**Experimental evidence that a songbird matches song-types to manage alignability, not to signal aggressive intent**

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**Running title**

The function of song-type matching

**Summary**

Song-type matching occurs when a bird sings the same song-type another bird has just sung. It has long been considered a signal of aggressive intent, but recent findings cast doubt on that hypothesis. The structural alignability hypothesis states that matching improves eavesdroppers’ abilities to accurately compare the performance of the two songs. Based on that hypothesis, we predict birds will tend to match low performance songs (emphasizing their own superiority), but avoid matching high performance songs (obscuring their inferiority). We conducted two playback experiments on Adelaide’s warblers (*Setophaga adelaidae*) to test these hypotheses. In each experiment we broadcast an accelerated (high performance) song, a slowed-down (low performance) song, and a minimally processed (control) song. In the second experiment we also gave the subject an opportunity to attack a simulated intruder. Subjects produced the most matches in response to low performance stimuli and the fewest matches in response to high performance stimuli in both experiments, supporting a prediction of the structural alignability hypothesis. Contrary to a key prediction of the aggressive intent hypothesis, song-type matching did not predict attack on the simulated intruder. This is the first experimental evidence supporting the hypothesis that structural alignability influences signaling behavior in non-human animals.

# Keywords

Animal communication, bird song, choice, performance, *Setophaga adelaidae*, structural alignability

In many songbird species, individuals sing repertoires of discrete, learned song-types. 'Song-type matching' is a phylogenetically widespread behavior that occurs when a bird sings the same song-type that another bird has just sung. Song-type matching occurs above chance levels in several species, indicating that it serves an adaptive function (Vehrencamp 2001; Burt & Vehrencamp 2005; Searcy & Beecher 2009). The most prominent functional hypothesis for song-type matching is that it signals the matcher's intent to act aggressively toward the matched bird (Vehrencamp 2001).

Searcy and Beecher (2009) identify three criteria that can be used to test whether a given signal qualifies as a signal of aggressive intent: (1) The signal must be given at an elevated rate during aggressive *contexts*, (2) It must *predict* aggressive escalation by the signaler and (3) receivers must *respond* appropriately to the signal (e.g., by escalating or fleeing). Reviewing the literature on song-type matching, they conclude that there is strong support for criterion 1 and some support for the criterion 3 but only a single study that supports criterion 2 (hereafter, 'the predictive criterion'). In that study, song sparrows (*Melospiza melodia*) that matched song behaved more aggressively than those that did not match in the three minute period after playback concluded (Vehrencamp 2001). Other experiments have failed to associate song-type matching with aggressive escalation by the signaler. Falls et al. (1982) found no correlation between type matching and measures of aggressive response in great tits (*Parus major*). Similar results were obtained in studies of western meadowlarks (*Sturnella neglecta*) (Falls 1985), western song sparrows (Beecher et al. 2000), and eastern song sparrows (Searcy et al. 2006). In their review of aggressive signaling, Searcy and Beecher (2009) conclude that song-type matching “is not a signal of attack but may be a signal of lower levels of aggressive escalation” (p1281).

Searcy et al. (2006) introduced a powerful experimental assay to test the predictive criterion. In its original form, the experiment begins with one minute of song playback from a speaker in the subject’s territory. The subject’s behavior, including any song-type matching, is recorded for five minutes. The experimenters then reveal a taxidermic mount of a conspecific male that had been hidden inside the territory. The mount is important because it gives the subject an opportunity to attack the simulated intruder, providing an unambiguous indicator of aggressive intent. Both the original study (Searcy et al. 2006), and subsequent studies using similar designs arrived at the conclusion that song-type matching does not predict aggressive behavior (Hof & Hazlett 2010; Akçay et al. 2011). The mount presentation assay has been used to show that signalling behaviors other than song-type matching, including low-amplitude ‘soft’ song (Searcy et al. 2006) and a visual display called ‘wing-waving’ (Ballentine et al. 2008) do predict attack, validating this experimental protocol as a useful test of the predictive criterion.

An alternative to the aggressive intent hypothesis views the choice to match as a strategy that can influence eavesdroppers' assessments of the signalers’ relative quality (Logue & Forstmeier 2008). ‘Structural alignabilty,’ is a term that Cognitive Psychologists use to describe the structural similarity between entities that are being compared (Gentner & Markman 1994). Consider a chooser that is comparing two advertisers’ signals. Similarities between the signals (e.g., both are 1 second long) are not useful for determining the superior signal. Thus, choice is based on differences, of which there are two kinds. Alignable differences are differences between shared aspects of the two signals, whereas unalignable differences are structurally distinct aspects of the signals. examples

Experiments on humans (*Homo sapiens*) have demonstrated that the structural alignability of options facilitates easy, rapid, and accurate choice (Markman & Loewenstein 2010). We propose that the effects of structural alignability on choice are not specific to humans (Akre & Jhonsen 2010). When options are alignable, choosers can directly compare the level of one or more features of the signal and choose the best one (see (Fawcett & Jhonstone 2003) for a model of choice based on more than one feature). Options that are non-alignable differ in their basic structure, so choosers must convert the value of each option to some common scale, increasing both the cognitive load and the error rate.

Logue and Forstmeier (2008) modeled a signaling interaction between two advertisers of variable quality. In the model, the fine-grained structure of the signal indicates the male's quality (Podos 1997; Draganoiu et al. 2002; Moseley et al. 2013), and one or more eavesdroppers use the signaling interaction to choose the superior singer (Otter et al. 1999; Mennill et al. 2002). The major prediction of the model is that advertisers can improve the probability that they will be chosen by modulating the structural alignability of their signals in response to the competitive environment. Specifically, advertisers should signal alignably when they can produce higher quality signals than their rivals (facilitating accurate assessment by choosers) and non-alignably when they cannot (increasing the probability that choosers will erroneously choose the focal advertiser). Returning to the language of bird song, the model predicts that singers should manage the alignability of their signals by matching only when they can sing the song-type better than their rival.

We conducted playback experiments to test the aggressive intent hypothesis and the managing alignability hypothesis. Our study species, Adelaide's warbler (*Setophaga adelaidae*), is a common year-round resident of low-elevation forests in Puerto Rico (Toms 2010). They are socially monogamous, but behavioral observations suggest the occurrence of extra-pair copulation (Toms 2012). Males sing repertoires of discrete song-types, comprising frequency modulated trills (avg. = 23 songs, (Staicer 1991; 1996a)) (Fig. 1). Most song-types are shared, and neighbors often match song-types (Staicer 1996b) (Medina et al. in prep). Like other wood-warbler species (Family: Parulidae), male Adelaide’s warbler have split song repertories. Songs from Categories A and B are structurally similar, but not identical (Staicer 1996b). Songs in Category A are sung thorughout the year during daylight hours. Males sing Category B songs before dawn during the breeding season and during close-range aggressive interactions between males (Staicer 1996b). A given song-type can be used as an A song by one male and as a B song by a different male, but individual males use a given song-type in only one category (Staicer 1996b).

We performed two playback experiments on male Adelaide’s warblers during their breeding season. The first was conducted during Category B singing before sunrise (hereafter the “pre-dawn” experiment), and the second was conducted during Category A singing after sunrise (the “post-dawn” experiment). In both experiments, males were subjected to playback of three types of song stimuli: Fast, control, and slow. The post-dawn experiment included a second phase in which the males had the chance to attack a taxidermic mount of an adult male Adelaide’s warbler. Our primary objective was to test key predictions of the aggressive intent and alignability hypotheses. Based on the aggressive intent hypothesis, we predicted that song-type matching would be a reliable predictor of attack on a taxidermic mount. Our data also allowed us to test the hypotheses that song overlapping (Naguib & Kipper 2005) and wing-waving (Anderson et al. 2013) signal aggressive intent. Based on the alignability hypothesis, we predicted subjects would produce the most song-type matches in response to low quality song stimuli, and the fewest song-type matches in response to high quality song stimuli. Our metric of song quality is trill rate (notes / s), which is a constrained parameter that has been linked to female preference in songbirds (Podos 1996; Ballentine et al. 2004; Moseley 2014).

**Methods**

All research was conducted at the Cabo Rojo National Wildlife Refuge in south-western Puerto Rico (17°59'N, 67°10'W), May–July, 2012. Each bird used in the study was marked with a unique combination of colored leg bands. Prior to the experiments, subjects were recorded both before and after sunrise, to obtain partial A and B song-type repertoires. We observed their movements to determine the location of territory borders. All recordings were made with a portable solid state audio recorder (Marantz PMD661) and a directional ‘shotgun’ microphone (Sennheiser ME67). Recordings were saved as .wav files (sample rate=44.1 kHz, 16 bits).

Recording and stimuli

Recordings were visualized as spectrograms in the program Syrinx PC v2.6f (John Burt, www.syrinxpc.com).We classified song-types based on visual inspection of spectrograms, which is the gold standard for song-type classification (Kogan & Margoliash 1998). Stimuli for each post-dawn trial were based on three songs from Category A, and stimuli for each pre-dawn trial were based on three songs from Category B. All stimuli were recorded from birds that were not neighbors with the focal male, and all stimuli represented song-types that were known to occur in the focal male’s repertoire. When there were multiple recordings available, we used the ones with the highest signal-to-noise ratio. No recordings were used to make more than one stimulus. We used the program Goldwave v5.58 (Goldwave Inc., http://www.goldwave.com/) to filter out low-frequency noise (“high-pass” filter function, cutoff at 1500Hz). We then applied the 'maximize' function in Syrinx to standardize the maximum amplitude of each stimulus. The three songs in a trial were randomly assigned to the three treatments: fast (speed increased 15%), control (speed decreased 1%), and slow (speed decreased 15%).

We used Goldwave's 'time warp' function to manipulate the speed of the songs. We chose the 'similarity' algorithm, which replicates or overlaps similar small section of the audio to modify the length without changing the frequency. This technique affects the duration of both the notes and the intervals between notes (compare to Mosely et al. 2013, in which only the spaces between notes were manipulated). All stimuli were within the natural range of trill rates of the species, and they all sounded normal to human observers.

Each playback file included ten copies of the three stimuli (total = 30 song stimuli per playback trial). We designed the order of playback stimuli to mimic natural song delivery in the pre-dawn and post-dawn periods. For the pre-dawn experiment, we simply randomized the order of the thirty stimuli to generate the immediate variety that characterizes Category B singing (e.g., B, A, A, C, B, C…). In the post-dawn experiment, the three stimulus types were randomly ordered, and all ten repetitions of one stimulus-type were played before switching to the next one (e.g., B [10x], A [10x], C[10x]). That delivery pattern simulates the eventual-variety singing style that characterizes Category A singing. We used Syrinx to insert ten seconds of silence between each stimulus, resulting in a song rate that was well within the natural range. We then saved the playback as a .wav file (sample rate = 44.1 kHz, 16 bits). The entire playback period lasted approximately five minutes.

Playback experiments

The same twenty-three males served as subjects in both experiments. All subjects completed pre-dawn trials before post-dawn trials, with at least four days between trials. Pre-dawn trials were started after males began singing, but at least twenty minutes before sunrise. Post-dawn trials started at least forty minutes after sunrise and ended no more than four hours after sunrise.

Stimuli were played from a Marantz PMD 661 solid state recorder driving an SME-AFS loudspeaker (5W RMS, Mineroff Electronics) mounted in an aluminum parabolic reflector (diameter = 1m) for increased directionality. Playback amplitude was standardized to a natural level (88dB at 1m) with a volume meter (Radio Shack analog VU-meter). An assistant operated the playback device, while the observer (author DAP) operated the recording device and took audio notes on the subject's behavior. We recorded all of the subject’s vocalizations and verbally noted the following behaviors: immediate matching, repertoire matching, song overlapping, and wing-waving displays. A song that matched a stimulus was classified as an immediate match if the male matched the stimulus before he sang another song and before the next stimulus, or as a repertoire matches if it did not meet those criteria (Beecher et al. 1996). Song overlapping was scored whenever the subject's song overlapped any part of the stimulus song. Wing-waving is a conspicuous visual display in which the bird crouches down and flutters its wings. Immediate matches, repertoire matches and song overlapping were later confirmed with spectrographic analysis. If a neighboring bird intruded on the focal bird’s territory at any point in the experiment, we aborted the trial and tried again on another day (n = 3).

In both experiments, the behavior of the focal bird was recorded for five minutes prior to the start of playback (hereafter referred to as the 'pre-trial period'). After the pre-trial period, the design of the two experiments diverged. In the pre-dawn experiment, the playback was conducted near the focal bird’s song post. When the playback was completed, we recorded the male’s behavior for five more minutes (the 'post-playback' period) and ended the experiment.

Prior to the post-dawn experiment, we afixed a taxidermic mount of an adult male Adelaide’s warbler to a treebranch ~2m off of the ground in the center of the territory and covered the mount with a cloth attached to a string. After the pre-trial period, we played the entire stimulus file from the border of the focal bird's territory (the ‘border playback’ phase). After the border playback was complete, we exposed the taxidermic mount in the center of the territory and played the same playback file from a speaker near the mount (the 'center playback' phase). If the focal bird attacked the mount we immediately stopped the playback, terminating the experiment. If the focal bird did not attack the mount after five minutes, we turned off the playback and continued to observe the focal bird for an additional five minutes.

Data analysis

Recordings were visualized as spectrograms in Syrinx. One person (DAP) scored behaviors in the program JWatcher v1.0 (Blumstein et al 2006). Assumptions of normality could not be met in the original dataset or after transformation, so all data were analyzed with non-parametric statistics. We used Wilcoxon matched pairs tests to compare song rates before and after the start of playback. We used the Friedman test to test the prediction that matching rates would differ among song treatments (alignability hypothesis). When Friedman tests were significant, we conducted LSD post-hoc tests based on the average ranks of each treatment. Mann-Whitney U tests were used to test whether matching, overlapping, and wing-waving predicted attack on the mount. For that analysis, immediate matching, repertoire matching and overlapping were converted to rates because the duration of the center-playback phase varied among individuals. Immediate matching rate was calculated as the number of immediate matches divided by the number of stimuli. Repertoire matching rate was calculated as the number of repertoire matches divided by the number of songs sung by the subject. Overlapping rate was calculated as the number of overlapping events divided by the number of stimuli. The post-hoc analysis for the Friedman test were conducted in Infostat v 2013 (Di Rienzo et al. 2013). All other statistical tests were done with SPSS v 21.0 Alpha levels for hypothesis tests were set to 0.05.

# Results

We compared subjects’ song rates between the pre-trial period and the initial five minutes of playback to test the hypothesis that they were responding to our playback stimuli. Subjects did not significantly increase their song rates in response to playback during the pre-dawn playback, but they did during the post-dawn playback (Wilcoxon matched pairs tests: pre-dawn: median pretrial = 31.0, median playback = 33.0, *n* = 23, *z* = -0.76 *p* = 0.45; post-dawn: median pretrial = 7.0, median playback = 11.0, *n* = 23, *z* = -3.48, *p* = 0.001).

Pre-dawn experiment

During the playback period, there was a significant effect of stimulus type on the number of *immediate matches* (Table 1). Specifically, birds gave the most *immediate matches* in response to the *slow* stimuli and the fewest in response to the *fast* stimuli. The post-hoc test revealed a significant difference in the number of *immediate matches* between the *slow* and *fast* treatments. A similar pattern was observed in *repertoire matching* during the playback and after the end of the playback, but the statistical tests were only marginally significant. We found a strong, statistically significant treatment effect on the number of total matches, which is the sum of the three previous measures. Here too, the post-hoc test indicated a significant difference between the response to the *slow* and *fast* songs.

## Post-dawn experiment

We found significant treatment effects on all measures of song-type matching during the post-dawn experiment (Table 2). All response variables showed the same pattern: Males matched the *slow* stimuli at the highest rate, the *control* stimuli at an intermediate rate, and the *fast* stimuli at the lowest rate. The pattern of separation in the post-hoc tests varied depending on how matching was measured.

## Aggressive signaling

Eight of the 23 subjects (35%) attacked during the mount trials (Table 3). Of the seven putative signals of aggressive intent that we measured, only wing-waving was given significantly more by attackers than by non-attackers. All of the other putative signals of aggressive intent, including various forms of song-type matching, tended to be given at a higher rate by non-attackers than by attackers. We were interested in testing whether birds that continued to match when the playback moved into the center of the territory were more likely to escalate than those that did not (Akçay et al. 2013) but all of the birds in our study matched at least one song during both the border playback and center playback, obviating statistical analysis.

**Discussion**

Our results support predictions of the managing alignability hypothesis for the function of song-type matching (Logue & Forstmeier 2008), but fail to support an important prediction of the hypothesis that song-type matching signals aggressive intent. Below, we discuss subjects’ overall responses to playback, the lack of evidence that song-type matching reliably predicts aggressive intent, and the evidence that song-type matching is a behavior that males use to manage the structural alignability of their signals relative to those of their opponents.

Response to playback

Playback stimulated the subjects to increase their song rates in the post-dawn trials, clearly indicating that the subjects responded to our stimuli. Song playback did not, however, induce a statistically significant change in song rate in the pre-dawn experiment. Nevertheless, we believe these birds were responding to our playbacks. Male Adelaide’s warblers are continuously engaged in intense vocal interactions during the dawn chorus (Staicer 1991). Song rates were much higher during the pre-dawn pre-trial period (median = 31 songs / 5 min) than they were during the post-dawn pre-trial period (7 songs / 5 min) or even the post-dawn trial period (11 songs / 5 min). Thus, the initiation of song playback during the dawn chorus represents a continuation of an interactive state, which explains the lack of significant change in song rate. We are confident that subjects were attentive to playback during the dawn chorus because they selectively matched low quality stimuli. .

Aggressive signaling

Our results do not support the hypotheses that song-type matching signals aggressive intent. Based on that hypothesis we predicted that attacking birds would match more than non-attacking birds, but our data show a trend in the opposite direction. The direction of the trend was not affected by the type of matching that we considered (immediate or delayed) or the time during which the data were collected (during border playback or center playback). Our results are consistent with the majority of studies that test the predictive criterion with respect to song-type matching (Vehrencamp 2001; Searcy & Beecher 2009; Akçay et al. 2013).

Recently, Akçay et al. (2013) found evidence that a Western population of song sparrows uses song-type matching as an early aggressive signal in a hierarchical signaling system (see also (Hof & Podos 2013)). As in our post-dawn experiment, they began playback at the territory border and then ‘escalated’ by moving to the interior of the territory where a taxidermic mount was revealed. Both wing-waving displays and attack were predicted by adherence to a matching strategy through the ‘escalation’ phase of the experiment. Searcy et al. (2013). performed a similar experiment on an eastern population of song sparrows, but found no evidence of hierarchical signaling. In our experiment, all subjects matched at least one song in both phases of the post-dawn experiment. This lack of variation suggests that continuing to match as an interaction escalates does not function as part of a hierarchical signal of aggressive intent in Adelaide’s warbler.

We can be confident that the mount presentation assay is effective at identifying signals of aggressive intent in this species because we found strong evidence that the signal wing-waving is associated with attack. Wing-waving is also a reliable signal of aggressive intent in swamp sparrows (Ballentine et al. 2008: Anderson et al. 2013). Song overlapping was not a reliable predictor of attack in our study. Overlapping has never been shown to reliably predict attack, suggesting that is unlikely to serve as a signal of aggressive intent, as some authors had argued (Searcy & Beecher 2009: Naguib & Mennill 2010).

Managing Alignability

We found strong support for our predictions that male Adelaide’s warblers would produce the most song-type matches in response to low quality (slow) song stimuli, and the fewest song-type matches in response to high quality (fast) song stimuli in both the pre-dawn experiment and the post-dawn experiment. The congruent pattern in the two experiments strengthens our confidence in these finding. The experiments should not be considered to provide completely independent data, because the same subjects (but different stimuli) were used in both experiments. The adaptive significance of split repertoires in warblers remains a mystery (Beebee 2004;Hof & podos 2013; Price & Crawford 2013). Our findings suggest that the rival’s singing performance has similar effects on the choice to match during Category A and Category B singing.

We found similar results whether we focused on immediate matches (a type-match of stimulus X that was also the first song sung after stimulus X) or repertoire matches (a song that matched a stimulus, but was not an immediate match). We interpret this result to suggest that birds manage the alignability of their signals relative to multiple other signals in the environment, not just the signal that immediately preceded the focal individual’s signal.

This is the first study to provide evidence that a non-human animal manages the structural alignability of its signals in response to the competitive environment. Several important parts of this hypothesis, however, have yet to be addressed. First, it is important to determine whether relative performance affects the decision to match in natural interactions between neighboring males (Medina et al., in prep). Second, we lack a direct test of the underlying hypothesis that female songbirds make more accurate choices when their options are alignable. Finally, it would be useful to conduct a playback experiment that incorporates the subjects’ own performance levels. Such an experiment could test the prediction that the decision to match depends on whether the stimulus outperforms the subject.

The broader hypothesis motivating this research is that the structural alignability of options influences choice in non-human animals. If true, this idea would have broad implications for our understanding of choice. Structural alignability effects are cognitive biases that affect comparative evaluation in animals (Bateson & Kacelnik 1995; Akre & Johnstone 2010; Rowe 2013). We suggest that alignability effects may influence choice and advertisement strategies whenever advertisers compete to be selected by choosers, as in choice-based mating systems, and pollination / nectarivory systems.

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# Table 1. Friedman tests for variation in median song-type matching in response to three kinds of stimuli during the pre-dawn experiment.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | Stimuli | Median | Mean Rank | Test results | |
|  |  | |  |  |  |
| Immediate | Slow | 3 | 2.26a | *X2* | 6.19 |
| Match | Control | 2 | 2.11ab | df | 2 |
|  | Fast | 1 | 1.63b | *P* | 0.045 |
|  |  |  |  |  |  |
| Repertoire | Slow | 2 | 2.35 | *X2* | 5.15 |
| Match | Control | 1 | 1.89 | Df | 2 |
| Playback | Fast | 1 | 1.76 | *P* | 0.076 |
|  |  |  |  |  |  |
| Repertoire | Slow | 4 | 2.30 | *X2* | 4.78 |
| Match | Control | 3 | 2.00 | df | 2 |
| Post-playback | Fast | 1 | 1.70 | *P* | 0.092 |
|  |  |  | |  | |
| All | Slow | 9 | 2.37a | *X2* | 8.29 |
| Matches | Control | 8 | 2.09ab | df | 2 |
|  | Fast | 3 | 1.54b | *P* | 0.016 |

# Results of LSD of average ranks of treatment are showed as letters, different letters indicate significant differences.For all tests, n = 23 individuals.

# Table 2. Friedman tests for variation in median song-type matching in response to three kinds of stimuli during the post-dawn experiment.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | Stimuli | Median | Mean Rank | Friedman test results | |
|  |  |  |  |  |  |
| Immediate | Slow | 2 | 2.39a | *X2* | 6.10 |
| matching | Control | 2 | 1.85b | Df | 2 |
| border | Fast | 1 | 1.76b | *P* | 0.047 |
|  |  |  |  |  |  |
| Repertoire | Slow | 0 | 2.28a | *X2* | 7.47 |
| matching | Control | 0 | 1.85b | Df | 2 |
| border | Fast | 0 | 1.87b | *P* | 0.024 |
|  |  |  |  |  |  |
| Immediate\* | Slow | 3 | 2.47a | *X2* | 9.12 |
| matching | Control | 2 | 2.07a | Df | 2 |
| center | Fast | 1 | 1.47b | *P* | 0.010 |
|  |  |  |  |  |  |
| Repertoire\* | Slow | 1 | 2.53a | *X2* | 11.35 |
| matching | Control | 0 | 1.77ab | Df | 2 |
| center | Fast | 0 | 1.70b | *P* | 0.003 |
|  |  |  |  |  |  |
| Repertoire\* | Slow | 2 | 2.43a | *X2* | 6.12 |
| matching | Control | 0 | 1.93ab | Df | 2 |
| post-playback | Fast | 0 | 1.63b | *P* | 0.047 |
|  |  |  |  |  |  |
|  | Slow | 12 | 2.57 a | *X2* | 8.52 |
| All\* | Control | 4 | 1.90 ab | Df | 2 |
| Songs | Fast | 3 | 1.53 c | *P* | 0.014 |

# Results of LSD of average ranks of treatment are shown as letters, different letters indicate significant differences*.*

# \* Data exclude the eight attacking birds, such that n = 15. In the other tests, n = 23 individuals

# Table 2. Behaviors given by attackers (*n* = 8) and non attackers (*n* = 15) during the post-dawn playback.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Behavior | Attack | Median | Median rank | Mann-Whitney test results | |
| Repertoire match border \* | No | 0.14 | 13.77 | *U* | 33.5 |
|  | Yes | 0.00 | 8.69 | N1, N2 | 15,8 |
|  |  |  |  | *P* | 0.065 |
| Repertoire match center \* | No | 0.17 | 13.27 | *U* | 41.0 |
|  | Yes | 0.00 | 9.63 | N1, N2 | 15,8 |
|  |  |  |  | *P* | 0.21 |
| Overlapping border \* | No | 0.17 | 13.03 | *U* | 44.5 |
|  | Yes | 0.12 | 10.06 | N1, N2 | 15,8 |
|  |  |  |  | *P* | 0.31 |
| Overlapping center \* | No | 0.17 | 12.60 | *U* | 51.0 |
|  | Yes | 0.15 | 10.88 | N1, N2 | 15,8 |
|  |  |  |  | *P* | 0.56 |
| Immediate matching border \* | No | 0.20 | 11.83 | *U* | 57.5 |
|  | Yes | 0.17 | 12.31 | N1, N2 | 15,8 |
|  |  |  |  | *P* | 0.87 |
| Immediate matching center \* | No | 0.23 | 12.80 | *U* | 48.0 |
|  | Yes | 0.15 | 10.50 | N1, N2 | 15,8 |
|  |  |  |  | *P* | 0.44 |
| Wing waving | No | 0.0 | 9.90 | *U* | 28.5 |
|  | Yes | 1.5 | 15.94 | N1, N2 | 15,8 |
|  |  |  |  | *P* | 0.029 |

\* Immediate matching, repertoire matching and overlapping data were analyzed as rates, rather than counts. See Methods.

# Figures

# C:\Users\Dany\Downloads\Fig 1 v2.0.png

**Figure 1.** Spectrograms of unmodified Adelaide warblers songs (top) and “time warped” songs (bottom) used as stimuli in playback experiments. The time warping algorithm was used to slow down some songs by 15% (compare *a* vs. *a’*) and speed up others by 15% (*b* vs. *b’*) without changing the frequency characteristics of the songs.