Articles

Journal of Avian Biology 48: 1254–1262, 2017
doi: 10.1111/jav.01357

Subject Editor: Alexandre Roulin. Editor-in-Chief: Thomas Alerstam. Accepted 31 May 2017

Rock wrens preferentially use song types that improve long distance signal transmission during natural singing bouts

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When animals are capable of producing variable signals they may preferentially use some signal types over others. Among songbirds, individuals are known to alter song type form and usage patterns in contest and mating situations, but studies have not examined how song choice improves signal efficacy during broadcast song. For this study we investigated rock wren *Salpinctes obsoletus* song type use rates during natural singing bouts. We tested three hypotheses for adaptive song use during broadcast song: 1) birds improve signal content by increasing the use of high quality songs, 2) birds optimize for signal propagation by preferentially using songs that transmit well, and 3) birds maintain energy by reducing the use of costly songs. The study included 19 058 songs sung by 12 individuals, each of which had a measured song repertoire of between 52 and 117 song types which were produced at highly variable rates. Results indicated that rock wrens did not preferentially sing song types with shorter durations or fewer frequency switches, as would be expected if they selected song types to minimize delivery costs. They also did not favor songs with more rapid trills or more frequency switches, as would be expected if they adjusted song use primarily to indicate quality. Focal birds did preferentially sing significantly longer songs with lower bandwidths, lower frequencies, and slower trill rates. Results suggest that natural broadcast singing patterns are shaped more by the benefits of long distance transmission than by the benefits of advertising performance ability or the costs of song production.

Many animals possess signal type repertoires (Searcy and Nowicki 2005, Bradbury and Vehrencamp 2011). Across avian species, song repertoire sizes can range from just a single song type to a seemingly infinite number of song types produced via mimicry or improvisation (Krebs and Kroodsma 1980, MacDougall-Shackleton 1997, Catchpole and Slater 2003). Decades of research have shown that large song repertoires may signal breeding quality and are attractive to potential mates in many species (Catchpole 1986, Hasselquist et al. 1996, Hosoi et al. 2005, Byers and Kroodsma 2009, Soma and Garamszegi 2011). Similarly, song repertoires may provide information about an individual singer's quality in contest situations, making birds with large repertoires more effective at defending resources (Krebs 1977, Yasukawa et al. 1980, Hiebert et al. 1989, Lapierre et al. 2011). Birds with large repertoires may also be able to increase total song output if frequent song type switching reduces costs associated with singing high-cost songs, or with repeatedly singing songs of the same type (Lambrechts and Dhondt 1988, Weary et al. 1991, Deoniziak and Osiejuk 2016, but see Brumm and Slater 2006).

In addition to having inherent signal value, a large song repertoire provides the potential for more flexible song behavior through differential song use. Among avian species with song repertoires larger than one, individuals must decide how and when to employ different song types (Hartshorne 1956, Kroodsma 1977). Birds can vary the timing and pattern with which they deliver songs, and are known to do so in functional ways. For example, many species of New World wood warblers sing two song types which they employ at different times of day and during different social contexts (Byers 1996, Beebee 2004). Song sparrows, with typical repertoires of about a dozen song types, adjust their song type use in response to the songs of neighbors in order to match or avoid matching types as agonistic signals (Beecher et al. 2000, Burt et al. 2001, Vehrencamp 2001). Similarly, banded wrens preferentially use shared song types with neighbors, and adjust song type usage in different contexts (Trillo and Vehrencamp 2005, Vehrencamp et al. 2007).

In the studies referenced above, researchers have shown that birds vary song type use patterns in and across mating and contest situations, but the field lacks studies testing whether birds produce adaptive song type use patterns when singing without an immediate threat or challenge. Virtually all studies of song type use have been done using playback experiments, which by their nature do not capture variation in natural broadcast song. General broadcast song is used daily for resource defense and likely comprises the majority of all song output produced by a given bird over the course of its life (Catchpole and Slater 2003). Natural selection is expected to favor individuals that maximize the effectiveness of broadcast song, and individuals with large and variable repertoires may accomplish this by varying song type use rates in this context (as they are known to do in other contexts) (Endler 1992, Searcy and Andersson 1986).

Researchers have noted that song delivery patterns vary across species and individuals during broadcast singing, but no studies have explored the functional consequences of variable song type delivery rates (Kroodsma 1977, Bradbury and Vehrencamp 2011). The potential for adaptive song type use certainly exists in the many species that have song repertoires consisting of multiple song types, particularly when individuals show heterogeneous patterns of song delivery (Kroodsma 1977, Ritchison 1988, Nowicki et al. 1994, Riebel and Slater 1999, Botero et al. 2008). By varying song type delivery, birds may improve signal efficacy in two primary ways; they may alter the content of the signal or the quality of signal propagation (Guilford and Dawkins 1991, Hebets and Papaj 2005). Alternatively, birds may adjust signaling patterns, not to improve signal efficacy, but to minimize the cost of signal production (Lambrechts and Dhont 1988, Gil and Gahr 2002). Accordingly, in this study, we examined the repertoire use of rock wrens *Salpinctes obsoletus* during broadcast singing and asked whether they show individually variable song delivery patterns during broadcast song, and if so, then do their song use patterns provide support for any of three hypotheses: 1) birds improve signal content by increasing the use of high quality songs, 2) birds optimize for signal propagation by preferentially using songs that transmit well, and 3) birds minimize energy use by using low-cost songs. These functions of song are not mutually exclusive, and all three are likely to shape overall repertoires. Use rates of song types within these repertoires, however, may promote one function over others within a given context.

Rock wrens provide an excellent model system within which to test for functional variation in song type use rates because individual males sing between 50 and 130 song types that vary in form, providing a singer with many potential song types to choose from at any given moment (Kroodsma 1975). This large repertoire size offers the opportunity to examine preferential use of not just one or a few song types, but of larger classes of song types with shared structural characteristics, including timing and frequency parameters. Rock wren songs vary in length, but not dramatically, with all songs being approximately one to three seconds long (Kroodsma 1975, Lowther et al. 2000) (Fig. 1). Each song type contains only a single syllable type that may vary substantially in length and be repeated a variable number of times (Fig. 1). Thus, every rock wren song may be considered a 'trill' since trills are defined as repeats of a single syllable (Catchpole and Slater 2003, Podos et al. 2004). Some song types (rapid trills) include many syllable (65+) repeats (Fig. 1a, b), while other song types include only one or a few repeats of a given syllable (Fig. 1d, e, f).

In order to test the hypotheses outlined above, we examined how rock wren song use varied in relation to several features that are known to relate to song quality, cost, and transmission potential. There is a well-studied tradeoff between propagation potential and signal content potential of song form, such that simple whistles with low bandwidths (which is associated with low entropy) transmit better through space, but song forms with wide bandwidths have higher entropy and may carry more information (Morton 1975, Titus 1998, Brown and Handford 2000, Podos et al. 2004, Brumm and Naguib 2009). Low frequencies also improve transmission and may reflect quality by indicating body size, attractiveness or resource holding potential (Morton 1977, Halfwerk et al. 2011, Byers et al. 2016). Research has shown that rapidly trilled, broadband songs with high entropy (i.e. Fig. 1b) are good indicators of individual quality and are challenging to produce, but do not transmit well over long distances (Morton 1975, Podos 1997, Drăgănoiu et al. 2002, Ballentine et al. 2004, Garamszegi et al. 2006, Illes et al. 2006, Brumm and Naguib 2009). When songs include many rapid frequency directional switches they are

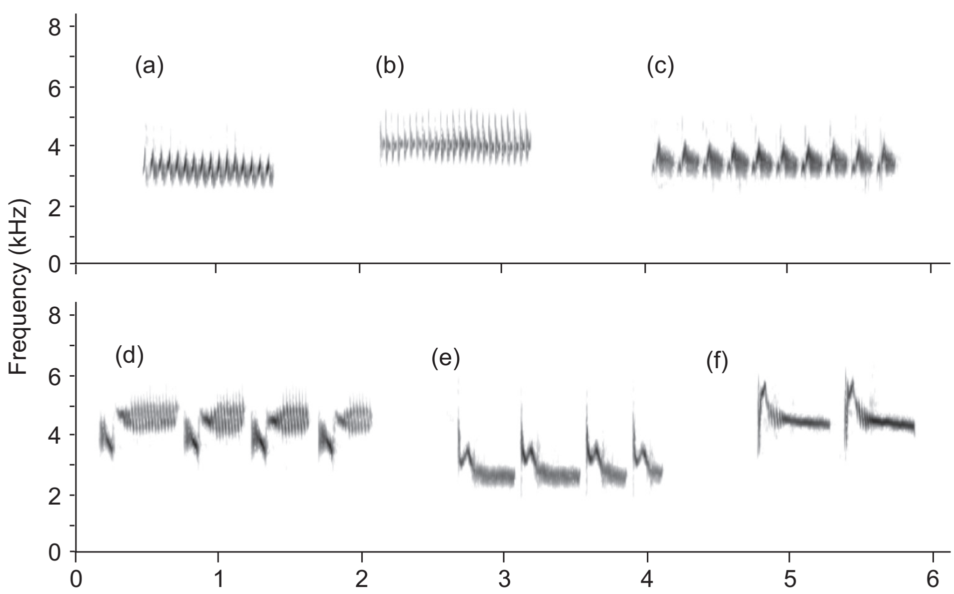

Figure 1. Six song types sung by one rock wren recorded in Larimer County, Colorado, USA during June 2014.

expected to be particularly physiologically difficult to sing, giving them the potential to indicate something about singer quality and energy investment in song (Geberzahn and Aubin 2014, Riede and Goller 2014, Podos et al. 2016). Energy investment in each song may also be indicated by a simpler metric: song duration.

Some avian species use both whistled and trilled elements in their songs, and researchers have postulated that this allows them to optimize for both transmission (whistles) and content (trills and other complex syllables) (Richards 1981, Naguib et al. 2008, Nelson et al. 2016). Rock wrens exhibit similar variation not within a song type, but between song types, allowing us to ask which of these song features the wrens favor by using song types with those features more often than song types with opposite features. Preferential use of classes of song types with particular structural features has the potential to reveal whether natural selection more strongly favors signal performance, signal propagation, or energy maintenance during broadcast singing.

Accordingly, we made the following predictions about differential use of song types by rock wrens (Table 1). If rock wrens preferentially use song types that indicate quality then they will more often sing song types with wide bandwidths (and high entropy), a rapid trill rate and many frequency switches (i.e. Fig. 1b), while less often singing song types with narrow bandwidths (and low entropy), a slow trill rate and few frequency switches (Table 1). If they preferentially use song types that maximize signal transmission over content, then they will more often sing types with narrow bandwidths (and low entropy) and slow trill rates (i.e. Fig. 1c), while less often singing song types with wide bandwidths (and high entropy) and fast trill rates (Table 1). Both the performance and transmission hypotheses predict that birds will preferentially sing songs with low maximum frequencies and longer durations (Table 1). In contrast, if rock wrens opt to sing song types that are energetically less costly then we predicted that they will more often sing songs with short durations, few frequency directional switches, and low performance trills (i.e. Fig. 1f), and they will less often sing song types with long durations, many frequency switches, and high performance trills (Table 1).

We did not make a prediction regarding the relationship between song frequency and energy reduction because there is little information available regarding the relative cost of songs with different predominant frequencies among oscine passerines (Gil and Gahr 2002, Catchpole and Slater 2003) (Table 1). We also did not make a prediction about how frequency switches would relate to song transmission. Wide bandwidth songs with many frequency switches may propagate relatively poorly, but at the same time, rapidly frequency modulated whistles are predicted to transmit better than buzzy songs with no or few frequency switches, leaving us with no clear prediction.

As a group, the hypotheses in Table 1 offer adaptive explanations for song use rates among rock wrens, but it is possible that individual birds select song types randomly with respect to their features. It is also possible that birds vary song use patterns to indicate quality, reduce energy use, and improve transmission simultaneously by cycling regularly through different song types that achieve each goal. In either of these cases, rock wrens should show no tendency to favor song types with particular timing or frequency parameters.

Methods

We recorded the natural broadcast songs of 12 male rock wrens in Larimer County, CO in 2013 and 2014. Recordings were made in late May through July of each year. Rock wrens typically return from migration, establish territories, and begin to breed in April and early May of each year at our study sites (unpubl.), so the timing of our recording was designed to capture the singing behavior of established males. During this period, males defend their territories and retain females using long (several hours per day) bouts of broadcast song (Lowther et al. 2000). All recordings were made using either a Sennheiser MKH 20 microphone with a Telinga 24-inch parabolic reflector, a Sennheiser MKH-70 shotgun microphone, or a Sennheiser MKH-60 shotgun microphone, connected to a Marantz PMD 670 or a Marantz PMD 671 solid-state digital recorder. Recordings were made in mono at a sampling frequency of 48 kHz and a 16-bit sample depth. Recording details for each bird are provided in Supplementary material Appendix 1.

We visited all but one territory more than once (average number of visits: 2.7 ± 1.4) in order to sample song types across multiple days and singing bouts. To ensure that we were recording unprovoked general broadcast song, we never used playback on the populations, and recordists watched for interactions between the focal male and conspecifics. Over the course of the study we never observed any direct confrontations, and we avoided recording when neighbors were countersinging. Recordists noted all activity of each focal bird and took care to record only when he was engaged in a long singing bout from a fixed perch, as is typical of broadcast singing. Most birds were not individually marked, but rock wrens show high site-fidelity and have large home ranges, making it feasible to consistently relocate the same individual (Lowther et al. 2000, Warning and Benedict 2015). We further verified individual identities on repeated visits by defining song features that were unique to each subject. All of our subjects lived in arid, exposed, rocky habitats. Although habitat may affect song transmission, our

Table 1. Predictions[a] for how song features will correlate with usage rates of rock wren song types under three hypotheses.

	Song duration	Song low frequency	Song bandwidth	Trill rate	Frequency switches
Performance hypothesis	+	–	+	+	+
Transmission hypothesis	+	–	–	–	
Energy reduction hypothesis	–		–	–	–

[a](+) indicates a predicted positive correlation with song type use frequency, (–) indicates a predicted negative correlation with song type use frequency, blank spaces indicate lack of a directional prediction.

study animals were all found in similar habitats, and habitat effects were not a focus of this study (Morton 1975, Wiley and Richards 1982).

Since rock wrens have large and variable song repertoires, we recorded many songs per individual. In total we examined 19 508 songs which represented an average of 1588.17 ± 418.49 (SD) songs per bird (range: 928–2077). Gathering so many songs from each bird was necessary to achieve the large within-individual samples that form the main basis of our statistical analyses. To examine song type use patterns, we began by building song type repertoires for each bird using a simple enumeration technique (Botero et al. 2008). We did this to verify that song type delivery patterns are variable among individuals, since this trait is a prerequisite for differential use rates. One person (LB) visualized all songs for every individual and assigned them to types by eye. This is straightforward to do for this species because rock wren songs are highly stereotyped (Kroodsma 1975). For each bird we recorded the order of delivery of all song types and we calculated a use rate of every song type as follows: use rate of song type x = (number of recordings of song type x)/(total number of songs recorded from that bird). This 'use rate' metric allows for comparison across birds when assessing how often they use individual song types, controlling for sampling effort. Once individual repertoires were built, we matched song types to a universal key to quantify the number of song types shared by individuals.

For every song type within each bird's repertoire we selected the example with the best recording quality for analysis of song features. We examined all songs by visualizing them in Raven Pro 1.3 Sound Analysis Software (Cornell Laboratory of Ornithology, NY, USA) as Hanning type spectrograms with a discrete Fourier transform of 512 samples, a frequency resolution of 11.7 Hz, and a time resolution of 5.33 ms. For each song we measured the following variables: duration (s), lowest frequency (Hz), and frequency bandwidth (Hz). We visually assessed spectrograms to calculate trill rate and frequency switches. Trill rate was calculated as the number of syllables in the song divided by song duration to provide a syllables/second value. A frequency switch was defined as either a change from increasing to decreasing frequency, a change from decreasing to increasing frequency, a switch between a pure tone and a buzz, or a change in frequency over a break in a continuous trace on the spectrogram (i.e. a period of silence). Our frequency switching metric was calculated as the number of frequency switches per song divided by song duration to yield a switches/second value. We used this measure because it reflects adjustments within the muscular control of the syrinx during singing (Suthers and Zollinger 2004). Our frequency switch measure also allows us to incorporate all types of sounds made during rock wren songs, including buzzes, which can cause analysis challenges using other performance metrics (Tchernichovski and Mitra 2011, Geberzahn and Aubin 2014, Podos et al. 2016). In general, existing measures of song performance consider bandwidth, trill rate, and frequency modulation, often combining them into a single metric (Tchernichovski and Mitra 2011, Geberzahn and Aubin 2014, Podos et al. 2016). By breaking down our performance measure into the three component parts we were able to assess how each of these song type features was used differentially during broadcast song.

We first assessed whether measured song repertoire sizes correlated with recording effort using simple linear regression. In order to test whether rock wrens preferentially use songs with particular features we built a standard least squares linear regression model that included number of uses of each song type as the response variable and each of the following as predictor variables: 1) song duration, 2) song low frequency 3) song bandwidth 4) trill rate, and 5) frequency switches. Within the model, all of these variables were nested within bird identity. This allowed us to combine data from all individual repertoires (n = 920 song types), while accounting for the fact that the we were assessing song type use rates across a series of twelve within-individual (n = 12) data sets that include song types with variable characteristics, variable inter-individual sampling, and repeated universal song types. Output from the model allowed us to statistically assess whether birds used song types with structural features at rates consistent with our predictions (i.e. are longer songs used more often than shorter songs? Are song types with fast trill rates used more often than song types with slow trill rates?). Statistics were performed in JMP, ver. 9. All values are reported as mean ± standard deviation unless otherwise noted.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.453v0> (Benedict and Warning 2017).

Results

The 12 rock wrens in this study were observed to sing between 52 and 117 different song types, with an average measured repertoire of 76.75 ± 17.54 song types. We note that these values represent the total number of song types recorded during a limited sampling period, and are therefore probably underestimates of full repertoire size. They are, however, likely to approach final repertoire sizes and reflect meaningful individual differences between birds, as rock wren song type accumulation curves typically level off once 1000 songs have been sampled (Kroodsma 1975, LB unpubl.). We verified this pattern by confirming that our sampling effort (number of songs recorded) did not correlate with measured repertoire size ($r^2 = 0.008$, $F = 0.0862$, $p = 0.775$). Furthermore, fully complete repertoires are not necessary in order to calculate the use rates of observed song types, as is our goal here.

Song measurements confirmed the expected typical song duration, and found that rock wren songs were quite variable in their frequency characteristics, number of frequency switches, and trill rates (Fig. 2). Song type delivery patterns were unpredictable and individually variable, with some types occurring more often than others (Table 2). Within a singing bout a bird would typically switch between several song types multiple times with no evident patterning, before moving on to new song types (Table 2). Many individuals did show a tendency to group particular song types together during different singing bouts, but these patterns were never

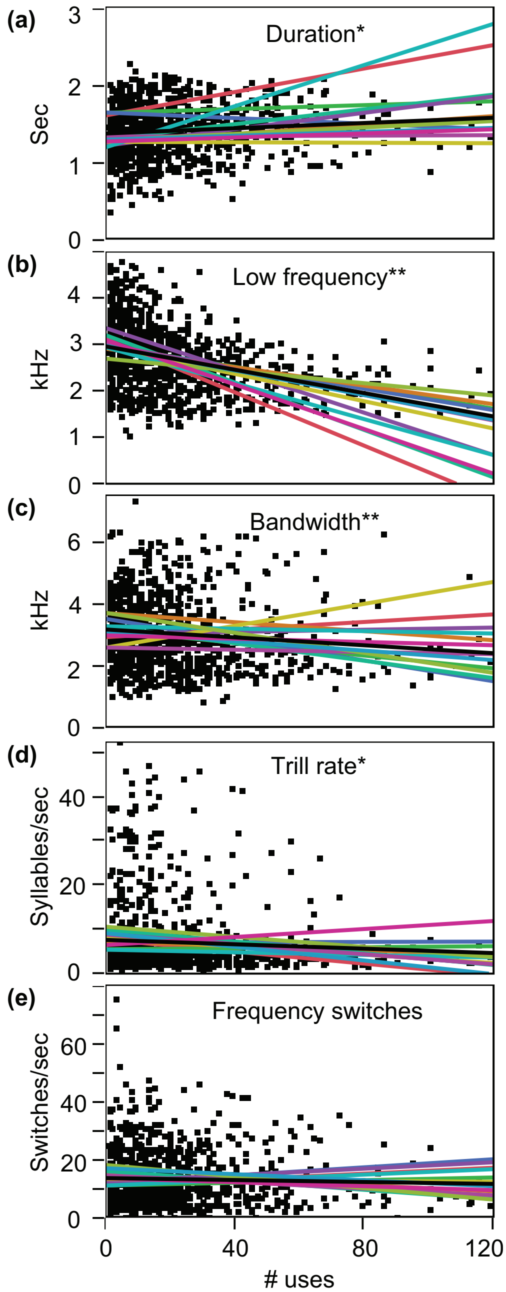

Figure 2. Correlations between song type use and five measures of song form. In (a) through (e) each point represents a song type and each colored line represents song type use patterns by a single rock wren. The black line on each graph indicates the linear trend across all birds. Asterisks indicate significant correlations between song type features and song type use according to linear regressing models nesting song type use within bird identity. (*) indicates significance at $0.05 > p > 0.001$. (**) indicates significance at $p < 0.0001$.

entirely consistent, and individual birds employed different patterns (Table 2).

Our song type use metric indicated that rock wrens did not use all of their song types at equal rates. On average, across all birds, a single song type made up 1.29 ± 1.26% of all songs delivered by that individual. The least frequently used song type made up only 0.048% of the songs sung by a single bird, while the most frequently used song type made up 13.11% of the songs sung by a single bird. On average, each bird sang its most used song type 90.33 ± 1.27 times more often than its least used song type, and showed a log-normal distribution of use frequencies for the song types in between. Individuals shared an average of 31.95 ± 5.26 song types with any other individual in the study, a value that represented 42 ± 4% of each bird's full song type repertoire. Each of 235 universal song types in the population was sung by an average of 3.9 ± 2.6 of the 12 birds. Individuals did not all prefer to use the same song types; the most preferred song types of ten birds were unique, while two shared a most preferred song type. Aggregated, the ten most preferred song types of each bird (120 total) included 74 different universal song types.

Across individuals, our regression model indicated that song type use correlated positively with song duration ($F_{12(920)} = 2.73$, $p < 0.0012$) (Fig. 2). Song type use correlated negatively with song low frequency ($F_{12(920)} = 24.47$, $p < 0.0001$) song bandwidth ($F_{12(920)} = 8.59$, $p < 0.0001$), and trill rate ($F_{12(920)} = 2.05$, $p = 0.0183$) (Fig. 2). Song type did not significantly correlate with frequency switches ($F_{12(920)} = 1.32$, $p = 0.204$) (Fig. 2).

Discussion

Our analyses confirmed that rock wrens have large song type repertoires which they deliver in variable ways (Kroodsma 1975). Song type use rates and delivery patterns were flexible, allowing individuals the potential to facultatively adjust them. We found that birds shared 42% of their song types with other birds in the population, and that not all birds preferred the same song types. Repertoire size, song delivery patterning, and song sharing rates for this species in Colorado (this study) matches data from Oregon, suggesting that rock wren song behavior may be relatively consistent across large geographic areas (Kroodsma 1975).

Individual rock wrens in our study delivered many song types, suggesting that there is a benefit to variety, but they also had favored song types, suggesting that some types bring more benefit than others during broadcast singing. On average the favored song types tended to be long in duration, contain low frequencies, have narrow bandwidths, and slow syllable trill rates. Individuals did share song types

Table 2. Song delivery patterns of the first 30 songs recorded from six rock wrens.

Bird	Song type delivery
1	A B A A A C D C D C E D C E E E F G H H H I H J K J K J L L
2	A B B B B A B A B B C C C C D D E F F F E F G G H G H G H G
3	A B A B A A B A C B C C C C C C D C D D D C D C D C D C D C
4	A B B B C C C C D C E F C E F E C E G F E G G G F G F H I F
5	A B C D D C D C D C D E F C F C F C F C B E B G B G H G H I
6	A B A B A B C B D A D E F E F E F G H I H I H J I J K J K G

but did not all used the same preferred song types, thus these common trends are individually based and are not due to identical use patterns across the population. The significant associations between song type use rates and structural features suggest that rock wrens do not choose song types randomly or equivalently when singing broadcast song. Instead, all of these features are consistent with the hypothesis that song type use most improves signal propagation. Our results supported all three predictions of the transmission hypothesis, and countered none (Table 1). Long, low frequency songs may also indicate singer quality, but other features predicted to be associated with quality, including rapid frequency switching and rapid trill rates were not preferred. These data fail to support all predictions of the performance hypothesis, and suggest that rock wrens do not maximize all signals of performance ability during broadcast singing (although they still may provide information about quality – see discussion below). We also failed to support all predictions of the hypothesis that rock wrens preferentially sing low cost song types. Birds showed no overall tendency to reduce the use of song frequency switches or to minimize song length. For some of the measured variables there were, however, birds that deviated from the population trends (Fig. 2), suggesting that individuals can pursue different behavioral strategies.

Many species of birds have distinct song types that are differentially employed and provide information about the singing individual, such as its quality, breeding status, or readiness to attack (Titus 1998, Nelson and Poesel 2011, Lohr et al. 2013). In contest and mate attraction situations, individuals may do best to highlight quality via song performance and complexity features (Gil and Gahr 2002, Podos et al. 2004). In this study we did not find that our subjects highlighted song performance or complexity, and this may be either a species difference or a difference in song delivery context. Patterns of song type use during broadcast singing bouts are likely to differ from those used in close interactions. During one-on-one interactions individuals are generally advertising in close proximity to each other as potential mates or rivals (MacDougall-Shackleton 1997, Catchpole and Slater 2003, Searcy et al. 2006, Dunning et al. 2014). In contrast, our data suggest that a rock wren's primary goal during broadcast singing is to make its presence known to as wide an audience as possible. Across avian species, long distance song transmission can be an important indicator of both species affiliation and individual identity, and wide dispersion of this information is likely to benefit singing rock wrens who must advertise to potential mates and rivals across large territories which average over 4 ha in size (Brenowitz 1982, Mouterde et al. 2014, Warning and Benedict 2015). Future studies should examine whether rock wrens favor a different set of song types when they are in close interactions.

During broadcast singing bouts rock wren song type selection improves signal transmission, but does not do so exclusively, as is evidenced by the fact that individuals produce many song types of varying form within each bout. To completely maximize transmission, an individual could produce only a single song type optimized for signal propagation (Morton 1975, Wiley and Richards 1982, Price 2013). Thus, although transmission may be most highly favored, there is likely still a benefit to singing multiple song types. This benefit may come through several avenues. Researchers have proposed that singing complex songs is costly and that birds may minimize the cost of repeatedly singing such songs by switching song types regularly (Lambrechts and Dhont 1988, Garamszegi et al. 2006, Deoniziak and Osiejuk 2016). Although we did not support most predictions of the energy reduction hypothesis, we also did not directly measure energy use, and so there may be an energetic advantage to song variability. Such an advantage, however, would not explain why some song types are sung more often than others.

Our performance hypothesis examined multiple potential indicators of male quality, including song length, song bandwidth, trill rate and frequency switch rate. These features may indicate different information about a singing bird, and although we did not support the quality hypothesis as a whole, some predictions were supported. In particular, we found that rock wrens preferentially sing long songs with low frequencies. Song length may advertise energy investment and therefore male condition, a result that has been found in other species (David et al. 2013, Grunst and Grunst 2014). Low frequency song generally correlates with body size and has the potential to indicate fighting ability. (Hall et al. 2013, Linhart and Fuchs 2015). Birds are known to adjust song frequencies downwards in contest situations, so by preferentially singing low frequency songs during broadcast singing, rock wrens might be advertising resource holding potential (Benedict et al. 2012, Geberzahn and Aubin 2014). Additionally, in some species, females prefer males with lower song frequencies, providing another sexual selection pressure favoring lower pitched songs (Cardoso 2011, Byers et al. 2016).

Although rock wrens employ song selection patterns that have the potential to reveal individual quality information about body size or condition, they do not preferentially sing songs that are more complex or difficult to perform. Bird song complexity may be measured in many ways. Researchers studying song complexity may quantify song repertoire size, syllable repertoire size, song bandwidth, the number of elements in a song, the structural complexity of a song form and more (Irwin 2000, Drăgănoiu et al. 2002, Gil and Gahr 2002, Kagawa et al. 2014, Podos et al. 2016). Songs with high structural complexity and many frequency switches require precise respiratory and motor control, making them challenging to sing and good candidate indicators of performance ability (Suthers and Zollinger 2004, Taft 2014, Podos et al. 2016). In our study we found that rock wrens do not maximize signals of complexity or song performance by preferentially using such songs during broadcast singing bouts.

Conclusions

Because rock wrens can vary the delivery patterns of many song types which each include just a single syllable type, they provide an excellent test system for assessing which avian song features are favored during broadcast song bouts. Rock wrens sing a range of song types with forms that include trills, relatively simple whistle-like notes, and complex rapidly frequency-modulated notes. The wide variety of songs produced is striking and suggests that there are benefits to song diversity, not the least of which may be the ability to adapt song use patterns to singing context. When singing natural song in a broadcast setting rock wrens favor song types that propagate well through environmental space, and have the potential to advertise aspects of quality related to body size and condition but not song performance or complexity (Gil and Gahr 2002). The hypotheses examined here have been difficult to assess in other species which have more variable song type syntax or smaller song repertoires, making this an informative test case for general hypotheses about broadcast signaling. Our results indicate that birds can vary signal type use rates to improve the propagation of advertisement song, and that this outcome is favored over minimizing costs or indicating song performance ability. Future work should assess whether the same outcomes may be seen in other animal species with variable signaling repertoires.

Acknowledgements – The authors wish to thank Colorado Parks and Wildlife, the Larimer County Dept of Natural Resources, the City of Fort Collins Natural Areas Program, and Lory State Park for access to field sites. Nadje Najar, Stephanie Pitt and four anonymous reviewers provided feedback on earlier versions of the manuscript. Mark Delorey provided valuable advice regarding statistical approaches.

Funding – This work was supported by The Univ. of Northern Colorado's Provost Fund and the Univ. of Northern Colorado's Summer Support Initiative.

Permits – The research reported here was conducted under the Univ. of Northern Colorado's Institutional Animal Care and Use permit #1506C, Colorado State collecting permit #TRb2041, and the United States Geological Survey's Bird Banding Laboratory permit #23741. As necessary, we obtained research permissions from local land management agencies. All research activities followed guidelines set forth by the ASAB/ABS (ASAB/ABS 2016), and the Ornithological Council (Fair and Jones 2010).

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Supplementary material (Appendix JAV-01357 at <www.avianbiology.org/appendix/jav-01357>). Appendix 1.