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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, Beebe 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, Heberts 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

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.

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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:  $2.7 \pm 1.4$ ) 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

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 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 data sets



is 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







*mexicanus*) and rock wrens (*Salpinctes obsoletus*

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