

# The structure and organization of song in Southern House Wrens (*Troglodytes aedon chilensis*)

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**Abstract** Studies of birdsong across very broad geographic scales, such as between the north temperate zone and the tropics, provide special opportunities to understand the role of variable ecologies, life histories and mating pressures on song structure and organization. The problem is typically studied through comparative, cross-species analyses because few species have such broad distributions to encompass both regions. The House Wren is an important exception, having the widest distribution of any native songbird in the Americas, from Canada to Tierra del Fuego. Across this range, they manifest considerable variation in life history, mating systems and migration, but there is no systematic research on corresponding song variation. Here we provide a first detailed characterization of song structure and organization for Southern House Wrens (*Troglodytes aedon chilensis*) in western Argentina and provide preliminary comparisons to Northern House Wrens. Songs of Southern House Wrens contained two distinct sections: an introduction of broadband noisy, or harmonic, notes followed by a louder terminal section of

tonal, frequency-modulated syllables with a mean of seven syllables and three syllable types per song. The syllable repertoire was large (28), mostly shared and used to construct very large song repertoires (up to 170 song types with no evidence of a ceiling), but much smaller repertoires of commonly produced song types (24). Males tended to repeat song types many times before switching (eventual variety) but, at times, sang with immediate variety. Compared to Northern House Wrens, there were differences in the detailed form of some notes and syllables as well as in the relative emphasis of the softer introduction versus louder terminal section of songs. In broader patterns of song construction, organization, delivery, and the size of syllable and song repertoires, the two populations were very similar. These patterns are discussed in light of differences in life history, mating and migration between them.

**Keywords** House Wren · Geographic variation · Song organization · Song repertoires · *Troglodytes aedon*

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## Zusammenfassung

### Gesangsstruktur und -organisation beim Südlichen Hauszaunkönig *Troglodytes aedon chilensis*

Untersuchungen von Vogelgesang über große Gebiete hinweg, zum Beispiel in der nördlichen gemäßigten Zone und in den Tropen, bieten besondere Gelegenheiten, die Rolle variabler Ökologie, Lebensgeschichte und Paarungsdruck hinsichtlich der Gesangsstruktur und -organisation zu verstehen. Dieses Problem wird typischerweise mit Hilfe vergleichender Analysen mehrerer Arten untersucht, da nur bei wenigen Arten das Verbreitungsgebiet so groß ist, dass es beide Regionen einschließt. Der

Hauszaunkönig, der die weiteste Verbreitung aller in Amerika heimischen Singvögel aufweist (von Kanada bis Feuerland), stellt hier eine wichtige Ausnahme dar. Über dieses Gebiet hinweg zeigt die Art beträchtliche Variation in Lebensgeschichte, Paarungssystem und Zugverhalten, doch gibt es keine entsprechende systematische Forschung bezüglich der Variation im Gesang. Hier liefern wir eine erste detaillierte Beschreibung der Gesangsstruktur und -organisation bei Südlichen Hauszaunkönigen (*Troglodytes aedon chilensis*) in Westargentinien und stellen vorläufige Vergleiche mit Nördlichen Hauszaunkönigen an. Die Gesänge der Südlichen Hauszaunkönige bestanden aus zwei unterschiedlichen Abschnitten: einer Einleitung aus verrauschten oder harmonischen Breitbandnoten, auf die eine lautere Endsektion tonaler frequenzmodulierter Silben folgte, mit im Mittel sieben Silben und drei Silbentypen pro Gesang. Das Silbenrepertoire war umfassend (28), wurde zum großen Teil gemeinsam genutzt und zum Aufbau sehr großer Gesangsrepertoires verwendet (bis zu 170 Gesangstypen mit keinen Hinweisen auf eine Obergrenze). Die Repertoires häufig produzierter Gesangstypen waren allerdings viel kleiner (24). Männchen tendierten dazu, Gesangstypen viele Male zu wiederholen, bevor sie wechselten (letztendliche Gesangsvielfalt), zeigten zeitweise jedoch auch unmittelbare Gesangsvielfalt. Verglichen mit Nördlichen Hauszaunkönigen bestanden Unterschiede in der genauen Form einiger Noten und Silben sowie in der relativen Betonung der leiseren Einleitung relativ zur lauteren Endsektion der Gesänge. Die beiden Populationen ähnelten sich sehr in den allgemeinen Mustern von Gesangsaufbau, Organisation und Darbietung sowie in der Größe der Silben- und Gesangsrepertoires. Diese Muster werden im Hinblick auf Unterschiede in Lebensgeschichte, Paarungs- und Zugverhalten zwischen den Populationen diskutiert.

## Introduction

A longstanding issue in the study of birdsong concerns variation in song patterns between populations. Such variation can arise from social processes related to the role of learning and cultural transmission in the cross-generational transmission of song, which, over time, can lead to divergence in song patterns between populations, traditionally referred to as song ‘dialects’ (Marler and Tamura 1962). Geographic, or dialect, variation can also arise through processes of ecological adaptation of song features to local habitat conditions and their associated acoustic transmission characteristics, which can differ between populations (Slabbekoorn and Smith 2002). Differences of either sort can occur even over very short distances, as

documented for White-crowned sparrows in northern California (*Zonotrichia leucophrys*: MacDougall-Shackleton and MacDougall-Shackleton 2001) and Rufous-collared sparrows in Argentina (*Zonotrichia capensis*: Tubaro et al. 1993; Kapouchian et al. 2004). Because song often plays an important role in reproduction, disjunct populations might ultimately diverge sufficiently to represent different subspecies or even species, as elegantly documented for greenish warblers in central Asia (*Phylloscopus trochiloides*: Irwin 2000; Irwin et al. 2008).

There is currently considerable interest in patterns of song variation at exceptionally broad geographic scales, such as might characterize birds inhabiting the north temperate zone versus the tropics arising from very broad differences in ecology, life history and selection regimes in the two regions (reviewed in Podos 2014). For example, it has been proposed that the pressures of sexual selection on song might often be greater for migratory birds in the north temperate zone compared to sedentary birds in the tropics because of the relatively short breeding season in the former, which provides only a limited time window in which to compete for territories and find mates (Catchpole 1987). As a result, we might expect more elaborate or complex song patterns in north temperate birds for efficient mediation of these behaviors. There is some support for this proposal (e.g., Collins et al. 2009; Botero et al. 2009a; Weir and Wheatcraft 2011), but the relationships are far from definitive, and there are a variety of exceptions and confounding factors (Byers and Kroodsma 2009; Cardoso and Hu 2011; Soma and Garamszegi 2011). One complication is that most such broadscale studies necessarily involve comparisons across different species inhabiting either the temperate zone or the tropics because there are very few species with sufficiently broad distributions to encompass both regions and thereby allow more focused testing within a single species.

There are, however, some exceptions that can shed additional light on our understanding of latitudinal differences in song structure and singing behavior. For example, it has been suggested that differences in residency and neighbor stability between north temperate and tropical-to-south temperate Sedge Wrens (*Cistothorus platensis*) can select for different song development strategies, which in turn affects song sharing between neighbors (Kroodsma et al. 1999). The House Wren (*Troglodytes aedon*) is another exceptional species with an extremely broad distribution that is ideally suited to detailed investigation of geographic variation in song, but no systematic studies of tropical-south temperate populations have been conducted to date.

House Wrens have the widest latitudinal distribution of any native songbird in the western hemisphere (Brewer 2001). They reach their northern limits in central Alberta,

Canada (58°N) and their southern limits in Tierra del Fuego (55°S). Across this range, there is tremendous variation in ecology, behavior and life history. For example, populations in the north-temperate zone are mainly migratory, show appreciable rates of social and genetic polygyny, and have large clutch sizes (reviewed in Johnson 2014). In contrast, populations in the south-temperate zone are sedentary, social polygyny is rare with only moderate rates of extra-pair fertilizations, and clutch sizes are small (Young 1996; Llambías 2009, 2012; Llambías and Fernández 2009; Ippi et al. 2012; Llambías et al. 2012, 2015; LaBarbera et al. 2010, 2012). Differences such as these in basic dimensions of life history, mating system and migration patterns are among the traits implicated in differences in song structure and complexity (Catchpole 1987; Read and Weary 1992; MacDougall-Shackleton 1997; Kroodsma et al. 1999; Collins et al. 2009; Irwin et al. 2008). As a result, there is considerable scope for variation in song patterns in House Wren populations across the Americas, and this represents a truly unprecedented opportunity to examine how variable ecology, life history, migration and mating systems influence song.

Previously, we provided a detailed description of song structure and organization for a population of Northern House Wrens breeding in southern Alberta, Canada (*Troglodytes aedon parkmannii*; Rendall and Kaluthota 2013). Here we provide a complementary study of song for Southern House Wrens from a population in western Argentina (*Troglodytes aedon chilensis*). This represents the first detailed account of song for the species in the southern hemisphere and is a critical first step toward allowing more detailed comparisons of population variation in this exceptionally widespread species group.

Given the many documented differences in life history and mating systems just noted, and following the proposal for latitudinal gradients in song elaboration and complexity, one would predict the songs of Southern House Wrens to be relatively simplified compared to those of their northern counterparts. Specifically, we might expect their songs to be shorter and to involve fewer elements and smaller song repertoires.

## Methods

### Study site and subjects

Research was conducted on a population of Southern House Wrens at a long-term study site in Mendoza province, Argentina, near the town of Uspallata (32.62°S 69.36°W). The site is in a montane habitat (1850 m) in the foothills of the Andes where the breeding habitat for House Wrens is a plantation of White Poplar (*Populus alba*). To

facilitate our broader research program on breeding biology, wooden nest boxes were provided and used by the birds (Llambías and Fernández 2009; Llambías 2012; Llambías et al. 2012). Since 2011, we have captured and marked individuals at this site with a numbered metal band and three color bands to facilitate long-term identification, and we have re-sighted marked individuals on their territories during the austral winter, suggesting that House Wrens are year-round residents at this site. The breeding season is from late October to mid-February. Maximum daytime temperatures range from 18 to 35 °C with little rainfall (mean annual precipitation = 134 mm; Carretero 2000).

The present study was conducted in the 2012 breeding season (October 2012–February 2013). An initial survey was conducted at the start of the breeding season to identify suitable males for song recording. Candidate males that were not yet marked were captured using mist nets and banded in the fashion just described and thereby added to the long-term sample. These males were then monitored daily for the remainder of the breeding season.

### Song recording and analysis

Song recordings of marked males were made primarily in the early morning (5:00–10:00 a.m.) when males were most active and singing. Recordings were made with a digital recorder (Sound Devices 702) and Sennheiser microphone system (Sennheiser MKH 816) at distances as close as possible (5–10 m) without disturbing the birds.

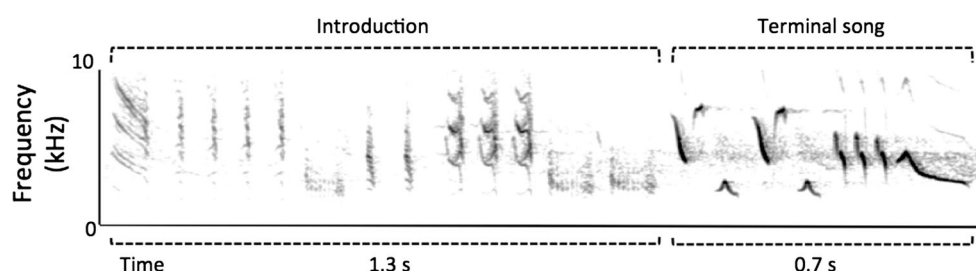
Our complete recording sample involved 30 males. However, for some males, we had very few recordings. Hence, for subsequent detailed analysis, we limited the sample to males for which we had more than 200 songs. The final sample thus comprised a total of 13,440 songs from 18 males (Table 1; see also Electronic Supplementary Material). Sample sizes for these males also varied, reflecting natural differences in singing activity among males at different breeding stages and associated differences in sampling effort. Recordings were analyzed in PRAAT, version 5.3 (Boersma and Weenink 2015), to capitalize on its robust modules for signal segmentation, annotation and database export. The first step was to characterize the basic structure of song. Songs lasted for 1–3 s and tended to be delivered in bouts in which consecutive songs were separated by relatively short silent intervals (2–5 s). We used a silent interval of  $\geq 30$  s to define different bouts of singing. The majority of songs were composed of two discrete sections, readily distinguished by ear and in spectrograms (Fig. 1). The opening section (labeled the introduction) was an arrangement of unstructured broadband notes that were either harsh (noisy) or tonal with multiple harmonic overtones, while the

**Table 1** Summary statistics (counts or means  $\pm$  SD) for the sample of recorded songs of 18 male House Wrens from a population breeding in western Argentina in 2012

Bird ID	Number of bouts	Number of songs	Syllables song <sup>-1</sup>	Syllable types song <sup>-1</sup>	SVI <sup>a</sup>	Syllables sec <sup>-1</sup>	Syllable types sec <sup>-1</sup>	Total syllable types	Total song types	Common song types <sup>b</sup>
UP211	85	711	6.9 $\pm$ 2.8	2.8 $\pm$ 1.0	0.43 $\pm$ 0.13	9.8 $\pm$ 2.7	4.1 $\pm$ 1.2	27	52	25
UP212	89	1458	7.5 $\pm$ 3.1	3.3 $\pm$ 1.4	0.46 $\pm$ 0.13	9.7 $\pm$ 2.6	4.4 $\pm$ 1.5	28	159	34
UP266	27	292	5.2 $\pm$ 2.0	2.7 $\pm$ 1.2	0.52 $\pm$ 0.11	8.8 $\pm$ 2.7	4.5 $\pm$ 1.5	20	33	22
UP403	45	223	7.3 $\pm$ 3.5	3.0 $\pm$ 1.4	0.44 $\pm$ 0.15	8.9 $\pm$ 2.7	3.9 $\pm$ 1.4	26	46	20
UP405	68	1481	6.5 $\pm$ 2.2	2.8 $\pm$ 0.7	0.46 $\pm$ 0.15	10.8 $\pm$ 2.9	4.8 $\pm$ 1.5	27	78	23
UP409	58	797	7.5 $\pm$ 3.5	3.0 $\pm$ 1.3	0.44 $\pm$ 0.16	9.7 $\pm$ 2.8	4.1 $\pm$ 1.3	28	170	29
UP411	151	1665	5.5 $\pm$ 2.8	2.6 $\pm$ 1.2	0.52 $\pm$ 0.15	8.8 $\pm$ 2.3	4.3 $\pm$ 1.0	28	114	24
UP414	51	336	7.4 $\pm$ 3.3	2.8 $\pm$ 1.0	0.41 $\pm$ 0.13	9.7 $\pm$ 3.1	3.8 $\pm$ 1.4	28	46	25
UP416	38	215	6.8 $\pm$ 3.7	2.6 $\pm$ 0.9	0.48 $\pm$ 0.22	10.5 $\pm$ 3.5	4.5 $\pm$ 1.6	19	25	17
UP417	46	483	7.9 $\pm$ 3.0	2.8 $\pm$ 0.9	0.39 $\pm$ 0.13	9.5 $\pm$ 3.0	3.5 $\pm$ 0.9	27	47	20
UP419	46	651	8.3 $\pm$ 4.4	3.3 $\pm$ 1.4	0.45 $\pm$ 0.16	9.2 $\pm$ 2.1	4.0 $\pm$ 1.1	27	118	18
UP422	41	613	6.1 $\pm$ 2.3	2.7 $\pm$ 1.0	0.45 $\pm$ 0.11	9.3 $\pm$ 2.4	4.1 $\pm$ 1.2	22	60	22
UP423	57	351	8.9 $\pm$ 2.6	3.7 $\pm$ 1.1	0.43 $\pm$ 0.10	10.9 $\pm$ 2.1	4.7 $\pm$ 1.5	22	38	20
UP424	22	230	9.8 $\pm$ 3.9	4.1 $\pm$ 1.8	0.44 $\pm$ 0.13	10.4 $\pm$ 2.7	4.5 $\pm$ 1.7	27	116	32
UP428	18	379	5.8 $\pm$ 2.5	2.8 $\pm$ 0.9	0.53 $\pm$ 0.15	9.2 $\pm$ 2.8	4.6 $\pm$ 1.1	22	44	25
UP438	70	1087	6.1 $\pm$ 2.4	2.6 $\pm$ 1.0	0.45 $\pm$ 0.12	9.7 $\pm$ 2.6	4.2 $\pm$ 1.3	26	78	20
UP466	123	2051	6.9 $\pm$ 3.0	3.0 $\pm$ 1.1	0.48 $\pm$ 0.17	9.3 $\pm$ 2.4	4.2 $\pm$ 1.1	28	143	26
UP475	32	417	8.0 $\pm$ 3.6	3.3 $\pm$ 1.4	0.44 $\pm$ 0.13	11.9 $\pm$ 3.1	5.0 $\pm$ 1.6	27	67	22
Mean			7.13	3.00	0.46	9.75	4.30	25	79	24

<sup>a</sup> Syllable Versatility Index (SVI): calculated by dividing the number of syllable types in a song by the number of syllables

<sup>b</sup> Count is limited to types representing more than 1 % of a male's song or syllable production



**Fig. 1** A representative song of a male House Wren illustrating the basic structural division of song into an introduction section composed of relatively low-amplitude broadband notes and a terminal

section composed of a concatenation of higher amplitude and tonal, frequency-modulated notes organized into discrete syllable types

second section (labeled the terminal section) was comprised of well-structured, tonal and frequency-modulated notes. The introduction section was often notably softer than the terminal section. As a result, it was sometimes difficult to delineate clearly the structure of some notes in the introduction section.

After characterizing the basic components of songs and song bouts, the next step was to develop a catalog of notes and syllables. In this, we focused our efforts on the terminal section of songs where the structure of notes was very clear and easily delineated. Because this section of songs was also generally louder than the introduction, it

also had greater potential to be heard by males and females in the wider area. Following conventional definitions and nomenclature, notes were defined as continuous signal traces in the song spectrogram, and syllables were defined as regularly grouped combinations of notes consistently produced together as a common unit. This conventional approach also mirrored our earlier analyses of song structure and organization for a population of Northern House Wrens (Rendall and Kaluthota 2013). We delineated different note and syllable types based on clear and constant differences in overall temporal-spectral shape that were repeatable across songs both within and between males.

Songs were then segmented and their syllable content annotated. Subsequent detailed analysis involved quantifying the note, syllable and song repertoires of individual males. For each song, we also quantified the syllable and syllable type production rate and calculated the ratio between different syllable types and the total number of syllables (the Syllable Versatility Index, SVI; Gil and Slater 2000). Finally, we analyzed variability in the sequencing of syllables within songs and in the sequencing of songs within bouts using first-order transition matrices. Statistics were performed in SPSS, version 20 (SPSS, Chicago, IL).

## Results

### General summary of singing, courtship and breeding behavior

Males sang at high rates at the start of the breeding season, often from relatively high perches. Early in the season, they delivered songs in long bouts of 30 min or more continuously. Males increased their singing rate even more when visited by females and showed additional signs of heightened arousal, chasing the female and wing-fluttering near her when she settled on a branch or inspected a specific nestbox. Additionally, male songs were interspersed with high-frequency “squeak” calls at such times (cf. Johnson and Kermott 1991). Most males continued to sing while their female partners completed nest building. However, they dramatically reduced their singing rate just before and during egg laying. During this stage, song bouts were usually much shorter with longer intervals between consecutive songs. Some males resumed singing when their mates had finished laying and began incubating eggs, but others only resumed singing just before, or shortly after, chicks from their first nest had fledged. Throughout the breeding season, males sang most often, and at higher rates, in the early morning, starting just before sunrise. They sang only infrequently in the afternoon or evening. Males tended to sing from specific locations within their territories, usually from the tree containing their nestbox or from a neighboring tree. Although males were provided with two nestboxes per territory, we did not observe any case of polygyny.

### Global song structure

Most songs (97 %) contained both introduction and terminal sections, with only 2.5 % lacking a terminal section and the remaining 0.5 % lacking an introduction. Individual song duration averaged 2.11 s ( $\pm$ SD = 0.62 s), with the introduction generally longer (mean = 1.38 s  $\pm$  SD =

0.54 s) than the terminal section (mean = 0.73 s  $\pm$  SD = 0.25 s). Notes in the terminal section were organized as a sequence of discrete syllable types. Many syllable types were repeated within a song before switching to a different type, and some syllable types appeared again later within the same song. Songs contained an average of three syllable types (range 1–10) and seven syllables (range 1–26) produced at an average rate of 4.3 syllable types  $s^{-1}$  and 9.75 syllables  $s^{-1}$  (Table 1; Fig. 2). The relative syllable diversity of songs (SVI index) averaged 0.46. The interval between songs in a bout averaged 2.77 s ( $\pm$ SD = 2.27 s).

### Note and syllable repertoires

A total of 15 different notes and 28 different syllable types were identified in the terminal section of songs (Fig. 3). The structure of notes and syllables was highly regular and consistent within and between individuals, showing no obvious intermediate forms (Fig. 4). Some syllable types were formed from only a single note, while others were composed of two or three notes (Fig. 3). The different syllable types varied in their position within songs, some syllables occurring primarily at the beginning or the end of songs, and others occurring primarily in the middle. Still others were more flexible and could occur in various positions (Fig. 5).

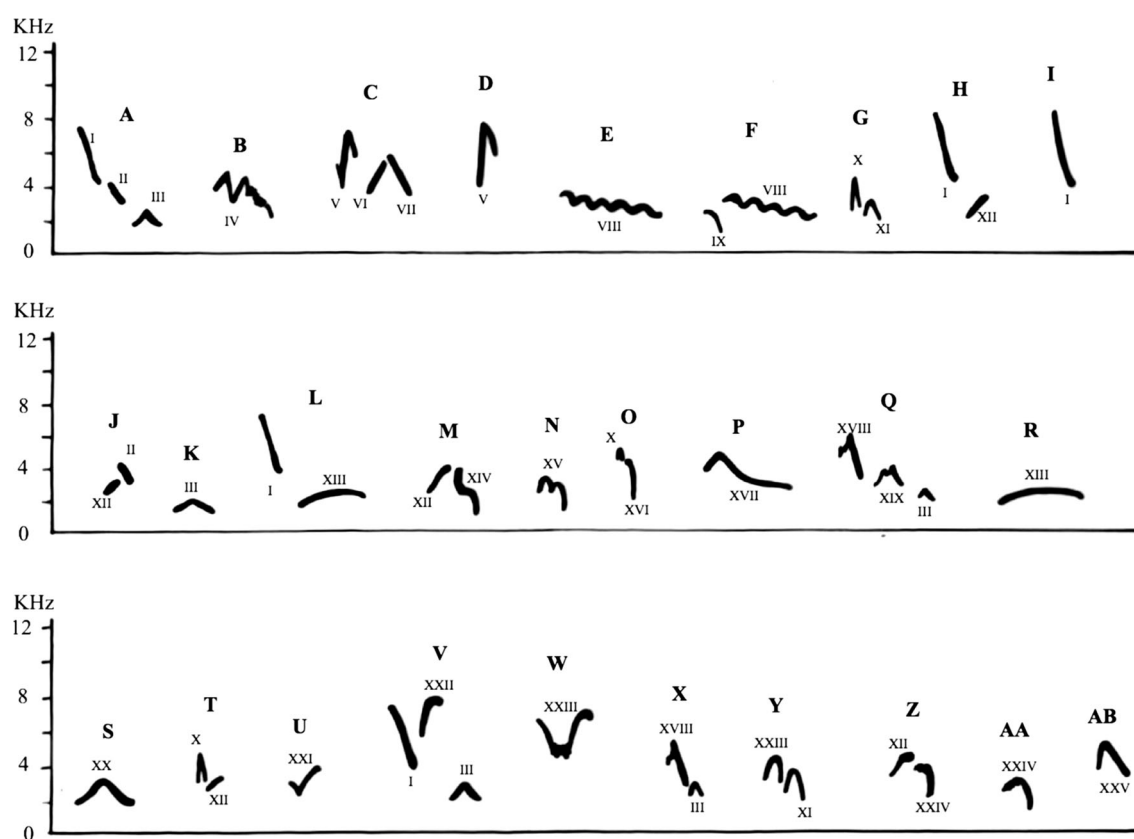
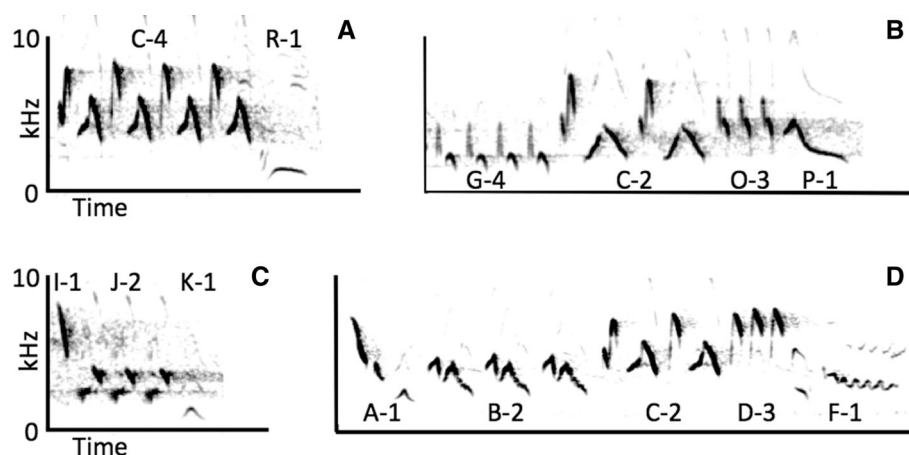
Syllable repertoires were strongly conserved across males, with individual males producing an average of 25 of the total 28 different syllable types (Table 1). Although they shared most of the syllable repertoire, males varied in their use of different syllable types. Some syllable types (e.g., C, I, P, Q, R) were produced and used frequently by all males, while others were used much less commonly (e.g., AB, D), and still others (e.g., K, W, R, T) were produced frequently by some males but rarely by others.

Figure 6 shows the time course over which syllable types were revealed in successive song recordings for each male. This figure shows that, for all males, syllable accumulation curves ultimately reached an asymptote typically within the first 500 songs recorded. However, the figure also shows some variation among males in the rate at which complete syllable repertoires were revealed. Some males revealed their full syllable repertoire within the first 200 songs, while others required up to 1000 songs to reveal an equal-sized repertoire of syllables.

### Syllable transition patterns

For the song sample for each male, we constructed a syllable transition matrix to summarize the first order transitions between adjacent syllable types within songs. In this analysis, transitions between the same syllable type (i.e.,

**Fig. 2** Four songs illustrating common variation in the number of different syllable types contained in the terminal section of songs



**Fig. 3** The note and syllable type repertoire for the study population based on the terminal section of songs. Notes are indicated by *Roman numerals* and syllable types by *capitalized letters*. Some notes appear

in several different syllable types (e.g., *I* is used in syllables *A*, *H*, *I*, *L* and *V*), while other notes are unique to only one syllable type (e.g., *XVII* is used in syllable *P*)

repetitions of the same syllable type) were ignored. Some syllable transitions were very common (e.g., *A*, *B*; *G*–*L*; *H*–*U*; *I*, *J*; *I*–*O*; *O*–*S*), while other transitions were much more rare (e.g., *A*–*I*; *I*–*K*; *B*–*L*), and many possible syllable-type transitions never occurred at all. Furthermore, some syllable types transitioned to one of many other syllable types (e.g., *C* was followed by 20 different syllable types), while others were followed by only one or a few

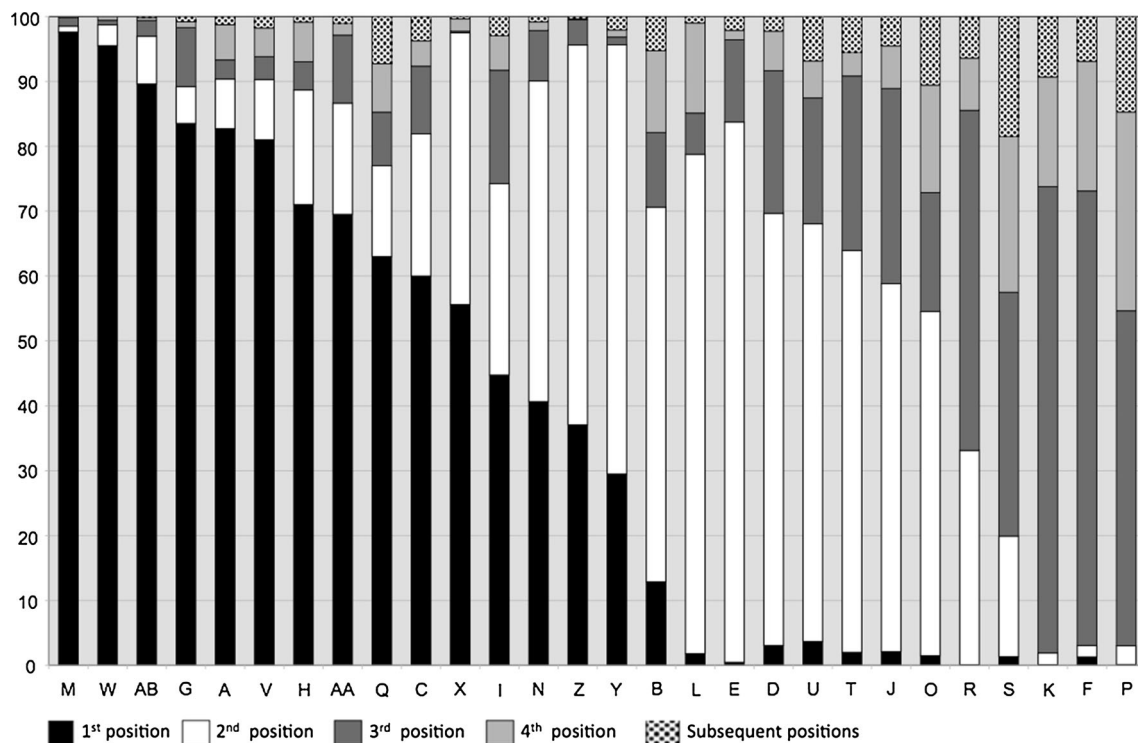
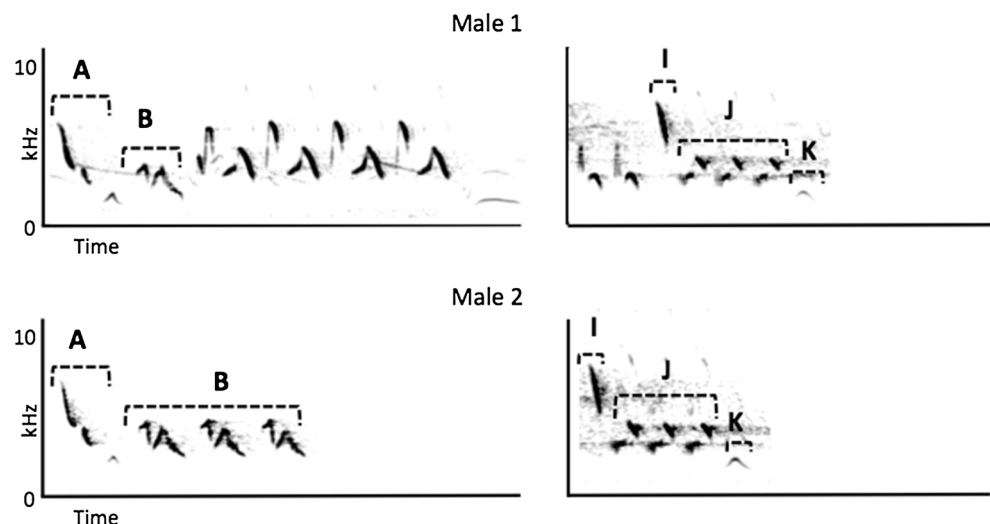
other syllable types (e.g., *E* was followed by only three different syllable types).

### Song type repertoires

We defined different songs, or song types, conservatively as a unique sequence of syllable types, ignoring variation in the number of times a particular syllable type might be



**Fig. 4** Two different songs from each of two different males. Syllable types common to songs used by both males are annotated to illustrate similarity in the forms of specific syllable types across males

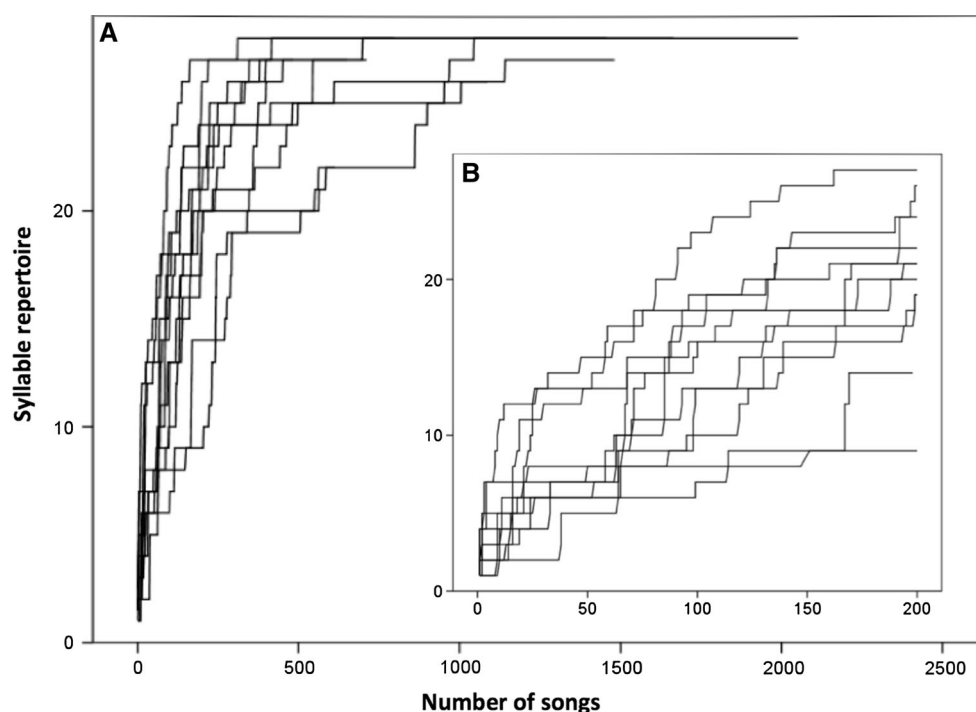


**Fig. 5** All syllable types in the study population's repertoire organized according to the frequency with which they occur in first, second, third, fourth and all other subsequent positions within songs

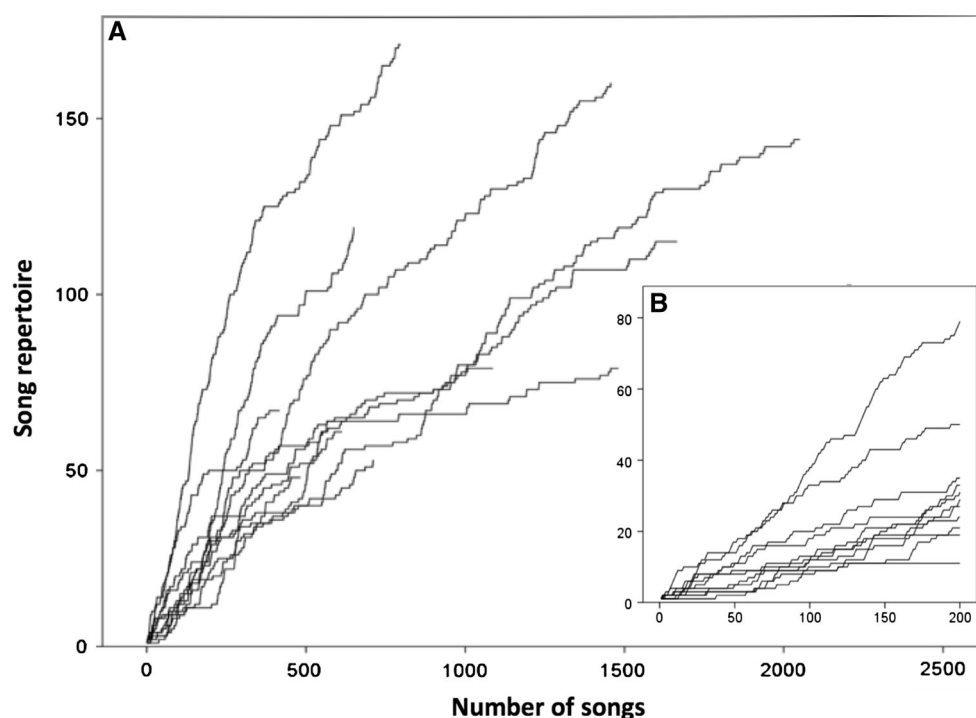
repeated in a given position within a song (Kroodsma 1977). If a syllable type was repeated in a different position in the song—that is, after the occurrence of other intervening syllables—this was counted as a distinct song type. Despite our conservative definition of song types, there was tremendous diversity in the song types recorded. The complete sample of 13,440 songs included 809 different song types. Males varied substantially in the size of their song type repertoires, from a low of 24 song types to a high

of 170 (mean = 79; Table 1). However, much of this variation among males was almost certainly due to unequal sampling effort. This is captured in Fig. 7, which plots the time course over which new song types were introduced in successive recordings for each male. Males with relatively small song repertoires were also males with a smaller overall recording sample. These males would probably show a larger song repertoire with additional recordings, as Fig. 7 also shows that, for all males, new song types were

**Fig. 6** Syllable repertoire size and accumulation functions for a subsample of male House Wrens ( $n = 11$ ). Each *line* represents a different male and shows the time course over which they introduced new syllable types into their songs across successive recordings. **a** Covers the the entire recording sample and illustrates the clear asymptote in the syllable repertoire, while the *inset b* zooms in on the first 200 songs recorded for each male to better illustrate differences in the early accumulation functions between them



**Fig. 7** Song repertoire size and accumulation functions for subsample of male House Wrens ( $n = 11$ ). Each line represents a different male and shows the time course over which males introduced new song types across successive recordings. Note that the accumulation functions show no sign of a plateau for any of the males regardless of the size of their recording sample. **a** Covers the entire recording sample and the *inset b* zooms in on the first 200 songs recorded for each male



introduced steadily and continuously, with no indication of an asymptote for any male, regardless of the size of the recording sample. Even for the male with the largest sample of recordings (UP466,  $n = 2051$  songs) and one of the largest documented song repertoires ( $n = 143$ ), there was no indication of reaching a ceiling.

Given the diversity of different song types sung by males, there was relatively little sharing of complete song types among them, defined conservatively as a complete matching of their syllable type sequences (irrespective of differences in syllable repetition). Of the total of 809 different song types produced, no single song type was shared



by all males, and only 26 different song types (3.2 %) were shared by more than half. Indeed, only 178 different song types (22 % of the total) were produced by more than one male. The remainder ( $n = 631$ , or 78 %) were unique to particular males. On average, the number of males producing a particular song type was 1.78.

Notably, although males had large repertoires involving many unique song types, they sang most song types only rarely. Of the 809 song types in the sample, 390 (48.2 %) were sung only once, and only 51 song types (6.1 %) were sung >50 times. Thus, individual repertoires of commonly produced song types were much smaller. To establish these, we defined a “commonly produced” song type as one that accounted for >1 % of a male’s song production. By this criterion, the repertoires of individual males were more consistent in size and averaged only 24 song types (range 17–34, Table 1). There was no relationship between the size of the repertoire of commonly produced song types for individual males and the number of song recordings for each (Pearson  $r = 0.351$ ,  $P = 0.2027$ ).

### Song-type transitions

To further examine the relative diversity of songs within bouts, we constructed a song type transition matrix quantifying the first order transitions between song types in adjacent positions in the sequence of songs within a bout. This analysis was limited to a set of 24 song types that accounted for more than 1 % of the entire sample. Even limiting the analysis in this way, the matrix is too large to display, but it revealed that despite the large number of song type transitions that are possible only a few actually occurred. By far the most common “transition” between successive songs was to the same song type. Of the total 5245 transitions involving this set of 24 common song types, 76.7 % ( $n = 4023$ ) were repetitions of the same song type. Only 22.3 % ( $n = 1222$ ) involved switching to a different song type. Hence, successive songs in a bout tended to involve repetitions of the same song type, with only occasional switching to a different song type, and most such switches involved song types that were only minimally different in their syllable type makeup. As a result, over long bouts of singing, the syllable content of songs tended to change gradually.

At the same time, though, males sometimes sang with much greater short-term variety and with much more rapid switching between song types. These differences in singing style are illustrated in Fig. 8. This figure depicts first-order transitions between successive songs in a protracted bout of singing by two different males on two different days. The data were standardized as much as possible to facilitate comparisons such that each example involves a continuous bout of singing involving a similar number of total songs. The figures show that for each male there is a clear

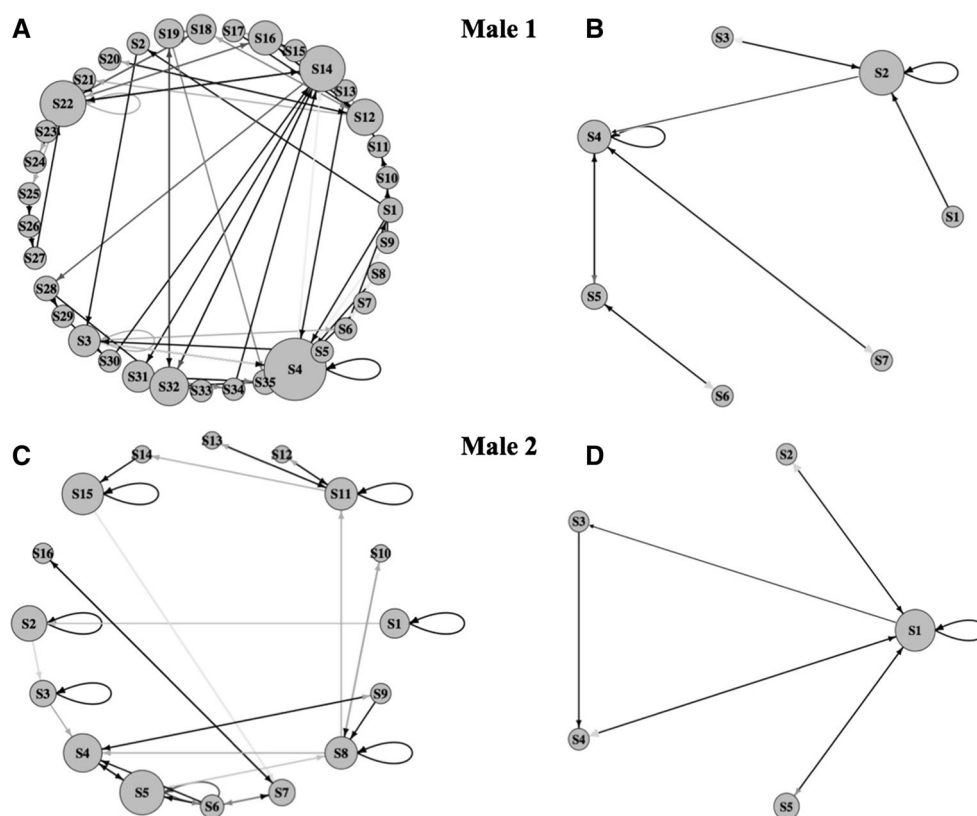
difference in singing style, with singing on one occasion involving production of a relatively large number of different song types with considerable switching among them, and on another occasion involving production of relatively few different song types with greater serial repetition of each.

### Discussion

The detailed patterns of song organization and singing style reported here for Southern House Wrens (SHOWR) were, in most respects, very similar to those reported recently for Northern House Wrens (NHOWR: Rendall and Kaluthota 2013). There were some differences between the two populations in the detailed form of individual notes and syllables (cf. Fig. 3 in Rendall and Kaluthota 2013). Differences at this level even over very short distances are not uncommon in the learned songs and calls of other species (e.g., Marler and Tamura 1962; Mundinger 1982; MacDougall-Shackleton and MacDougall-Shackleton 2001; Kapouchian et al. 2004); hence, it is not surprising to find note and syllable structure differences across the macro-geographic scale involved for NHOWR and SHOWR.

There were some other differences in song structure related to differences in the relative length and emphasis of the introduction versus terminal sections of song in the two groups and in the number of syllables and syllable types they contained (see Table 2). The introduction section of songs in SHOWR was longer relative to the terminal section, by comparison to NHOWR. As a consequence, the proportionately shorter terminal section of songs in SHOWR also contained fewer syllables and syllable types than the terminal section of songs in NHOWR. However, because the reduction in the number of elements contained in the terminal section of songs in SHOWR was not quite proportional to the reduction in the duration of this section, syllables and syllable types were actually delivered at slightly faster rates in SHOWR (Table 2).

Most of these differences were not large but nevertheless might be important and functional with respect to additional differences in life history and mating system between the two populations. For example, the longer terminal section of songs with a greater number of syllables and syllable types in NHOWR is consistent with the prediction of greater song elaboration or complexity in populations at higher latitudes with shorter breeding seasons (Catchpole 1987; Collins et al. 2009). It is also consistent with higher rates of polygyny and extra-pair fertilizations in NHOWR compared to SHOWR (LaBarbera et al. 2010, 2012; Llambías et al. 2012; Johnson 2014) and with the manner in which social polygyny can arise in the two groups. In NHOWR, social polygyny arises when a male



**Fig. 8** Diagrams illustrating variation in male singing styles. Each panel is constructed from a single bout of protracted singing from a particular male. The structure was developed using a custom R code implemented in the iGraph software package (Csardi and Nepusz 2006). It operates on the string of successive songs in a bout and the first-order transitions between them. Each circle represents a different song type, and differences in the size of the circles capture variation in the relative frequency with which the different song types were produced during that bout. Lines between circles represent song type switching, with the arrow indicating the direction of the transition and the darkness of the line signifying the relative frequency of that particular song type change. Looped connections (curved lines that loop back onto the same song type) indicate instances in which a song type is repeated in succession. The top two panels (a, b) correspond to

two different bouts of singing from the same male (UP409) on two different days. They illustrate a clear difference in singing style: on one occasion a bout of 114 songs from this male involved production of a large number of different song types (35) and considerable switching among them; on another occasion, a similar bout of 81 songs involved production of a much smaller number of song types (7), many of which were therefore repeated frequently. The bottom two panels (c, d) capture a similar difference in singing style from a second male (UP466), once again based on single bouts of 75 and 98 songs, respectively, recorded on 2 different days. In this case, UP466 shows lower overall song diversity on both occasions, but greater diversity (16 song types) with more switching among song types on one day versus the other (5 song types)

attracts a second female to his territory. In contrast, in SHOWR social polygyny is rare but can arise when a monogamously paired male replaces a neighboring male and then breeds with the female resident there (Llambías 2012; Johnson 2014). Taken together, these patterns point to a possibly increased emphasis on female attraction in NHOWR and on territorial defense in SHOWR.

It is also possible that the softer introduction section of songs is absolutely longer in SHOWR because it reflects an increased emphasis on close communication and coordination with a female partner. Johnson and Kermott (1991) suggested previously that some aspects of male song in NHOWR functioned to coordinate close-range nest activities between male and female post-pairing. It might then

be that the more protracted pair bonds between males and females in SHOWR select for some extension of the softer introduction section for close-range communication between them compared to the much louder terminal section, which has far greater broadcast potential. These possibilities remain speculative at this stage and require further study and experimentation.

In most other respects, the organization of songs and patterns of song delivery were very similar in the two populations. Thus, the note and syllable repertoires of the two populations were similar in size (NHOWR: 22 different notes and 27 syllable types; SHOWR: 15 different notes and 28 syllable types), and notes were organized into discrete syllable types in a similar fashion. Syllable types

**Table 2** Comparison of basic song features between Northern and Southern House Wrens

Song feature	Southern House Wrens <sup>a</sup>	Northern House Wrens <sup>b</sup>
Song duration (s)	2.11	2.25
Introduction section (s)	1.42	0.92
Terminal section (s)	0.69	1.33
Syllables/song	7.13	10.5
Syllable types/song	3.0	3.9
SVI	0.43	0.39
Syllable production rate	9.75	8.0
Syllable type production rate	4.3	3.1
Syllable repertoire size	28	27
Song repertoire size	19–170 (79)	38–194 (109)
Common song type size	24	24

<sup>a</sup> This study<sup>b</sup> From Rendall and Kaluthota (2013)

were then concatenated together into songs in very similar ways, showing similar patterns of serial repetition within songs (trills) and similar patterns of transition diversity and constraint. For example, in both populations there were clear biases in the positioning of particular syllable types within songs, some syllables occurring primarily only at the beginning, others only at the end and still others occurring more flexibly in different positions within songs (cf. Table 2 in Rendall and Kaluthota 2013). Likewise, there were similar patterns of flexibility and constraint on transitions between particular syllable types in the two populations, where transitions between some syllable types were quite common, others were much rarer, and many possible syllable type transitions never occurred at all.

Similarities in the organization of notes and syllables were paralleled by similarities at higher organizational levels as well. Thus, there was tremendous diversity in the song repertoires of both populations. In NHOWR, we recorded 996 different song types in a sample of 15,608 song recordings from 15 males, while in SHOWR we recorded proportionately similar numbers: 809 different song types in a sample of 13,440 song recordings from 18 males. The song repertoires of individual males were also similarly large in the two populations (NHOWR range 38–194 song types; SHOWR range 25–170 song types) and showed no evidence of reaching a ceiling with increasing numbers of recordings (cf. Fig. 7 in Rendall and Kaluthota 2013) and limited overlap, or sharing, of complete song types between males. The size of these song repertoires in both populations puts them at the very high end of the continuum for song diversity, alongside some other wren species (Sedge Wrens and Marsh Wrens, *Cistothorus palustris*: Kroodsma and Verner 1978; Kroodsma et al. 1999) and members of the *Mimidae* (e.g., Brown Thrashers, *Toxostoma rufum*, and possibly Gray Catbirds, *Dumetella carolinensis*: Boughey and Thompson 1981; Kroodsma 2005).

At the same time, males in both NHOWR and SHOWR had much smaller repertoires of commonly produced songs (defined identically as those sung more than 1 % of the time), which averaged exactly the same number (24 song types). Hence, in both populations, males tended to focus their singing on a much smaller number of song types than they were capable of producing.

Males in both populations also showed similar patterns of song delivery during protracted song bouts. Typically, males sang in a fairly monotonous fashion, repeating the same song type many times before switching and, when switching song types, doing so only gradually via incremental addition, deletion or substitution of one syllable type at a time. Hence, although males in both populations had very large observed song repertoires and a clear capacity for even larger song repertoires than were recorded, their typical singing style tended not to reveal this capacity for diversity but rather concealed it. We referred earlier to this juxtaposition for NHOWR as one of ‘global diversity combined with short-term monotony’ (Rendall and Kaluthota 2013), and it seems to apply similarly to SHOWR. It is important to note, however, that males sometimes showed a capacity for greater short-term diversity in their singing, at times producing a larger number of song types within a single protracted bout and switching among song types more frequently (illustrated for SHOWR in Fig. 8), and this capacity for greater short-term variety has also been noted previously for males in North America (Rendall and Kaluthota 2013; Platt and Ficken 1987). Hence, males in both populations seem to have a capacity for singing with either eventual or immediate variety. We speculated previously for NHOWR that this capacity might point to selection simultaneously for elements of both consistency and diversity in song performance. In fact, recent work on a species of *Mimidae*, the Tropical Mockingbird (*Mimus gilvus*), supports this

possibility (Botero et al. 2009b). Mockingbirds have very large and diverse song repertoires but nevertheless tend to repeat song themes over short intervals, and the consistency of repeated performance correlates with age, social status and reproductive success.

It is also possible that the use of different singing styles in House Wrens is associated with different breeding stages or target audiences (female mates versus rival males), as in the simple ‘repeat’ and more diverse ‘serial’ singing styles of America redstarts (*Setophaga ruticilla*: Lemon et al. 1993). For House Wrens, these possibilities remain speculative and are an important focus of future planned work.

Overall, the pattern of song construction in both NHOWR and SHOWR appears quite similar and based on a core repertoire of syllable types common to all males in a local population. These syllable types are used as the building blocks for songs, with song variety arising from the flexibility with which different syllable types are combined in song construction. The corollary is that song learning in this species probably does not entail learning entire songs, as complete songs, as typifies many other oscines (Catchpole and Slater 2008). Instead, it likely involves learning the repertoire of common syllable types and then constructing songs from them through an improvisation-like process as hypothesized for some other species with exceptionally large song repertoires (e.g., Northern Sedge Wrens, Brown Thrashers and Gray Catbirds, Kroodsma 2005). Notably, improvisation has also been proposed to account for large song repertoires in north temperate populations of closely related Sedge Wrens, while sedentary, populations of Sedge Wrens in the tropical-south temperate zone are proposed to learn their songs in more canonical fashion from adjacent neighbors (Kroodsma et al. 1999; Kroodsma 2005). This pattern points to an interesting possible difference in how the selective forces on song learning and repertoire size might differ in migratory and sedentary populations between Sedge Wrens and House Wrens.

That many of the features of song organization and singing style in SHOWR were so similar to those in NHOWR is a bit unexpected in light of the many documented differences in life history and mating system between them. This might suggest that some conventional metrics of song variability and complexity—such as song repertoire size—are not straightforwardly applied to all species (Byers and Kroodsma 2009; Cardoso and Hu 2011; Soma and Garamszegi 2011) or that effects are more likely to be found in more detailed features of song not yet measured (reviewed in Gil and Gahr 2002; Sakata and Vehrencamp 2012; but see Cramer 2013a, b), and these too are a central focus of future work.

Nevertheless, the high degree of similarity between NHOWR and SHOWR in many features of song

organization and structure bears on an additional important topic in geographic variation, namely the taxonomic status of different populations. Currently, NHOWR and SHOWR are classified as part of a single species (*Troglodytes aedon*; Remsen et al. 2013), but at times in the past they have been split into separate species. There has been renewed interest in the taxonomy of this broadly distributed species complex and new proposals to consider recognizing additional divisions based on certain detailed features of song (Sosa-Lopez and Mennill 2014). While some of the differences we found in the detailed form of notes and syllables between NHOWR and SHOWR might further substantiate this proposal, in the main, our analyses highlighted considerable similarity between the two at higher organizational levels including how songs are constructed from constituent notes and syllables; how those syllables are organized serially to produce songs; how many such songs males produce; how many songs they produce commonly; how many songs they share; and how songs are actively delivered during protracted singing bouts. Hence, at this point, it is perhaps still premature to make definitive proposals about taxonomic status for this broadly distributed species group based on the limited available song data.

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