SEXUAL SELECTION, BREEDING BEHAVIOUR AND SONG COMMUNICATION IN HOUSE WRENS (*Troglodytes aedon*)

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Abstract

Elaborated male displays, such as the complex songs of some songbirds, are thought to have evolved via processes of sexual selection addressing two main functions: attracting mates and repelling rivals. House Wrens (*Troglodytes aedon*) are a good model species because, while not yet systematically studied, the species' song is noted for being elaborate and complex. The first step in research was to establish basic patterns of male breeding success under natural conditions. The second step was to provide a detailed characterisation of song organization and diversity and begin to identify dimensions of song performance and complexity likely relevant in female choice of male partners or in male defence of territories against rivals. The final step involved a broad-scale latitudinal study of song patterns across the Americas testing the relevance of these elements of sexual selection on song performance and complexity in House Wrens.

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Chapter 1

The mechanisms, functions, and evolution of variable bird song

Bird song, a remarkable natural phenomenon, has attracted human minds for centuries. A seemingly unlimited variety of bird songs coupled with the extraordinary diversity of birds across the world must have aroused the curiosity of humans. Diversity of songs attracted the special attention of scientists who to this day are still studying the puzzle of species diversity in relation to the variability of songs among birds.

Both diversity of species and variability of songs exist at multiple levels. There are more than 10,000 different varieties of birds, identified as biological species. However, even within such defined species, extraordinary variety can be identified. For example, there could be high variability in size, plumage, and behavioural patterns in different populations of the same species, separated geographically. Moreover, even within the same population, there can be substantial variation among individuals in some traits. Song is one such trait that can vary across species as well as within populations. Most species have specific vocalizations that facilitate species identity. Among songbirds, most species sing different song types, even though they have morphological characters similar to closely related species in some cases. This uniqueness in bird songs is believed to be functional in species recognition, and especially in mate recognition. However, these species-specific songs can vary from very simple to highly complex renditions. For example, species like Chipping Sparrow (*Spizella passerina*) possess a very simple song, while some species such as Lyre birds (*Menura spp.*) and Mockingbirds (*Mimus spp.*) have extraordinarily complex songs. Moreover, song variation exists across populations which are isolated geographically, as well as within such populations by way of individual variations. Analogous to geographic variations in human languages, birds show song dialects, which are stable geographic differences in songs within species, probably originating from processes similar to human language diversification. Individual variation of songs within populations, adds another dimension to the diversity, as it could be important in attracting mates and defending territories from rivals, which are critical in reproduction and survival.

As songs are an important part of breeding behaviour in many bird species, it has very important implications in speciation and evolution. This suggests that there is an important relationship between song diversity and species diversity of birds. However, for many species, little is known on the origin and maintenance of song variation.

1.1. General functions of bird song in mate attraction and territory defence

Scientists have studied many species of birds to understand the functions of songs, especially in mate attraction and mate choice. For example, Johnson and Searcy (1996) studied the responses of female House Wrens to playback of male songs, and showed that female House Wrens are attracted to male songs, and also compete with each other for access to nest boxes from which the songs were broadcasted. They observed significantly higher visitation rates of females to nest boxes from which male songs were broadcast compared to visitation rate to control nest boxes which didn't broadcast any song. Females were not only attracted to the nest boxes that broadcast male songs, but also showed signs of settling in the territory by staying for longer periods around the nest box, and commenced nest-building by bringing sticks to the nest box. This observation clearly demonstrates the effectiveness of male songs in attracting females; even when the male is not physically present. Similarly, for many other species, evidence have been obtained to show that male song functions in mate attraction.

The effects of bird songs in territory defence have been shown in numerous studies. For example, in a study of Ochre-bellied Flycatchers (*Mionectes oleaginous*), Westcott (1992) showed that males that were experimentally muted either lost their territory or had it reduced in size. Further, he observed that the number of intrusions of territories owned by muted males increased 22 fold during the period of experiment. Similarly, many studies on songbird species, including Red-winged Blackbirds –*Agelaius phoeniceus* (Peek, 1972; Yasukawa, 1981), Northern Cardinals –*Cardinalis cardinalis* (Conner et al., 1986) and Scott’s Seaside Sparrow –*Ammodramus maritimus* (McDonald, 1989) showed that songs are functional in territory defence.

Other functions of songs include recognition of species, mates, and specific individuals including kin (Catchpole & Slater, 2008). As some species have local dialects of songs, it is possible that songs provide cues to the natal area of the individuals, if songs are learned before the natal dispersal (Kroodsma & Byers, 1991). Communication function of songs in coordinating the behaviour of mated pairs, was also studied and found important; especially in the breeding season when birds provision their offspring (Johnson & Kermott, 1991b).

Based on the growing literature, it is evident that bird songs are functional in a variety of basic social functions. However, it is yet to be conclusively understood the functions of high variability which exist in bird songs and the remarkable diversity of such patterns.

1.2. Song variability

One important factor that contributes to the generation of higher variability is the role of learning in the acquisition of song. Species in only three of the 36 avian orders (Dickinson & Christidis, 2014), namely the Psittaciformes (parrots), the Caprimulgiformes (hummingbirds) and the Passeriformes (songbirds) possess the ability of learning their songs. In general, birds in these taxonomic groups show more variability in their songs or vocalisations compared to those species in other orders which have simple vocalisations that are not learned. However, even among species in these three groups where song is learned, there is a remarkable variation in song complexity. For example, the Chipping Sparrow - a songbird species, has a simple trill of a single note as its song. On the other hand, many other species of songbirds are able to produce a variety of song types that are often composed of many different notes and syllables. For example, the wrens (Troglodytidae), thrushes (Turdidae), mockingbirds (Mimidae), larks (Alaudidae) and warblers (several families including Parulidae) have highly complex songs.

Song variability can occur at multiple levels, as songs can consist of several components. Notes which are defined as a single continuous trace in a spectrogram are the most basic level of organization. Notes are probably produced by a single exhalation, passing through the syrinx, the sound production organ of birds. Notes, then contribute to build syllables, which are either single notes or combinations of notes that always occur together in a song. Hence, syllables can consist of one to many different notes (Catchpole & Slater, 2008). Syllables are considered as minimum units of production similar to phonemes in human languages (Podos et al., 1992). The number of syllables produced by an individual, population or species, identified as syllable repertoire, is an important measure of song variability. Song type diversity, which is the next level of song organization, is influenced by the syllable repertoire size.

Song types are probably the most widely used unit of song variability or complexity in recent bird song studies (Searcy et al., 1999). Generally, song type is defined as a unique sequence of syllable types, although some researchers used variations of this definition. Similar to syllable repertoire, number of song types an individual (or population or species) possess is defined as song repertoire. There is a tremendous variation in song repertoire of songbird species. For example, species like the Ovenbird (*Seiurus aurocapilla*) or the Chipping Sparrow possess only a single song type, while species like Brown Thrasher (*Toxostoma rufum*) can sing upwards of 1,500 different song types (Kroodsma & Parker, 1977). While this enormous variation in song complexity across species creates a puzzle, scientists propose several explanations in solving this puzzle.

1.3. The adaptive functions of song variability

Since song variability is an important aspect of bird communication, understanding the functions of such variability is essential. Krebs (1977) proposed three hypotheses for the functions of song repertoire size. The first hypothesis is that song variation facilitates individual recognition in a population. Godard and Wiley (1995) showed that individual recognition is possible for Hooded Warblers (*Wilsonia citrina*) that have a moderate repertoire size of 3-9 song types, and sing in immediate variety. However, this idea is largely discounted by Krebs (1977) on the grounds that species with lower song variability, as few as a single song, have the capacity for higher individual recognition. The other two main hypotheses on the functions of song variability proposed by Krebs (1977) are female attraction and territory defence.

1.3.1. The role of song variability in mate attraction

In the recent past, an enormous number of studies have been conducted on the effects of song variability on female attraction and male mating success. In these studies, various proxy measures have been used in identifying female attraction towards variable songs. For example, Searcy and Marler (1984) showed that female Song Sparrows (*Melospiza melodia*) perform more copulation solicitation displays towards presentations of larger repertoires compared to smaller repertoires. Further, Reid et al. (2004) showed that song repertoire size predicts the initial breeding success, as measured by mating success and early egg laying by the partners. Similarly, in a study of Sedge Warblers (*Acrocephalus schoenobaenus*), Buchanan and Catchpole (1997) showed that males with larger song repertoires are able to mate earlier compared to males with smaller song repertoires. Likewise, Mountjoy and Lemon (1996) were able to show that male European Starlings (*Sturnus vulgaris*) with larger song repertoires attracted females earlier in the breeding season.

Polygyny potential of males is considered as another proxy for female choice towards certain individuals. Hence, the effect of song repertoire size on the polygyny potential of songbirds have been extensively studied. For example, song repertoire size of Great Reed-warbler (*Acrocephalus arundinaceus*) males was positively correlated with polygyny rates (Hasselquist, 1998). In the same study, it was found that older males have larger song repertoires and therefore are preferred by females. Similarly, Hasselquist (1998) showed that females obtain extra-pair fertilizations from neighboring males that have higher song repertoires. Female preference towards neighboring males who doesn't provide any direct benefit, strongly suggests that larger song repertoires may be in part indicative of male quality that is beneficial for females by increasing their fitness. This idea was supported by the finding that higher survival rate of fledglings fathered by neighbors (extra-pair fertilizations) that had higher song repertoires (Hasselquist, 1998). In a cross species analysis, Kroodsma (1977) showed that, North American wren species that have higher song repertoires and sing complex songs tend to be polygynous, while monogamous species show comparatively lower song repertoires.

Similarly, many studies support the hypothesis that females are attracted to the song complexity and thus enhance the reproductive success of males. In fact, it was shown that reproductive success of males is correlated with the song repertoire size. For example, in a study of Song Sparrows, Potvin et al. (2015) were able to show that males with larger song repertoire have greater reproductive success, irrespective of territory quality.

However, there are many studies which failed to make such correlations; therefore these do not support the female attraction hypothesis. For example, Great Tits (*Parus major*) did not show any mating advantage by having larger song repertoires, probably due to the fact that pairing occurs before the peak of song delivery in the season (Krebs et al., 1978). In a study of Red-winged Blackbirds, it was shown that females are attracted to males with larger song repertoires (Yasukawa et al., 1980). However, authors suspected that this outcome is largely due to better territory quality, where males with higher song repertoire are better capable of defending their territories from rivals. In a study on Song Sparrows, female Song Sparrows showed preference for males with larger song repertoire, however, song repertoire of males did not correlate with other indices of male quality such as age, dominance status, territory size, and body size (Searcy et al., 1985).

In a comparative analysis of New World blackbirds (subfamily Icterinae), Irwin (1990) examined the relationship of song repertoire-size with mating systems and territoriality of five different clades within the subfamily. This study failed to find an overall pattern linking repertoire size with mating system and territoriality. For example, polygyny in grackles was associated with song repertoire, but other groups did not show such a relationship (Irwin, 1990).

Growing literature on bird song suggests that evidence for mate attraction function of variable songs are mixed and inconclusive (Byers & Kroodsma, 2009; Kroodsma & Byers, 1991). Interestingly, laboratory studies tend to confirm female attraction towards larger song repertoires, while many of the field studies failed to find such relationships (Byers & Kroodsma, 2009). Further, studies on some songbird species resulted in both positive and negative evidence regarding the mate attraction function. Byers and Kroodsma (2009) emphasized the fact that correlations between song complexity and male quality, do not actually confirm cause and effect. They argue that in some species, males use their larger repertoire once paired, rather than before paring. Also, song complexity may not be the only or most important factor used by females when choosing their mates. Instead, territorial quality may be equally or more important than song complexity of males, in the decision making process (Alatalo et al., 1986). Thus, the evolutionary function of complex songs in mate attraction remains inconclusive due to mixed evidence obtained from large number of studies on many different songbird species (Byers & Kroodsma, 2009).

1.3.2. The role of song variability in territory defence

The other proposed major function of song variability is intra-sexual selection. Krebs (1977) proposed that there are three main pathways in this occurrence. The first way of mediating male-male competition is through counter singing in territorial interactions between rival males. In such a scenario, song matching the ability to sing the songs of rivals, is thought to be important in mitigating aggression (Vehrencamp, 2001). So, males that have larger song repertoires should have an opportunity to win; over males with lower song repertoire, by way of counter singing. In fact, song matching has been observed in many songbird species, including Banded Wren –*Thryothorus pleurostictus* (Vehrencamp et al., 2007), Song Sparrows (Beecher et al., 2000) and Tropical Mockingbird (*Mimus gilvus*) that has a very large repertoire (Price & Yuan, 2011). The second possible pathway of mediating territorial competitions is by avoiding the habituations of neighboring males. Having larger song repertoire is useful in breaking the monotony and reduces the habituation of rivals towards similar singing patterns. In this way, males are able to maintain effects of the song in repelling neighboring males from intrusions. In a study of Red-winged Blackbirds, Searcy et al. (1994) were able to demonstrate the habituation towards repeated songs, and change of behaviour in response to dissimilar songs. According to the "Beau-Geste" hypothesis, the third pathway proposed by Krebs (1977), large song repertoires of males are functional in territory defence by deceiving new-coming males. Arriving males would perceive the area as already densely occupied by several males, due to the different song types it hears, and would be discouraged to settle in such an area.

The effectiveness of larger song repertoires in acquiring and defending territories were shown in many songbird species, including Great Tits (Krebs et al., 1978), Red-winged Blackbirds (Yasukawa, 1981), Brownish-flanked Bush Warbler –*Cettia fortipes* (Xia et al., 2015) and European Penduline Tits –*Remiz pendulinus* (Pogány et al., 2013). In a study of Song Sparrows, Hiebert et al. (1989) showed that males with larger song repertoire are capable of acquiring territories earlier, had a longer territory tenure, and had higher life time reproductive success compared to males with smaller song repertoires.

However, as for the female attraction function, evidence for territorial function of song variability are mixed and inconclusive. For example, in a study of Red-winged Blackbirds, Searcy and Yasukawa (1990) found that males sing more song types towards female models, and song switching frequency was three times higher towards female stimuli compared to male stimuli. Therefore, they concluded that evidence strongly supported the female attraction function of song variability, but not convincingly for the male competition function. Similar patterns were observed in Western Meadowlarks – *Sturnella neglecta* (Horn & Falls, 1991). Likewise, Song Sparrow males with larger song repertoires were no more likely to acquire larger territories than males with smaller repertoires (Reid et al., 2004).

1.4. Song variability and song learning

The origin of song variability is partly due to its acquisition process by birds, which occurs through vocal learning. Song learning processes have been studied extensively (e.g. Beecher & Brenowitz, 2005; Jarvis, 2006; Nowicki & Searcy, 2014), while early studies were focused on how and when birds learn their songs (Marler, 1970; Nottebohm, 1969a). According to the classical "Auditory template model" of song development (Konishi, 1965), young birds listen and memorize songs sung by other males in their natal area, including those by their fathers and neighbors. Exposure to correct songs during this early "sensitive period" is critical in acquiring species-specific song patterns later in life (Konishi, 1965; Marler, 1970). In the following spring, as adults these young birds begin to sing memorised songs, and go through a series of steps to acquire fully crystallized species-specific songs. First, young birds sing a poor version of adult song which has a rudimentary similarity to species-specific songs. Then they pass the stages of sub song, plastic song and achieve fully crystallized song that resembles species-specific song structure and temporal patterns. This classical method of song learning has been observed in many species.

However, studies revealed that some species deviate from this model (Marler, 1997). For example, the duration of the sensitive period varies among species. Some species have a very restricted short-time window of learning in the first year of their life (e.g. European Chaffinch- Fringilla coelebs, Slater & Ince, 1979). Such species that have fixed song repertoires for life are known as “closed learners” (Kroodsma, 1982). However, many species have an extended period of song learning. For example, the sensitive period for Song Sparrows encompasses five months in their first year (Nordby et al., 2001). Nightingales (*Luscinia megarhynchos*) are able to learn new songs that they hear in the spring following their birth year (Todt & Geberzahn, 2003). Some other species such as Village Indigobird-*Vidua chalybeata* (Payne, 1985) and European Starlings (Mountjoy & Lemon, 1995) are able to learn songs every year. This latter group of birds that has greater flexibility in learning are referred to as “open-ended learners”. Due to this flexibility in learning, birds of these species possess greater song variability. Subsequent studies showed that such species have greater neuroplasticity with annual neurogenesis, which enables flexible song learning process (Brenowitz, 2008; Nottebohm, 2004).

1.4.1. Song learning, local dialects and population sub-structuring

As described above, the song learning process involves copying and reproducing previously learned songs. This process is prone to making mistakes, as young birds can inadvertently introduce new variations into their original song patterns. Since song is locally learned, the novel variations in songs can possibly be established in local populations, leading to divergence of song characteristics from other populations over time. This phenomenon, which is analogous to human language dialects, was observed in many species of songbirds (Catchpole & Rowell, 1993; Marler & Tamura, 1964; Seibt et al., 2002).

Due to increasing information on local song dialects in songbirds, scientists started to study the functional explanations for such phenomena (Podos & Warren, 2007) and proposed several hypotheses. According to the "local adaptation hypothesis", females gain fitness advantage by choosing males better adapted to their natal region. Males reflect their adaptability to natal region by singing songs best suited to that particular environment where acoustic transmission of songs is at its best (Marten & Marler, 1977; Morton, 1975; Nottebohm, 1969b; Wiley & Richards, 1978). This facilitates assortative mating where females can recognize males adapted to local environment, and discriminate against immigrant males. The "social adaptation hypothesis" proposes that males gain a fitness advantage by singing dialects of local population, where singing songs of a different dialect would subject them to penalising by local males. Hence, immigrant males have to learn songs later in life as in open ended learning, which is shown in many songbird species. However, evidence for both these hypothesis are mixed and inconclusive (Podos & Warren, 2007). It is also possible that, song dialects are functionless by-products of learning mechanism and dispersal (Andrew, 1962; Slater, 1986).

1.4.2. Song learning, song variation and speciation

Song dialect variation among populations may be important in evolution, because song is also important in species recognition and mate choice. Regional differences in song patterns, which facilitate assortative mating, might ultimately contribute to genetic divergence of populations as strong as speciation events. In fact, Baker and Cunningham (1985) suggested that the song learning process and dialect variations might be an important factor accounting for the remarkable species diversity that exist within the songbirds, the most diverse of all bird taxa. There is some evidence in support of the idea that learned song variations might support speciation. For example, female Zebra Finch (*Taeniopygia guttata*) can differentiate male songs from two different subspecies (Clayton, 1990). Additionally, in a playback experiment with cross-fostered birds, female Zebra Finches showed preference for songs of their cross-fostered fathers, regardless of songs of natal subspecies. Similar patterns of assortative mating was shown in some other species such as White-crowned Sparrows, in which limited genetic differentiation was also observed (MacDougall-Shackleton & MacDougall-Shackleton, 2001). This suggests that, if sustained over a long time period, such assortative mating could lead to genetic divergence large enough to differentiate populations.

However, evidence to support the idea of genetic divergence through song divergence, is relatively limited. But, some authors argue that the process of song learning, with its inherent potential for introduction of novel variations might be able to accelerate the rate of speciation in songbirds (Lachlan & Servedio, 2004).

1.5. Importance of natural breeding biology

Indices of male quality, such as song performance or song variability may not be the only or most important factor used by females when choosing their mates. Instead, territory quality may be equally or more important in the decision making process (Alatalo et al., 1986) as it can be crucial in survival of nestlings in the latter stages of breeding season. Similarly, nest characteristics which are important in the protection and survival of nestlings, might be considered by females when pairing.

However, territory and nest characteristics could also be related to male quality. For example, good quality males should be able to secure better territories and nest sites. Therefore, arriving early in the breeding grounds, securing and defending high quality large territories may be indicative of male quality. If so, there should be a positive relationship between conventional male quality characters such as larger song repertoire, body size, etc. and indirect male quality indicators such as territory size and nest quality. For example, cavity nesting songbirds that have better territory and a quality nest cavity may also have higher song variation indicative of male quality. In such case, breeding success could be higher due to better genes, increased resources, and better protection provided by the male. Therefore, it is important to study breeding ecology of birds together with effects of male quality indicators such as song variation.

Studies of breeding biology of cavity nesting species, especially secondary cavity nesters were more extensive when compared to other species due to increased use of artificial nest boxes. Use of nest boxes allows researchers to perform regular monitoring while experimental manipulations of eggs, nestlings and also brooding adults is made easy (Griffith et al., 2008). Artificial nest boxes helped to advance ornithological research in many sub-disciplines including behavioural ecology, cognitive ecology, conservation biology, ecotoxicology, evolutionary ecology, functional ecology, molecular ecology, population ecology (Lambrechts et al., 2010). As a result, cavity nesting species such as Great Tit, swallows, and bluebirds became model species, and in fact resulted in far more scientific publications compared to other bird species.

However, scientific studies involving nest boxes have been scrutinised on the basis that artificial boxes differ from natural cavities in many ways. As a result, findings derived from such studies may fail to reflect true natural variation. Therefore, validity of those findings obtained from nest box studies remain questionable (Møller, 1992). Hence, it is highly important to understand the breeding ecology of cavity nesting species under natural conditions, although studies pose many challenges.

1.5.1. Breeding in nest boxes compared to natural cavities

Many of the secondary cavity-nesting species readily breed in artificial nest boxes (Llambias & Fernandez, 2009; Zingg et al., 2010). However, there are many positive and negative effects of nest boxes that can be critical in conclusions drawn from such studies. Hence, effects of nest boxes on the breeding success, and related aspects were studied for many species of secondary cavity nesting species (e.g. East & Perrins, 1988; Lambrechts et al., 2010; Llambias & Fernandez, 2009; Zingg et al., 2010).

In many species, higher reproductive success rates are reported in nest boxes compared to natural cavities. Among many species, examples include House Wren (Llambias & Fernandez, 2009), Eurasian Kestrels -*Falco tinnunculus* (Fargallo et al., 2001), Tree Swallows -*Tachycineta bicolor* (Robertson & Rendell, 1990), Gouldian Finch-*Erythrura gouldiae* (Brazill-Boast et al., 2013) and Eastern Bluebirds-*Sialis sialis* (Gowaty & Bridges, 1991). Birds breeding in nest boxes are reported to have lower nest predation rates (Purcell et al., 1997; Robertson & Rendell, 1990) compared to birds nesting in natural cavities. Similarly, birds nesting in nest boxes lay larger clutches (Brazill-Boast et al., 2013; Fargallo et al., 2001; Purcell et al., 1997) and fledge more nestlings (East & Perrins, 1988; Fargallo et al., 2001; Purcell et al., 1997) than birds nesting in natural cavities. Also, higher polygyny rates were reported among birds nesting in nest boxes (Johnson & Kermott, 1991a; Petit) particularly when nest box density creates an unusual high availability of nesting sites in the area, compared to natural cavities. Further, increased rate of extra-pair paternity was reported among birds nesting in nest boxes, where nest density is higher in many experimental setups, compared to natural conditions (Gowaty & Bridges, 1991; Stewart et al., 2009).

All this evidence, suggests that findings related to breeding biology obtained from nest box studies should be interpreted with caution. Comparative studies involving nest boxes and natural cavities would be useful in understanding the true nature of breeding biology of cavity nesting species.

1.6. Summary

Song variability remains an important aspect of evolution as it connects with a number of important mechanistic, functional and evolutionary issues. The song learning process may be the driving force that creates song variability; however, the idea that such variation is driven primarily by mistakes in the song copying process remains ambiguous. Although several hypotheses including mate attraction and territory defence are proposed as possible functions of song variability, none of the hypotheses have been proved conclusively to date.

In order to understand the sexual selection process of a species, it is important to have better knowledge of breeding biology and ecology of such species. Most of the knowledge on breeding biology of many cavity-nesting bird species has been generated under artificial nesting conditions, in which some findings remain questionable. Therefore, the importance of the studies of breeding biology under natural conditions is emphasized by many scientists.

1.7. Thesis objectives and organisation

The objectives of the thesis are threefold. The first objective is to provide detailed characterization and analysis of breeding ecology of northern House Wrens under natural conditions. Much of the knowledge on the breeding of the species is known from nest box studies, where findings may not reflect true conditions. The second objective of the thesis is to provide characterization of song organization and variation in the northern House Wren. In order to understand the functional, mechanistic, and evolutionary issues related to song variation, an essential first step would be to characterize the existing variation and organisation patterns. The final objective of the thesis is to characterize the song variation on a much larger scale, in which songs of the species would be analyzed across its full breeding range covering the western hemisphere. Effects of latitude on the song performance and complexity will be examined.

In chapter 2, the breeding phenology of House Wrens in South Western Alberta, Canada is examined. In this chapter, the manner in which breeding events unfolded during the spring and summer, and possible effects of latitude on delaying the events in contrast to the breeding in southern latitudes are discussed. Also, some characteristics of nest cavities and nest sites that can be influential in choosing particular nests and territories by males and females for their breeding are examined. Some of those nest parameters affected the breeding outcome, thereby showing that selection and protection of certain nests can improve reproductive success of birds. This provides important insights in to the breeding behaviour of cavity nesting birds in natural conditions opposed to findings obtained from nest box studies. Further, the possible effects of nest boxes on the breeding outcomes of cavity nesting birds, and thereby on certain conclusions we make in scientific studies are discussed.

In chapter 3, detailed account of song variation in male House Wren songs is given. Here, characterization of the sources of variation in male songs and how that variation affects performance of males are discussed. As singing behaviour in House Wren is sexually dimorphic, in which only males have elaborate song systems, it is hypothesized that male song is subjected to female choice. So, to understand how female choice acts on the male songs it is important to understand the song variation within and among individuals. Since, a very high individual variation in song characters is observed, it is important to understand how the songs are organized and delivered. Hence, in this chapter, detailed description of song organization of House Wren males is presented.

In chapter 4, song variation of House Wrens on a much wider scale, i.e. in its full breeding range across Americas, is examined. Here, the study focuses on both song performance and complexity measures which can be influential in sexual selection. House Wrens, as a species distributed in almost all of the Americas, provided excellent opportunities to test the effects of latitudinal variation on song complexity across an enormously wide range. Previously such studies on other taxa were confined to shorter ranges of latitudes mostly in Northern hemisphere. Another approach was to study sister taxa present in higher and lower latitudes. This study is possibly the first to examine the song variation across whole range from northern temperate to southern temperate regions for a single species. Very interesting patterns of variation in song performance and complexity were found. The range of possible reasons for such variation across the latitudinal distribution, are discussed in this chapter.

Chapter 5 summarizes the findings of these studies on House Wren song variation and nesting ecology. Possible implications of these findings are discussed. Some future directions of these studies, especially for song studies, are presented.

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Chapter 2

Nest site selection and breeding biology of House Wrens (*Troglodytes aedon parkmanii*) using natural cavities in Western Canada

Abstract

House Wrens (*Troglodytes aedon*) are among the best studied songbirds in North America, but most of what is known about this model species derives from studies using artificial nest boxes. Consequently, we know comparatively little about the naturalistic breeding biology of House Wrens and whether it corresponds to patterns reported from nest boxes. To address these issues, we report a study of nest site selection, breeding phenology and success in House Wrens using natural cavities in aspen forests in southwestern Alberta, Canada. A total of 96 breeding pairs, representing 77 different banded males, were studied across a four year period (2011-14). In total, 78% of arriving males paired, with 52% of nests successfully fledging. More than 30% of males attempted polygyny, but only 3% succeeded. Preferences were observed for many characteristics of the nest site and cavity including the type of tree favored, and the cardinal direction and dimensions of the cavity entrance, its location on the nest tree and height above the ground. Many of these had consequences for pairing and breeding success. Results are compared to studies of House Wrens using artificial nest boxes with potentially broader application to other model species likewise studied primarily using nest boxes.

Key words: breeding phenology, breeding success, cavity nesting, House Wrens, nest boxes, nest site selection, polygyny, *Troglodytes aedon*

2.1. Introduction

House Wrens are a New World passerine with the widest latitudinal distribution of any native songbird in the western hemisphere. They are distributed from approximately 58^0N in Alberta, Canada to the extreme southern tip of South America at 55^0S in Tierra del Fuego (Brewer, 2001). Currently, populations across this vast range are recognized as a single species with 31 subspecies (AOU, 1998; Dickinson & Christidis, 2014). With such a vast distributional range, encompassing a diversity of habitat types, House Wrens "*present an almost unparalleled opportunity to study how environmental conditions shape the morphology, physiology and, especially, the behaviour of birds"* (Johnson, 2014). Not surprisingly, the species has become one of the best studied "model passerines" with many hundreds of papers encompassing virtually every aspect of behaviour, ecology, and biology (Albrecht & Johnson, 2002; Bowers et al., 2011; Cavitt & Thompson, 1997; Forsman et al., 2010; Forsman et al., 2008; Johnson & Barclay, 1996; Johnson et al., 2001; Johnson et al., 2005; Masters et al., 2003; Masters et al., 2011).

At the same time, the majority of what is known about House Wrens derives from studies that involve breeding in artificial nest boxes. Nest boxes can be a tremendous advantage to research. They allow some standardization, and controlled manipulation of core elements of the breeding environment, thereby permitting refined experimental testing of research hypotheses. Because nest boxes also allow ready access to eggs, chicks and, at times brooding parents, they also permit collection of additional and more detailed types of data.

Nest boxes necessarily also eliminate variation in many factors related to the ecology and quality of the types of cavities normally used for nesting that have presumably shaped the natural breeding biology and behaviour of the species. For example, it is possible that natural variation in cavity and nest tree characteristics are as important to breeding success as many other ecological characters (Cockle et al., 2015). It is also possible that in selecting where to settle and breed, females place as much, or more, emphasis on characteristics of the nest site and cavity compared to those of the resident male (Johnson & Kermott, 1991, 1994)

It is also true that breeding in nest boxes may have advantages over natural cavities in terms of protection from predators and from environmental elements such as wind and rain (Brazill-Boast et al., 2013; East & Perrins, 1988; Fargallo et al., 2001; Møller, 1989; Purcell et al., 1997; Robertson & Rendell, 1990). Such advantages are documented to lead to a variety of improved breeding outcomes, including reduced losses to predators, increased clutch size, improved nestling survival, and higher rates of polygyny (Johnson & Kermott, 1991; Llambias & Fernandez, 2009; Purcell et al., 1997).

It is possible, therefore, that studies using artificial nest boxes do not present an entirely accurate picture of a species' natural behaviour and breeding biology. For example, Johnson et al. (1994) argued that although certain strategies of female mate choice (e.g., pairing with already mated males) appears maladaptive when all males have access to several high-quality nest sites in the form of nest boxes, such strategies may be favored under conditions where males have limited access to natural nest sites that vary substantially in quality. Concerns like this apply not only to House Wrens but to other model passerines that also have been studied heavily using nest boxes, including Great Tits (*Parus major*), Blue Tits (*Cyanistes caeruleus*), Pied Flycatchers (*Ficedula hypoleuca*), Tree Swallows *Tachycineta bicolor*) and bluebirds (Barber et al., 1996; Dunn et al., 1994; Robertson & Rendell, 1990).

Here we report a multi-year study of House Wrens breeding in natural cavities. We had two broad goals: 1. to help fill a critical gap in our understanding of the natural breeding phenology and nesting success of this otherwise well-studied species; and 2. to compare the resulting patterns with those obtained from nest box studies to assess the potential validity and generality of conclusions drawn from nest box studies for House Wrens, in particular, but with much broader application to other model species.

2.2. Methodology

General breeding biology and behaviour—Our research focused on House Wrens in southwest Alberta, Canada, recognized as *T. a. parkmanii*. This subspecies is broadly distributed throughout western North America, where it is very well-studied in central Illinois, northern Wyoming, and Ohio (Johnson & Kermott, 1991, 1994; Soukup & Thompson, 1997, 1998). A second subspecies, *T. a. aedon*, is distributed across much of the eastern part of North America where it has been particularly well-studied in northwestern New York (Cramer, 2012; Cramer et al., 2013; Llambias, 2009; Llambías et al., 2015).

The two North American subspecies are similar in many aspects of life-history and breeding biology(Reviewed in Johnson, 2014). Males arrive on the breeding grounds and survey the local area for suitable breeding sites, often moving one or more times locally before settling on a territory that they then defend from rival males (Johnson & Albrecht, 1993). Their survey of possible territories includes inspecting various types of natural cavities, foremost among them cavities previously excavated by woodpeckers (Haggard & Gaines, 2001; Li & Martin, 1991; Raphael & White, 1984). However, other sorts of natural cavities are inspected and sometimes used for nesting including natural crevices in bark, tree snags, and broken stumps and branches (see Figure 1 for sample of cavities used by House Wrens in southwest Alberta). Males then begin to make initial preparations to one or more cavities by removing previous nesting material and then adding sticks to the base of the nest cavity (Johnson, 2014; Kendeigh, 1941).

Females arrive a short time after males and survey available males and breeding sites. In this process, females spend considerable time inspecting cavities in a male's territory. The male often follows the female during her inspections, at times seeming to lead the female among the candidate cavities by flying ahead and singing loudly at the entrance to a particular cavity. Some females appear to settle relatively quickly (within hours of being first observed on a territory), while others are observed to sample multiple territories before settling. The 'decision' to settle often appears to have been made when the female herself begins to make concerted modifications to the contents of one or more cavities by repeatedly removing material and then beginning to add sticks of her own. Females then finish nest construction typically with no further contributions by the male.

However, males are active again later in feeding nestlings (Barnett et al., 2012; Johnson et al., 1992; LaBarbera et al., 2011; Llambias et al., 2012).

Many males also actively court second mates once their first mate has begun incubating eggs, and males resume vigorous singing at this time typically from the location of a second cavity in their territory (Johnson & Kermott, 1991; Rendall & Kaluthota, 2013). Previously reported rates of successful polygyny vary among populations (10–24%) possibly reflecting variation in the number and quality of additional suitable nest cavities that are available within a male’s territory (Drilling & Thompson, 1991; Johnson & Kermott, 1991).

Study sites and subjects.—Research reported here was conducted between 2011 and 2014 at two sites in the foothills of the Rocky Mountains of southwest Alberta. One site, the Whaleback (WB), located in the Bob Creek Wildlands of the Whaleback region (49.86°N, 114.27°W; mean elevation = 1 360 m). The second site, Lundbreck Falls (LF), located on private lands near Lundbreck Falls, Alberta (49.56°N, 114.29°W; mean elevation = 1 280 m). The two sites were separated by 35 km, and both were in montane habitat at similar elevation where the vegetation was a mosaic of open grasslands punctuated by small stands of quaking aspen (*Populus tremuloides*) and occasional douglas-fir (*Pseudotsuga menziesii*). The Lundbreck Falls site was used occasionally for light cattle grazing, while the Whaleback site was regularly used for more intensive grazing. The primary disturbance from grazing at both sites involved reduction in the understory ground cover. Otherwise, the forest habitats at both sites were largely undisturbed.

Research was conducted at the Lundbreck Falls site in all four years and at the Whaleback site in only two years (2011 and 2012). Each year, we started preliminary surveys in early May to find first arrivals in the area. Observations continued until the nestlings of the last active nest had fledged, typically in mid-August.

Once male House Wrens started to arrive and settle in territories, we commenced capture and banding. When captured, each bird was marked using a numbered metal band and a unique combination of three colored bands to facilitate individual identification. Because females were wary and difficult to capture early in the season prior to nesting, and because this study was part of a larger project focused on male song patterns (e.g. Rendall & Kaluthota, 2013), we chose to capture and band only males.

Territory Monitoring – The nest trees of all males were marked, and the territory and male occupant were then monitored regularly (2-4 times/week) for the remainder of the season. During each visit, we spent at least one hour in the territory between 06.00h and 12.00h to confirm male breeding status. Soon after birds were paired, we monitored female behaviour for signs of incubation, such as extended stays in the cavity and less frequent movements away from the nest site. When the first eggs were suspected, the nest was accessed using a mini-camera fixed on a bendable gooseneck cable (Meerkam wildlife inspection camera) to confirm eggs and, where possible, a count of their number. Based on the number of eggs present, and a pattern of subsequent daily increments in egg number, we estimated the first egg laying date assuming a standard pattern of adding one egg per day (Bowers et al., 2013). Similarly, we monitored the activities of parent birds for signs of hatching, such as male and female feeding visits, and removal of fecal sacs.

The camera was used again to obtain nestling counts. Some nests were not accessible either because of their location on the tree or because the interior architecture of the nest did not permit camera access.

Nest tree and cavity measurements – A variety of data were collected concerning the nest tree and cavity. Data about the nest tree included its species, condition (live or dead), overall height, diameter at breast height (DBH), and the number of suitable cavities it contained. Cavities with unusually large entrances and shallow cavities are not generally used by House Wrens and thus were considered to be unsuitable. Data about the cavity included its height above the ground, tree diameter at cavity height (DCH), and the height, width, and cardinal direction of the cavity entrance. Overall height of the nest tree and the height of the nest cavity were obtained using a clinometer.

We subsequently calculated an index of cavity entrance shape as the ratio between the entrance width and height. A value of 1 indicates a perfectly circular entrance, while values greater than 1 indicate a more horizontal entrance, and values less than 1 indicate a more vertical entrance.

Nesting Success – Overall nesting success was calculated using the Mayfield method to facilitate comparison with other studies that have used this method (Mayfield, 1961, 1975). By this method, nest survival is calculated as the probability that a nest fledges at least one bird. The first step in the calculation is to establish the daily survival probability as follows:

Daily survival probability = 1 – [total number failed nests/total number exposure days]

In this formula, the total number of exposure days is the sum of the number of days all nests were active, and thus were susceptible to failure. To then calculate nesting success (the survival probability for the entire nesting period), the daily survival probability is raised to an exponent equal to the number of days in the nest (i.e., the nesting period). For this analysis, we used the mean nesting period for the population which was 30 days.

Statistical testing was done in SPSS v.23. Data normality was checked using the Shapiro-Wilk's test.

2.3. Results

A total of 81 different males were captured on the two study sites across the four year period, though not all of these males ultimately settled and successfully held territories. At the same time, some males returned and thus were present in two (*N*=15), three (*N*=4) or all four years (*N*=1). A total of 65 different cavities were used by this sample of males, many cavities being re-used within and across years.

2.3.1. Breeding phenology and success

First males arrived on the study sites in mid-May with later arrivals continuing until mid-June. Arrival of new males peaked 9 to 11 days after the arrival of the first male

(Figure 2.2). For first breeding attempts, the mean date of first eggs was 9th June (SD=6.8 days, range 29th May – 28th June, *N*=46 nests) and the mean hatch date was 23rd June (SD=4.2 days, range 15th June–6th July, *N*=33 nests). The mean duration of incubation for all broods was 15 days (SD=3.3, Range= 12-22, *N*=61 nests) and of nestlings was 15 days (SD=1.3, Range= 13-22, *N*=47 nests), yielding a mean breeding cycle duration of 30 days (SD=3.11, Range= 27 - 36, *N*=47 nests).

Focusing only on these first breeding attempts, the date of male arrival was positively correlated with pairing dates (Pearson r=0.506, P<0.01, N=58, Figure 2.3), and early arriving males, defined as those that arrived within 3-weeks of the first arrival, were significantly more likely to breed successfully than late arriving males (Fisher's Exact Test: χ^2=4.67, df=1, P=0.05, N=73).

Collapsed across years and males, there was a total of 111 attempts by males to settle and breed. In 96 of these cases (86%) males paired successfully. For 88 (79%) of the males, their nests made it further to the stage of eggs; 63 (57%) went on to nestlings; and 48 (43%) ultimately fledged at least one young (Table 2.1).

Nesting success was 52% across the four year period, with only slight differences between years (Table 2.1). This level of nesting success is marginally lower (10%) than has been reported for other populations of House Wrens breeding in natural cavities and considerably lower (30%) than reports for House Wrens breeding in nest boxes (Figure 2.4).

A total of 18 males paired with more than one female within the same season. Six of them did so polygynously while the first nest was still active (further details for these males are provided below). All others did so serially (i.e., only one female partner at a time). One male paired with 4 females having failed with each of the previous three. The remaining eleven males paired with two different females, after either failing, or breeding successfully, with their first partner.

Of the 88 breeding attempts that proceeded to the stage of producing eggs, 28 males (31.8%) were observed attempting to attract a second mate while their first mate was incubating by singing vigorously from another location in their territory. Six males (8.2%) succeeded in pairing with a second mate while the first nest was active. Of those males, five succeeded to the egg stage (polygynously), while the sixth did not. However, only two males successfully bred polygynously (i.e., fledged young from two overlapping clutches). For the other males, one or the other of the first or second nest failed. An additional male succeeded with a second clutch after completing its first attempt successfully**.**

2.3.2. Nest cavity selection and characteristics

Data on nest cavity characteristics are available only for the first 3 years of the study (2011-2013) and are summarized in Table 2.2 alongside comparable available data from other studies of House Wrens. Figure 2.1 illustrates a sample of the types of natural cavities used by males in the study population.

Nest tree characteristics— A total of 91 different nesting attempts in tree cavities were recorded over the four year period. All involved cavities on quaking aspen which was also by far the predominant tree species available. Of the 91 total nesting attempts, 60 (65.9%) involved cavities on dead trees. However, there was no significant difference in the nesting success of cavities on dead versus live trees (χ^2=1.82, df=1, P=0.18, N=91). For 87 breeding attempts, we were able to establish the number of suitable cavities available on the nest tree and 60 (68.9%) were on trees that contained only a single cavity (Figure 2.5). There was a non-significant trend toward higher probability of breeding success in such trees compared to trees that contained more than one suitable cavity (χ^2= 3.14, df=1, P=0.076, N=87).

Cavity orientation—The cardinal direction of the nest cavity entrance ranged widely from 0^0 to 330^0. There was, however, some bias in orientation. Of 81 nests for which cardinal direction could be definitively established, 55 (68%) were oriented within a 90^0 swath from East to South (Figure 2.6). The orientation of successful nests (M=147.1, SD=83.5) was significantly different from that of failed nests (M=185.4, SD=79.9; $F_{2, 70}$ =3.95, P=0.051) with successful nests generally oriented in an E-SE direction (Figure 2.6).

Nest entrance dimensions— The dimensions of the cavity entrance varied considerably, from circular shaped entrances to vertical slot-shaped entrances (Figure 2.1). Birds showed some selectivity in nest entrance dimensions, which, in turn, had some effect on nesting success. Of the 39 cavities whose entrances could be definitively measured, 17 (44%) had circular, or near circular shapes (Cavity shape index = 0.8-1.2).

Male pairing date was positively correlated with cavity entrance height and negatively correlated with cavity entrance shape index: males that paired earlier selected cavities with shorter entrance heights (Pearson *r*= 0.52, *P*<0.01, *N*=25; Figure 2.7) and more circular entrances (Pearson *r*=-0.51, *P*=0.01, *N*=25). Pairing date was also negatively correlated with the diameter of the tree at cavity height (DCH: Pearson *r*= -0.60, *P*<0.01, *N*=23, Figure 2.8). Males that paired earlier selected cavities located closer to the ground. Ultimately, there was a significant effect of entrance width (*U*=120.5, *P*<0.05, *N*=39, two tailed) but not height (*U*=227.5, *P*=0.27, *N*=39, two tailed) on nesting success, with successful nest cavities having a smaller entrance width compared to failed nests.

Cavity re-use—A total of 65 different cavities were used for breeding at the two study sites across the study period, many of which were re-used in subsequent years by the same or different males. For example, of 22 different cavities used in the first year (2011), 10 (45%) were re-used the following year (2012); and in 2013, 14 of 28 cavities (54%) from the previous year were re-used. Three cavities were used for three consecutive years, while one cavity was used in all four years. There were seven instances in which a male settled in exactly the same cavity it used the previous year.

2.4. Discussion

2.4.1. Breeding phenology and success

The breeding phenology of House Wrens in southwest Alberta was broadly similar to patterns reported for other populations with some natural shifts based on variable latitude. Thus, males breeding in southwest Alberta began arriving in mid-May, and the dates of first eggs and first hatchlings were, respectively, 9th June and 23rd June. These dates are somewhat later than those reported for other populations of House Wrens in North America (reviewed in Johnson, 2014), but this almost certainly reflects the fact that our study sites, at 49^0 N latitude, are substantially farther north than previously studied populations and are approaching the northern breeding limit of the species. However, this comparatively late start of the breeding season in southwest Alberta has implications for other aspects of breeding phenology such as the potential for second broods as considered further below.

The duration of the breeding cycle (30 days) and of both the incubation (15 days) and nestling periods (15 days) were also broadly similar to other House Wren populations (reviewed in Johnson, 2014). The mean nestling period, and the overall breeding cycle duration were slightly shorter than reported for more southern latitudes (17 and 33 days, respectively; Johnson, 2014), while the duration of the incubation period in southwest Alberta was somewhat longer (15 days versus 12-13 days elsewhere; Johnson, 2014).

Similar to patterns reported for other House Wren populations, and for many other songbird species (Choi et al., 2010; Møller, 1994; Reudink et al., 2009; Velmala et al., 2015), males arriving earlier in southwest Alberta also generally paired and nested earlier, and these breeding milestones in turn were associated with improved breeding success

Overall rates of nesting success (at least one fledgling) averaged 52% across the 4-year period in southwest Alberta. This level is notably lower than success rates reported from the few previous studies of northern House Wrens breeding in natural cavities in California, Wyoming and Arizona, where success rates have ranged from 62 – 70% (Johnson & Kermott, 1994; Li & Martin, 1991; Purcell, 1995; Figure 2.4). It is difficult to reconcile the discrepancies with confidence because this sample of studies is relatively small and encompasses a range of habitats, from primarily oak-pine vegetation in California, to a more mixed forest habitat in Arizona and Wyoming, to almost exclusive stands of aspen in southwest Alberta. Levels of disturbance from activities like cattle grazing also vary across the populations studied.

Nevertheless, what is consistent across these populations is that levels of successful breeding in natural cavities are considerably lower than those associated with breeding in artificial nest boxes, which generally exceed 80% (Figure 2.4). Notably, some nest box studies have been conducted in parallel on populations using natural cavities, thereby controlling for most factors that would otherwise complicate comparisons, and, in these populations, birds breeding in nest boxes enjoy about a 20% increase in breeding success (Czapka & Johnson, 2000; Newhouse et al., 2008; Purcell, 1995). This difference reflects a variety of well-known advantages to breeding in nest boxes including reduced predation risk (by minimizing cavity entrance dimensions) and better protection from environmental factors like wind and rain (East & Perrins, 1988; Lambrechts et al., 2010; Nilsson, 1986). Studies of House Wrens, in particular, have shown that the birds prefer nest boxes over natural cavities and that this indeed translates into lower rates of predation, increased clutch size, improved nestling survival and higher overall breeding success (Johnson & Kermott, 1991; Llambias & Fernandez, 2009; Purcell et al., 1997).

The documented advantages of breeding in nest boxes also include elevated rates of polygyny, which was very rare in our population. Although many males in our population (31.8%) attempted to attract a second mate while their first nest was active, very few (6.8%) managed to pair and produce a second clutch. This pattern matches reports for House Wrens using natural cavities in Wyoming, where 47% of males attempted to be polygynous but only 9% were successful in pairing with a second mate (Johnson & Kermott, 1991). These outcomes for populations using natural cavities are dramatically different from nest box studies which have shown rates of polygyny two to three times higher: 16% in Wisconsin (Poirier et al., 2004) and 24.2% in Illinois (Drilling & Thompson, 1991). Success in acquiring a second mate can be even higher still when territories are supplied with additional nest boxes: 53.3% in Wyoming (Johnson & Kermott, 1991), and 13-40% in New York (Llambias et al., 2012). Thus, it seems that the distribution of cavities and males' ability to defend territories containing more than one suitable cavity limit the natural polygyny potential of House Wrens using natural cavities.

Taken together, the differences in breeding patterns and in the level of successful breeding in natural cavities compared to nest boxes make it useful to consider the preferences House Wrens have when breeding in natural cavities and how these may influence naturalistic breeding success.

2.4.2. Nest cavity selection and characteristics

One of the clearest patterns in the selection of natural cavities by House Wrens was the cardinal orientation of the cavity entrance, which involved a bias for entrances facing in easterly to southerly directions. There are very few studies of House Wrens with natural cavity orientation data for comparison, one in California reporting the same sort of bias we observed (Purcell, 1995), and another in Arizona finding no such bias (Li & Martin, 1991). In our population, the bias was also influential in breeding outcomes, as cavities with easterly exposures showed increased breeding success, which might be attributable to a variety of factors.

Cavities with easterly orientations might experience greater morning sun exposure and increased radiant heating of cavity interiors. This might be particularly functional at higher latitudes where overnight temperatures can drop below freezing in early spring. At the same time, the prevailing winds in southwest Alberta are from the west-southwest. In early spring, these winds can be cold and are often accompanied by rain and sometimes even snow, with May and June being by far the wettest months of the year (EnvironmentCanada, 2015) and coinciding with the primary period of nesting and incubation for House Wrens. Hence, cavities with eastern exposures might be multiply beneficial. They may improve rapid radiant heating of cavity interiors in the morning and thereby reduce incubation costs, while also reducing exposure to cold westerly winds and the risk of cavity flooding from accompanying rain, both advantages contributing to improved egg and nestling survival. While intuitive, these possibilities remain speculative.

At the same time, it is not clear that the bias in cavity orientation that we observed necessarily reflects an active preference on the part of House Wrens. As secondary cavity nesters, House Wrens rely heavily on cavities originally excavated by woodpeckers (Haggard & Gaines, 2001; Li & Martin, 1991; Raphael & White, 1984). While some studies of woodpeckers have failed to find any orientation bias in their nests (Stauffer & Best, 1982), a meta-analysis involving 23 woodpecker species found that populations at higher latitudes prefer southerly orientations (Landler et al., 2014). At the same time, in a study focused specifically on aspen trees, Losin et al. (2006) found that heartwood rotting is higher on the south to southeast sides of the trunk, and that this in turn corresponds with the frequency of cavities excavated by Red-naped Sapsuckers (*Sphyrapicus nuchalis*).

As a result, it is possible, that the bias in cavity orientation observed for House Wrens in our populations was partially passive, reflecting the original preference of the woodpeckers that excavated the cavities, which created a biased distribution of entrance directions available to the House Wrens. However, the fact that we nevertheless found differential breeding success within the range of cavity orientations used by House Wrens, suggests that the proposed functional advantages of easterly facing entrances might nevertheless apply to House Wrens even if they do not necessarily explain the original preference of the woodpeckers before them.

In selecting natural cavities, House Wrens also showed a clear preference for those with smaller entrances, 81% of nests having widths of 5 cm or less, which agrees well other studies (Dobkin et al., 1995; Gutzwiller & Anderson, 1987; Raphael & White, 1984; Sedgwick & Knopf, 1990), including some using nest boxes (Pribil & Picman, 1997). In our population, nests with smaller entrance widths were also more successful, which is likely a result of reduced predation, as this is the primary reason for nest failures in House Wrens in both temperate and tropical populations (Auer et al., 2007; Li & Martin, 1991; Llambias & Fernandez, 2009). Reported or suspected nest predators of House Wrens include snakes, a variety of small mammals (e.g. rats, raccoons, squirrels, chipmunks, weasels, etc.) and birds (reviewed in Johnson, 2014), and nests with smaller entrances are almost certainly functional in reducing predation by many of them.

It is also possible that selection of smaller cavity entrances helped to reduce competition for cavities with other secondary cavity nesters (Dobkin et al., 1995; Purcell, 1995). A variety of other secondary cavity nesters were common at our field sites in southwest Alberta and were frequently observed harassing House Wrens, including European Starlings (*Sturnus vulgaris*), Tree Swallows (*T. bicolor*), Mountain Bluebirds (*Sialia currucoides*), Red-breasted Nuthatch (*Sitta Canadensis*), White-breasted Nuthatch (*Sitta carolinensis*), and Black-capped (*Poecile atricapillus*) and Mountain Chickadees (*Poecile gambeli*). Selecting a cavity with a smaller entrance may reduce competition from some of the larger-bodied competitors among these, such as starlings and bluebirds. The importance of reducing competition from other cavity nesters may also help to account for the bias observed in House Wrens of nesting in trees containing only a single cavity.

There was a further preference for nest entrances that were circular or near circular in shape as opposed to slot shaped. This finding contradicts a preference noted previously by Kennedy and White (1992) who reported a bias toward slot shaped entrances in House Wrens using nest boxes. Those authors argued that a preference for slot shaped entrances was functional in facilitating the addition of the typical sticks and twigs House Wrens use to build their nest platform, and, indeed, we also observed many birds struggling to enter circular shaped nests carrying sticks that were much longer than the diameter of the entrance.

However, the advantage of slot shaped entrances may be more applicable to nest boxes than to natural cavities because nest boxes often have a much larger inner cavity space to fill with nesting materials. For example, Purcell et al. (1997) found that the natural cavities selected by House Wrens had an average bottom area of 48 cm^2, while the majority of nest box designs have more than 100 cm^2 of bottom area (Lambrechts et al., 2010). Hence, the mass of nesting material required, and thus the overall costs of nest construction, might be considerably higher in nest boxes. Consistent with this possibility, Kennedy and White (1992) reported that larger nest boxes did indeed contain higher nesting material mass, and that the rate of adding nesting material was higher in boxes with slot shaped entrances. In consequence, the cost of adding materials might be requisitely lower in natural cavities compared to nest boxes, and the further advantages for reduced predation risk and competition with other cavity nesting species may account for the preference for circular shaped entrances in natural cavities.

The majority of cavities were also located on the main trunk (bole) of trees, relatively close the ground (mean 4.68 m). Studies of some other populations have not found such a clear preference for bole- as opposed to branch-nesting (Gutzwiller & Anderson, 1987; Sedgwick & Knopf, 1990), but these studies have also been conducted in areas containing quite large species (e.g., floodplain cottonwoods, *Populus deltoids*) with very large branches. In contrast, the predominant tree species at our study sites in southwest Alberta were quaking aspen which accounted for 96% of the stems and seldom attained sizes large enough to support branches of sufficient diameter to contain cavities.

The bias we found towards cavities closer to the ground appears to be a general one (Johnson, 2014) and may be functional in allowing rapid escape to the surrounding shrub layer at the approach of danger, and reducing travel time and allowing more cryptic approach from this layer when provisioning nestlings. It is also possible that cavities located lower on the trunk, at a place where trunk diameter is wider, provides a larger interior space for nestling growth.

Finally, all of the nest cavities used by House Wrens in our study were on aspen trees, and nearly 2/3 was on dead trees. Aspen was also the predominant tree species available at our site, but even in mixed vegetation types where aspen is not so predominant, there is a clear preference for aspen among excavator species and secondary users (Martin et al., 2004). This preference seems to reflect the high susceptibility to heartwood decay in aspen compared to other tree species (Basham, 1958), which facilitates excavation and promotes the formation of other sorts of natural cavities, and likely for these reasons, woodpeckers show a preference for excavating in unhealthy live and recently dead aspen trees (Blanc & Martin, 2012).

In conclusion, while some elements of the basic breeding phenology of House Wrens using natural cavities were broadly similar to reports from nest box studies, such as the seasonal timing and duration of major events in the breeding cycle (e.g., nest initiation, incubation, nestling period), there were substantial differences in a variety of other aspects of breeding behaviour and success. Notably, these included rates of polygyny and the overall level of breeding success which were both substantially lower in our population of House Wrens breeding in natural cavities compared to those breeding in artificial nest boxes. These differences highlight a key constraint on the natural breeding behaviour and success of House Wrens arising from limitations in the number and quality of good breeding cavities. Under natural conditions, good quality breeding cavities are likely a critical limiting resource for this and other cavity nesting species, serving to depress breeding success and polygyny potential.

At the same time, the breeding success of House Wrens in natural cavities was affected by a number of additional details of those cavities that are also either minimized or eliminated altogether by artificial nest boxes. These include the specific tree species involved and variation in the height, dimensions and cardinal orientation of the nest entrance. Importantly, because House Wrens are actually secondary cavity users, the influence of these factors may ultimately be attributable to the behaviour and biases of the primary users and excavators of these cavities, namely woodpeckers. As a result, the breeding patterns of House Wrens under natural conditions might depend a lot on the particular community of tree and primary excavator species present, and differences in both across populations, factors that are entirely glossed in studies using artificial nest boxes.

Altogether then, there are a number of factors relevant to the natural breeding behaviour and success of House Wrens, and other species of secondary cavity nesters that are overlooked or eliminated in studies using artificial nest boxes, with effects on metrics of breeding biology as basic as overall breeding success and polygyny potential. Caution must then be used in extrapolating from nest box studies to the behaviour of a species under fully natural conditions.

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Table 2.1. The number and proportion of nesting attempts reaching various breeding milestones of the study population of House Wrens (*Troglodytes aedon*) in southwestern Alberta.

Year	**No. settled**	**Paired (%)**	**Eggs (%)**	**Chicks (%)**	**Fledged (%)**	**Nesting success***
2011	23	15 (65)	15 (65)	12 (52)	8 (35)	53.1
2012	42	35 (83)	32 (76)	22 (52)	17 (40)	46.1
2013	44	34 (77)	31 (70)	22 (50)	18 (41)	57.3
2014	12	12 (100)	10 (83)	7 (58)	5 (42)	50.8
Total	111	96 (86)	88 (79)	63 (57)	48 (43)	52.0

Note: Eggs, Chicks and Fledglings are number of nests that produced at least one egg, chick or fledgling and, for these, the percentage values are based on the paired number.
*Nesting success was calculated by the Mayfield method

Table 2.2. Basic characteristics of the habitat, nest site and dimensions of natural cavities used by House Wrens in SW Alberta, compared to available data for other North American populations of House Wrens breeding in natural cavities.

Study	Location	Latitude (^{0}N)	Vegetation	Sample size	Cavity height	Entrance width	Entrance height	DCH	Nest tree DBH	Nest tree height
Current study	SW Alberta	49	Aspen	117	4.7	4.2	7.0	18.1	21.3	9.4
Haggard & Gains, 2001	Washington	48[a]	Pine and Fir	18	8.5	-	-	-	42.0	18.9
Gutzwiller & Anderson, 1987	Wyoming	42[a]	Cottonwood-Willow	32	6.9	4.8	-	16.9[c]	53.9	-
Dobkin et al. 1995	Oregon	42	Aspen	31	3.6	5.1	5.8	24.5	27.6	12.9
Stauffer & Best, 1982	Iowa	41[a]	Mixed riparian	82	5.4	-	-	19.6	-	8.4
Sedgewick & Knopf, 1990	Colorado	40[a]	Cottonwood-Willow	29	4.9	4.9	-	17.4[c]	52.1	13.1
Raphael & White, 1984	California	39	Pine and Fir	21	4.1	4.4[b]	-	47.6	51.8	9.3
Purcell, 1995	California	37[a]	Oak-Pine	45	4.5	5.8	-	-	-	-
Li & Martin, 1991	Arizona	34[a]	Aspen-Maple	120	9.0	-	-	-	33.6	-

a- Latitudes not provided by authors, but estimated based on site names provided in the work.

b- n=9 nests

c- DCH is low compared to DBH because most nests were on tree limbs not on the main trunk.

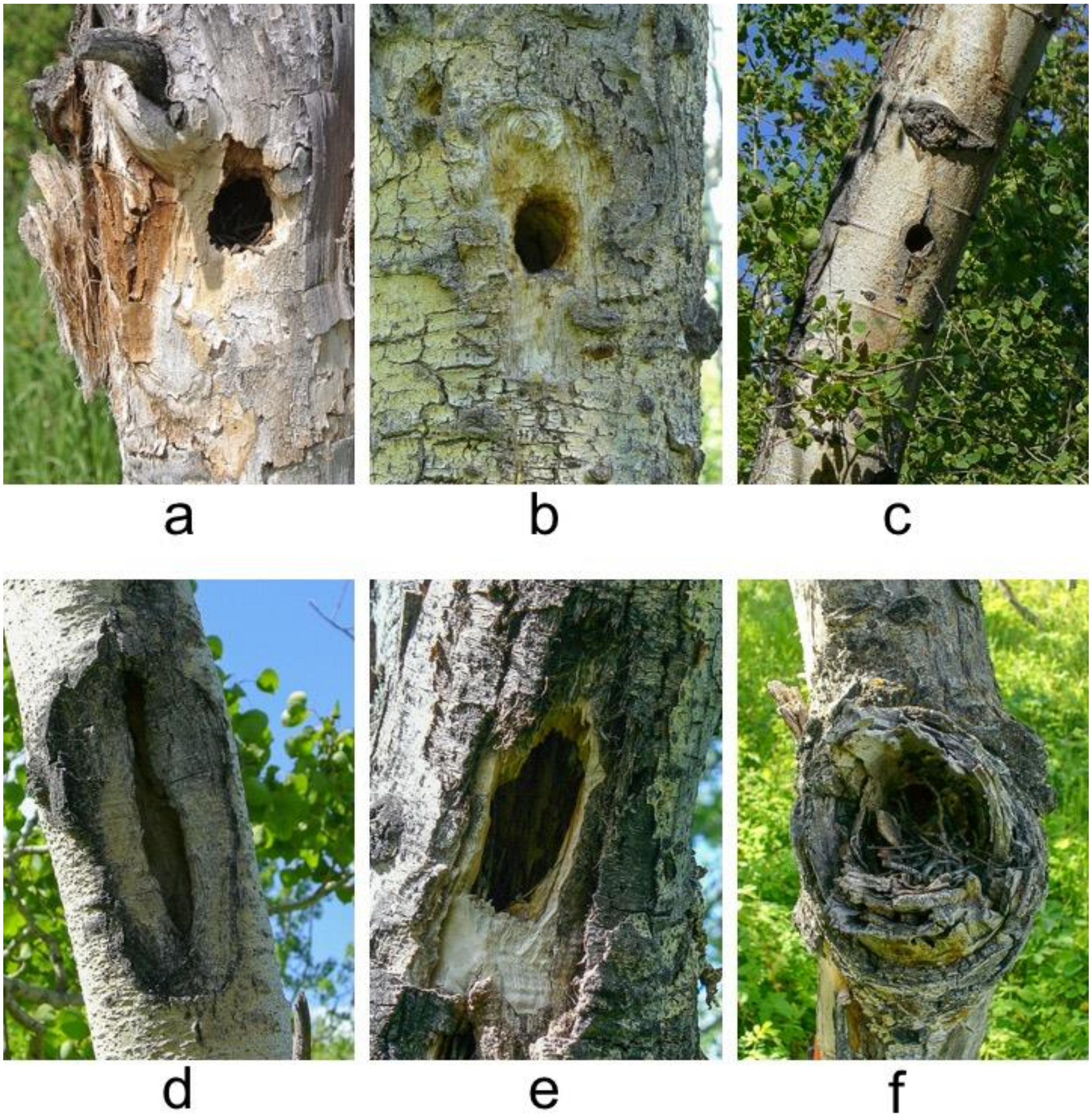

Figure 2.1. A sample of the types of natural cavities used by House Wrens (*Troglodytes aedon*) in southwest Alberta. The most common cavities were those previously excavated by woodpeckers with circular (a, b, c) or slot-shaped entrances (e) but House Wrens also used other naturally formed cavities on trunks (d) or in snags (f).

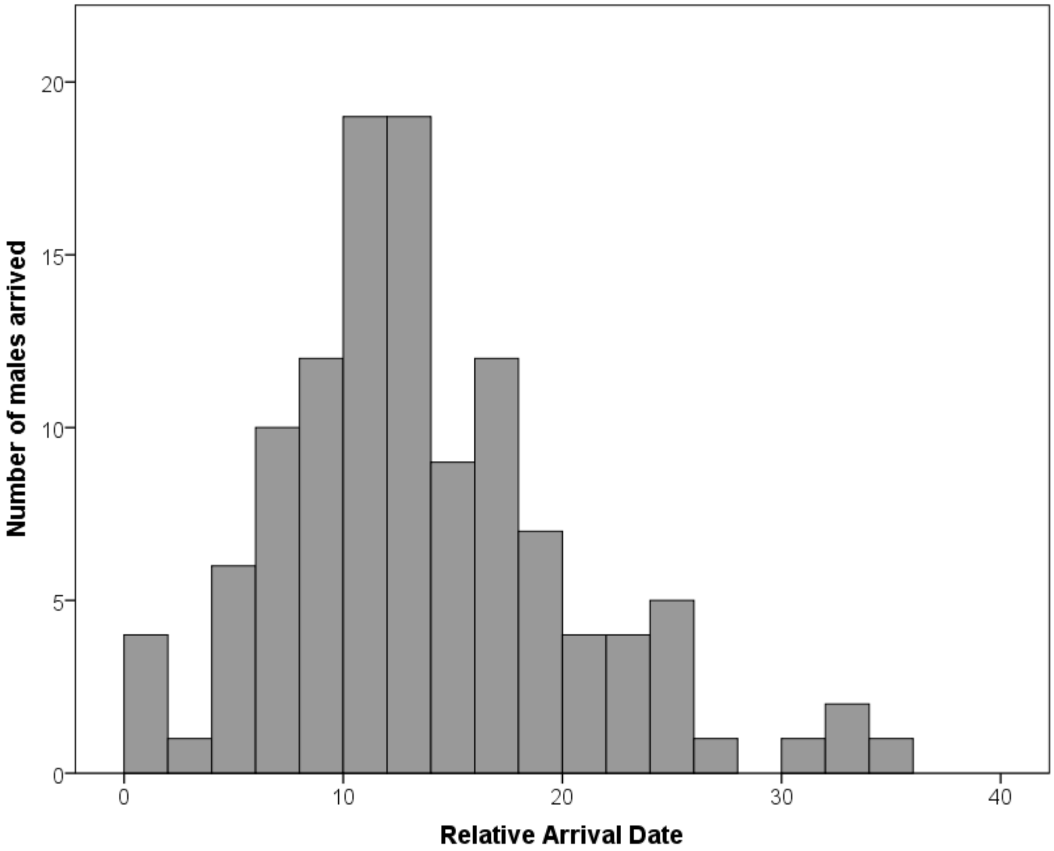

Figure 2.2. Number of male arrivals relative to date of first male's arrival of the study population of House Wrens. Arrivals peak 9 to 11 days after the first male's arrival.

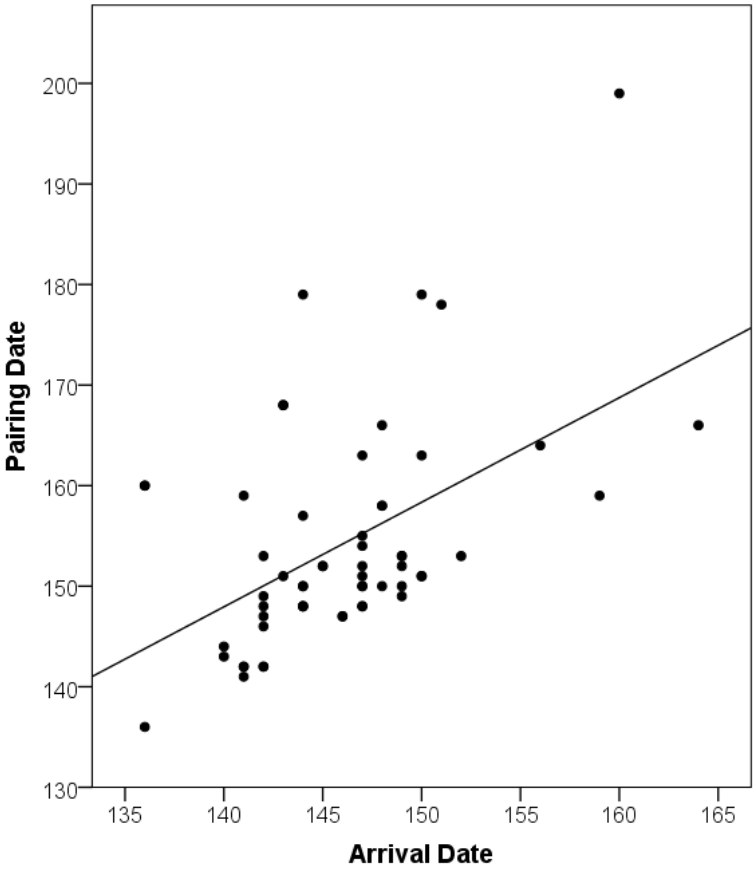

Figure 2.3. Male arrival date correlates positively with date of pairing (r^2=0.256)

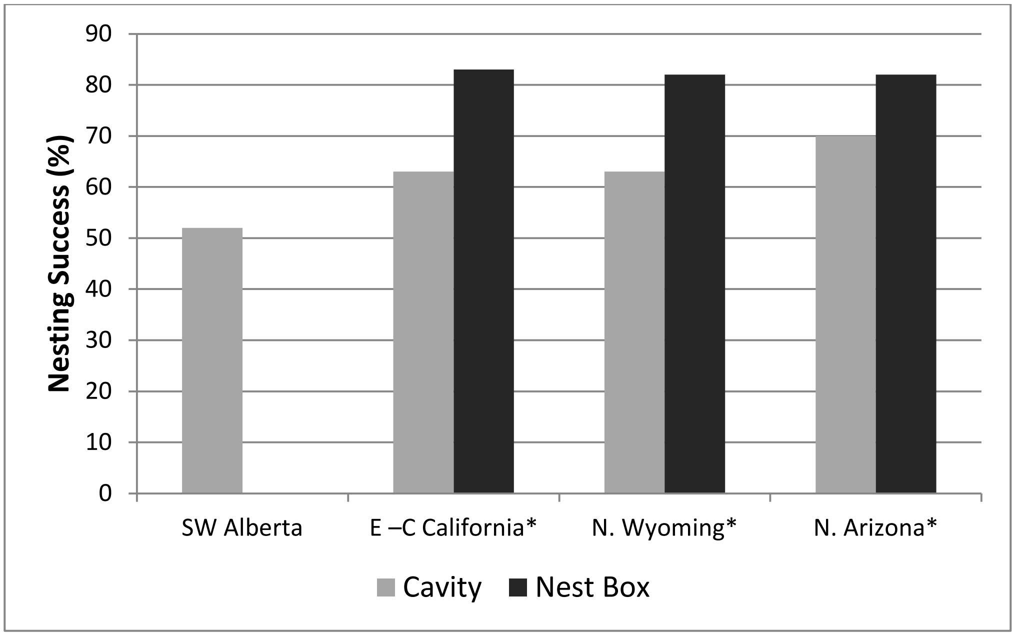

Figure 2.4. Nesting success of House Wrens using natural cavities in southwest Alberta compared to other populations of House Wrens using either natural cavities or nest boxes.

*E-C California = Purcell et al. 1997; N. Wyoming = Johnson & Kermott, 1994; N. Arizona = Clark & Martin, 2007

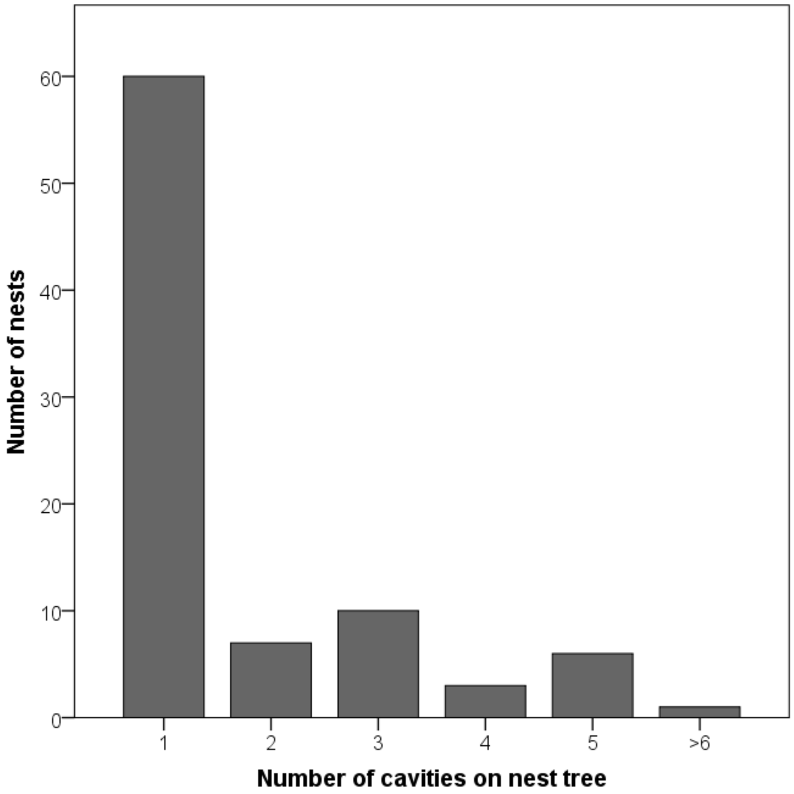

Figure 2.5. Number of nests used by House Wrens as a function of the number of suitable cavities available on the nest tree. There was a strong bias to nesting in trees containing only a single suitable cavity.

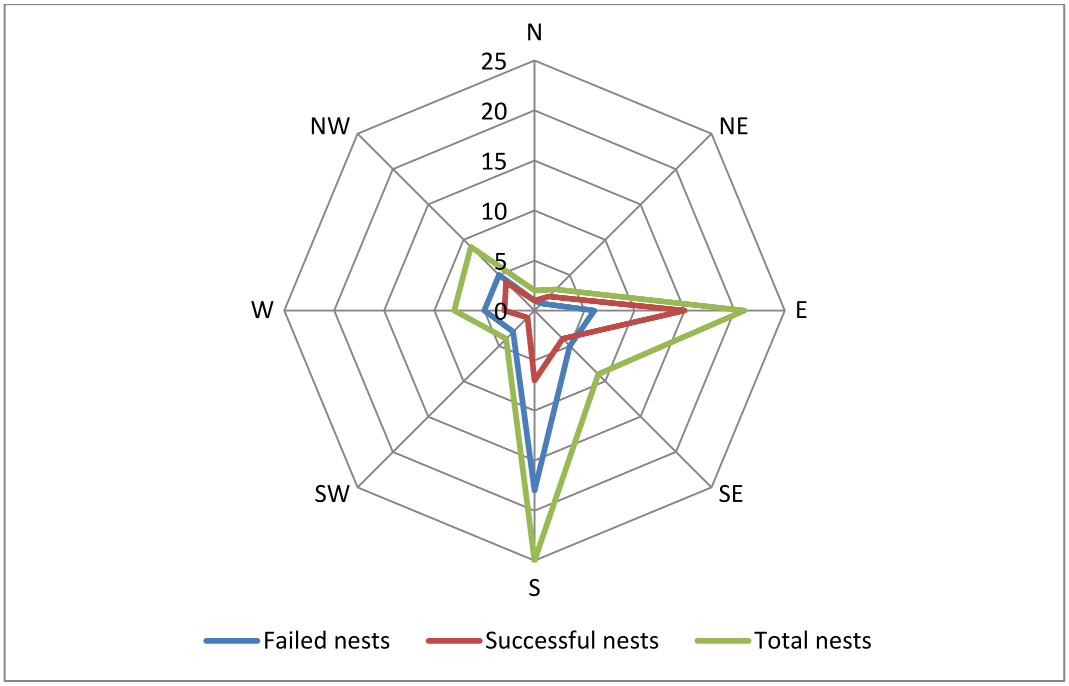

Figure 2.6. The success or failure of House Wren nests based on the cardinal direction of the cavity entrance. The outermost (green) line captures the orientation of all nests, while the inner red and blue lines capture, respectively, the orientation of those that succeeded or failed.

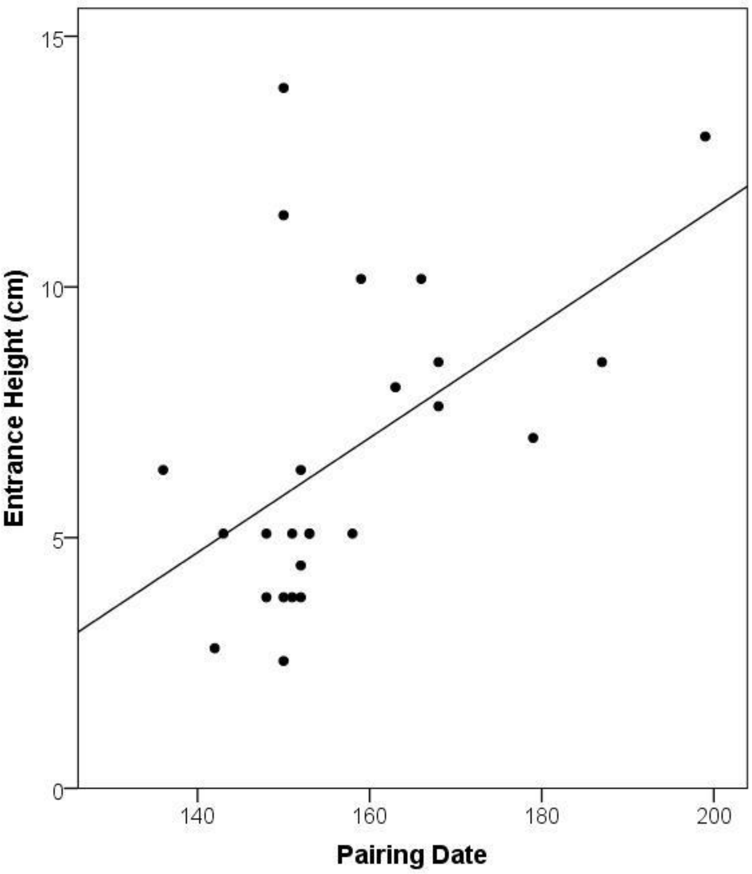

Figure 2.7. Relationship between male pairing date (given as the absolute date of the year) and the height of the cavity entrance (r^2=0.274).

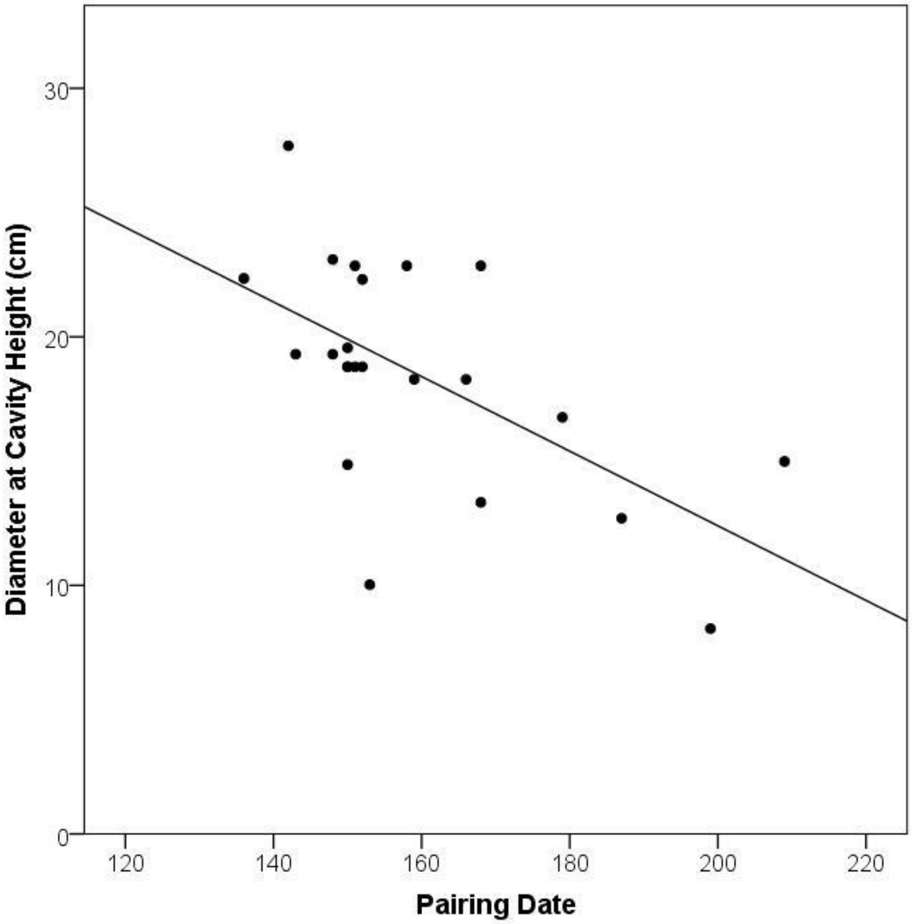

Figure 2.8. Relationship between male pairing date (given as the absolute date of the year) and the diameter of the nest tree at the height of the cavity entrance (r^2=0.361).

Chapter 3

Song organisation and variability in Northern House Wrens (*Troglodytes aedon parkmanii*) in Western Canada*

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Abstract

Detailed descriptions of song structure are critical to understanding the ontogeny, evolution, and function of bird song, particularly for species with large song repertoires. We provide a first detailed characterization of song organization and variability in a migratory population of House Wrens (*Troglodytes aedon*) breeding in western Canada, using a sample of 15,608 songs from 15 males. Males sang with high intensity in protracted bouts prior to pairing and often resumed high-intensity singing later in the breeding cycle to attract a second mate. The high-amplitude terminal portion of songs comprised rapid trills of frequency-modulated notes organized into discrete syllable types with a mean of 10 syllables and 4 syllable types per song. The population syllable repertoire was large (n =27) and mostly shared but was used to produce much larger repertoires of song types, most of which were unique. Individual males sang up to 194 different song types, with no evidence of a ceiling. However, males sang most song types only rarely and, thus, had much smaller "effective" repertoires of ~25 song types. Within singing bouts, males also repeated song types many times before switching and modified the syllable contents of successive songs gradually. Hence, they combined tremendous global song diversity with limited real-time song variability. This mix may reflect central neural or peripheral motor constraints on short-term song diversity or, perhaps, selection simultaneously favoring both diversity and consistency in song performance.

Key words**:** House Wren, song diversity, song organization, song repertoire, *Troglodytes*.

3.1. Introduction

Detailed descriptions of song structure are critical to understanding the ontogeny, evolution, and function of bird song (Catchpole & Slater, 2008; Marler & Slabbekoorn, 2004). However, for practical reasons, baseline knowledge of species' song structure and organization is often incomplete because large samples of song and behaviour can be required to fully characterize a species' singing patterns (e.g., Trillo & Vehrencamp, 2005). These practical challenges are further exaggerated for species with very large or complex song repertoires, and this is problematic because understanding the origins and evolution of large song repertoires is a particular focus of contemporary research, which increasingly shows that the relationships between song structure and function are more diverse and complicated than was previously thought (Byers & Kroodsma, 2009; Cardoso & Hu, 2011; Catchpole & Slater, 2008; Slater, 2003; Soma & Garamszegi, 2011).

Here, we use a large sample of song recordings from northern House Wrens (*Troglodytes aedon parkmanii*) to provide a detailed account of song organization and variability as a necessary first step in more focused studies of the evolution and function of large song repertoires in this species. House Wrens are ideally suited for such research. There are only a few previous studies of song in this group, and they are consistent in suggesting that House Wrens produce highly variable song and, possibly, large song repertoires (Cramer, 2012; Johnson & Kermott, 1990, 1991b; Kroodsma, 1977; Platt & Ficken, 1987). However, the extent and form of the variation—and, ultimately, the size and complexity of the song repertoires—are unknown. At the same time, House Wrens are very common and have the widest latitudinal distribution of any songbird in the Western hemisphere, breeding from central Canada to Tierra del Fuego. Across this broad range, populations in the north temperate zone are well studied in the United States (Barnett et al., 2012; Bowers et al., 2011; DeMory et al., 2010; Dobbs et al., 2006; Johnson, 1998; Masters et al., 2003; Soukup & Thompson, 1998), as are subtropical populations in Argentina (Fernandez et al., 2012; LaBarbera et al., 2010; LaBarbera et al., 2011; Llambias, 2009; Llambías, 2011; Llambias et al., 2012), and these studies have documented considerable variation in life history and mating systems; birds in the subtropics are sedentary and socially monogamous, with small clutch sizes, but birds in the north temperate zone are migratory and show appreciable rates of polygyny and large clutch sizes. The species and subspecies status of many populations are also uncertain and debated (Barker, 2004; Brewer, 2001; Brumfield & Capparella, 1996; Dickinson, 2003; Kroodsma & Brewer, 2005).

Given their broad distribution and behavioural variability, there is also considerable scope for differences in song diversity among House Wren populations and, therefore, important opportunities for research to help clarify the functional pressures that influence the size and complexity of song repertoires. A critical step in this process is to obtain a more complete picture of the form and extent of song variation in House Wrens. Here, we provide a comprehensive description and qualitative analysis of patterns of song organization and variability for one population of House Wrens breeding near the northern limits of the species' range in Western Canada.

3.2. Methods

3.2.1. Breeding biology and behaviour

North temperate populations of House Wrens are well studied in central Illinois, northern Wyoming, and northwestern New York. The resulting body of work, together with our own observations, confirms several aspects of the species' breeding biology and behaviour that are relevant to the singing patterns of north temperate populations. Males establish territories early in the breeding season that they then defend from rival males (Johnson and Albrecht 1993). Males contribute to nest building (Kendeigh, 1941) and are active in feeding nestlings (Barnett et al., 2012; Johnson et al., 1992; LaBarbera et al., 2011; Llambias et al., 2012). Males sing throughout the breeding season and in multiple contexts, including in interactions with potential female mates and with neighboring males (Johnson & Kermott, 1991b). Females are specifically attracted to male song and may use song as well as nest-site characteristics in choosing where to settle (Johnson & Searcy, 1993, 1996). Male song appears to play a role later in the breeding cycle in coordinating the female's safe departure from the nest (Ziolkowski et al., 1997) and in attracting additional mates (Johnson & Kermott, 1991b). Many males attempt polygyny. They actively court a second mate when their first mate is incubating eggs, and they sing again at this time (Johnson & Kermott, 1991b). Rates of successful polygyny may vary (10–24%), in part based on the availability of additional suitable nest cavities in male territories (Drilling & Thompson, 1991; Johnson & Kermott, 1991a). Rates of extra-pair copulation are also appreciable (Johnson et al., 2002; Masters et al., 2003; Soukup & Thompson, 1997). Taken together, these patterns suggest that song may function in establishing and defending territories and also in attracting females as either first or second mates, and possibly also as extra-pair mating partners.

3.2.2. Study sites and subjects

Research reported here was conducted in 2011 at two sites in the foothills of the Rocky Mountains of southwest Alberta. One site, Whaleback (WB), was located in the Bob Creek Wildlands of the Whaleback region (49.86°N, 114.27°W; mean elevation = 1,360 m), and the other, Lundbreck Falls (LF), was located on private lands near Lundbreck Falls, Alberta (49.56°N, 114.29°W; mean elevation = 1,280 m). The two sites were separated by 35 km, and both were in montane habitat at similar elevation where the vegetation was a mosaic of open grasslands punctuated by small stands of quaking aspen (*Populus tremuloides*) and occasional Douglas-firs (*Pseudotsuga menziesii*). In these undisturbed and nonurban habitats, House Wrens nest primarily in cavities previously excavated in quaking aspen by woodpeckers, but they also utilize other natural cavities, hollows, or cracks in quaking aspen and Douglas-firs. We did not erect nest boxes but chose instead to study birds using natural cavities.

First arriving males were documented on 17 May. On arrival, males immediately began to establish territories, to identify and prepare candidate nest cavities, and to sing. Once males appeared to have committed to a territory (i.e., had started initial nest preparation), they were captured using mist nets, measured, and then marked with a numbered aluminum band and three color bands in unique combinations to allow reliable individual identification. Females arrived shortly after males and visited males, inspected their territories, and investigated the cavities in them. First pairings, as evidenced by repeated inspections of specific cavities and concerted delivery of nest material by females, occurred as early as 19 May.

3.2.3. Song recording and analysis

Marked males (*n* =25) were sampled regularly for the remainder of the breeding season. Observation and recording were concentrated between 0530 and 1200 hours, when birds were most active. Recording was done in 1-h samples, with an effort to sample each male at least twice per week. Northern House Wrens are not generally disturbed by human presence, which makes it possible to obtain high-quality recordings at relatively close range (<10 m). Prior to recording, focal birds were confirmed by their colored leg bands. Recordings were made using digital recorders (Marantz PMD 670 and Sound Devices 702) and shotgun microphones (Sennheiser MKH 816).

The recording sample available for analysis comprised a total of 15,608 songs from 15 males (Table 3.1). The sample of recordings for individual males varied considerably because males varied in the speed with which they paired and their rate of singing tended to decrease dramatically shortly after pairing. Songs were analyzed in PRAAT, version 5.3 (Boersma & Weenink, 2012). The first step was to characterize various basic metrics of song structure and organization. As noted previously by others (Johnson & Kermott, 1991b; Kroodsma, 1977; Platt & Ficken, 1987), songs are obvious and discrete units of rapidly concatenated notes and syllables typically lasting 1–3 s followed by a conspicuous silent interval of similar duration (2–5 s). Most songs also involve two discrete sections that are readily distinguished by ear and in spectrograms (Fig. 3.1). The first section ("introduction") is a jumble of relatively unstructured, broadband notes that are either harsh (noisy) or tonal with multiple harmonic overtones. This section tends to be soft and difficult to hear clearly beyond ~20 m, and the individual notes can be difficult to delineate clearly in spectrograms. By contrast, the second ("terminal") section of songs is composed of a sequence of clearly structured, tonal and frequency- modulated notes. This section is also much louder and can be heard at considerable distances, often >100 m. Songs tend to be delivered in bouts in which consecutive songs are separated by relatively short silent intervals (2–5 s). We used a silent interval of ≥30 s to define different bouts of singing.

After delineating the basic components of songs and song bouts, the next step was to develop a catalog of notes and syllables using conventional nomenclature and definitions. In this analysis, we focused on the terminal section of songs, both because the notes and syllables in this section are far more clearly structured and therefore easier to delineate and because this section of the song is also much louder, with greater potential to be heard by males and females in the wider area. By comparison, the soft and unstructured notes of the introduction are unlikely to be heard clearly much beyond the immediate vicinity of the singer. "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. The delineation of different note and syllable types was based on clear and consistent 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; assessing additional metrics of syllable and song production variation, including variability in the sequencing of syllables within songs and in the sequencing of songs within bouts; and, finally, generating song templates that summarized common patterns of song construction. Statistics were performed in NCSS, version 8 (Hintze, 2010), or SPSS, version 20 (SPSS, Chicago, Illinois).

3.3. Results

3.3.1. General features of singing behaviour

Males sang at very high rates early in the breeding season, immediately on arrival on the breeding grounds. At this time, they produced songs in protracted bouts that could last for 30 min or more of continuous singing with very short intervals between successive songs (i.e., 8–12 songs min^{-1} and ≥600 songs h^{-1}). When visited by a female prospecting for a territory to settle in, males sang at especially high rates and showed other visible signs of heightened arousal, including following (chasing) the female closely, hopping around and above her when she settled on a branch, producing additional high-frequency “squeak” calls (cf. Johnson & Kermott, 1991b) between songs, and trying to direct her to specific cavities to which he had already made initial preparations. Males that remained unpaired continued to sing at high rates. After pairing, most males continued to sing as their female partners completed nest construction, but then curtailed their singing prior to and during egg laying. Song bouts were then generally much shorter, with longer intervals between consecutive songs. Some males resumed singing again after their mates had finished laying and begun incubating eggs, and some resumed singing later in the season when chicks from their first nest were close to fledging. In both cases, males generally sang from another location in their territory that contained a suitable nest cavity, apparently attempting to attract a second mate. Regardless of breeding stage, males sang most in the early morning, starting just before sunrise, until midday, and only infrequently in the afternoon or evening. Males tended to sing from a few specific locations within their territories, typically either immediately adjacent to their nest cavity or on a neighboring tree. Much less frequently, they sang near boundaries with neighboring males.

3.3.2. Global song structure

Most songs (93.5%) contained both introduction and terminal sections, but occasionally songs lacked either an introduction (4.8%) or a terminal section (1.7%). Collapsed across males, song duration averaged 2.25 s (range: 0.36–4.73), with the introduction generally shorter (mean = 0.92) than the terminal section (mean = 1.33). Notes in the terminal section were organized as a sequence of discrete syllable types, each type typically repeated several times before switching to a different type but then not repeated again within the same song. Songs contained an average of 3.9 syllable types (range: 1–9) and a total of 10.5 syllables (range: 1–25) produced at an average rate of 3.1 syllable types s^{-1} and 8.0 syllables s^{-1} (Table 3.1 and Figure 3.2). The relative syllable diversity of songs, evaluated as the ratio of the number of different syllable types to the total number of syllables produced within songs, averaged 0.39. The interval between successive songs averaged 5.4 s.

3.3.3. Note and syllable repertoires

A total of 22 different notes and 27 different syllable types were identified in the terminal portion of songs (Table 3.2 and Figure 3.3). Note and syllable structures were generally highly regular and extremely consistent within and between individuals, without obvious intermediate forms (Figure 3.4). Some syllables were formed from a single note, whereas others comprised the regular combination of two or three notes (Figure 3.3). Some syllables occurred primarily at the beginning or end of songs, whereas others occurred primarily in the middle. Still others were more flexible and could occur in various places in a song (Table 3.2). Some syllables could be shifted upward or downward in frequency and retain their overall form. Such frequency shifts depended in part on the placement of a particular syllable type within a song, in that most songs showed a tendency to decline in frequency from beginning to end. There were four pairs of syllables that resembled each other in many features of their overall temporal-spectral shape (M-G; N-R; AE-E; AD-F). However, in each case, there were also consistent differences in overall form that were stable within and between individuals, and there were no clear continua of intermediate forms between the two types in a pair; hence, we kept them distinct for present purposes but allow that future analyses might warrant collapsing them.

Syllable repertoires were highly conserved across males, with each male averaging 22 syllable types (range: 18–24), most of which were the same for all males. Only a few syllable types (BF, BG, BI, BH, and BJ) were produced by just one or a few males. Despite their common repertoire of syllable types, males varied in their use of different syllable types. Some syllable types (e.g., C and U) were produced by all males and were also used frequently by all of them. By contrast, other syllable types (e.g., K, AD, and AE) were produced relatively rarely by any male. Still other syllables (e.g., BF, N, Q, R, and Z) were produced commonly by some males but much less commonly by others.

The time course over which syllable types were revealed in successive song recordings for each male is illustrated in Figure 3.5. This figure shows that, for all males, syllable accumulation curves reached an asymptote, generally within the first 300–400 songs recorded. The figure also shows that there was variation in the rate at which males revealed their syllable repertories, with some males revealing their full syllable repertoire within the first 200 songs recorded and others requiring >800 songs to reveal a similarly sized repertoire of syllables.

3.3.4. Syllable transition patterns

We constructed a syllable transition matrix summarizing the frequency of observed (first order) transitions between adjacent syllable types within songs (Figure 3.6). For this analysis, transitions between the same syllable type (i.e., repetitions of the same syllable type) were ignored. Some syllable transitions were very common (e.g., AE-AD, D-E, E-F, and F-G), whereas others were much rarer (e.g., AE-F, D-AD, and L-E), and many possible syllable-type transitions never occurred at all. Furthermore, some syllables could transition to one of many other syllable types, whereas others could be followed by only one or a few different syllable types. For example, the syllable AG could be followed by 20 other syllable types, whereas the syllable F could be followed by only 5 other syllable types and was actually followed by only 1 other syllable (G) with any frequency.

3.3.5. Song type repertoires

A song type was defined conservatively as a unique sequence of syllable types, ignoring variation in the number of times particular syllable types might be repeated within a song. Even so, there was tremendous diversity in the song types recorded. The complete sample of 15,608 songs included 996 different song types. Song-type repertoires for individual males varied considerably, from a low of 38 song types to a high of 194 (mean = 109; Table 3.1). However, much of this variation among males was likely due to unequal sampling effort, as seen in Figure 3.7, 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. With additional recordings, these males would likely also have been found to have larger song repertoires because, as this figure also shows, novel song types were 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 (male ID LF14: n = 3,493 songs) and the largest documented song repertoire (n = 194), there was no indication of reaching a ceiling.

Given the diversity of song types among males, it was unsurprising that there was relatively little sharing of song types among males. Of the total of 996 different song types produced by the entire sample of 15 males, only a single song type was shared by all 15 males, whereas 14 song types (1.4%) were shared by ≥10. A substantially larger number (*n* = 231, or 23.1%) were shared by ≥2 males, but by far the majority of song types (*n* = 765, or 76.8%) were unique to particular males. On average, the number of males producing a particular song type was 1.6.

Notably, although males had large repertoires involving many unique song types, they sang most song types only rarely. Of the 996 song types in the sample, 427 (42.8%) were sung only once, and only 56 song types (5.6%) 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: 17–35). There was no relationship between the size of these "effective repertoires" of commonly produced song types for individual males and the number of song recordings for each of them (Pearson *r* = 0.065, *P* = 0.818).

3.3.6. Song type transitions

To further assess the relative diversity of songs within bouts, we developed a song-type transition matrix, exactly analogous to the syllable-type transition matrix. The song transition matrix quantified the first-order transitions between different song types in adjacent positions in the sequence of songs within a bout. We limited this analysis to the set of 56 song types that were sung > 50 times in the sample overall. Even limiting the analysis in this way, the resulting transition matrix is too large to display (56 × 56), but it revealed that, despite the large number of song-type transitions that are possible, very few actually occurred. By far the most common "transition" between successive songs was to the same song type. Of the total 7,975 transitions involving this set of 56 common song types, 84.1% (*n* = 6,707) were repetitions of the same song type. Only 15.9% (*n* = 1,268) 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. As a result, over long bouts of singing, the syllable content of songs tends to change very gradually. Only rarely did males switch to a song type with a dramatically different syllable structure.

3.3.7. Song templates

Combining the data on common song types and on syllable-type transition frequencies, we constructed a set of song templates that summarize the common patterns of song construction for this population. For this analysis, we limited the number of syllable types in a template to four, corresponding to the average number of syllable types observed in songs in the overall sample. Song templates were then seeded with the most common starting syllable types, which were C, AG, AI, AM, and S, and together accounted for 77.2% of all songs in the sample. Starting from these syllable seeds, song templates were constructed by concatenating the most frequent following syllable types at each successive stage, using a threshold syllable-type transition frequency of 30%. Figure 3.8 illustrates the set of common song templates that result from this process. Overall, there were 10 common pathways followed to generate the average four-syllable song, and some of these pathways were relatively subtle variants of one another (e.g., C.U.E.F and C.U.Z.M). Furthermore, many additional song types produced by males were relatively straightforward modifications of one of these 10 common pathways. For example, one song template was the C.U.E.F song type, and it was the basis for producing several common variants that differed only in the addition or deletion of one or two syllable types (e.g., C.U., C.U.E., C.U.E.F.G., and C.U.E.F.G.N).

3.4. Discussion

3.4.1. General patterns of song organization and variability

Songs of male House Wrens in western Canada were structurally delineated into a soft introductory section of relatively noisy, unstructured notes and a much louder terminal section composed of an extended trill of frequency-modulated notes organized into discrete syllable types. The repertoire of syllable types in the terminal section of songs was finite and totaled 27 syllable types for the population, most of which were shared by all males. Males used this large repertoire of common syllable types to produce much larger repertoires of different song types, with individual males producing up to 194 different song types with no evidence of a ceiling. These basic patterns agree well with previous descriptions and predictions about song-type diversity by Kroodsma (1977) and Platt and Ficken (1987).

It is important to emphasize that our estimates of song type diversity are conservative in two important respects. First, our definition of a song type did not incorporate differences in the number of times that particular syllable types were repeated within and between songs, which was an additional common source of variation. We also did not try to identify and categorize note and syllable diversity in the softer introductory section of songs. Incorporating these two additional sources of variation in future analyses could reveal even larger overall song repertoires.

Even so, song-type diversity for this population was very high, with 996 different song types sung by the sample of 15 males. Notably, the great majority of these song types (76.8%) were not shared but rather were unique to particular males. Hence, not only did males have large individual song repertoires by the conservative definition used, but there was also considerable diversity among males in the particular song types they sang.

3.4.2. Global diversity but short-term monotony

At the same time, the short-term diversity of male singing was limited. Thus, although the very large individual song-type repertoires attest to the tremendous potential diversity of male singing, the actual real-time song output of males revealed relatively little of this potential over short intervals. Within protracted bouts of singing, males tended to repeat the same song types many times before switching and, thus, sang with “eventual” rather than “immediate” variety, as originally predicted by Kroodsma (1977; cf. Kroodsma et al., 1999). Occasionally, males switched between different song types more abruptly, or toggled back and forth between two song types before converging on one of them, which they then repeated multiple times. In such instances, their singing exhibited more immediate variety, as emphasized by Platt and Ficken (1987) for House

Wrens in Wisconsin. This mode of singing was far less common than the more repetitive style, but future work should examine the extent to which the alternative singing styles may be used in different functional contexts (cf. Catchpole & Slater 2008, Johnson and Kermott 1991b, Trillo & Vehrencamp 2005,).

Furthermore, when males switched song types within a protracted bout of singing, they tended to do so gradually and incrementally via the addition, deletion, or substitution of only a single syllable type at a time. Hence, the syllable constitution of successive songs changed relatively slowly and, thus, the short term syllable diversity of a male's singing was comparatively low. Finally, while obviously capable of producing a very large number of different song types, males tended to focus on a much smaller number of ~25 song types that they sang regularly. They sang the remainder of the songs in their large repertoires very infrequently.

In general, then, the short-term singing style of males in Alberta tended to be quite repetitive and not especially diverse, at least with respect to our focus only on the syllable-type constitution of songs and in relation to the much greater capacity for variation at this level of which males were clearly capable. Consequently, over short time intervals, male House Wrens seemed to be concealing their singing potential more than they were revealing it (Byers, 1995; Byers & Kroodsma, 2009).

This coupling of tremendous potential global song diversity with a repetitive and relatively monotonous short-term singing style is an interesting combination. One possibility is that the pattern is pointing to potential constraints on song organization and variability, constraints that might operate at multiple different levels (Gil & Gahr, 2002). For example, there may be peripheral motor, or central neural, constraints on the variety of song types a male can maintain in his short-term (“active”) production repertoire. There may also be constraints on the syllable constitution of song types and on the ability to modify them dramatically over short intervals in successive songs. Certainly, our syllable transition analysis showed that transitions between some syllable types were routine whereas others were rare, and the majority of all possible transitions never occurred at all. This pattern suggests that the types of transition that can occur may be constrained: some transitions may be relatively easy whereas others may be more difficult or even impossible.

This potential constraint may be buttressed by the song template analysis (Figure 3.8), which showed that the great majority of songs produced by males in this population were based on a relatively small number of common song-construction pathways. Furthermore, many of the additional song types that males produced to yield their much larger global repertoires involved relatively straightforward modifications of one of these 10 common pathways by the simple addition, deletion, or substitution of one or two syllable types. One interpretation of these findings is that the regularity in song construction patterns is highlighting some fundamental syllable-sequencing constraints, which thereby limit the short-term song diversity observed.

Another possibility is that the combination of global song diversity with a relatively repetitive short-term singing style reflects selection for both diversity and consistency in male singing (Byers et al., 2010; Podos et al., 2009; Sakata &

Vehrencamp, 2012). Although these pressures are traditionally conceived of as opposing and relatively exclusive pressures on song organization and variability, they may not be. Perhaps selection on song can favor males capable of both singing a variety of different song types and singing each with high fidelity. Indeed, recent research on Tropical Mockingbirds (*Mimus gilvus*) supports this possibility by demonstrating that males have very large syllable repertoires and even larger song repertoires. Nevertheless, they tend to repeat song themes over short intervals, and the consistency of syllable repetitions has been shown to correlate with male age, social status, and reproductive success (Botero et al., 2009). Hence, there appears to be selection for consistency in singing patterns, even in species with very large and diverse syllable and song repertoires, which then also favors an element of repetitiveness in song delivery. Something similar may explain the juxtaposition of diversity with repetitiveness in the singing style of House Wrens. If so, an important corollary is that there may then be a host of other performance-related factors at play that could be manifest in additional detailed aspects of song structure and likewise favor an element of repetitiveness in singing to facilitate evaluation by receivers (Byers et al., 2010; Cramer, 2012; Logue & Forstmeier, 2008; Podos, 1997; Podos et al., 2004; Sakata & Vehrencamp, 2012), and these too should be investigated further.

Taken together, the juxtaposition of global song-type diversity with short-term monotony in the singing of male House Wrens may highlight important mechanistic constraints on the expression of song diversity over short intervals, or it may reflect a combination of functional pressures that simultaneously favor both diversity and consistency in singing performance. Testing and disentangling these alternatives are priorities for future research. In this respect, the detailed song patterns described here represent an important baseline for comparison with House Wren populations in other parts of the Americas, particularly as they manifest important differences in migratory behaviour and other life-history and mating-system factors that are thought to influence the evolution of large and complex song repertoires. Such comparisons offer an important opportunity to further illuminate the variety of factors affecting the evolution of singing in this widespread and otherwise well-studied species.

3.5. Acknowledgements

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Table 3. 1. Summary statistics (counts or means ± SD) for the sample of recorded songs of male House Wrens from a migratory population breeding in western Canada in 2011

Bird ID	Number of songs	Syllables song^{-1}	Syllable types song^{-1}	SVI[a]	Syllables second^{-1}	Syllable types second^{-1}	Song types	Common song types[b]	Syllable types	Common syllable types[b]
LF 02	1744	12.03	3.73	0.32	8.03	2.53	169	22	21	14
LF 04	312	9.94	2.92	0.35	8.38	2.89	48	21	18	15
LF 06	869	9.59	4.18	0.46	8.14	3.67	109	26	23	19
LF 08	1447	9.79	4.20	0.45	7.99	3.60	133	35	23	20
LF 09	629	8.96	3.31	0.39	7.73	2.96	95	20	23	17
LF 10	560	9.74	4.16	0.44	8.22	3.60	98	24	21	18
LF 11	1327	12.18	3.94	0.33	8.14	2.69	142	17	24	16
LF 12	529	9.64	3.71	0.44	8.04	3.57	38	18	18	16
LF 13	1357	10.26	3.99	0.40	7.87	3.14	170	21	24	18
LF 14	3493	10.80	4.25	0.40	8.08	3.23	194	25	22	18
LF 15	1052	12.89	4.74	0.38	7.83	2.99	117	30	23	17
WB 01	1147	11.14	3.89	0.36	7.86	2.88	105	25	24	19
WB 02	390	9.96	3.94	0.41	8.43	3.49	78	33	21	19
WB 05	419	10.90	3.57	0.34	7.31	2.50	81	26	21	18

Bird ID	Number of songs	Syllables song^{-1}	Syllable types song^{-1}	SVI[a]	Syllables second^{-1}	Syllable types second^{-1}	Song types	Common song types[b]	Syllable types	Common syllable types[b]
WB 08	235	9.47	3.67	0.40	7.66	3.10	55	21	18	16
Mean		**10.49**	**3.88**	**0.39**	**7.98**	**3.12**	**108.8**	**24**	**22**	**17**

[a] SVI (Syllable Versatility Index): calculated by dividing the number of syllable types in a song by the number of syllables.

[b] Count is limited to types representing more than 1% of a male's song or syllable production.

Table 3. 2. Syllable-type repertoire and characteristics for the sample of recorded songs of male House Wrens from a migratory population breeding in western Canada in 2011.

Syllable	Number of notes	Note identity	Position in song [a]
AD	3	XLIII, XVIII,XVI	Middle
AE	2	XLIII, XLV	Beginning, Middle
AG	2	XLII, XVIII	Beginning, Middle
AI	1	VIII	Beginning
AM	1	XXXIV	Beginning
AW	2	XXVIII, XXIX	Beginning, Middle
BB	1	XVIII	Beginning, Middle
BF	2	XVIII, XLV	Middle
BG	2	VIII, IX	Beginning
BH	2	VIII, XLVIII	Beginning
BI	2	VIII, VI	Beginning
BJ	1	XLIX	Beginning
C	2	VI	Beginning, Middle
D	1	VII	Middle
E	2	XLIII, XLIV	Middle, End
F	3	XLIII, XVIII, XVI	Middle
G	2	XVIII, XVI	Middle, End
K	1	XVII	Beginning
L	2	XVIII, XIX	Middle
M	2	XVIII, XVI	Beginning, Middle, End
N	2	XVIII, XXVI	End

Syllable	**Number of notes**	**Note identity**	**Position in song** [a]
Q	2	XVI	Beginning, Middle
R	2	XVIII, XXVII	Middle
S	1	IX	Beginning
T	2	XXVIII, IX	Middle
U	3	XVIII, XLI	Middle, End
Z	3	XVIII, XX,XXI	Middle, End

[a] Indicates where each syllable typically occurs within the main section of the song.

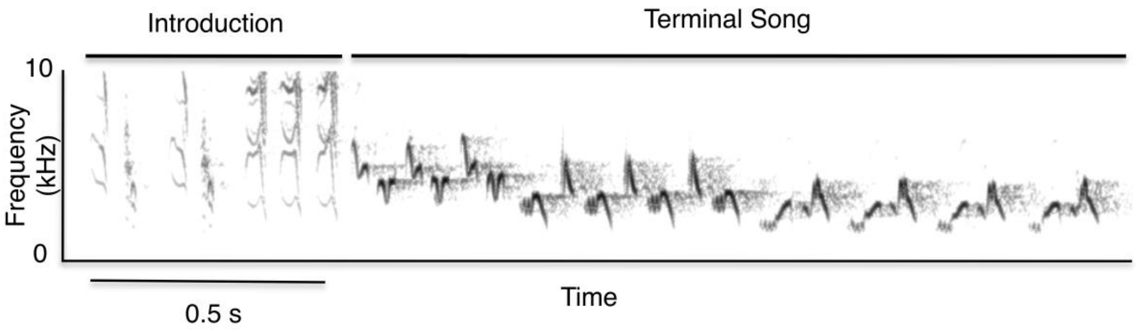


Figure 3. 1. A representative song of a male House Wren, illustrating the common structural division of song into an "introduction" section composed of relatively low-amplitude broadband notes and a "terminal" section composed of a concatenation of much higher-amplitude and tonal, frequency-modulated notes organized into discrete syllable types.

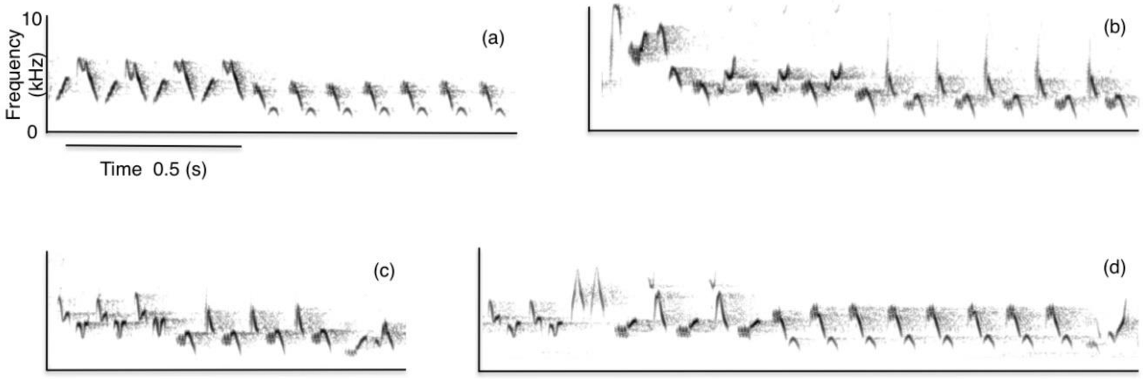


Figure 3. 2. Four songs of male House Wrens from a migratory population breeding in western Canada in 2011, illustrating common variation in the number (n) of different syllable types contained in the "terminal" section of songs. (A) n = 2. (B) n = 4. (C) n = 3. (D) *n* = 6.

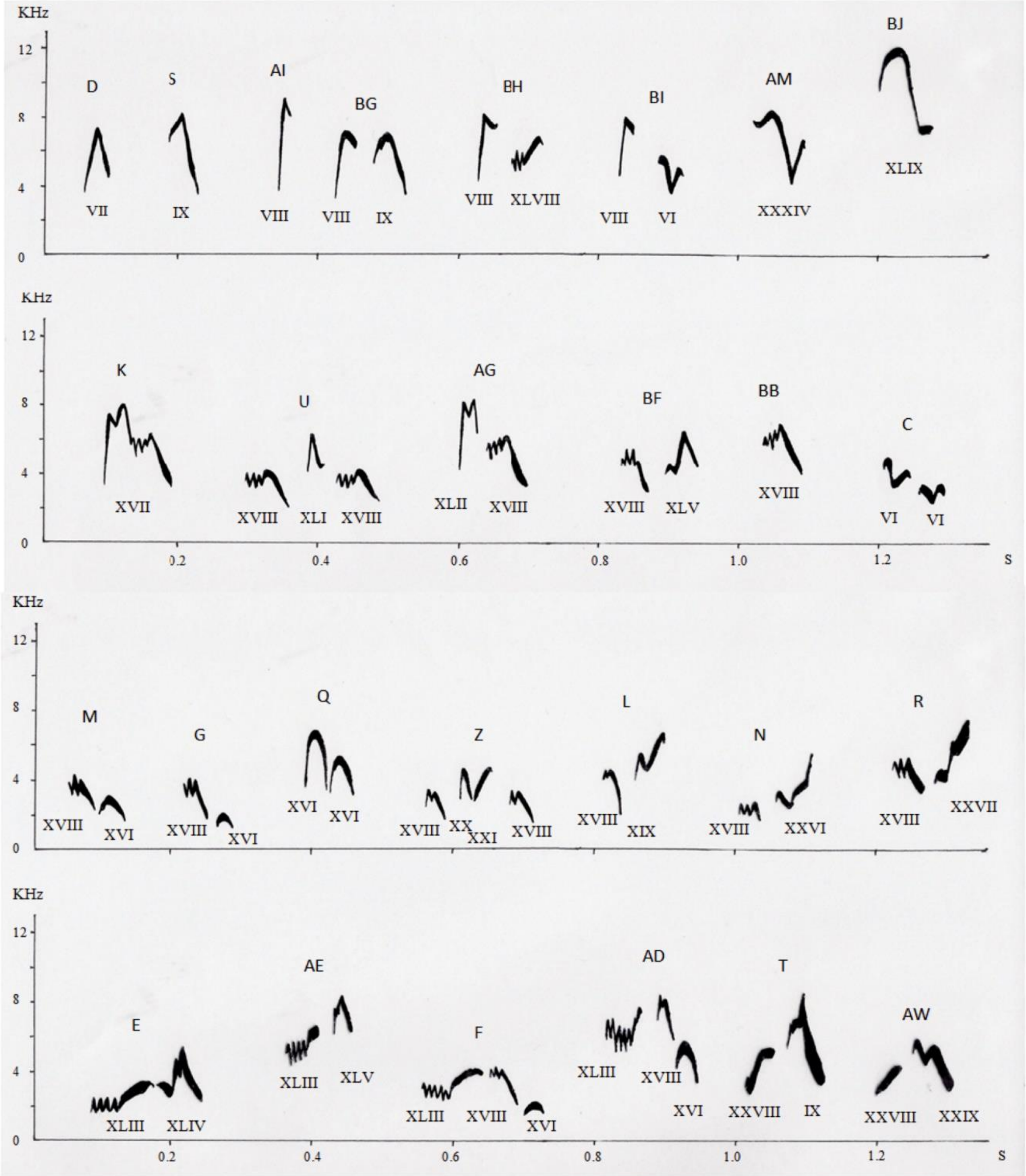


Figure 3. 3. The complete note and syllable-type repertoire for the study population of male House Wrens from a migratory population breeding in western Canada in 2011, focusing on the "terminal" section of songs. Notes are indicated by Roman numerals and syllable types by capital letters. Some notes appear in several different syllable types (e.g., XVIII is used in syllables U, AG, BF, BB, M, G, Z, L, N, and R) whereas other notes are unique to only one syllable type (e.g., XVI is used in syllable Q).

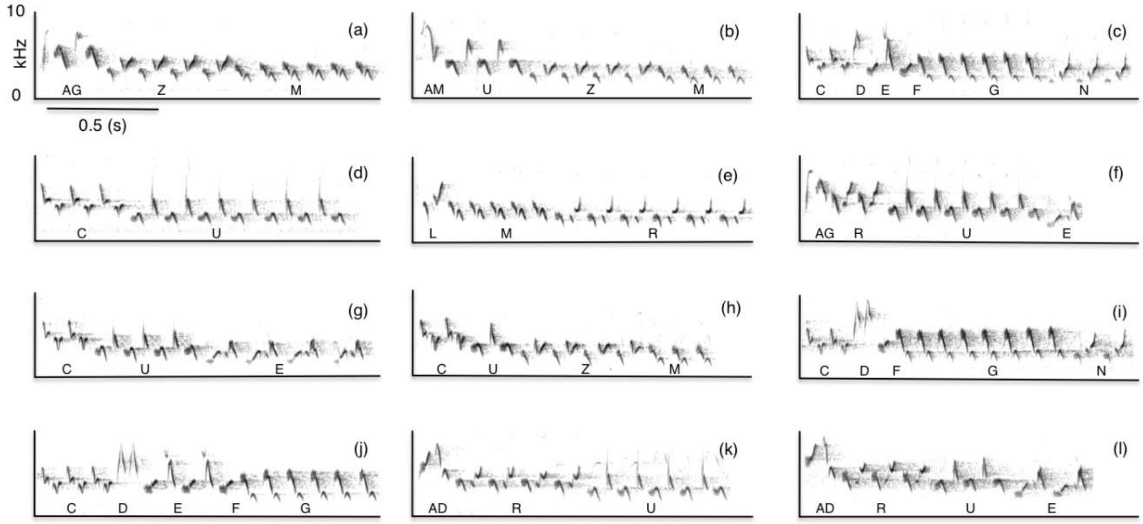


Figure 3. 4. Six different songs from each of two male House Wrens from a migratory population breeding in western Canada in 2011. (A–F) Male 1. (G–L) Male 2. The syllable-type sequence of each song is annotated in capital letters (e.g., AG.Z.M. for the song in panel A). Note the similarity in the forms of specific syllable types within and between males even when they occur in different places in a song and are thus shifted either up or down in frequency (e.g., the syllable U in panels B and H, where it occurs toward the beginning of the song, versus in panels F, G, and L where it occurs in the middle and panels D and K where it occurs at the end as the final syllable type).

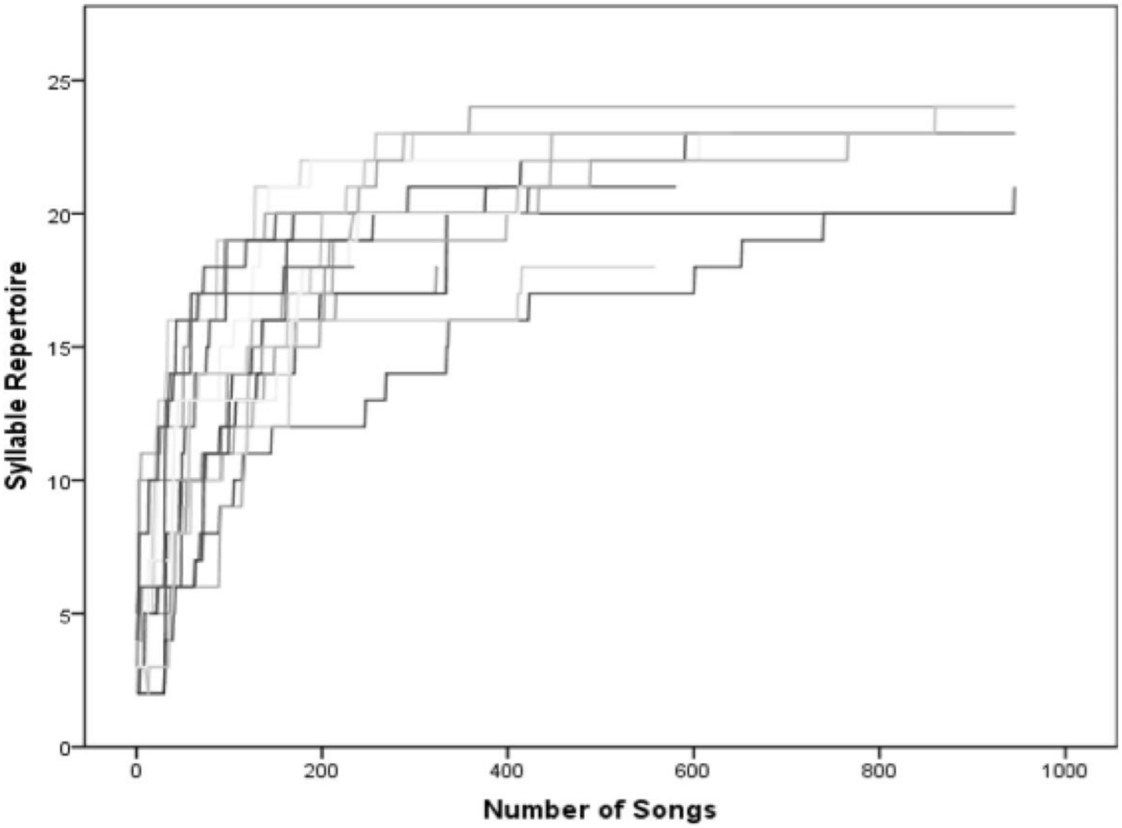
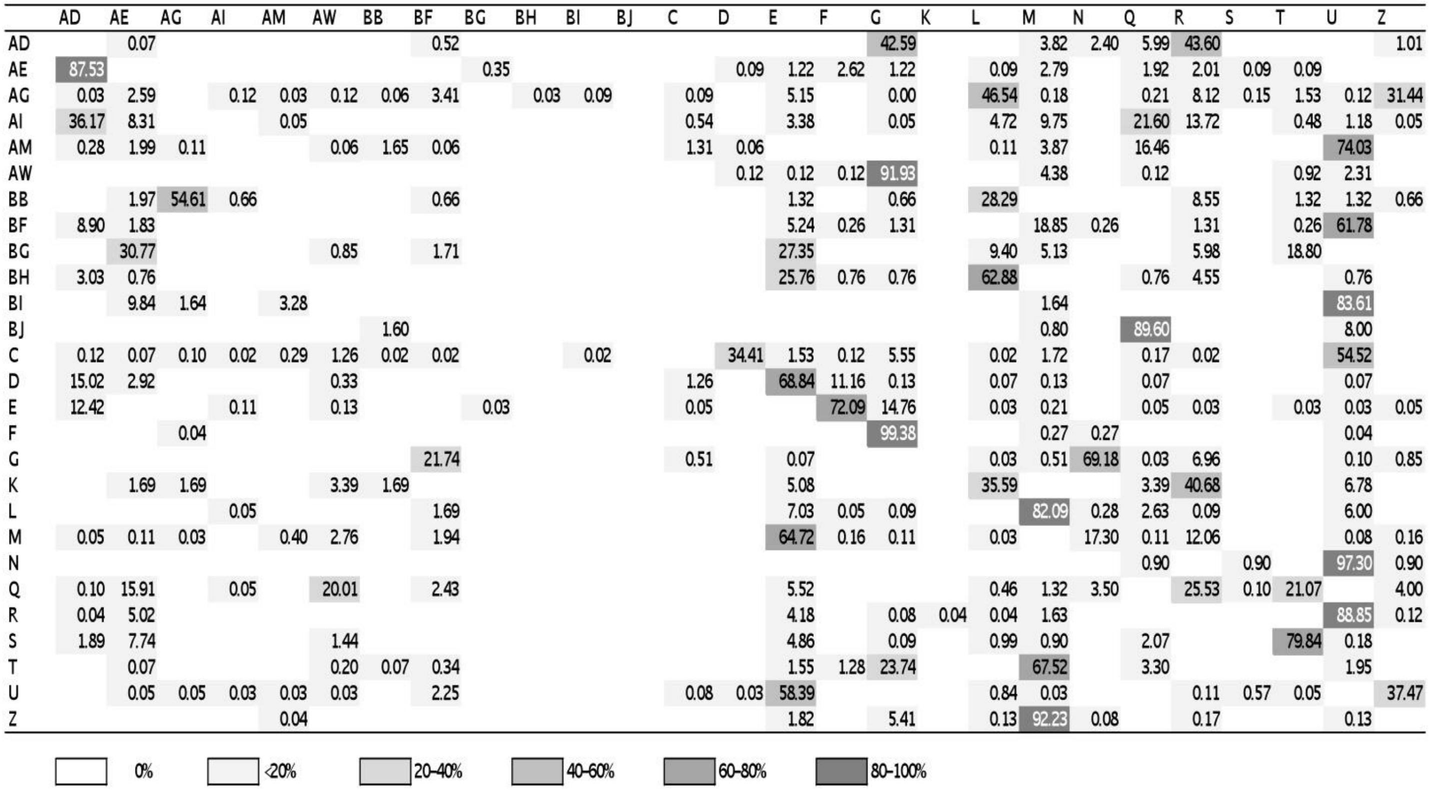


Figure 3. 5. Syllable repertoire size and accumulation functions for each individual in the sample of male House Wrens from a migratory population breeding in western Canada in 2011. Each line represents a different male (n = 15) and shows the time course over which males introduced new syllable types into their songs in successive recordings.



	AD	AE	AG	AI	AM	AW	BB	BF	BG	BH	BI	BJ	C	D	E	F	G	K	L	M	N	Q	R	S	T	U	Z
AD		0.07						0.52									42.59			3.82	2.40	5.99	43.60				1.01
AE	87.53								0.35					0.09	1.22	2.62	1.22		0.09	2.79		1.92	2.01	0.09	0.09		
AG	0.03	2.59		0.12	0.03	0.12	0.06	3.41		0.03	0.09		0.09		5.15		0.00		46.54	0.18		0.21	8.12	0.15	1.53	0.12	31.44
AI	36.17	8.31			0.05								0.54		3.38		0.05		4.72	9.75		21.60	13.72		0.48	1.18	0.05
AM	0.28	1.99	0.11			0.06	1.65	0.06					1.31	0.06					0.11	3.87		16.46				74.03	
AW														0.12	0.12	0.12	91.93			4.38		0.12			0.92	2.31	
BB		1.97	54.61	0.66				0.66							1.32		0.66		28.29				8.55		1.32	1.32	0.66
BF	8.90	1.83													5.24	0.26	1.31			18.85	0.26		1.31		0.26	61.78	
BG		30.77				0.85		1.71							27.35				9.40	5.13			5.98		18.80		
BH	3.03	0.76													25.76	0.76	0.76		62.88			0.76	4.55			0.76	
BI		9.84	1.64		3.28															1.64						83.61	
BJ							1.60													0.80		89.60				8.00	
C	0.12	0.07	0.10	0.02	0.29	1.26	0.02	0.02			0.02			34.41	1.53	0.12	5.55		0.02	1.72		0.17	0.02			54.52	
D	15.02	2.92				0.33							1.26		68.84	11.16	0.13		0.07	0.13		0.07				0.07	
E	12.42			0.11		0.13			0.03				0.05			72.09	14.76		0.03	0.21		0.05	0.03		0.03	0.03	0.05
F			0.04														99.38			0.27	0.27					0.04	
G								21.74					0.51		0.07				0.03	0.51	69.18	0.03	6.96			0.10	0.85
K		1.69	1.69			3.39	1.69								5.08				35.59			3.39	40.68			6.78	
L				0.05				1.69							7.03	0.05	0.09			82.09	0.28	2.63	0.09			6.00	
M	0.05	0.11	0.03		0.40	2.76		1.94							64.72	0.16	0.11		0.03		17.30	0.11	12.06			0.08	0.16
N																						0.90		0.90		97.30	0.90
Q	0.10	15.91		0.05		20.01		2.43							5.52				0.46	1.32	3.50		25.53	0.10	21.07		4.00
R	0.04	5.02													4.18		0.08	0.04	0.04	1.63						88.85	0.12
S	1.89	7.74				1.44									4.86		0.09		0.99	0.90		2.07			79.84	0.18	
T		0.07				0.20	0.07	0.34							1.55	1.28	23.74			67.52		3.30				1.95	
U		0.05	0.05	0.03	0.03	0.03		2.25					0.08	0.03	58.39				0.84	0.03			0.11	0.57	0.05		37.47
Z					0.04										1.82		5.41		0.13	92.23	0.08		0.17			0.13	

☐ 0% ▢ <20% ▢ 20–40% ▢ 40–60% ▢ 60–80% ▢ 80–100%

Figure 3. 6. Matrix of first-order transitions between successive syllable types within songs of male House Wrens from a migratory population breeding in western Canada in 2011. Cell contents summarize the frequency with which a given syllable type (in rows) is followed by each of the other possible syllable types (in columns) tabulated as a percentage of the number of occurrences of the preceding syllable (i.e., tabulated within rows). As an example, the first syllable type in the matrix (AD) was followed by eight other syllable types (AE, BF, G, M, M, Q, R, and Z), but two of these (G at 42.59% and R at 43.60%) were by far the most common following syllables and together accounted for >85% of transitions from AD to a succeeding syllable type. Cell shading is used to highlight larger-scale differences in transition probabilities summarized in 20% intervals

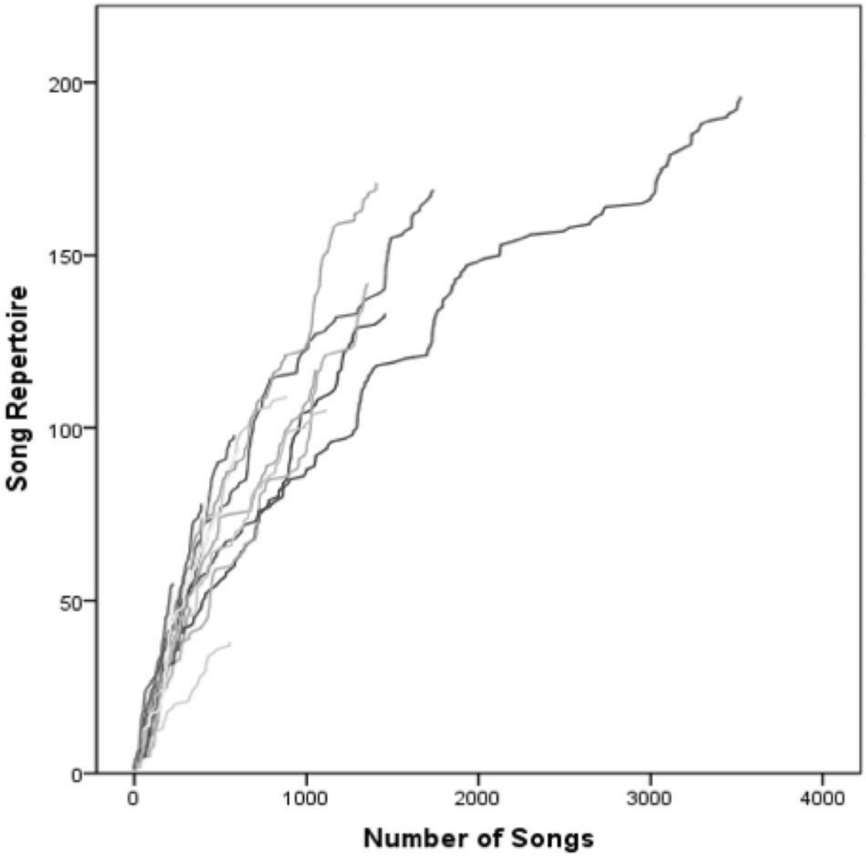


Figure 3. 7. Song repertoire size and accumulation functions for each individual in the sample of male House Wrens from a migratory population breeding in western Canada in 2011. Each line represents a different male (n = 15) and shows the time course over which males introduced new song types during 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.

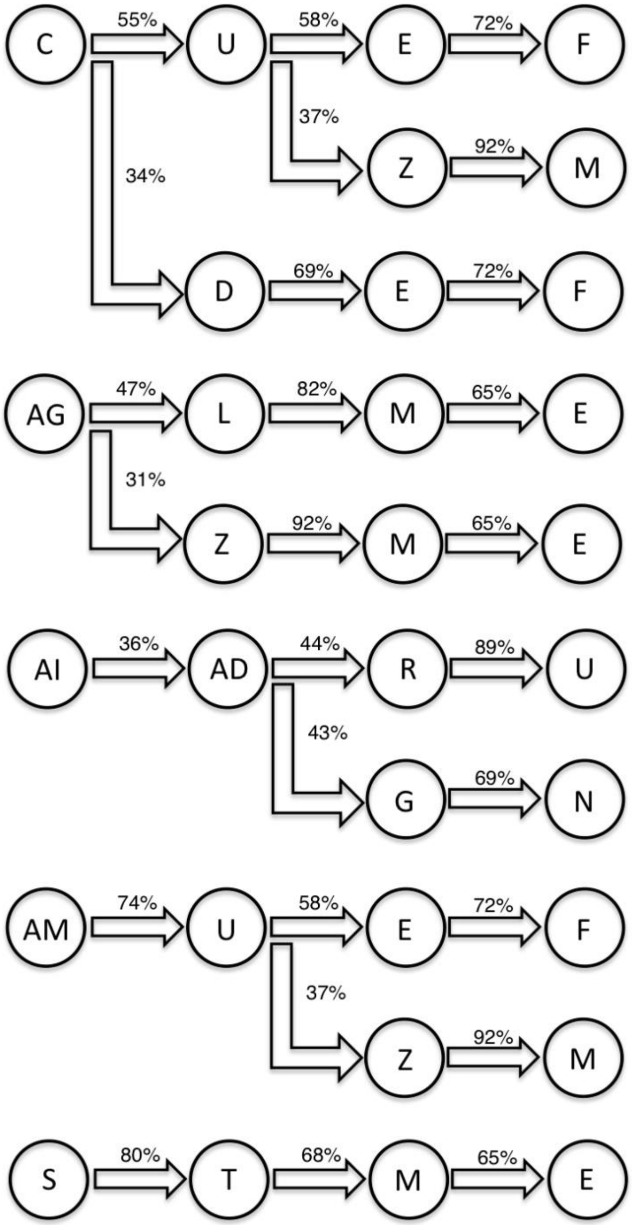


Figure 3. 8. Song templates summarizing patterns in the construction of the most common song types of male House Wrens from a migratory population breeding in western Canada in 2011, containing the average number of syllable types for the population (n = 4). Templates were seeded from five different syllable types that represented the most common starting syllables in the entire song sample, collectively accounting for 77.2% of all songs (C, AG, AI, AM, and S). Additional syllables were then concatenated to the seed on the basis of their successive syllable transition probabilities. These transition probabilities are reported at successive steps in each template as percentage values and are derived from the data summarized in Figure 6. This process yields 10 song templates that were among the most common song types sung by males.

Chapter 4

Transcontinental latitudinal variation in song performance and complexity in House Wrens (*Troglodytes aedon*)*

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Abstract

There is growing interest in latitudinal effects on animal behavior and life history. One recent focus is on birdsong, which is hypothesized to be more elaborated or complex in the North temperate zone compared with the tropics. Current evidence is mixed and based on cross-species comparisons, or single species with restricted distributions. We circumvent these limitations using a transcontinental sample of 358 songs from House Wrens (*Troglodytes aedon*) at 281 locations spanning more than 100^0 of latitude (52^0 N–55^0 S) across the Americas. We found a significant latitudinal gradient in several basic elements of song performance and complexity between north temperate and tropical populations. Furthermore, we document convergence in song patterns between populations at higher latitudes in the Northern and Southern Hemispheres. Effects were strongest for the number of elements in a song, and the rate of element production, both increasing towards the poles, with similar but weaker effects for other song dimensions (e.g. number of unique elements, trills and trill rate). We consider possible causes related to variable habitats and morphology, concluding that the shorter breeding seasons at higher latitudes in both hemispheres may favour greater song elaboration to mediate territory competition and mate choice.

Keywords: songbirds, song performance, song complexity, geographical variation, latitudinal gradient, sexual selection

4.1. Introduction

A longstanding issue in the study of birdsong concerns variation in song patterns between populations that can arise through a variety of social and ecological processes (Slabbekoorn & Smith, 2002). There is considerable recent interest in geographical variation at exceptionally broad geographical 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 in seasonally variable environments (Botero et al., 2009) and for migratory populations (Collins et al., 2009) in the north temperate zone compared with sedentary birds in the tropics due to 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 the development of more elaborate or complex song patterns in north temperate birds for efficient mediation of male competition for territories and for female choice of mates.

There is some support for this proposal (e.g. Botero et al., 2009; Collins et al., 2009; Weir & Wheatcroft, 2011), but the relationships are far from definitive, and there are a variety of exceptions and confounding factors (Byers & Kroodsma, 2009; Cardoso & Hu, 2011; Soma & Garamszegi, 2011). At the same time, most broad-scale studies of song variation have involved comparisons across different species inhabiting either the temperate zone or the tropics. It is possible that focused studies of single species inhabiting both regions could shed additional light on our understanding of latitudinal differences in song structure and singing patterns. While the number of species with sufficiently broad distributions to allow such testing are limited, there are some species that fit the bill, and the House Wren (*Troglodytes aedon*) is one. House Wrens have the widest, continuous latitudinal distribution of any native songbird in the Western Hemisphere (Brewer, 2001) being distributed from central Alberta, Canada (58^0 N) to Tierra del Fuego (55^0 S). The species thus provides a unique opportunity to examine patterns of song variation at the transcontinental scale.

Here we use a sample of song from recordings of House Wrens at 281 locations distributed across their entire range to test predictions about some basic elements of song performance and complexity stemming from the hypothesis that sexually selected pressures on song are magnified at higher latitudes. According to this hypothesis, we should find evidence of increased elaboration or complexity in the songs of populations at temperate latitudes compared with the tropics. We are particularly interested to test an additional (and to our knowledge largely untested) prediction arising from the hypothesis of latitudinal variation in sexual selection: that song patterns of populations at more extreme latitudes in the Southern Hemisphere might converge on those observed in the more commonly studied temperate regions of the Northern Hemisphere reflecting a convergence in the functional pressures of sexual selection associated with similarly short breeding seasons at higher latitudes in both hemispheres. Testing of this prediction is uniquely afforded by the exceptionally broad distribution of House Wrens.

4.2. Material and methods

4.2.1. Study species

House Wrens are a small songbird species distributed broadly across North, Central and South America, having the widest distribution of any native songbird in the Western Hemisphere (Brewer, 2001). There have been proposals to split the species (Brumfield & Capparella, 1996), but currently it is recognized as a single species (AOU, 1998; Dickinson & Christidis, 2014) with 31 subspecies (Dickinson & Christidis, 2014). The species reaches its northern limits in Central Alberta, Canada (58^0 N) and its southern limits in Tierra del Fuego (55^0 S). Across this range, there is considerable variation in ecology, behaviour and life history.

For example, populations in the North temperate zone, which are well studied in the United States, are migratory, show appreciable rates of polygyny and produce large clutches (Dobbs et al., 2006; Johnson, 2014; Soukup & Thompson, 1998). By contrast, populations in the tropics and the South temperate zone tend to be sedentary, socially monogamous and produce small clutches (Fernandez et al., 2012; LaBarbera et al., 2011; Llambias, 2009; Llambías et al., 2015; Llambias et al., 2012). Hence, there is considerable scope for corresponding variation in sexual selection pressure and associated influences on song performance and complexity across this range (dos Santos et al., 2015; Rendall & Kaluthota, 2013; Sosa-López & Mennill, 2014).

Populations of House Wrens at higher latitudes in the Southern Hemisphere have not been studied systematically. So there is outstanding uncertainty concerning the migratory status, life history and mating system of these populations. Nevertheless, climate and geography at higher latitudes in the Southern Hemisphere yield seasonal environments convergent in many respects with those of the North temperate zone, which may also contribute to convergent influences on song complexity.

4.2.2. Song sample

To properly assess potential latitudinal variation in song patterns, we attempted to obtain a sample of songs spanning the entire latitudinal range of House Wrens. To do so, we made use of the Xeno-Canto online database of bird songs (www.xeno-canto.org) as the primary source of song recordings, downloading all available recordings in the database for House Wrens up to October 2014. A preliminary examination was undertaken of all recordings to first eliminate those of poor quality resulting from weak signal levels, high levels of background noise or interference from signals produced by other species. For most geographical locations in the resulting sample, there was only a single recording available, but most of these recordings contained more than one song. To further standardize the sample for analysis, we selected only a single song from each recording, and selected not more than two recordings (randomly chosen) from any sample location, presumably representing different males. For each recording, the song selected for subsequent analysis was selected based on overall quality, with the highest signal-to-noise ratio and relatively free of interference from other sound sources. Because the original recordings were sometimes made at different sampling frequencies, we resampled all songs at 20.5 kHz.

This sample of songs from the Xeno-Canto database was supplemented by our own recordings of House Wren songs made between 2011 and 2014 at two long-term field sites, one in Southern Alberta, Canada (Rendall & Kaluthota, 2013) and the other in Mendoza Province, Argentina (dos Santos et al., 2015), as well as from 16 additional locations sampled in Argentina and Chile. To match the Xeno-Canto sample procedure, for each of these additional sample locations, we likewise used only one song from up to two recordings and involving two different males. For our own field recordings, we used digital recorders (Marantz PMD660, PMD670 or Sound Devices 702) and a Sennheiser microphone system (MKH 816).

The final sample available for analysis comprised a total of 358 songs, presumptively all different males, from 281 locations covering almost the entire range of the species from 52^0N to 55^0S (Figure 4.1).

4.2.3. Song organization and complexity

House Wren song comprises two distinct sections. The opening section (labelled the introduction) is comparatively soft and is composed of relatively unstructured broadband notes that are either harsh (noisy) or tonal with multiple harmonic overtones, while the second section (labelled the terminal section) is much louder and composed of well-structured, tonal and frequency modulated notes organized into discrete syllable types (Figure 4.2). Both northern and southern House Wrens have large but finite note and syllable repertoires, and they combine syllables in a non-random pattern to produce much larger repertoires of different song types (dos Santos et al., 2015; Rendall & Kaluthota, 2013).

One metric of complexity commonly used in the birdsong literature concerns the overall size of the repertoire of songs, syllables or notes. The utility of some of these metrics is subject to continuing debate and uncertainty (Byers & Kroodsma, 2009), and in any case, they could not be used in this study because the Xeno-Canto database contains too few recordings at any given location to allow credible assessments of repertoire sizes for any of them.

Past research has identified a number of other potential metrics of song performance or complexity similarly influenced by pressures of sexual selection (Cardoso et al., 2012; Palmero et al., 2014; Podos et al., 1992; Tietze et al., 2015; Weir & Wheatcroft, 2011). These include the duration of individual songs; the number of distinct elements (notes or syllables) they contain; the rate at which successive elements within songs are produced; the number of trills contained in songs; and the frequency range covered by trilled notes (Podos, 2014). Following past work, we thus identified a set of parameters to measure from each song in our assembled database. Some were relevant to both the introduction section and the terminal section of songs, while others were relevant only to the louder terminal section. Measured song parameters were: (i) overall song duration and (ii) the duration of the introduction and (iii) terminal sections; the (iv) minimum and (v) maximum frequency of elements in the terminal section; (vi) the number of elements in the entire song and in (vii) the introduction and (viii) terminal sections; (ix) the number of unique elements in the terminal section; and (x) the number of trills (defined as the repetition of an element three or more times in succession). From these basic metrics, we developed a number of derivative measures including (xi) the element production rate across the entire song, and in (xii) the introduction and (xiii) terminal sections; (xiv) the trill production rate; (xv) the rate of production of unique elements; and (xvi) frequency bandwidth (max–min frequency). Spectrographic measurements were made using the software PRAAT v. 5.4 (Boersma & Weenink, 2012).

4.2.4. Statistical analysis

Our statistical analysis proceeded in two steps. First, to address the more conventional prediction that song performance or complexity is greater in (migratory) north temperate populations compared with those in the tropics (Catchpole, 1980; Collins et al., 2009), we conducted simple linear regressions of song metrics and latitude, limiting the sample to locations in the dataset north of the equator. Second, to address the additional specific prediction that metrics of song performance or complexity at higher latitudes in the Southern Hemisphere might converge on those in the north temperate region, we conducted both linear and quadratic regressions on the complete dataset encompassing locations at all latitudes. If this latter prediction is supported, we would expect to find patterns of latitudinal variation in song complexity better explained by quadratic than linear equations. Statistical analyses were conducted using SPSS (v. 23). Because our analyses involved multiple individual regression tests (n=48), we applied a Bonferroni correction to adjust the standard family-wide α-level of 0.05 for multiple comparisons (0.05/ 48). This yielded an adjusted α of 0.001 for evaluating the statistical significance of individual tests.

4.3. Results

Summary descriptive statistics for the entire song sample are presented in Table 4.1, as are the results of analyses of latitudinal variation in each of the measured song metrics. Across the entire sampled range, the mean (±s.d.) duration of House Wren songs was 2.18 s (±0.58 s), with the introduction section (1.13±0.50 s) slightly longer than the terminal section (1.09±0.41 s). Songs contained an average of 26.71 elements (±8.94), with a greater proportion contained in the relatively shorter terminal section (16.54±6.86 elements) compared with the longer introduction section (10.64±5.61 elements). Consequently, elements were also generally produced at faster rates in the terminal section of songs (15.72±5.26 elements s^{-1}) compared with the introduction section (9.78±4.16 elements s^{-1}).

In our first set of regression analyses, limited to song variation among populations only in the Northern Hemisphere (i.e. 0^0–52^0 N), there were significant positive relationships between song performance or complexity and latitude for most (12 of 16) of the measured variables (see Table 4.1 for detailed statistics). For some, the relationships were clear and relatively strong ($R^2 > 0.20$). This was the case for the number of elements (Figure 4.3) and the element production rate (Figure 4.4) across the entire song, as well as in just the terminal section of songs (Figure 4.5): songs contained more elements, delivered at faster rates in northern latitudes compared with the tropics. For other metrics, there were also significant positive relationships, but they were not as strong ($R^2 <0.20$). This was the case for the number of elements and the element production rate in the introduction section of songs; the number of unique elements in the terminal section of songs and their rate of production; and the number of trills and the rate of trill production. In each of these cases, the number and rate of production was, once again, greater in northern latitudes compared with the tropics but the differences were less dramatic. There were also significant but weak relationships for the minimum and maximum frequency of elements in the terminal section of songs, the frequency of both being higher at northern latitudes compared with the tropics. There was no significant effect of latitude on the overall duration of songs or the duration of either the introduction or terminal sections. Nor was there an effect of latitude on the frequency bandwidth of elements in the terminal section.

In the second set of analyses, encompassing the full range of latitudinal variation, the patterns were a bit different. Here, there were significant linear relationships for only a few metrics (6 of 16). These were the number of unique elements in the terminal section of songs; the rate of element production in the terminal section of songs; the duration of both the introduction and terminal sections of songs; and the maximum frequency and bandwidth of elements. In each case, however, the relationships were relatively weak ($R^2 < 0.10$).

By contrast, there were significant quadratic relationships for almost all song metrics (14 of 16). In fact, only two song metrics did not vary significantly with latitude in this analysis, namely the overall duration of songs and the minimum frequency of elements (Table 4.1). For all other metrics, there was a significant U-shaped effect of latitude on song patterns, with convergence observed between populations at higher latitudes in the two hemispheres, sometimes strongly so. For example, the overall number of elements (Figure 4.3) and rate of element production (Figure 4.4), as well as the rate of element production in the terminal section of songs (Figure 4.5), varied strongly with latitude: songs contained more elements produced at faster rates in populations at the latitudinal extremes in both hemispheres compared with those occupying sub-tropical and tropical latitudes. Similarly U-shaped functions, with convergence in parameters in populations closer to the poles, were observed for all remaining song metrics, although the strengths of the relationships were generally weaker (Table 4.1).

4.4. Discussion

Our results confirm transcontinental latitudinal variation in several basic metrics of song performance and complexity within a single species, the House Wren. Most previous studies of latitudinal variation in song patterns have been based on comparisons between species occupying different latitudinal zones (Cardoso et al., 2012; Greig et al., 2013; Lawson & Weir, 2014; Weir & Wheatcroft, 2011; Weir et al., 2012). Relatively few studies have focused on a single species, and in these cases, the species' distribution has tended to be fairly limited in extent, lying entirely within the north temperate zone, or being distributed from tropical to temperate zones, primarily in the Northern Hemisphere (Collins et al., 2009; Irwin, 2000; Kroodsma, 1985; Singh & Price, 2015). Hence, ours is one of the first systematic reports of transcontinental variation in song characters for a single species, spanning more than 100^0 of latitude and encompassing the temperate and tropical zones of both the Northern and Southern Hemispheres (cf. Sosa-López & Mennill, 2014).

We found that several very basic characteristics of song showed continuous variation across both Northern and Southern Hemispheres. The strongest relationships were observed for the overall number of elements in the song and in the rate of element production. Both showed strong correlations with latitude, decreasing towards the equator and increasing towards the poles. Song length did not vary significantly with latitude but remained similar across the entire distributional range. Hence, male House Wrens at higher latitudes in both hemispheres produced more song elements per song, not by extending song length but by singing at increased rates. Several other song characteristics, including the number of trills, trill production rate and the number of unique element types in the terminal section of songs, showed a similar pattern of increasing number or rate towards the poles. These patterns are broadly similar to those reported in another recent, continent-wide study of the House Wren complex, confirming the phenomenon of latitudinal gradients in multiple components of song structure and organization across very broad geographical scales (Sosa-López & Mennill, 2014). Collectively, these patterns indicate that the songs of tropical populations may be simpler in a number of very fundamental respects compared with those in north and south temperate populations, and that songs can become increasingly elaborated towards the poles in both hemispheres.

There are a number of hypotheses proposed to account for latitudinal effects on song complexity (Singh & Price, 2015). One predominant hypothesis is that metrics of song performance and complexity reflect variation in the intensity of sexual selection, including intra-sexual competition among males in the establishment and maintenance of breeding territories, and inter-sexual mate choice by females (Catchpole, 1980; Collins et al., 2009). These functional pressures on song are proposed to be exaggerated in migratory populations, or populations occupying strongly seasonal environments at higher latitudes, because of the annual requirement for territory establishment and mate selection and the necessarily shorter time windows available, which together place increased pressure on song to mediate both processes.

Our findings are consistent with this hypothesis in showing strong positive relationships between latitude and almost all song metrics for populations distributed from equatorial regions to higher latitudes in the Northern Hemisphere, as previously hypothesized and reported for some other species (Botero et al., 2009; Catchpole, 1987; Collins et al., 2009; Weir & Wheatcroft, 2011). Furthermore, we documented convergence in these patterns in the Southern Hemisphere. This latter finding is relatively novel in the animal signaling literature, but it is fully anticipated by the original hypothesis in as much as populations at higher latitudes in the Southern Hemisphere face strongly seasonal environments convergent in many respects (e.g. temperature, day length) with those in the Northern Hemisphere and hence might be expected to show similarly elaborated song patterns.

The role of migration, by itself, in accounting for song pattern convergence across the two hemispheres is unclear. Populations of House Wrens in the north temperate zone are highly migratory, while populations in the tropics and subtropical zones of the Southern Hemisphere are sedentary (dos Santos et al., 2015; Johnson, 2014; Llambias, 2009). However, the migratory status of House Wren populations at more extreme southern latitudes (40^0 S–54^0 S) is unclear (Ippi et al., 2012; Johnson, 2014). There are some reports that birds in the extreme south may be resident year around (Bernath, 1965; Jaramillo et al., 2003). However, there are no systematic studies of the species in these regions to confirm such reports. At the same time, there are reports that House Wrens in Patagonia and Tierra del Fuego are migratory (P. Llambias 2015, personal communication). Ultimately, it may prove difficult to separate the effects of migratory behaviour and shorter breeding seasons, as the two factors are often coincident. Nevertheless, more focused research on the migratory status of House Wren populations at higher latitudes in South America might provide further insights.

One alternative hypothesis for latitudinal variation in song complexity concerns the effects that variable habitat characteristics have on the transmission of acoustic signals (Wiley, 2006; Wiley & Richards, 1978). Habitat effects can be quite complicated, making it difficult to develop clear predictions for a particular species. However, in general, forest habitats in the tropics have higher tree and foliage densities that impede signal propagation compared with many temperate forests at higher latitudes which can be comparatively open. Animals of many types have adapted signal patterns that minimize signal degradation to facilitate transmission in these broadly different habitat types (Morton, 1975; Weir et al., 2012; Wiley, 1991), and some of the latitudinal effects observed in our sample of House Wren songs (e.g. songs containing fewer elements and produced at slower rates in tropical populations) might appear consistent with such habitat-based adaptations. However, House Wrens do not generally occupy forest interiors but instead are specifically noted to avoid such locations and to show a very strong preference for more open and edge type habitats wherever they occur (Finch, 1989; Johnson, 2014). Hence, despite representing an exceptionally wide geographical range, it is unlikely that the House Wren populations studied would have occupied qualitatively different habitats of the sort required to generate the different song patterns observed for environmental reasons alone.

Another important alternative is that some of the observed patterns of song variation could be traceable to basic morphological differences across the Americas as other recent analyses have identified a similarly U-shaped latitudinal gradient in overall body and beak size in the House Wren complex, with both characteristics being larger in the tropics and decreasing towards the poles (Sosa-López & Mennill, 2014). Larger-bodied individuals with larger and more robust beaks might be expected to produce longer, lower-frequency songs due to size-related effects on lung volume, syrinx size and beak gape effects on the transfer function of the vocal tract (Huber & Podos, 2006; Nowicki, 1987; Ryan & Brenowitz, 1985; Westneat et al., 1993). Beak size might also influence additional metrics of song performance and complexity such as trill rate and bandwidth given inherent motor constraints on the capacity for rapid modification of beak gape (Podos, 1997; Podos & Nowicki, 2004). The latter relationships, in particular, are consistent with our finding of faster trill rates in populations of House Wrens with smaller bodies and beaks at temperate and higher latitudes in both hemispheres compared with the tropics. However, the expected effects of body and beak size variation are not consistent with the patterns observed for either song duration or minimum frequency, which were not either longer or lower among larger bodied tropical populations as would be predicted but rather were consistent across the entire latitudinal range.

At the same time, variation in body and beak size alone cannot account for the other latitudinal song patterns observed such as the number of elements, unique elements and trills that songs contained. Indeed, the effects of variable beak morphology on metrics of song performance and complexity are not yet fully understood with different studies yielding sometimes mixed results. For example, some studies have found clear effects of beak size on performance metrics such as trill rate and vocal deviation (Huber & Podos, 2006; Podos, 2001), whereas other studies have not (Ballentine et al., 2004; Slabbekoorn & Smith, 2000). Further, in some cases, the reported effects run counter to the patterns observed here for House Wrens. For example, among European Reed Buntings -*Emberiza schoeniclus* (Matessi et al., 2000), populations with longer and more curved beaks are reported to produce songs with greater syllable diversity, while in House Wrens, the larger-beaked tropical populations were characterized by reduced syllable diversity.

It may also be the case that the influence of variable beak morphology on song performance is more relevant for some species than others. For example, in species with large repertoires of syllables and songs, motor performance limits might not be equally tested by all syllable and song types (Huber & Podos, 2006). In such cases, broad summary evaluations of performance and morphology may fail to identify relationships. Indeed, House Wrens are a species noted for having extremely large song repertoires (dos Santos et al., 2015; Kroodsma, 1977; Rendall & Kaluthota, 2013), and recent tests of frequency- bandwidth : trill-rate performance trade-offs in songs of northern House Wrens (*T. aedon aedon*) have failed to find clear correlations with standard metrics of male quality or breeding success (Cramer, 2012; Cramer, 2013).

Taken together, the patterns of latitudinal variation in song performance and complexity observed in House Wren populations across the Americas align well with hypothesized pressures based on variable sexual selection (Catchpole, 1987; Collins et al., 2009). Nevertheless, other factors, such as those related to variable body size and beak morphology, are almost certainly at play, and they might serve either to reinforce or potentially to counter effects related to sexual selection pressures. At the same time, it is clear that we studied only a small number of the most basic elements of song structure and organization and that we lacked detailed information on many additional relevant social, ecological and life-history factors (e.g. migration status, absolute length of breeding season, population density) for the many populations sampled. Hence, future analyses incorporating an expanded set of song metrics (Gil & Gahr, 2002; Podos, 1997; Searcy, 1992) and a richer set of potential causal factors will surely help both to resolve the detailed patterns of latitudinal variation in song elaboration that exist for this and other broadly distributed species, and to clarify the specific selective processes shaping them.

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Table 4. 1. Summary descriptive and analytic statistics for song metrics in House Wrens.

	Mean (SD)	**Linear regression (Northern Hemisphere)**		**Linear regression (Full range)**		**Quadratic Regression (Full range)**	
		F (1,215**)**	$\mathbf{R^2}$	**F (**1,356**)**	$\mathbf{R^2}$	**F (**2,355**)**	$\mathbf{R^2}$
Number of elements	26.71 (8.94)	75.81*	0.261	0.0	0.0	60.92*	0.256
No. elements in introduction	10.64 (5.61)	20.92*[a]	0.093	8.16[b]	0.023	32.30*[c]	0.160
No. elements in terminal section	16.54 (6.86)	54.88*	0.203	6.95	0.019	32.24*	0.154
Element production rate	12.52 (3.49)	121.35*	0.361	0.36	0.001	67.49*	0.275
Element production rate – Introduction	9.78 (4.16)	24.48*[a]	0.107	0.5[b]	0.001	17.80*[c]	0.095
Element production rate – Terminal Section	15.72 (5.26)	85.47*	0.284	16.25*	0.044	61.38*	0.257
Number of unique elements	5.69 (2.43)	43.13*	0.167	19.52*	0.052	24.53*	0.121
Unique element production rate	5.54 (2.34)	37.29*	0.148	0.24	0.001	13.75*	0.072
Number of trills	2.05 (1.17)	21.80*	0.092	0.23	0.001	26.75*	0.131
Trill production rate	0.94 (0.48)	21.93*	0.093	0.02	0.0	23.49*	0.117
Minimum frequency (kHz)	1584 (356)	13.88*	0.061	0.01	0.0	2.35	0.013
Maximum frequency (kHz)	7398 (1220)	12.36*	0.054	28.37*	0.074	16.29*	0.084
Bandwidth (kHz)	5814 (1268)	4.95	0.022	25.95*	0.068	13.80*	0.072
Song duration (s)	2.18 (0.58)	0.04	0.0	0.21	0.001	0.90	0.005
Duration –Introduction (s)	1.13 (0.50)	0.14[a]	0.001	11.11*[b]	0.032	6.93*[c]	0.039
Duration- Terminal section (s)	1.09 (0.41)	0.42	0.002	29.95*	0.078	15.01*	0.078

[a] df= (1,205), [b] df= (1,340), [c] df= (2,339),

* p=<0.001 (threshold reflecting Bonferroni correction).

Figure 4. 1. Map of the Americas indicating the provenance of House Wren song recordings used in this study (n = 281 locations).

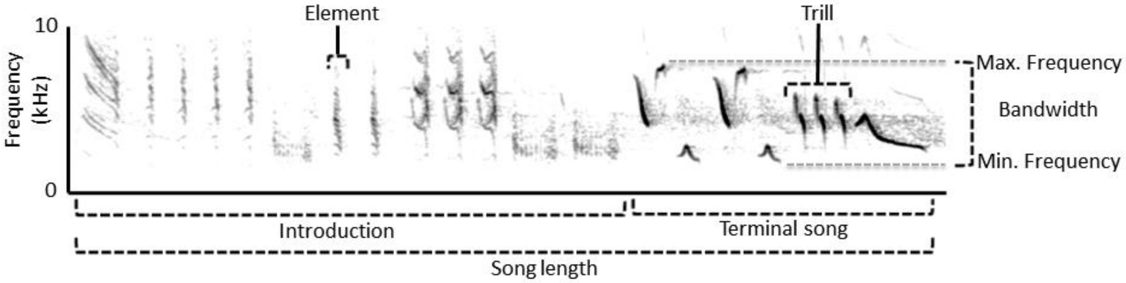

Figure 4. 2. Spectrogram of a typical House Wren song illustrating the division into an introduction and terminal section and the features of each section used as metrics in this study.

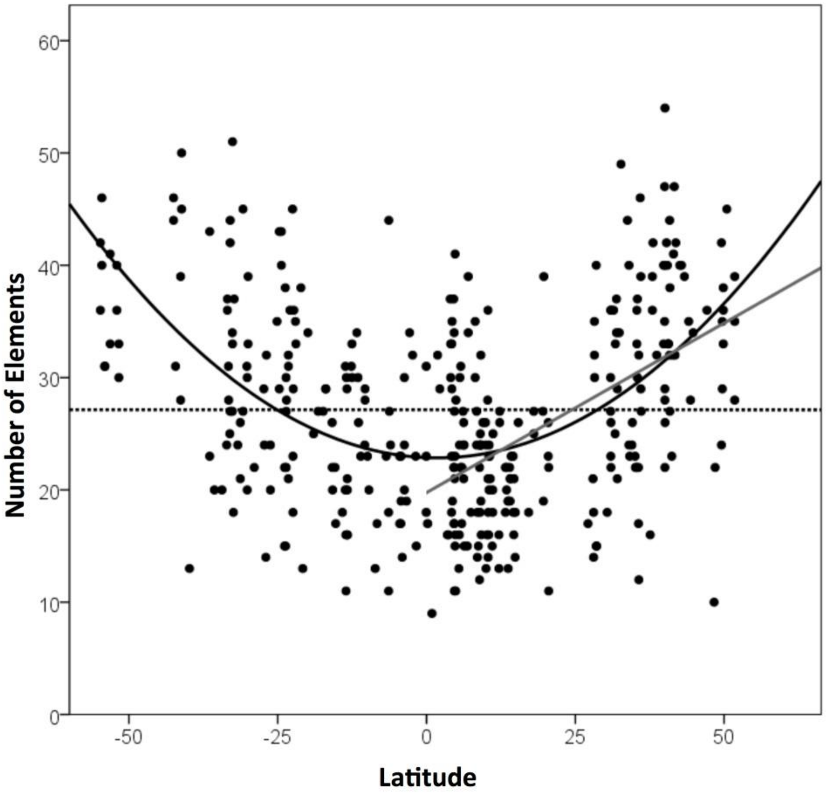

Figure 4. 3. The relationship between latitude and the total number of elements contained in House Wren songs. The solid grey line represents the significant positive relationship between the two variables for sample locations in the Northern Hemisphere (0^0–52^0 N: $F_{1,215} = 75.81$, $p > 0.001$, $R^2 = 0.261$), while the dotted and solid black lines represent, respectively, the non-significant linear relationship and the significant quadratic relationship ($F_{2,355} = 60.92$, $p > 0.001$, $R^2 = 0.256$) between the two variables for sample locations across both hemispheres (55^0 S–52^0 N).

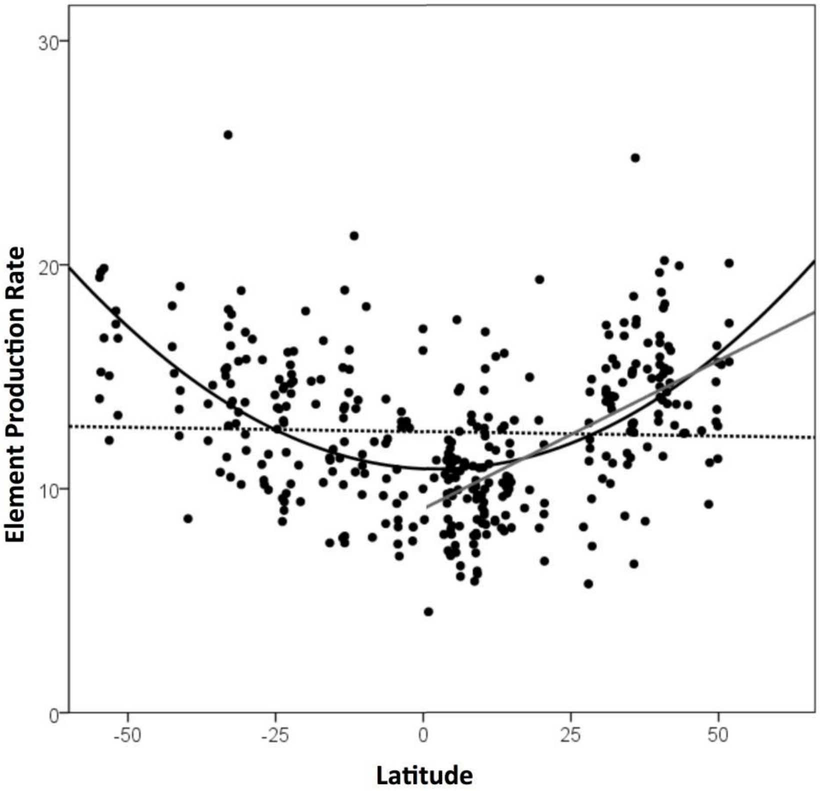

Figure 4. 4. The relationship between latitude and the rate at which elements are produced in House Wren songs. The solid grey line represents the significant positive relationship between the two variables for sample locations in the Northern Hemisphere (0^0–52^0 N: $F_{1,215} = 121.35$, $p > 0.001$, $R^2 = 0.361$), while the dotted and solid black lines represent, respectively, the non-significant linear relationship and the significant quadratic relationship ($F_{2,355} = 67.49$, $p > 0.001$, $R^2 = 0.275$) between the two variables for sample locations across both hemispheres (55^0 S–52^0 N).

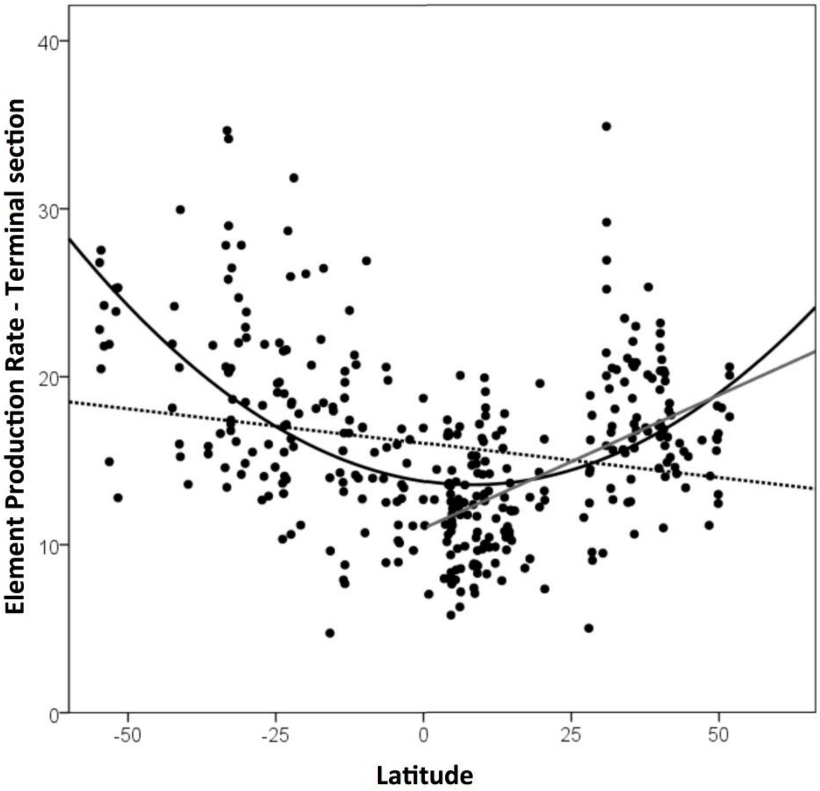

Figure 4. 5. The relationship between latitude and the rate at which elements are produced in the terminal section of House Wren songs. The solid grey line represents the significant positive relationship between the two variables for sample locations in the Northern Hemisphere (0^0–52^0 N: $F_{1,215} = 85.47$, $p > 0.001$, $R^2 = 0.284$), while the dotted and solid black lines represent, respectively, the significant but weak negative linear relationship ($F_{1,356} = 16.25$, $p > 0.001$, $R^2 = 0.044$) and the significant quadratic relationship ($F_{2,355} = 61.38$, $p >0.001$, $R^2 = 0.257$) between the two variables for sample locations across both hemispheres (55^0 S–52^0 N).

Chapter 5

General discussion, research limitations and future directions

There were three primary objectives of this thesis. The first was to characterize the natural nesting ecology of House Wrens, which to this point was known primarily from studies using artificial nest boxes. While nest box studies provide improved ability to track landmark events in the breeding cycle (e.g., egg laying, hatching and fledgling) and so provide more detailed insight into breeding phenology, it is also widely established that nest boxes represent a premium nesting environment that removes many important sources of natural variation in breeding success among males and therefore exaggerate levels of breeding success (Lambrechts et al., 2010). By extension, attempts to understand the evolved, sexually-selected pressures on male song patterns (i.e., examine potential links between song patterns and prospective breeding success) must ultimately be grounded in metrics of male breeding success obtained under natural conditions. The second objective was to characterize the organization and variability of male song, and begin to understand how it might be related to the two most common, sexually-selected pressures on song, namely male-male competition for territories and female mate choice, both of which contribute to variable breeding success. The third objective was to conduct an explicit test of the hypothesis that song variation in this species might be directly influenced by its role in mate attraction and territory defence. This test was undertaken using a very broad, transcontinental sample of song under the hypothesis that the sexually selected pressures of mate attraction and territory establishment and defence would vary latitudinally and favor increasing song complexity at higher latitudes where the breeding season is comparatively short. In what follows, a summary is provided of work supporting each of these objectives and the connections between them. Some limitations of the work and possible future directions are considered.

5.1. Natural nesting ecology

In the current study in southwestern Alberta, the overall success of House Wrens breeding in natural cavities was 52%, a level that is substantially lower than that reported for studies using artificial nest boxes and therefore confirms the value of naturalistic studies of breeding behaviour. The level of breeding success in southwest Alberta was also somewhat lower than studies of the species using natural cavities at lower latitudes, a finding that might be attributable to the additional challenges of breeding at higher latitudes, in this case near the northern limit of the breeding range for the species.

It was also found that male arrival dates positively correlated with pairing dates, and that males that arrived earlier had higher breeding success compared to late arriving males. This pattern agrees well with findings from many other songbird species (Lozano et al., 1996; Mitrus et al., 2012; Møller, 1994; Velmala et al., 2015). Hence, male arrival date may serve as a fairly reliable proxy for male quality in House Wrens, as is commonly assumed for other migratory species. In addition, pairing date correlated with several characteristics of the nest cavities selected, including cavity entrance dimensions and shape, tree diameter at cavity height, and height of the cavity on the nest tree. Males that paired earlier had cavities with circular and smaller cavity entrances located closer to the ground where tree diameter was greater. In general, these characteristics appeared to reflect attempts to choose secure nests that were better protected both from competitors and from predators which represent significant threats to egg and nestling survival.

There was also a strong bias in the cardinal orientation of the cavity entrance. The majority of nest cavities used by House Wrens in this study were facing east to south directions, and breeding success was higher in east-facing cavities. The importance of nest cavity orientation has likewise been shown for many other species, especially in the northern hemisphere where microclimatic conditions and protection from adverse weather conditions are critical for egg and nestling survival (Ardia et al., 2006; Landler et al., 2014; Rendell & Robertson, 1994).

Collectively, these findings confirm the relevance of natural cavity characteristics for breeding success and thus also the importance to males of establishing territories containing cavities suitable for successful breeding. Suitable cavities are rare in nature and therefore a limiting factor, particularly for secondary cavity nesting species (Lambrechts et al., 2010; Lõhmus & Remm, 2005). As a result, competition for territories containing suitable cavities is high and possessing and protecting a good quality nest cavity could be an important indicator of male quality relevant in female mate choice.

5.2. Song organisation and variability

The work conducted here represents the first comprehensive description of song organization in House Wrens using a large sample of males and song recordings. In addition to providing a core description of general patterns of song organization as a baseline for future research, it revealed a number of patterns relevant to the potential roles played by pressures of sexual selection. For example, there was considerable variation among males in many song performance metrics, including bout length, song duration, song rate, and syllable and song complexity. Similarly there was considerable variation among males in the overall size of their song repertoires, which is a standard metric of song performance often connected to variable pressures of intra- or inter-sexual selection. Indeed, male House Wrens appeared to be capable of an unlimited variety of song types from their diverse but finite repertoire of syllable types. At the same time there were some apparent constraints on song construction, which seemed to impose some limits on the diversity of song construction. For example, some possible syllable type combinations never occurred, while others were very common, and many song types were only subtle variations on common themes, reflecting a more limited set of common song templates.

Ultimately, the style of song delivery best corresponded to the traditional category of ‘eventual’ as opposed to ‘immediate’ variety because the typical pattern of singing involved many repetitions of the same song type before switching. Furthermore, successive song types in extended bouts tended to reflect rather modest, incremental changes in syllable type contents rather than wholesale differences in their syllable constitutions. A further important, and novel, finding made in this study was that, while capable of producing several hundred different song types, individual males nevertheless focused their singing on a much smaller repertoire of song types commonly, with the many other song types in their repertoires sung only very rarely. The average repertoire of such “common song” types for individual males in the study population was quite consistent, around 25.

This juxtaposition of seemingly unlimited overall variety in song type repertoires with relatively little short term variation in singing style was characterized as “global variability with short-term monotony". This combination of variety and monotony was hypothesized to reflect a combination of the traditional pressures on song that can favor both variety and consistency in singing patterns in support of the dual functions of song in male-male competition and female mate choice. Thus, for example, song variety, and large song repertoires in particular, are commonly taken to be reliable metrics of male quality because they are thought to make greater demands on motor skill performance, and on neurocognitive systems associated with motor control and the coordination of song learning and memory (Buchanan & Catchpole, 1997; Catchpole, 1987; Nowicki et al., 1998; Peters et al., 2014). The converse is that sustained consistency in repetitive song performance has emerged as another potentially important index of male quality (Byers, 2006; Sakata & Vehrencamp, 2012; Taff et al., 2016). And both traits – i.e., variety and consistency – may be relevant in the contexts of both male-male competition and female mate choice.

It is difficult to say with any further certainty at this stage whether and to what degree male competition or female choice is responsible for specific details of song organization, variation and delivery in House Wrens. Certainly, the pattern of song production across the breeding season points to a clear and general role in mate attraction as males produce louder and longer bouts of song at the beginning of the breeding season while single and they sing at very high rates when a prospecting female visits the male's territory and inspects cavities. Once paired, males dramatically reduce their rate of singing and song volume is also low when they do sing, especially during the incubation period when the female remains inside the cavity. These 'soft songs'(whispering songs) are hypothesized to function in other ways to coordinate male-female behaviour (Johnson

& Kermott, 1991). Males often resume high rates of singing later in the breeding season, either late in the incubation period or when chicks fledge, and their behaviour at this time mirrors their courtship activity at the beginning of the season. Hence, song at this stage appears very clearly to reflect attempts to attract a second mate.

However, because male House Wrens song delivery involves serial repetition of song types rather than rapid song type switching, it does not allow prospecting females at the beginning of the breeding season to assess their full song repertoires in a short time window. As a result, short-term evaluation of male song performance by prospecting females may be based instead on song consistency, rather than variety. In this respect, it is possible that the “common song types” males produce in much larger numbers represent a subset of the repertoire that is the target of exactly this form of assessment by females.

However, these possibilities leave unexplained why males produce much larger overall repertoires of song types. To fully appreciate that level of song variety would require much longer periods of assessment. Perhaps assessment at this level is made by females that are already paired and settled and thus reflects ongoing efforts by males (and females) to obtain extra-pair copulations. Previous work confirms appreciable levels of extra-pair mating in House Wrens, with 27-40% of nests involving at least one egg sired by an extra-pair male (Soukup & Thompson, 1997), and, on average 28% of eggs in a clutch sired in this way (Scott Johnson et al., 2009). While extra-pair matings cannot be confirmed in the study population, the behaviour of both males and females was consistent with this activity. Males were observed commonly leaving their territories and intruding on those of others throughout the breeding season (Johnson & Kermott, 1989).

Females were also observed roaming widely on neighboring territories, sometimes a considerable distance from their own ‘home’ territory, particularly early in the breeding season. Both activities are consistent with attempts to obtain additional matings outside the pair-relationship. It is also the case that the interval between pairing and egg-laying was longer early in the season compared to later in the season. So, it is at least possible that females, already paired with a male, might nevertheless delay laying in order to prospect for extra-pair copulations from (better quality) neighboring males, and that such assessment might be made based on more protracted evaluation of global song variety.

It is also possible that the female’s interest in extra-pair copulations, mediated through evaluation of the singing of neighboring males, plays a role in their original selection of nest sites. For example, females might prefer nest sites located toward the periphery of a male’s territory because this specifically allows better monitoring of the long-term singing variety of neighbor males. Nest sites on the periphery could also facilitate visiting and mating with such neighbor males without detection by the resident male. The focus in this work was on ecological factors affecting nest site selection; however, it is certainly possible that functional pressures related to female evaluation of singing behaviour, not just of their social partner but of other males in the community, can also influence decisions about the location of a nest site.

Taken together, a variety of aspects of male behaviour and singing, points to a suggested role of female choice in influencing. It is less clear exactly how this pressure determines any more detailed patterns of song variety and delivery and future work could profitably explore the question further in two parallel ways: first, through more detailed analysis of the relationship between song and male quality metrics, and second, through complementary perceptual studies of female responsiveness to particular features of song organization and delivery. Both are common methods for testing the role of female choice on male song and are natural next steps to undertake for House Wrens.

How and to what degree male-male competition influences song patterns in House Wrens is even more difficult to assess. Males do at times sing at high rates and amplitude during obvious territorial encounters with neighboring males. These interactions tend to occur early in the season when males are prospecting for and establishing territories, and so are consistent with a role in male-male competition. However, these interactions are relatively rare and are generally limited to this very early period in the breeding season. Once territories are established such encounters are quite rare, unless the nest trees of neighbors happen to be situated near a common boundary and thus very close together. Later in the season, males will intrude on neighbor territories but generally do so entirely silently. And detection by the resident male tends not to involve singing but rather simply a quick chase and possible scuffle. It is possible that the pattern of continuous singing early in the breeding season could be effective in territory maintenance, but, as outlined above, many of the features of singing at this time appear more consistent with a role in mate attraction.

It is also the case that there were very high rates of syllable sharing among all males in the population but very low rates of song type sharing, a pattern also noted in a previous short study by Platt and Ficken (1987). This lack of song type sharing, in particular, is not consistent with a role in male-male competition, at least in so far as that process is, for many species, believed to involve a process of song matching, wherein neighboring males escalate or de-escalate territorial aggression, respectively, by flexibly producing songs that either match or do not match songs recently produced by a neighbor (Logue & Forstmeier, 2008; Vehrencamp, 2001). Such mediation of territorial encounters through song matching seems unlikely then among House Wrens given the very low levels of song sharing observed. If the criterion for sharing were relaxed from the requirement of matching the entire syllable type constitution of songs to only a portion of them, then the capacity for some degree of 'song matching' in support of territory mediation may be possible in House Wrens. A much more focused investigation on song sharing and, in particular, on the real-time song-type production dynamics among neighboring males would help to adjudicate the role of male-male competition in influencing song organization and delivery in House Wrens.

5.3. Latitudinal variation in song performance and complexity

The final component of the thesis involved a study of latitudinal variation in basic metrics of song performance and complexity for House Wren populations distributed across the Americas. The objective was to provide an explicit test of the hypothesis that song variation in this species might be directly influenced by its role in mate attraction and territory defence. The preceding work did not allow definitive conclusions concerning the role of either pressure on patterns of song organization and delivery in House Wrens. It would certainly be possible to pursue the questions further in a variety of ways including: more focused analyses of the relationship between song metrics and metrics of male quality; complementary studies of female responsiveness to different elements of the organization and variety or consistency of male song; and detailed study of song patterning in the context of clear competitive interactions between males.

However, given the species exceptionally broad distribution and the emerging emphasis on broad-scale latitudinal variation in sexual selection, it was possible to provide an additional global test of the potential role of either or both pressures of female mate choice and male-male competition on House Wren song by evaluating elements of song performance and complexity across the species range.

This test was undertaken then using a very broad, transcontinental sample of song under the hypothesis that the sexually selected pressures of mate attraction and territory establishment and defence would vary latitudinally and favor increasing song complexity at higher latitudes where the breeding season is comparatively short. This work revealed a very interesting pattern of song variation not previously reported in any songbird species. Metrics of song performance and complexity increased towards the poles in both northern and southern hemispheres, while tropical populations showed lower complexity and performance levels. In other words, metrics of higher song performance and complexity converged at higher latitudes in both hemispheres suggesting convergence in corresponding pressures of sexual selection in both regions. To this point, within species latitudinal variation in complexity has been observed primarily only within the northern hemisphere, and over much smaller latitudinal ranges (Collins et al., 2009; Singh & Price, 2015). Similarly, analysis of variable song complexity across species has reported increased complexity at higher latitudes (Weir & Wheatcroft, 2011), but again primarily in the northern and not southern hemisphere and not across both.

The pattern of hemispheric variation and convergence in song patterns could be attributable to a variety of factors beyond those directly related to sexual selection, including ecological variation associated with broad-scale differences in habitats occupied by birds in different regions and their differential effects on song transmission; or to similarly broad scale variation in body and or beak size and shape and the differential constraints they impose on details of song production. However, on balance, the evidence is consistent with a role for sexual selection where the pressures associated with both territorial establishment and female choice of mates may be exaggerated at higher latitudes due to the necessarily truncated time window available for breeding compared to temperate and tropical regions. At higher latitudes males may face greater pressure to establish territories and obtain mates to complete the breeding cycle in a short period which in turn places a premium on song to mediate both processes. Here again it is not really possible to delineate which of the two processes of male competition or female mate choice may have the greater influence on the song patterns observed. The results do nevertheless serve to support the more general thesis, outlined throughout this dissertation, that one or other, or both, processes of sexual selection have likely been important in shaping patterns of song organization and variability in House Wrens.

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