

RESEARCH ARTICLE

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**AB AC**

Researchers studying the evolution of animal communication often ask what generates and maintains signal complexity, but they define and measure complexity in different ways. If different metrics are not concordant, then studies using them are probably not comparable. In this study, we asked whether 7 metrics of bird song complexity vary in tandem among individuals of a single species, the Rock Wren (*Salpinctes obsoletus*). The included metrics were chosen because they are regularly used by researchers in the field to test hypotheses within the literature. Results indicated that none of the metrics positively correlated with any others, suggesting that bird songs are not under general selective pressures favoring increased complexity across multiple features. If metrics of signal complexity are not correlated, then care should be taken when designing analyses and comparing results. Researchers should always clearly define the “complexity” under investigation and verify that it has significance to the study species. Contradictory outcomes among existing

hypotheses to different metrics of complexity. Multiple studies have found that different song features have different functions (Botero and Vehrencamp 2007, Wilkins et al. 2015) and yet traits relating to song or syllable repertoire sizes, song structure and delivery patterns are regularly discussed together as components of monolithic complexity, and parallel predictions are made for all metrics (e.g., Palmero et al. 2014, Kaluthota et al. 2016). This can cause confusion when comparing studies. For example, the hypothesis that song complexity increases with latitude has been both supported and refuted by studies that measured complexity in different ways (Soma and Garamszegi 2011, Singh and Price 2015, Najar and Benedict 2018). Similarly, researchers testing the “Cognitive Capacity Hypothesis” have found that song complexity shows no

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We did not use playback to stimulate singing, and we avoided recording birds that were involved in countersinging or other social interactions (for more details on recording and measurement methods see [Benedict and Warning 2017](#) or [Hedley et al. 2018](#)).

Rock Wrens have large, diverse song repertoires providing an excellent model system for quantification of multiple complexity metrics ([Kroodsma 1975](#)). They sing brief songs and present them in sequences that include some

these measures we measured the duration, bandwidth or frequency inflections per s in one exemplar of each song type per bird (Figure 1). Because Rock Wrens have large repertoires, these measurements came from a total of 922 song types across all birds. For each song type we chose the highest quality recording for measurement. We multiplied measured values for each song type by the number of times the appropriate song type was used by that bird, summed all multiplied values and divided by the total number of songs sampled from that individual in order to calculate individual average song duration, bandwidth or frequency inflections per s. Across all individuals these calculations included all 19,058 songs in our dataset. Measuring just one exemplar of each song type per bird is representative of the features of all songs of that type because song types are highly stereotyped (Kroodsma 1975, Benedict and Warning 2017).

Traits were correlated against all others using pairwise linear regression between all seven variables, yielding 21 potential correlations with 12 data points each. Because individual complexity maximums may be as informative as averages for some variables, we also identified the maximum Duration, Bandwidth and Inflections per s values produced by each individual, and ran a second set of analyses with those values instead of the average trait values.

Because our dataset included only 12 individuals, non-significant results could reflect a lack of power. Therefore, we assessed the potential for our existing dataset to yield positive results by examining relationships between variables that have been shown to correlate in previous studies (e.g., Duration and Inflections per song rather than Inflections per s). We also ran a set of analyses designed to test whether our observed correlations fall above or below a random null expectation. To produce a null expectation, we created a model that used our data to generate a set of randomized correlations. The model randomly assigned one of the 12 data points within each of our 7 variables to each individual and correlated the randomized variables using the same method that we used for the observed data. This process was iterated 1,000 times, and our observed mean  $r^2$  value was compared with the distribution of 1,000 randomly generated  $r^2$  values. Modeling was performed in R 3.4.0 and linear regressions in JMP 9.0.

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All 7 complexity metrics were variable across individuals (Table 1), but none showed significant positive correlations with any other (i.e. birds with large repertoires did not tend to have high rates of song delivery, switch song types more often, sing longer songs, etc.) (Table 2). Out of 21 relationships between complexity variables we found 9 positive correlations and 12 negative

correlations (Table 2). The only significant regression analysis ( $P = 0.0039$ ) reflected a negative correlation between song length and song delivery rate: birds that sang longer songs delivered them more slowly (Table 2). Because individual complexity maximums may be as informative as averages for some variables, we also identified the maximum song length, bandwidth and inflections per s values for each individual, and ran similar analyses with those values instead of the trait means. That analysis yielded 7 positive correlations, 14 negative correlations and no significant relationships among complexity metrics (Table 3).

Our randomized data model yielded 1,000 correlations with a mean average  $r^2$  of 0.092. Our observed mean  $r$

**ABLE 2.** Results of linear regressions describing correlations between complexity measures of the songs of 12 Rock Wrens.<sup>a</sup>

	Repertoire	Delivery	Switching	Variety	Length	Bandwidth	Inflections s <sup>-1</sup>
Repertoire		$r^2 < 0.001$	$+ r^2 = 0.043$	$r^2 = 0.043$	$r^2 = 0.014$	$+ r^2 = 0.20$	$+ r^2 = 0.05$
Delivery	$P = 0.99$		$+ r^2 < 0.001$	$r^2 = 0.034$	$r^2 = 0.58 *$	$+ r^2 = 0.052$	$r^2 < 0.001$
Switching	$P = 0.52$	$P = 0.93$		$+ r^2 = 0.30$	$r^2 = 0.0048$	$+ r^2 < 0.001$	$+ r^2 = 0.16$
Variety	$P = 0.52$	$P = 0.56$	$P = 0.066$		$r^2 = 0.0027$	$r^2 = 0.11$	$+ r^2 = 0.16$
Length	$P = 0.71$	$P = 0.0039 *$	$P = 0.83$	$P = 0.87$		$r^2 = 0.049$	$r^2 = 0.020$
Bandwidth	$P = 0.15$	$P = 0.48$	$P = 0.97$	$P = 0.29$	$P = 0.49$		$r^2 < 0.001$
Inflections s <sup>-1</sup>	$P = 0.49$	$P = 0.97$	$P = 0.20$	$P = 0.20$	$P = 0.66$	$P = 0.95$	

<sup>a</sup> Correlation direction and strength (– and +) are indicated in the upper right. Significance of the linear regression is indicated in the lower left. Asterisk (\*) indicates significance at  $P < 0.05$ .

**ABLE 3.** Results of linear regressions describing correlations between complexity measures of the songs of 12 Rock Wrens using maximum duration, bandwidth and frequency inflections s<sup>-1</sup>.<sup>a</sup>

	Repertoire	Delivery	Switching	Variety	Maximum length	Maximum bandwidth	Maximum inflections s <sup>-1</sup>
Repertoire		$r^2 < 0.001$	$+ r^2 = 0.043$	$r^2 = 0.043$	$-r^2 = 0.14$	$-r^2 = 0.0006$	$-r^2 = 0.17$
Delivery	$P = 0.99$		$+ r^2 < 0.001$	$r^2 = 0.034$	$-r^2 = 0.0084$	$-r^2 = 0.074$	$-r^2 = 0.063$
Switching	$P = 0.52$	$P = 0.93$		$+ r^2 = 0.30$	$+ r^2 = 0.065$	$-r^2 = 0.0058$	$-r^2 = 0.054$
Variety	$P = 0.52$	$P = 0.56$	$P = 0.067$		$+ r^2 = 0.18$	$+ r^2 = 0.0022$	$-r^2 = 0.038$
Maximum length	$P = 0.24$	$P = 0.78$	$P = 0.43$	$P = 0.17$		$-r^2 = 0.034$	$-r^2 = 0.056$
Maximum bandwidth	$P = 0.94$	$P = 0.39$	$P = 0.81$	$P = 0.89$	$P = 0.56$		$+ r^2 = 0.012$
Maximum inflections s <sup>-1</sup>	$P = 0.18$	$P = 0.43$	$P = 0.47$	$P = 0.55$	$P = 0.46$	$P = 0.27$	

<sup>a</sup> Correlation direction and strength (– and +) are indicated in the upper right. Significance of the linear regression is indicated in the lower left. Asterisk (\*) indicates significance at  $P < 0.05$ .

repertoire should display a higher song switching rate and a higher local song variety, but those predictions were not supported. In fact, the only significant relationship between complexity metrics was a negative one between delivery rate and song length. This adds some support (albeit minimal) to the notion that tradeoffs in complexity may be more common than positive correlations (Gil and Gahr 2002, Cardoso and Hu 2011).

Our study included only 12 birds, but provided a comprehensive measurement of average song behavior in those individuals. As such, the dataset used here differs from those used in some studies of signal complexity, which may rely on only a few sampled vocalizations from each individual or species under investigation (Buskirk 1997, Cardoso and Hu 2011, Kaluthota et al. 2016). By sampling many songs per individual we ensured that our measurements of complexity represent true individual average behavior, and the lack of correlations between those averages is not due to short-term variation in song form and context. Instead, results indicate that the different metrics of song complexity used in this study do not correlate tightly across individuals. It is possible that the lack of significant correlations stems from a relatively low sample size. If the traits measured in this study are weakly correlated, we may not have detected that with our linear regressions. However, 2 sets of results argue against this interpretation. First, the presence of strong correlations between structurally related variables (e.g., high frequency

and bandwidth) confirms that our approach could detect such relationships within the dataset. Second, the average measured  $r^2$  value for any 2 complexity metrics was smaller than the average randomly generated  $r^2$  value for those same metrics in our model, suggesting that Rock Wren song complexity traits are less correlated than we would expect by chance. Weak, non-significant, correlations would be predicted to fall above the average value within the model. Instead, our results suggest that over prolonged singing periods, which display the full repertoire and range of broadcast singing behavior, Rock Wren song “complexity” measures vary independently. Patterns may be different in short-term contexts, such as one-on-one contest or mating situations, but our results are likely to be relevant to any research that examines the complexity of general broadcast signals.

Existing studies have found mixed support for the idea that aspects of bird song repertoires, delivery patterns and form are biologically linked. For example, multiple syntactical or structural song features correlate in some species, but those correlations are often between variables that are non-independent, such as multiple frequency measures or duration and frequency inflections per song (Cardoso and Mota 2007, Soma and Garamszegi 2011, Woodgate et al. 2012, Kaluthota et al. 2016). Other work has shown that different elements of song form and complexity may be independent or serve different functions, making them likely to be under different selective

pressures (Botero and Vehrencamp 2007, Cardoso and Hu 2011, Wilkins et al. 2015, dos Santos et al. 2018). Our results add to that evidence and extend it to include multiple song features that have not often been previously compared. Many existing studies use either song repertoire size or single-song structural traits to measure song complexity, but for most species we do not know whether those repertoire-based and song-based metrics are correlated. If traits do correlate, they might represent multiple ornaments with redundant or distinct signal content (Moller and Pomiankowski 1993, Gil and Gahr 2002). If traits do not correlate, as is the case for Rock Wren song, this may indicate no need for multiple ornaments, such that elaboration of a single feature provides sufficient information. Among Rock Wrens, repertoire sizes are remarkably large, making this trait an obvious candidate target for selection, and future work will investigate the factors promoting large repertoires. The results presented here suggest that the same factors will not pro-

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**Author contributions:** L.B. collected acoustic data and conducted analyses. L.B. and N.A.N. conceived the idea and wrote the manuscript.

**Data availability:** Supporting data can be found at <http://datadryad.org/resource/doi:10.5061/dryad.453v0/1>

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#### 7. Inflections s<sup>-1</sup>

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