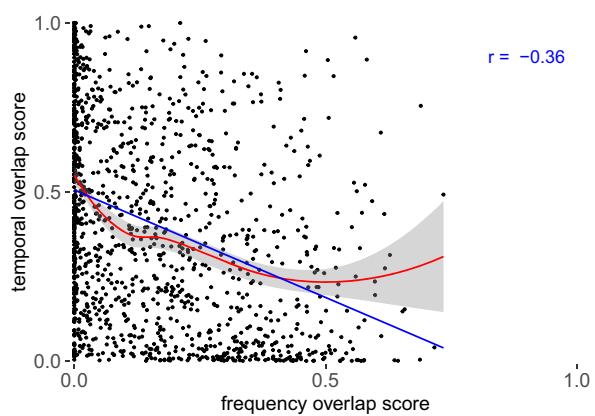


Figure 2. Frequency overlap score vs. temporal overlap score for all pair-clip combinations analysed. The red line with grey shading is a fitted loess curve. The blue line shows the linear correlation. The Pearson's correlation coefficient is displayed in blue text.

we analysed as well as in 12 species in that community. This correlation may suggest that rather than discretely avoiding or not avoiding other species within the community, birds modulate the strength of their temporal avoidance behaviour according to how disruptive other birds' vocalizations are to their own. Playback experiments could clarify how this apparent modulation of temporal avoidance occurs. We also note that the relatively limited scale of this study suggests that few individuals of each species may be included here, and future studies should expand to larger spatial scales.

In a similar prior study to this one, Planqué and Slabbekoorn (2008) also examined the correlation between frequency and temporal overlap in a tropical Peruvian bird community but found no significant correlation except in a single species. Instead, they found that only those birds occupying the same crowded frequency bands significantly avoid temporal overlap with one another. To our knowledge, no other significant correlations between frequency overlap and temporal avoidance have been reported in birds, although temporal avoidance has been investigated alongside frequency overlap several times (Planqué & Slabbekoorn 2008, Malavasi & Farina 2013, Hart *et al.* 2021). A scarcity of previous reports of a linear correlation between frequency overlap and temporal avoidance may relate to variation in the species assemblages and acoustic conditions across different communities which could constrain signal partitioning in different ways and affect the modes by which separation can be achieved. For instance, tropical communities, which have received a great deal of attention in the literature on avian signal partitioning, have been found to have higher levels of high-frequency background noise (Weir *et al.* 2012, Robert *et al.* 2019)

Table 1. Species, *P*-value from single-species permutation tests, Pearson's correlation coefficient and number of pair-clip combinations representing the species.

| Species | <i>P</i> -value | Pearson's <i>r</i> | <i>n</i> |
|--|-----------------|--------------------|----------|
| American Crow <i>Corvus brachyrhynchos</i> | 0.0559 | -0.1385 | 192 |
| American Redstart <i>Setophaga ruticilla</i> | 0.0169 | -0.2578 | 84 |
| Black-and-white Warbler <i>Mniotilla varia</i> | 0.0032* | -0.2988 | 97 |
| Black-capped Chickadee <i>Poecile atricapillus</i> | 0.0001* | -0.3234 | 167 |
| Blue Jay <i>Cyanocitta cristata</i> | 0.0008* | -0.4032 | 66 |
| Black-throated Green Warbler <i>Setophaga virens</i> | 0.0001* | -0.2498 | 222 |
| Common Yellowthroat <i>Geothlypis trichas</i> | <0.0001* | -0.4978 | 82 |
| Eastern Towhee <i>Pipilo erythrourhynchus</i> | <0.0001* | -0.3445 | 364 |
| Kentucky Warbler <i>Geothlypis formosa</i> | 0.0014* | -0.3304 | 91 |
| Northern Cardinal <i>Cardinalis cardinalis</i> | 0.0001* | -0.3121 | 192 |
| Ovenbird <i>Seiurus aurocapilla</i> | 0.0069 | -0.1914 | 197 |
| Red-eyed Vireo <i>Vireo olivaceus</i> | 0.0002* | -0.4472 | 69 |
| Scarlet Tanager <i>Piranga olivacea</i> | <0.0001* | -0.5205 | 106 |
| Tufted Titmouse <i>Baeolophus bicolor</i> | 0.0001* | -0.3014 | 160 |
| Wood Thrush <i>Hylocichla mustelina</i> | 0.0002* | -0.2902 | 168 |

Significant *P*-values are those below Bonferroni-corrected $\alpha = 0.0033$ and are marked with an asterisk (*).

and greater bird species richness compared with temperate communities (Schumm *et al.* 2019). In addition, tropical bird species appear to use songs that are more restricted in frequency range and overlap less in frequency with other bird species within the same community compared with temperate bird species (Weir *et al.* 2012, Robert *et al.* 2019). Indeed, only 16% of pair-clip combinations that we analysed had very limited interference in frequency (a frequency overlap score of 0). Large amounts of overlap in frequencies occupied by birds in temperate communities may necessitate variation in the strength of temporal avoidance for birds in these communities. Future studies should compare the short timescale temporal avoidance among birds in both tropical and temperate communities.

Frequency alone almost certainly is not the sole driver of temporal avoidance behaviour in the birds recorded by Chronister *et al.* (2021), and behaviours used to limit interference other than strictly temporal avoidance may also play a role. Abundant evidence exists describing a broad diversity of avian acoustic niche partitioning. Many species may be listening not only for songs in the proper frequency range (Nelson 1989) but also for the specific pattern of notes within a song (Beckers *et al.* 2002, Luther & Wiley 2009). Thus, similarly structured songs in the same frequency range may interfere with one another more than dissimilar songs. In a study of one temperate avian community during the dusk chorus, Malavasi and Farina (2013) found that instead of strictly temporally avoiding one another, different species that occupy different frequency ranges would form pairs that sing concurrently. Curiously, some birds do not even appear to avoid temporally overlapping with other birds in the soundscape at all, and

instead drive other birds in the soundscape to avoid them in an asymmetrical relationship (Suzuki & Cody 2019). In the present study, we do not distinguish whether any such asymmetry is shown. Evidence even suggests that birds can to some extent modify the frequency range of their songs to avoid interference from sources such as traffic noise (Verzijden *et al.* 2010). As the data collected by Chronister *et al.* (2021) are publicly available, future studies using this dataset may uncover more interesting behaviours within the avian community it records.

We performed a set of single-species permutation tests in this study to show that the pattern of correlation between frequency overlap and temporal avoidance is consistent at levels other than that of the whole community. We used 50 as our minimum number of pair-clip combinations for a species to be considered commonly occurring and thus included in single-species permutation tests because there is a great variation in the power of these tests due to variation in representation of each species in the dataset (see Table S1 for single-species permutation tests for all others). By far the most common species was the Eastern Towhee, which was a member of 28% of pair-clip combinations. This overrepresentation of a single species could mean that the pattern we have observed is due largely to that species' influence. However, we performed the same community-wide permutation test excluding Eastern Towhee and found that our results did not differ in significance (Supporting Information Appendix S2).

Zollinger *et al.* (2012) recognized several problems with the use of spectrograms for analysis of bird vocalizations. Importantly, the frequency content and timing of sounds may be incorrectly represented through

spectrograms. We account for such issues in part by using power spectra in calculating the amount of frequency interference between two bird species, and by using the same independently annotated 5-min clips as our unit of comparison. However, there could still exist the possibility that annotations to spectrograms were systematically shortened only for overlapping vocalizations, thus leading to a spurious correlation between frequency and temporal overlap. To investigate this possibility, we performed an additional test whereby we systematically lengthened all overlapping annotations by 0.5 s only where they overlap in time, and then performed community and species permutation tests. The community-wide permutation test did not differ in significance from that of our primary analysis, and 11 of 12 species tests which were significant in our primary analysis did not rise above $\alpha = 0.00333$, demonstrating that these results are robust to moderate errors in annotation (Supporting Information Appendix S3).

CONCLUSION

In this case study of a temperate eastern North American bird community, we predicted that we would find evidence of birds increasingly avoiding short-timescale temporal overlap with other bird species, as the frequencies at which they give their vocalizations increasingly overlap, and we found significant supporting evidence for this. Community-wide, there was a significant negative correlation between our measure of frequency overlap and temporal overlap. Twelve species showed the same significant negative correlation when measured against other species in the community. This adds to the growing body of evidence that birds modulate their temporal avoidance behaviour in response to other ways in which their signals are already partitioned in acoustic space.

We would like to thank Aidan Place for his contributions in creating the dataset used in this study, which included identifying species present in recordings and providing feedback on initial annotations to timing and frequency of sounds. We would also like to thank Samuel Lapp, Louie Freeland-Hayes, Lydia Katsis and R. Patrick Lyon for their helpful comments on the manuscript.

AUTHOR CONTRIBUTIONS

Justin Kitzes: Conceptualization; formal analysis; funding acquisition; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Tessa A. Rhinehart:** Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Lauren M. Chronister:**

Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

ETHICAL NOTE

None.

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Data Availability Statement

The data that support the findings of this study are openly available in *Ecology* at <https://doi.org/10.1002/ecy.3329>, reference number ecy.3329 or in *Dryad* at <https://doi.org/10.5061/dryad.d2547d81z>, reference number dryad.d2547d81z.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Python code used in the generation of frequency and temporal overlap scores.

Appendix S2. Community permutation test excluding Eastern Towhee.

Appendix S3. Additional tests investigating potential systematic errors.

Figure S1. Frequency vs. temporal overlap scores for 15 commonly occurring species.

Table S1. Results of single-species permutation tests for uncommon species.