

Fight song: variation in singing behaviour and song structure during natural agonistic interactions in a tropical songbird, Adelaide's Warbler (*Setophaga adelaidae*)

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Birds may use their singing behaviours and song structure as agonistic signals in territorial encounters. We conducted an observational study to test this hypothesis in male Adelaide's Warblers *Setophaga adelaidae*, a tropical songbird that defends a territory year-round. We described two singing behaviours and nine song structure variables (including vocal performance measures) around the time of natural territorial encounters. We found that birds decreased their song rate and song type switching around the time of encounters. Our findings allow us to reject the hypotheses that male Adelaide's Warblers use high song type diversity or high song rates as agonistic signals. They are, however, consistent with the hypothesis that repetitive singing may be an agonistic signal. Our results also suggest that song may not be an important agonistic signal in close range encounters and low song rates may provoke aggression. This study demonstrates how an observational approach grounds our understanding of aggressive signalling in the reality of natural agonistic encounters. Interestingly, our findings suggest that male Adelaide's Warblers mediate aggressive encounters with repetitive songs rather than high vocal performance or song diversity.

Keywords: agonistic signal, observational study, singing behaviour, song structure, vocal performance.

Songbirds use agonistic signals to mitigate the costs of conflicts over resources (Logue *et al.* 2010, Bradbury & Vehrencamp 2011). There are various classes of agonistic signals, including signals of aggressive intent, motivation signals, submission signals and victory signals (Bradbury & Vehrencamp 2011). Many song playback experiments have tested the hypothesis that birds use their songs to signal aggressive intent (Searcy *et al.* 2006, Laidre & Vehrencamp 2008,

Briffa 2015). Few studies, however, describe song use during natural agonistic encounters (Horn & Falls 1991, Nelson & Poesel 2010, Byers 2017).

A thorough description of singing behaviour and song structure before and after the time of agonistic encounters can clarify the role of song during agonistic encounters. The context criterion (Searcy & Beecher 2009) states that agonistic signals should occur around the time of agonistic encounters. Therefore, singing behaviours and song structures that change around the time of agonistic encounters may function as agonistic signals, whereas those that do not change are unlikely to function in this way. The magnitude of the behavioural change, its timing relative to an agonistic interaction and how it correlates with changes in

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other behaviours can all provide clues about its signalling function. Description of behaviour around the time of agonistic encounters can also inform playback study design by indicating which behaviours and functions should be tested further.

We used an observational approach to describe changes in two singing behaviours around the time of natural agonistic encounters in a Neotropical songbird, Adelaide's Warbler *Setophaga adelaidae*. We chose singing behaviours that have been hypothesized to function as agonistic signals: song type switch rate and song rate. Song type switching rate measures how often a bird changes its song type (Searcy *et al.* 2000). By rapidly switching song types, the signaller displays the size of its repertoire, which may be a reliable signal of quality (Potvin *et al.* 2015). Bachman's Sparrows *Peucaea aestivalis*, Song Sparrows *Mesospiza melodia* and Pale-legged Leaf Warblers *Phylloscopus tenellipes* increase their song type switch rate and respond more aggressively towards higher song type switch rates in simulated territorial encounters (Searcy & Beecher 2009, Searcy *et al.* 2014, Ali & Anderson 2018, Opaev 2024). In contrast, Red-winged Blackbirds *Agelaius phoeniceus* decrease their song type switch rates and Eurasian Chaffinches *Fringilla coelebs* respond more aggressively towards low switch rates in simulated territorial encounters (Searcy & Yasukawa 1990, Deoniziak & Osiejuk 2020). Our study species, Adelaide's Warbler, tends to use Type I (a.k.a., Category A) singing – which is characterized by a low song type switch rate – during natural territorial interactions (Staicer 1992). Song rate describes the number of songs produced over a given time. Signal rate indicates aggressive motivation in many animals (Baker *et al.* 2012, Barnett *et al.* 2014, Szymkowiak & Kuczyński 2017). Song Sparrows, Black-capped Chickadees *Poecile atricapillus*, Canyon Wrens *Catherpes mexicanus* and Wood Warblers *Phylloscopus sibilatrix* elevate their song rate in response to simulated territorial intrusions (Searcy *et al.* 2000, Baker *et al.* 2012, Benedict *et al.* 2012, Szymkowiak & Kuczyński 2017). However, Black-bellied Wrens *Pheugopedius fasciatoventris* lower their song rate in response to simulated territorial intrusions (Logue & Gammon 2004).

We also described changes in song structure around the time of agonistic encounters to determine whether such changes could function as agonistic signals. Some of the structural variables we

measured are indicators of vocal performance, which is a bird's ability to closely approach a physiological limitation when singing (Podos 1997, Cardoso 2017, Logue & Bonnell 2023). Songbirds may use vocal performance to signal their condition or motivation to defend a resource (Podos & Sung 2020). Swamp Sparrows *Melospiza georgiana*, Common Chiffchaffs *Phylloscopus collybita*, Eurasian Skylarks *Aulada arvensis* and European Serins *Serinus serinus* all increase their vocal performance in response to simulated territorial intrusions (Dubois *et al.* 2009, Linhart *et al.* 2013, Geberzahn & Aubin 2014, Funghi *et al.* 2015). Chipping Sparrows *Spizella passerine* and White-crowned Sparrows *Zonotrichia leucophrys* respond more aggressively towards simulated territorial intrusions with high vocal performance (Goodwin & Podos 2014, Phillips & Derryberry 2017), but the Common Reed Warbler *Acrocephalus scirpaceus* responds more aggressively towards playbacks that represent low performance (Hoi *et al.* 2023). Northern House Wrens *Troglodytes aedon* respond the same way to both low and high performance (Cramer 2013) and Pale-legged Leaf Warblers use both low- and high-performance songs in response to simulated territorial intrusions (Opaev 2022).

Logue *et al.* (2020) identified three axes of vocal performance in Adelaide's Warbler songs. *Recovery time* describes a bird's ability to 'fill the song with sound' by singing with relatively long notes and short silent gaps. At the limit of performance, longer notes require longer subsequent silent gaps, presumably because birds require long mini-breaths to replenish the air that they exhaled singing a long note (Hartley & Suthers 1989, Suthers & Zollinger 2004, Cardoso *et al.* 2007). Voiced frequency modulation (*voiced FM*) measures how fast a bird can modulate a note's fundamental frequency. Unvoiced frequency modulation (*unvoiced FM*) describes how fast a bird can modulate frequencies between the end of a note and the beginning of the next note. At the limit of performance, birds require more time to make a large frequency jump than a small one, suggesting that *voiced FM* and *unvoiced FM* are constrained. We examined changes in these three vocal performance metrics, the simple acoustic measures that contribute to them (*note duration*, *gap duration*, *note bandwidth* and *gap bandwidth*), and two measures of song length (*song duration* and *number of notes*) around the time of agonistic interactions.

Song length is not known to be constrained in Adelaide's Warblers but results from other studies suggest that it may indicate aggressive motivation (Cardoso *et al.* 2009, Osiejuk & Jakubowska 2017). Male Dark-eyed Juncos *Junco hyemalis* sing long song types in response to simulated and natural territorial intrusions (Cardoso *et al.* 2009) but European Serins produce short songs in response to simulated intrusions (Funghi *et al.* 2015).

Adelaide's Warblers are well-suited for a study of song during natural agonistic encounters because males sing and engage in conflict at high rates (Staicer 1992, present study). We analysed continuous recordings and behavioural observations of individually marked, free-living male Adelaide's Warblers to characterize changes in singing behaviours and song structure around the time of natural agonistic encounters. Our goals are to ground our understanding of song's agonistic functions in the reality of natural behaviour based on the prediction that signal traits that function as agonistic signals change in consistent ways around the time of agonistic encounters.

METHODS

Study population

Adelaide's Warbler is a socially monogamous wood warbler endemic to Puerto Rico (Fig. S1, Toms 2020). Mated pairs defend all-purpose territories throughout the year. Most pairs retain their territories from year to year, but territory borders frequently shift (P.C. Mower personal observation). Neighbours negotiate borders with territorial skirmishes. Non-territorial 'floaters' also come into conflict with territory owners. During an agonistic territorial encounter, competitors perform aggressive wing-waving displays and emit chitburst calls. Neither of these signals are observed outside of agonistic contexts. Escalated agonistic encounters include chases and, occasionally, physical fights (Staicer 1992). Females sometimes participate in aggressive encounters alongside their mates, but males take the primary role in territory defence (Staicer 1992).

Males of our study population have a repertoire of 29.0 ± 4.0 (mean \pm standard deviation) song types (Staicer 1992, Kaluthota *et al.* 2019). All song types are frequency-modulated trills (Fig. 1). Males share some of their song types with other males in the population, but we did not attempt

to determine which song types were shared across individuals for the present study.

We collected the data for this study from a population of Adelaide's Warblers at the Cabo Rojo National Wildlife refuge in southwestern Puerto Rico (17.975°N, 67.168°W). We used mist-nets and acoustic lures to capture males before observation. All males used in this study were fitted with Fish and Wildlife Service numbered metal bands and a unique combination of three coloured plastic bands on their legs for individual identification. All the males in the study were mated and held territories.

Data collection and processing

Fieldwork was conducted from 13 April to 6 May 2017, and from 12 March to 26 April 2018, periods that correspond to the height of the Adelaide's Warbler's breeding season (Toms 2020). At our study site, suitable habitat appeared to be saturated with Adelaide's Warbler territories (Figs S2 & S3). Recordists conducted continuous focal observations beginning with the first song of the day, until approximately 2 h after sunrise. Recordings were made with Marantz PMD 661 digital recorders and Sennheiser ME67 shotgun microphones (file format = wav; sampling rate = 44.1 kHz; bit depth = 16 bits). Recordists attempted to record all sounds produced by the focal male and made verbal annotations of behaviour and interactions with other birds. Recordists visually confirmed the identity of the focal male during or after every recording session. We recorded 19 males in 2017 and 17 males in 2018. Thirteen males were recorded in both field seasons, for a total of 23 unique individuals. We conducted 3.61 ± 1.82 recording sessions per bird, allowing 7.21 ± 4.82 days between subsequent recording sessions of the same individual.

Recordings were scored by trained annotators with the acoustic analysis software Raven Pro v 1.5 and 1.6.1 (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology 2024, Hann window size = 512, brightness = 60, contrast = 60, 50% overlap). The annotators scored songs and other behaviours, including calls, agonistic behaviours and territorial interactions with neighbours. We excluded the early morning 'dawn chorus' from our analyses because males rarely engage in agonistic encounters during this time (Staicer 1992, D.M. Logue

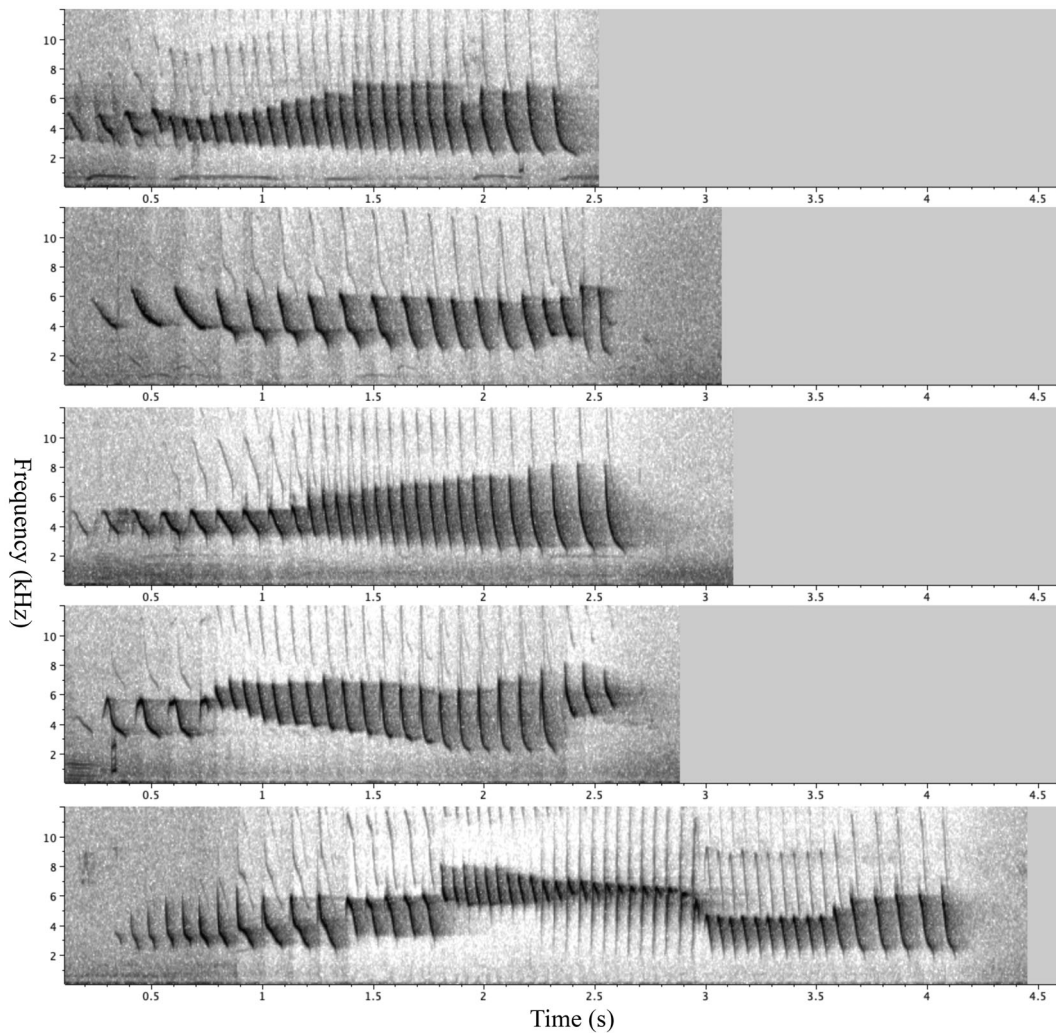


Figure 1. Spectrograms of five different Adelaide's Warblers' song types. Spectrograms were generated in Raven 1.6.3 (window shape = Hann, window size = 512, overlap = 50%, high-pass filter = -3 dB, 124 Hz).

unpublished data). We analysed recordings beginning at 700 s after sunrise (Kaluthota *et al.* 2019) until the end of the recording period (8101.62 ± 2279.98 s after dawn). During this period, males typically patrol their territory, sing, forage and engage in agonistic territorial encounters.

Song type classification

Song type scoring occurred in two phases. First, individual repertoires of song types were categorized during the annotation process. When the annotators encountered a song, they compared its

spectrogram to spectrograms of the known repertoire of the focal bird, and either assigned the song to an established song type, or created a new song type if it did not match any types in that male's repertoire. Each repertoire was independently reviewed by two reviewers. Song type categories were consolidated if they were judged to be 80% similar in (1) overall frequency contour, (2) note shape and (3) number of notes in each phrase. If two reviewers disagreed, they evaluated the spectrograms together until an agreement was reached. If they could not resolve their disagreement, a third reviewer (P.C. Mower) determined how to classify the song. Three songs were excluded from

the *song type switch* analysis because low signal-to-noise ratios precluded song type classification.

Independent variables

We used three aggressive behaviours to define agonistic encounters: 'chitburst' calls, aggressive posture and chases. Chitburst calls comprise a series of loud, broad-frequency 'chit' calls. Adelaide's Warblers give chitburst calls during agonistic territorial encounters (Staicer 1992), and territory holders will fly across their territory to approach chitbursts (D.M. Logue & P.C. Mower personal observation). A bird in aggressive posture assumes a distinctive hunched position with the bill pointed forward and slightly spread and vibrates the wings (Staicer 1992, Anderson *et al.* 2013). Chases occur when one bird pursues the other closely in the air. The occurrence of any of these behaviours was taken as evidence of an agonistic encounter. Males may exhibit multiple aggressive behaviours during a single agonistic interaction. We grouped aggressive behaviours that occurred within 30 s of each other into a single 'agonistic encounter'. This mitigates the risk of pseudoreplicating aggressive behaviours that are not independent. Each agonistic encounter was assigned a unique identifier (*EncounterID*).

We calculated the temporal distance of each song to the temporally closest agonistic encounter within 20 min (*TimeRelAE*). No songs were compared to more than one agonistic encounter and songs that were more than 20 min from an agonistic encounter were not included in the analysis. If the time between agonistic encounters was less than 20 min (as was common), the time between encounters was divided in half, and songs were assigned to the encounter on their side of the division (see Fig. S7 for distribution of sampling periods). *TimeRelAE* was negative if the nearest agonistic encounter within 20 min was after the song, and positive if it was before the song (Fig. 2).

We included the time since sunrise (*TimeRel-Sun*) and day of year (*DOY*) in our models, to account for temporal variation in singing behaviour and song structure (Staicer 1992, Schraft *et al.* 2017, Vazquez-Cardona *et al.* 2023). Sunrise times were retrieved from timeanddate.com and verified using the Solar Calculator Global Monitoring Laboratory of the National Oceanic and Atmospheric Administration (National Oceanic and

Atmospheric Administration n.d., Thorsen 1995–2022).

Dependent variables

All dependent variables were scored for 20 min before and 20 min after agonistic encounters. We chose this timeframe for two reasons. First, it seemed reasonable that agonistic signalling would occur over short-to-medium timescales. Playback studies typically influence behaviour over similar timescales, and our observations of natural agonistic interactions suggested that the strongest effects on behaviour typically emerge and dissipate within this timeframe. Second, each data point 'belongs' to only the nearest agonistic interaction, so data become sparse with increasing temporal distance from an interaction. Data were dense enough to fit the Bayesian model with confidence in the 20 min before and after aggressive encounters.

We scored *song type switch* as 0 if the song type was the same as the type that the bird previously sang, and 1 if it was not. To calculate *song rate*, we made a special dataset in which recordings were divided into 60-s bins measured from the beginning and the end of the agonistic encounter. The *song rate* was the number of songs in each bin. The bins furthest from agonistic encounters were typically less than 60 s long, because bins were measured from both the beginning and end of the encounter. These partial bins were excluded from the *song rate* analysis.

We measured acoustic variables and calculated vocal performance for all songs that had a high enough signal-to-noise-ratio that the acoustic measurement software could identify the signal. We measured acoustic variables in Luscinia v.2.14 (Lachlan 2007; Settings: max. freq. = 10 kHz, frame length = 5 ms, time step = 1 ms, dynamic range = 35 dB, dynamic equalization = 100 ms, de-reverberation = 100%, de-reverberation range = 100 ms, high pass threshold = 1.0 kHz, noise removal = 10 dB). We extracted the *number of notes*, the total *song duration*, the duration of each note (*note duration*), the duration of each silent gap between the notes (*gap duration*), the minimum and maximum peak frequency of the note, and the peak frequency at the beginning and end of each note. We used the minimum and maximum peak frequencies to calculate note bandwidth (*note BW*) and gap bandwidth (*gap BW*) as the ratio of the higher frequency to the lower

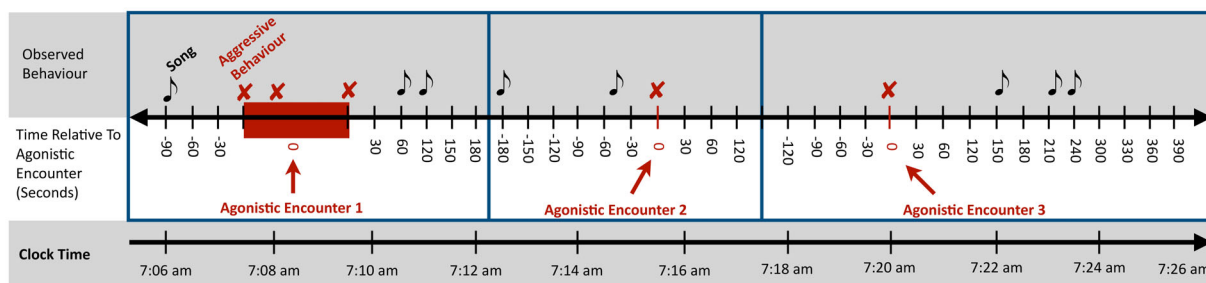


Figure 2. A hypothetical timeline of a 20-min recording segment, showing aggressive behaviours (red X), agonistic encounters (red lines/red bar) and songs (represented by musical notes). Vertical bars mark the temporal mid-point between agonistic encounters. We did not cross these lines when calculating songs' time relative to agonistic encounter (*TimeRelAE*), so *TimeRelAE* refers to the temporally closest agonistic encounter.

frequency (Cardoso 2013). We excluded the final note of each song to calculate *note duration*, *gap duration*, *note BW* and *gap BW*, because it is not possible to calculate *gap BW* or *gap duration* for those notes.

We used the note structure data to calculate the performance variables *recovery time*, *voiced FM* and *unvoiced FM*. *Recovery time* was measured as the deviation score (i.e. the distance to the estimated limit of performance; see below for more information) from a plot of *note duration* versus *gap duration*. *Voiced FM* is the deviation score from a comparison of *note BW* and *note duration*. *Unvoiced FM* is the deviation score from a plot of *gap BW* versus *gap duration* (Geberzahn & Aubin 2014). We first generated three scatterplots (*note duration* versus *gap duration*, *note BW* versus *note duration* and *gap BW* versus *gap duration*) with songs recorded in 2012 and 2017 (Vazquez-Cardona *et al.* 2023) and used the R package *lqmm* to run mixed quantile regressions with *Bird ID* as a random term (Geraci 2014, Logue *et al.* 2020).

Quantile regression estimates a quantile (like a percentile that uses decimals rather than percentages), specified by the parameter τ , of y conditional on x . For example, if we set $\tau = 0.05$, the model would attempt to find the straight line that best separates the bottom 5% of data from the top 95% of data for each value x . The goal of this analysis is to produce a regression line that parallels the constrained edge of the distribution. The angle of that line characterizes how the two variables trade-off at the limit of performance (Logue & Bonnell 2023). The value of τ that best achieves this goal depends on the shape of the data cloud (Wilson *et al.* 2014, Logue *et al.* 2025).

We set $\tau = 0.05$ to fit the data (Vazquez-Cardona *et al.* 2023).

We calculated each note's deviation score as the orthogonal distance between the note and the quantile regression line (see figure in Data S2, Podos 2001). We then multiplied deviation scores by -1 so that low scores indicate low performance, and high scores indicate high performance. We averaged the song structure variables *recovery time*, *voiced FM*, *unvoiced FM*, *note duration*, *gap duration*, *note BW* and *gap BW* over all notes within a song.

Statistical analysis

We followed McElreath's workflow for Bayesian analysis (McElreath 2020). All data analysis was in R x64 4.1.0 (R Core Team 2021). We used the package *DAGitty* to create directed acyclic graphs (DAGs; Textor *et al.* 2017) and *brms* to fit the Bayesian mixed-effects models (Bürkner 2018). We standardized all independent variables by mean-centring and scaling them with the *scale* function before analysis. We also standardized the dependent variables after analysis to facilitate comparison of effect sizes. We made DAGs to control factors that may serve as confounds in our analysis (Westreich & Greenland 2013, McElreath 2020). DAGs permit us to specify causal hypotheses between the variables in the question to be tested and other variables that may affect this relationship. With further analysis, DAGs help us to identify what variables to include in our models. DAG analysis indicated that we should include both *TimeRelSun* and *DOY* as covariates in our models (details in Data S1 and Fig. S4).

We built Bayesian multilevel models to estimate the influence of *TimeRelAE* on singing behaviours and song structure (McElreath 2020). The Bayesian framework facilitates complex modelling approaches, such as the use of splines – which show non-linear relationships between the dependent and independent variables – and multiple random terms. Bayesian models require the user to input prior estimates of the model parameters. We used weakly informative priors centred on zero. This approach sets the model's initial state to assume that the independent variables have no effect on the dependent variable. We estimated posterior distributions by training the model on our data. The *brms* package uses a Markov chain Monte Carlo conditioning engine to estimate posterior distributions. We used four chains with 3500 iterations each. We describe the magnitude of change of the singing behaviours and song structure variables around agonistic encounters based on these posterior distributions. We fit splines for all three predictor variables in our models (*DOY*, *TimeRelSun* and *TimeRelAE*) to allow for non-linear relationships with the dependent variables.

We included *Year* nested within *BirdID* as a random term because some birds were recorded in both years and we assumed that changes in behaviour between years were idiosyncratic to individuals and not broadly applicable to all birds. We included *EncounterID* as a random term to acknowledge the non-independence of songs around a single agonistic encounter. For the song structure models, we also included song type (*ST*) nested within *BirdID* as a random term to account for the non-independence of song structure within song type and individual. The inclusion of *ST* as a random variable means that any observed trend in the response variables should be interpreted as variation within, rather than among, song types. Models that did not include *ST* as a random variable showed similar patterns to those that did (not shown).

We constructed one model for each dependent variable. *Song rate* is a count (songs per 60-s bin), so we used a Poisson error distribution. *Song type switch* required a Bernoulli distribution because the variable was binary (each song is either a switch or not). All models for song structure variables used a Gaussian distribution. We validated the fit of our models with posterior predictive checks (see Data S1 and Figs S5 & S6). Finally, we used the function *conditional_smooths* from the

brms package (Bürkner 2018) to examine the model parameters and visualize the singing behaviour and song structure variables around agonistic encounters. We described the magnitude of change of our dependent variables around agonistic encounters as 'small' for effect sizes ≥ 0.2 sd, 'medium' for effect sizes ≥ 0.5 sd, and 'large' for effect sizes ≥ 0.8 sd (Leppink *et al.* 2016).

To further validate our models' predictions, we used the function *sample* to randomly reorder the values of the dependent variable within each bird-day, and then we fit the model to the randomized data. We repeated this five times for each model and compared the results from the randomized data with those from the observed data.

RESULTS

Our singing behaviour dataset includes 3106 songs and 236 agonistic encounters. The acoustic analyses are based on 1064 songs (26 212 notes) and 137 agonistic encounters. The acoustic analysis contains fewer agonistic encounters because some sampling periods did not include any recordings with a high signal-to-noise ratio. See Figure S7 and Table S1 for descriptive statistics.

Singing behaviours

The estimated conditional effects showed a small-to-moderate decrease in *song type switch* around the time of agonistic encounters (Fig. 3a). *Song type switch* declined in the time leading up to agonistic encounter, reaching a nadir about 15 min after the encounter (decrease = 0.34 sd), after which point it increased gradually. *Song rate* dropped slightly before agonistic encounters (decrease = 0.24 sd) and rebounded shortly after encounters (increase = 0.25 sd; Fig. 3b). For both singing behaviour variables, the models based on shuffled data produced flatter estimates than the models based on observed data (Fig. 3a,b), but the difference was weak in the *song type switch* analysis, so we interpret that result cautiously. See Figure S8 for the effects of *TimeRelAE* on singing behaviours with data points and Figures S9 and S10 for the effects of *DOY* and *TimeRelSun* on singing behaviours.

Song structure

The acoustic variables we tested showed effects on a par with or weaker than those that we observed

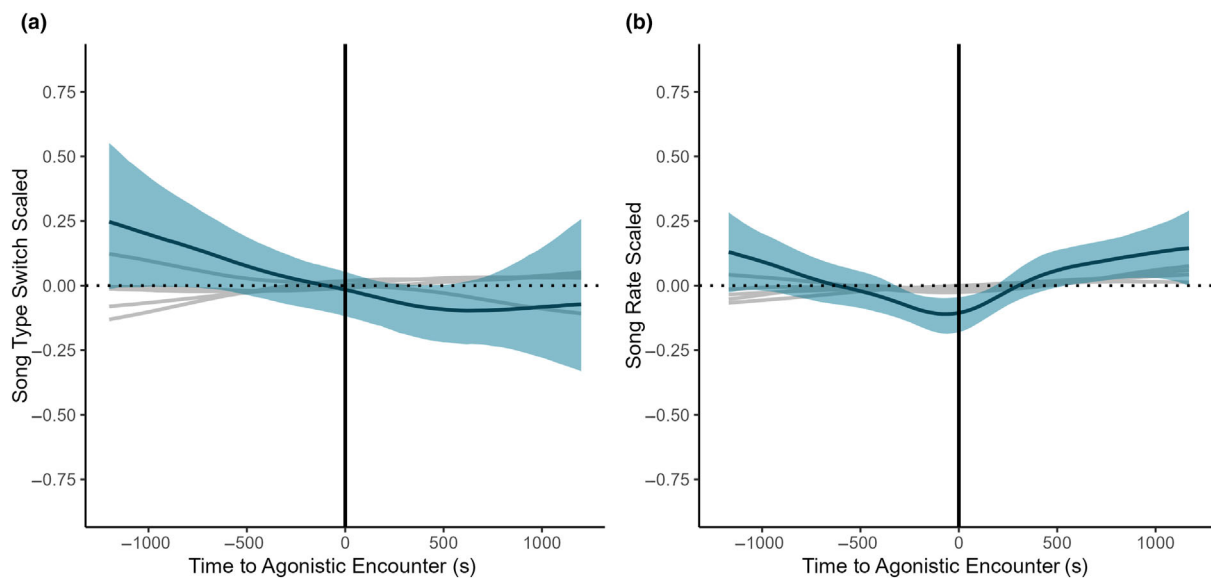


Figure 3. Estimates of (a) *song type switch* and (b) *song rate* as splines (dark blue curve) in the time around natural agonistic encounters (indicated by the black vertical line) in male Adelaide's Warblers; 95% credible intervals are indicated by the light-blue band. The mean level of each singing behaviour is indicated by the horizontal dotted line. Grey curves show the estimated conditional effects of *TimeRelAE* based on shuffled data.

for the randomized data, so we do not interpret those results further (Fig. 4a–i). There is a debate in the literature over whether to use single or double quantile regression to estimate vocal performance (Cardoso 2019, 2024, Logue *et al.* 2025). We repeated the analysis with recovery time metrics based on double quantile regression and the results were weaker than those shown in Figure 4a (unpublished data). See the effects of *TimeRelAE* on song structure with data points in Figure S11 and the effects of *DOY* and *TimeRel-Sun* on song structure variables in Figures S12 and S13.

DISCUSSION

We described male Adelaide's Warblers' singing behaviours and song structure around the time of natural agonistic encounters to improve our understanding of the agonistic signalling functions of bird song. We predicted that signal traits that function as agonistic signals would change in consistent ways around the time of agonistic encounters. We found strong evidence that *song rate* tends to change around the time of agonistic encounters, and weaker evidence that *song type switch* does. The acoustic variables, including

several indicators of vocal performance, did not change appreciably around the time of agonistic encounters.

We found that *song type switch* decreased in the time leading up to an agonistic encounter and continued decreasing for several minutes after the encounter, reaching its lowest point about 15 min after an encounter (Fig. 3a). The magnitude of the estimated change was small-to-moderate, only slightly exceeding the amount of change in the random data, so we interpret the evidence for a decrease cautiously. Our results, however, allow us to be confident that males do not increase their switch rate around the time of an agonistic encounter. A decrease in song type switches around the time of an agonistic encounter would be consistent with previous reports that male Adelaide's Warblers use Type I (a.k.a. Category A) singing around the time of territorial interactions (Staicer 1992). This result would also parallel findings from Red-winged Blackbirds, which decrease their song type switch rate in response to simulated territorial encounters (Searcy & Yasukawa 1990). Receiver side studies on Eurasian Chaffinches also parallel this result. Eurasian Chaffinches respond more aggressively towards low switch rates (Deoniziak & Osiejuk 2020).

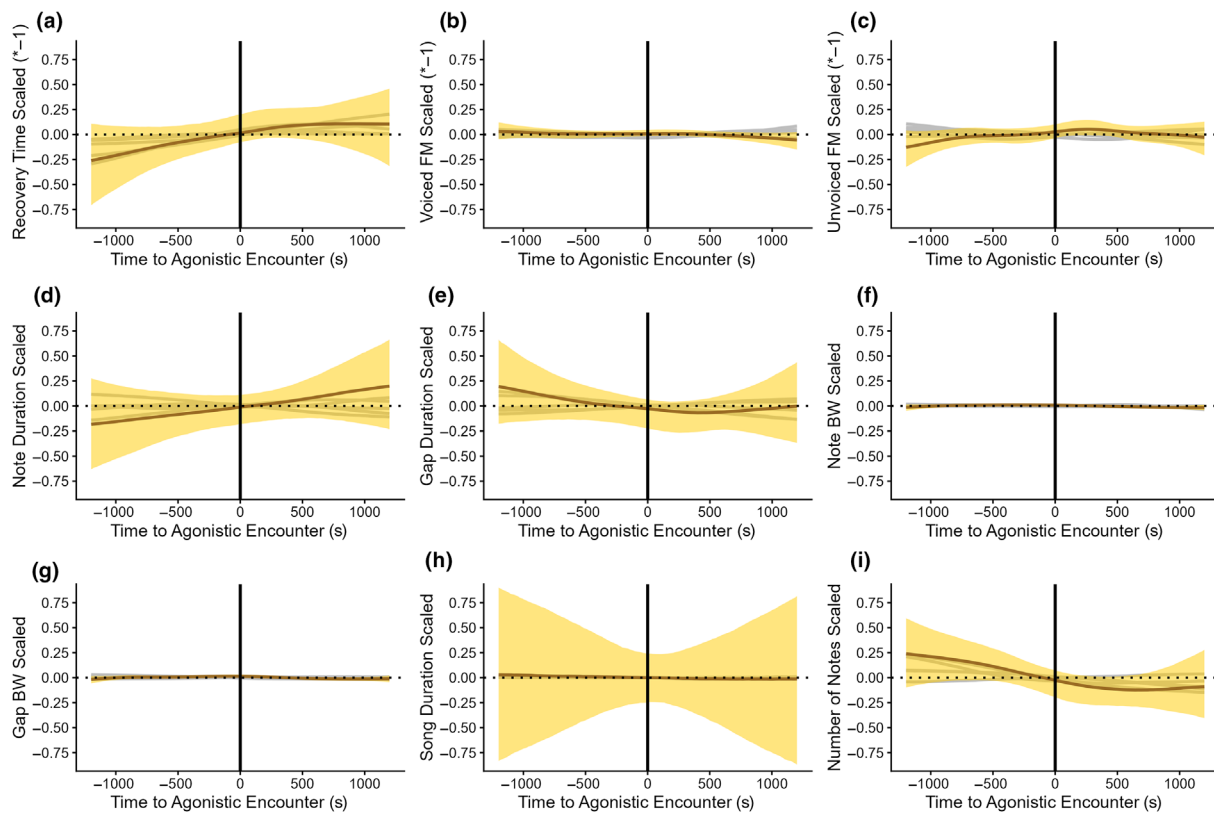


Figure 4. Estimates of (a) *recovery time*, (b) *voiced FM*, (c) *unvoiced FM*, (d) *note duration*, (e) *gap duration*, (f) *note BW*, (g) *gap BW*, (h) *song duration* and (i) *number of notes* (brown curves) around the time of agonistic encounters (black line); 95% credible intervals are indicated by the yellow bands. The mean level of each song structure variable is indicated by the horizontal dotted line. The dependent variables were mean centred to facilitate comparison. Grey curves show the estimated conditional effects of *TimeReIAE* based on shuffled data.

Contrasting results have been reported in Bachman's Sparrows, Song Sparrows and Pale-legged Leaf Warblers (Searcy & Beecher 2009, Searcy *et al.* 2014, Ali & Anderson 2018, Opaev 2024), which respond with higher song type switch rates or more aggressively towards higher song type switch rates in simulated territorial encounters.

The finding that male Adelaide's Warblers do not increase and may in fact lower their *song type switch* around the time of agonistic encounters offers clues about the agonistic function of song type switching. The finding that birds do not increase their switch rate around the time of agonistic encounters allows us to reject the hypothesis that signallers attempt to display the size of their repertoire as a signal of quality during agonistic encounters (Potvin *et al.* 2015). Reduced song type switching during agonistic encounters would be consistent with the hypothesis that low switch

rate is an agonistic signal. For example, repetitive singing might signal aggressive intent. Alternatively, males may use certain song types as general agonistic signals or as signals to communicate with specific neighbours during border disputes (Logue 2021). If either of these hypotheses are correct, a decrease in song type switch rates during agonistic encounters would be a byproduct of males singing a limited set of song types in agonistic contexts. We emphasize, however, that the observed negative trend was weak and should not be taken as strong evidence that switch rate decreases around the time of agonistic encounters.

Song rate decreased before the agonistic encounter and increased again several minutes after the agonistic encounter (Fig. 3b). This result contrasts with findings from Song Sparrows, Black-capped Chickadees, Canyon Wrens and Wood Warblers, which elevate their song rates during simulated

agonistic encounters (Searcy *et al.* 2000, Baker *et al.* 2012, Benedict *et al.* 2012, Szymkowiak & Kuczyński 2017). However, lower song rate in response to simulated territorial intrusions has been documented in the Black-bellied Wren *Thryothorus fasciatoventris*, another tropical species (Logue & Gammon 2004). It would be interesting to know whether this pattern is typical of tropical or year-round-territorial species. In any case, we can confidently reject the hypothesis that male Adelaide's Warblers signal aggressive motivation with high song rates. The low song rate immediately before and after agonistic encounters further suggests that songs are probably not important agonistic signals at these times, although they may be important over longer timescales.

We doubt that a low song rate, *per se*, serves as an agonistic signal. Low signal rates make poor signals because they can occur for many different reasons (e.g. the would-be signaller is busy, distracted or absent). Further, low signal rates are unlikely to be salient in the way that we would expect an agonistic signal to be. If a low song rate is not an agonistic signal, why do males reduce song rates around the time of agonistic encounters? Perhaps once birds are close to their rivals, they choose close-range aggressive signals such as aggressive posture and chitburst calls (Staicer 1992). Males may also reduce their song rate during escalated encounters to gain the element of surprise. Alternatively, the direction of causation may be reversed if low song rates increase the likelihood of intrusion and conflict (Krebs *et al.* 1978). Regardless of the reason that song rates drop before agonistic encounters, the rebound in song rate after encounters suggests that males resume long-distance territorial signalling shortly after an agonistic encounter.

Conditional effects plots indicated that our *song structure* variables did not vary around the time of agonistic encounters any more than would be expected from random data (Fig. 4a–i). This finding is evidence against the idea that an increase in vocal performance signals the singer's motivation in agonistic encounters in this system (reviewed in Podos & Sung 2020, Logue 2021). However, we cannot completely rule out this hypothesis because we had less statistical power to analyse song structure than we did for the singing behaviour analysis, and the trends were in the predicted direction in some cases (e.g. Fig. 4a,d,e).

Our sampling strategy has implications for the interpretation of our results. While *song rate*

returned to its baseline level before the end of the sampling period (Fig. 3b), our estimates of *song type switch* were lower at the end of the sampling period than they were at the beginning (Fig. 3a). It appears that agonistic encounters affect this behaviour for longer than 20 min. If this is true, we would expect some behavioural carryover from earlier agonistic encounters to later ones. This kind of carryover would tend to reduce the apparent effect of agonistic encounters on the dependent variables, leading to Type II (conservative) error.

We conducted an observational study to better understand how male Adelaide's Warblers use song as an agonistic signal. We found evidence against the hypotheses that male Adelaide's Warblers signal (1) quality by showcasing their vocal repertoire and (2) aggressive motivation with increased song rates around the time of agonistic encounters. We failed to find compelling evidence that vocal performance signals aggressive motivation, but we cannot reject that hypothesis on the basis of the current data. Our findings are consistent with the hypotheses that (1) repetitive singing and (2) shared song types are agonistic signals, (3) birds switch from song to other aggressive signals when they are close to rivals, and (4) low song rates provoke aggression. All these hypotheses are amenable to testing with observational studies and experiments in the future.

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AUTHOR CONTRIBUTIONS

Peter C. Mower: Conceptualization; data curation; formal analysis; visualization; writing – original draft; writing – review and editing; methodology; investigation; validation. **Juleyska Vazquez-**

Cardona: Writing – original draft; methodology; visualization; writing – review and editing; formal analysis; investigation; data curation; validation. **Samantha W. Krause:** Conceptualization; investigation; methodology; data curation. **Tyler R. Bonnell:** Writing – review and editing; visualization; formal analysis; methodology. **David M. Logue:** Conceptualization; funding acquisition; writing – original draft; methodology; writing – review and editing; resources; formal analysis; supervision; project administration; visualization; investigation; data curation.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

ETHICAL NOTE

This study adheres to ethics guidelines from the Institutional Animal Care and Use Committee at the University of Puerto Rico, Mayagüez (17 September 2010) and the Animal Welfare Committee at the University of Lethbridge (protocol #1605). Fieldwork was conducted with permission from the U.S. Fish and Wildlife Service (permit 2012-01, 41521-2016-11) and the Departamento de Recursos Naturales y Ambientales (permits 2016-IC-068-1). Bird handling was conducted under David M. Logue's USGS master bird banding permit (no. 23969).

DATA AVAILABILITY STATEMENT

The data and R code that support the findings of this study are openly available at: <https://doi.org/10.5683/SP3/EZSYJJ>.

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SUPPORTING INFORMATION

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

Figure S1: Picture of a male Adelaide's Warbler *Setophaga adelaidae*.

Figure S2: Map of the distribution of male Adelaide's Warblers in 2017.

Figure S3: Map of the distribution of Adelaide's Warblers in 2018.

Figure S4: A directed acyclic graph (DAG) describing the hypothesized patterns of causality for variation in singing behaviour and song structure.

Figure S5: Posterior predictive checks showing how well the models of singing behaviour fit the data.

Figure S6: Posterior predictive checks of the song structure variables (A) *recovery time*, (B) *voiced FM*, (C) *unvoiced FM*, (D) *note duration*, (E) *gap duration*, (F) *note BW*, (G) *gap BW*, (H) *song duration* and (I) *number of notes*.

Figure S7: Histogram of the distribution of sampling period durations in seconds, showing variability in the duration of sampling periods around agonistic encounters.

Figure S8: Estimates of (a) *song type switch* and (b) *song rate* as splines (dark blue line) in the time around natural agonistic encounters (black vertical line) in male Adelaide's Warblers.

Figure S9: Estimate of the effect of day of year on (a) *song type switch* and (b) *song rate* (blue curves).

Figure S10: Estimate of the effect of time relative to sunrise in seconds on (a) *song type switch* and (b) *song rate* (blue curves).

Figure S11: Estimates of (a) *recovery time*, (b) *voiced FM*, (c) *unvoiced FM*, (d) *note duration*, (e) *gap duration*, (f) *note BW*, (g) *gap BW*, (h) *song duration* and (i) *number of notes* (brown curves) in the time around natural agonistic encounters (black vertical line) in male Adelaide's Warblers.

Figure S12: Estimate of the effect of day of year on (a) *recovery time*, (b) *voiced FM*, (c) *unvoiced FM*, (d) *note duration*, (e) *gap duration*, (f) *note BW*, (g) *gap BW*, (h) *song duration* and (i) *number of notes* (brown curves).

Figure S13: Estimate of the effect of time relative to sunrise in seconds on (a) *recovery time*, (b) *voiced FM*, (c) *unvoiced FM*, (d) *note duration*, (e) *gap duration*, (f) *note BW*, (g) *gap BW*, (h) *song duration* and (i) *number of notes* (brown curves).

Table S1: Descriptive statistics for our samples of Adelaide's Warblers' songs.

Data S2: Mixed-quantile regression ($\tau = 0.05$) illustrating the trade-off between *note duration* in milliseconds (ms) and *gap duration* (ms) used to calculate the performance variable *recovery time*. The orange line represents the 5th quantile regression, which is an estimate of the performance limit. Data points closer to this limit have lower deviation scores, indicating higher vocal performance. Hovering over each data point reveals *Recov_time* (the deviation score derived from the trade-off).