THE ORGANIZATION AND VARIABILITY OF SONG

IN NORTHERN HOUSE WRENS

(*Troglodytes aedon parkmanii*)

CHINTHAKA DHANYAKUMARA KALUTHOTA

B.Sc., Sabaragamuwa University of Sri Lanka, 2000

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Abstract

Hypothesized functions of complex song in birds include a role in mate attraction and territory defense and, through regional dialects, in genetic substructuring of populations and speciation. The necessary first step in testing such functions is a detailed characterization of song organization and variability. This is provided for the Northern House Wren (*Troglodytes aedon*), a species noted for complex song, but lacking detailed descriptions. The species was studied at two sites in Alberta with a sample of 15,000 songs from 15 males. Males sang in long bouts, each song composed of multiple syllable types and repeated many times before switching. The population repertoire of 27 syllables was almost entirely shared, but used to construct novel repertoires of up to 200 different song types for individual males without evidence of a ceiling. Additional flexibility and constraints in song construction are discussed in view of the above noted functions of song complexity.

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Chapter 1

An Introduction to the Mechanistic, Functional and Evolutionary Significance of

Variability in Bird Song

Bird song is a remarkable natural phenomenon. The diversity of bird species and the seemingly limitless variety of songs they produce has attracted popular attention for centuries. Birds have also attracted the attention of scientists who are interested to know how the diversity of species that exist and the variability of the songs they sing might be related to one another.

The puzzle exists at multiple levels because the diversity of species and the variability of song both exist at multiple levels. Thus, there are many different varieties of birds, defined biologically as species. But, even within such biologically defined species, there also exists considerable diversity. For example, there can be considerable variation in the size, plumage and behavior patterns of different populations of the same species separated geographically, and even within populations there can be substantial variation in these traits among individuals (Catchpole and Slater 2008). Similarly, there is tremendous variation in song patterns both among and within species. Most species sing a song that is distinct from other species, particularly other species that live in the same area, and indeed part of this variation almost certainly marks species identity for purposes of mate recognition. So, each species has, in some sense, its own characteristic or species-specific song. Some of these are relatively simple (e.g. Chipping Sparrow, *Spizella passerina*), while others are far more complex (e.g. Superb Lyrebird, *Menura*

novaehollandiae). Hence, there is considerable variation in song among species.

However, there can also be considerable variation in song within species, variation that

once again exists among populations of the same species separated geographically as well

as variation within populations in song produced by different individuals (Marler and

Tamura 1964). Stable geographic differences in song are often referred to as dialects

analogous to geographic variation in human languages and may arise through similar

processes (see below). Variation among individuals within populations represents another

very important source of variation that is likely associated with critical behavioral tasks,

such as attracting mates and defending territories from rivals.

Research on the diversity of bird species and on the diversity of songs they

produce are conceptually linked in large part because song in many species mediates

breeding behavior with direct implications for the evolution of species. Hence, there is

good reason to think that song diversity and species diversity are causally related. Exactly

how the two are related and how song variation arises and persists remain unclear for

many species, but there are a variety of general factors to consider.

1.1 General Functions of Bird Song in Mate Attraction and Territory Defense

A growing literature provides many examples of how song functions in mate

attraction and mate choice. For example, based on a study of the House Wren

(*Troglodytes aedon*), Johnson and Searcy (1996) showed not only that females were

attracted to male song, but also that females competed for access to the nest boxes from

which male songs were being broadcast. Thus, there were significantly higher rates of

female visitation to next boxes where male songs were being broadcast compared to control nest boxes where song was not broadcast. Johnson and Searcy (1996) further observed that many of the females attracted to nest boxes broadcasting song showed additional signs of settling at the territory, for example, by starting to build nests or staying for prolonged periods around the nest boxes, even though no male was present. This is an especially clear demonstration of the role that song, by itself, can play in mate attraction. Additional evidence in support of the mate attraction function of song has been obtained in numerous other species (see below).

Similarly, numerous studies have been conducted to study the function of bird songs in territory defense. For example, based on a study of Ochre-bellied Flycatchers (*Mionectes oleaginous*), Westcott (1992) showed that males that were experimentally muted either lost their territory or had it shrink in size during the experimental period. He also noted that intrusions on the territories of muted males by other males increased 22-fold during the experimental period. Many studies of other species, including Red-winged Blackbirds (*Agelaius phoeniceus*) (Peek 1972) and Scott's Seaside Sparrow (*Ammodramus maritimus*) (McDonald 1989) have shown similar effects of songs on territory defense.

At the same time, there are a range of other potential functions of bird song including, for example, the recognition of species, mates, kin and even specific individuals, all of which can play additional important roles in the social behavior of birds (Catchpole and Slater 2008). Songs can potentially also provide cues to the

birthplace, or natal area, of a singer or signal its resident status in a local population, when songs are learned prior to natal dispersal (Kroodsma and Byers 1991). Finally, song may play a more subtle role in coordinating the behavior of mated pairs as they move about their shared territory and share in the care and provisioning of young (Johnson and Kermott 1991a).

Collectively, a variety of basic social functions of song are fairly widely supported and endorsed. However, what is much less clear is why there can be such tremendous diversity in the variety and complexity of song patterns within and between species.

1.2 Song Variability

One factor strongly implicated in the generation of variable song patterns is the role of learning in the acquisition of song. Learned song occurs in only three of the 28 avian orders, namely the Psittaciformes (parrots), the Apodiformes (hummingbirds) and the Passeriformes (songbirds). In general, species in these orders have more variable and complex songs than those in all other orders which have relatively simple songs, or vocalizations, that are not learned. Hence, the fact of learning a singing pattern seems to entail greater potential for variability (discussed further below). However, even among species where song is learned, there can be considerable variation in the complexity of song. For example, some oscine birds like the Chipping Sparrow have relatively simple songs in which males sing a single song composed of a simple, one-note trill. In contrast, many other species of oscine songbirds are able to produce many different songs that are

often highly variable and complex, including especially the Wrens (Troglodytidae), Thrushes (Turdidae), Mockingbirds (Mimidae), Larks (Alaudidae) and Starlings (Sturnidae).

This variability in learned songs can occur at multiple levels. The most basic level of song variation occurs at the level of notes, where notes are defined as a single continuous trace in spectrogram representations of the acoustic signal, corresponding to a single concerted expiration of air from the song production organ (the syrinx). Notes, in turn, are the building blocks of syllables, which are defined on analogy to the phonemes of language as consistent clusters of associated notes, ranging from a single note (like the letter 'a' in English which can stand alone as a word) to two or more notes that always occur together (like the letters 'ba' in English that form the prefix of words like 'baby' and 'balloon'). Syllables are considered by many authors to be analogous to phonemes of language as minimum units of production (Podos et al. 1992). The number of syllables produced by a population or species – its so-called syllable repertoire – is a common and important measure of song variability as it can, in turn, determine the range of different song types that can ultimately be formed. Thus, a larger repertoire of syllables (by comparison to a smaller one) can be recombined in more ways to create an even larger repertoire of discrete song types.

Song types are widely used as the basic units for assessing song complexity or variability (Searcy et al. 1999). Although there is no common agreement on the definition of a song type, it is most often defined as a unique sequence of syllable types (a bit like

the unique sequence of letters or phonemes in language defines different words). The number of distinct song types that are sung by an individual (or a population or species) is referred to as its song repertoire. There can be tremendous variation in song repertoire size ranging from species that sing only a single song type (a song repertoire of one), like the Ovenbird (*Seiurus aurocapilla*) or the White-crowned Sparrow (*Zonotrichia leucophrys*), to those like the Brown Thrasher (*Toxostoma rufum*) that can sing upwards of 1,500 different song types (Kroodsma and Parker 1977). Why there is such tremendous variation in song complexity across species remains a puzzle, but there are several possibilities, which are outlined below.

1.3 The Adaptive Functions of Song Variability

Krebs (1977) outlined three basic hypotheses for the functions of song variability measured by song repertoire size, namely in facilitating individual recognition, in attracting female mates and in defending territories. However, he largely discounted the role of variable song in individual recognition given that species with simple, single-song repertoires show as much evidence for individual recognition as those with large song repertoires. Hence, the capacity for individual recognition cannot reside in song variability *per se*. Therefore, he focused more on the latter two hypotheses for song variability, an emphasis which has continued to the present.

1.3.1 The Role of Song Variability in Mate Attraction

In the years since Krebs (1977) classic paper, a variety of studies have been conducted to test the effects of song variability in female mate attraction and male mating

success. For example, studying Song Sparrows (*Melospiza melodia*), Searcy and Marler (1984) showed that females performed more copulation displays in response to experimental playbacks simulating larger compared to smaller song repertoires. Buchanan and Catchpole (1997) showed that male Sedge Warblers (*Acrocephalus schoenobaenus*) with larger song repertoires acquired a mate earlier in the mating season than males with smaller song repertoires. Likewise, Mountjoy and Lemon (1996) found that male European Starlings (*Sturnus vulgaris*) with larger song repertoires attracted females earlier in the breeding season, even when they controlled for potential variation in the condition of nest boxes possessed by different males.

Studying Great Reed-warblers (*Acrocephalus arundinaceus*), Hasselquist (1998) found a correlation between larger song repertoires and higher polygyny rates. Males with larger song repertoires obtained more female mates. He also found that, in general, older males have larger song repertoires than younger males and, hence, that the female preference for larger song repertoires may, in part, be a preference for older males. At the same time, though, he showed that females were attracted to neighboring males with larger repertoires to obtain extra-pair fertilizations. Because neighboring males were providing no direct benefits in these cases, this female preference strongly suggests that larger song repertoires may be preferred in part because they indicate older males that make better mates. It is also possible that they indicate some inherent quality difference among males that is beneficial to females even when the male provides nothing further. In support of the latter possibility, it was found that survival was higher for fledglings born from extra pair fertilizations when the father had a larger song repertoire. These

fledglings received nothing from their fathers beyond his genetic contribution. Similarly, Reid et al. (2004) found that female Song Sparrows prefer males with larger song repertoires, even though there was no correlation between male repertoire size and territory size; and Kroodsma (1977) found that, among wrens, (family Troglodytidae) species that are more polygynous also sing more complex songs.

Taken together, studies like these support the hypothesis that song variability is attractive to females and thus enhances male mating success. At the same time, however, other studies are not so supportive. For example, Krebs et al. (1978) found no mating advantage of larger song repertoires in the Great Tit (*Parus major*), possibly because in this species pairing occurs before the peak period of singing in the spring breeding season. Yasukawa et al. (1980) found female Red-winged Blackbirds preferred males with larger song repertoires. However, they suspected this outcome was an indirect effect of males with larger song repertoires competing more effectively with other males for better territories. Hence, the female preference may have been for better territory quality rather than song repertoire size *per se*. Further, while Searcy et al. (1985) found that female song sparrows preferred males with larger song repertoires, they were unable to find any correlations between song repertoire size and other indices of male quality such as age, dominance status, territory size, body size.

Irwin (1990) conducted a broad comparative study of the new world Blackbirds (subfamily Icterinae) to examine the evolution of large song repertoires in relation to mating systems and spacing patterns. She examined the relationship between song

repertoire size, mating system and territoriality in five independent clades within the subfamily and found no overall pattern for repertoire size to be associated with mating system or with territoriality. She did find that repertoire size was associated with polygyny in one group (Grackles), but not in other groups within the subfamily.

Reviewing additional studies like these, Kroodsma and Byers (1991) and Byers and Kroodsma (2009) concluded that the evidence for a mate attraction function of variable song remains surprisingly mixed. For example, they found that laboratory studies tend to confirm female preferences for larger repertoire, while the majority of field studies fail to replicate this finding. They noted that studies of some species provided both positive and negative evidence. They further emphasized that some of the reported correlations between song complexity and male quality do not actually confirm cause-and-effect. For example, they emphasized that in some species, males actually use larger repertoires of song after pairing, rather than before. So, even if there is a correlation between repertoire size and breeding success, it is not clear that this relationship could have been evident to females when choosing their male mates. They also stress that song complexity is not the only or even most important cue females might be using, but rather that territory quality (Alatalo et al. 1986) is equally or more important. Ultimately, they concluded that the available evidence does not yet support a definitive conclusion on the evolutionary function of large song repertoires in female mate choice.

1.3.2 The Role of Song Variability in Territory Defense

The second major function proposed by Krebs (1977) for the evolution of song variability is its role in intra-sexual selection, specifically in mediating male territory competition and defense. Krebs proposed three ways this can occur. First, variable song may function in territory defense through the process of counter-singing that occurs between rival males in many species. Here, an ability to match the songs of neighbors is thought to be important in mitigating aggression (Vehrencamp 2001). If true, then males with larger song repertoires should be more effective in territorial competition because they can counter-sing with a larger number of rival male neighbors. A second possible function of song variability in territory defense could arise because variable song reduces a neighbors' ability to habituate to its distracting effects. Hence, neighbors spend more time and energy than necessary in unwarranted territorial patrol and response. Finally, a third way Krebs (1977) proposed that larger repertoires might be functional in territory defense he dubbed the Beau Geste hypothesis. Specifically, he proposed that newcomers assess suitable areas to settle based on the density of males already present. In this process, a larger song repertoire might give resident males an advantage by creating a false impression for newcomers of the density of the local neighborhood, thereby discouraging them from trying to settle there as well.

In an early experimental study of Great Tits by Krebs et al. (1978), larger repertoires proved effective in maintaining territories, by reducing the probability of intrusion by neighbors. Specifically, they found that areas from which repertoires of song were broadcast were the slowest to be invaded, while those from which single song types

were broadcast were faster to be invaded. They concluded that song is an effective 'keep out' signal for neighboring males, and that larger song repertoires are more effective in this compared to single song types. Similar results were obtained by Yasukawa (1981), who found that a larger repertoire was more effective than a single song type in discouraging intrusion by other males in the Red-winged Blackbird.

However, once again, there is evidence inconsistent with a territorial function of song variability. For example, using stuffed and live conspecific presentations, Searcy and Yasukawa (1990) found that the number of song types sung by male Red-winged Blackbirds was higher when presented with a female conspecific (i.e. a potential mate) than when presented with a male conspecific (i.e. a territorial rival). Also, the rate of song type switching was higher when presented with a female stimulus compared to a male stimulus. Hence, Searcy and Yasukawa (1990) concluded that the evidence is stronger for a function of song repertoires in this species being related to female mate attraction than to territory defense.

Similarly, Horn and Falls (1991) found that males sing shorter song bouts with less song switching during chases and boundary interactions with neighboring males than when courting females in Western Meadowlarks (*Sturnella neglecta*). Reid et al. (2004) found that, for song sparrows, males with larger song repertoires did not acquire territories earlier or obtain larger territories compared to males with smaller repertoires.

Here again, then, there is some residual uncertainty about the specific function of variable song in territory defense, or at least about how ubiquitous this function of song is across songbird species.

1.4 Song Variability and Song Learning

Some of the puzzle of song variability can be traced to the mechanistic process by which song is acquired, because much of the variability in song is thought to derive from the song learning process (Marler 1970). Most of the early studies of song learning focused on how and when birds learn their songs (e.g. Nottebohm 1968) from which developed a canonical model of song learning. In this model, young birds hear and memorize songs sung by other males in their natal community, including their father. Exposure to song during this early 'sensitive' period is critical for accurate production of species-specific song patterns in adulthood (e.g. Marler 1970, Konishi 1965). In the following spring, as adults now themselves, these young birds begin to sing and, at first, produce relatively poor versions of adult song that proceed through a series of recognized steps from sub-song, to plastic song, and finally to crystallized song that converges on faithful renditions of species-specific note and syllable structure and temporal patterns. During this process, young males often produce a wider variety of songs than they ultimately end up singing on a regular basis. This canonical model of song development is widely accepted for many species. However, later research has shown that the song learning process can also involve deviations from this model (Marler, 1997).

For example, the duration of the sensitive period can vary among species. Some species have a very restricted sensitive period early in life (e.g. Eurasian Chaffinch, *Fringilla coelebs*, Nottebohm 1968, 1969). They can acquire songs heard only during this short period and they then sing those songs for the remainder of their adult life without further changes or evidence of additional learning. Such species are referred to as 'closed learners' because their song repertoire is fixed for life (Kroodsma 1982). However, other species have a more extended period of sensitivity and more flexible learning capacities. For example, the sensitive period for Song Sparrows extends for five months into their first year (Nordby et al. 2001). Nightingales (*Luscinia megarhynchos*) can learn new songs that they hear in the spring following their birth year (Todt and Geberzahn 2003). Still other species are able to learn even later into adulthood. For example, in the Village Indigobird (*Vidua chalybeata*), males change their songs from year-to-year (Payne 1985). European Starlings appear to do the same (Mountjoy and Lemon 1995). These latter species are referred to as 'open ended learners' and, all else equal, they would seem to have a greater inherent capacity for song variability and complexity given their ability to continue to add new song variation to their repertoires throughout life. This capacity has important implications for the neurobiology of the species and brain evolution, as open-ended learners may generally have greater neuroplasticity with annual cycles of neurogenesis (Brenowitz 2008).

1.4.1 Song Learning, Local Dialects and Population Sub-structuring

An additional creative element of the song learning process involves, paradoxically, mistakes or errors in the copying process where young birds inadvertently

introduce new structural variation into the local song patterns by virtue of copying the songs of other adults with incomplete fidelity. The song learning process can introduce novel variation in more active ways as well, via innovation or improvisation of novel song patterns not present in preceding generations. By either route, variation of this kind can create local varieties of song, because songs tend to be learned locally, and thus song copying errors, innovations or improvisations occur and are perpetuated locally. The songs of different populations can then potentially diverge over time, creating what are often referred to as regional dialects, analogous to dialect differences in human languages (Marler and Tamura 1964).

It is not always possible to determine how song dialects arise and are perpetuated, and whether or not they are immediately functional (Catchpole and Slater 2008). One possibility is that dialect variation can arise and be perpetuated as a response to habitat variation. For example, if birds disperse to a new habitat, or if there is a change in their local habitat, song patterns may change to match the modified acoustic transmission profile of the environment (Marten and Marler 1977, Morton 1975, Slabbekoorn et al. 2002, Slabbekoorn and Smith 2002b, Wiley and Richards 1978, Wiley 1991). It is also possible that dialects provide some adaptive advantages. For example, females may prefer to mate with local males because their genome is better adapted to the local environment than the genome of immigrant males, and one way females might identify local males, and distinguish them from immigrant males, is based on their differing song patterns. Hence, dialects might arise and be maintained by assortative mating pressures (Podos 2010). The evidence for either of these hypotheses is mixed and it is, of course,

also possible that dialects are simply functionless byproducts of vocal learning (Catchpole and Slater 2008).

Nevertheless, by whatever route and for whatever possible functions, dialect variation may be important in evolution because song is also important in species recognition and mate choice, as reviewed already. Hence, regional differences in song likely contribute to genetic differentiation between populations, perhaps ultimately facilitating speciation. Indeed, Baker and Cunningham (1985) suggested that the song learning process and its creation of dialect variation might be an important factor accounting for the tremendous species diversity of songbirds, which is the most diverse of all bird orders.

1.4.2 Song Learning, Song Variation and Speciation

Mating signals have important taxonomic value and have been often used in the delineation of different species in several animal groups, especially insects and birds with unlearned, innate vocalization patterns (Wells and Henry 1999, Claridge 1985, Slabbekoorn and Smith 2002a, Price 1998). Indeed, many so-called cryptic species have been revealed by their distinctive signaling patterns (e.g. Lloyd 1966). This phenomenon has been studied far less commonly among birds that learn their songs. Nevertheless, there are similar examples of cryptic songbird species delineated based on their distinctive song patterns (Valderrama et al. 2007, Toews and Irwin 2008, Lara et al. 2012). There is also other evidence consistent with the possibility that learned song variation might support speciation. For example, Clayton (1990) found that female Zebra

Finch (*Taeniopygia guttata*) can differentiate male songs from two different subspecies and females preferred the songs of males of their own subspecies. Furthermore, in playback experiments with cross-fostered birds, females preferred songs of their cross-fostered fathers, irrespective of natal subspecies. These results indicate that, at least in some species, females use song characters that are learned during development to discriminate mates. Similar local dialect preferences have been obtained for populations of White-crowned Sparrows, which also show limited genetic differentiation (MacDougall-Shackleton and MacDougall-Shackleton 2001, Hernandez et al. 2009). If sustained over time, such assortative mating could support genetic divergence of local populations over time.

Additional evidence of this sort of process comes from work by Irwin (2000) who studied speciation in a ring species, the Greenish Warbler (*Phylloscopus trochiloides*). This species was historically dispersed from a common population with relatively simple songs in the Himalayas northwards to central Siberia, following two different geographical pathways. Along each pathway, adjacent populations have very similar songs, but where the two pathways converge in central Siberia, the songs are now long and complex and quite different, such that the populations do not inter-breed at their point of re-contact. Hence, it appears that mating signal divergence in allopatric populations has facilitated speciation in this group.

Documented examples like this are still relatively rare for songbirds, but some authors argue that the process of song learning, with its inherent potential for regular

introduction of novel song variation, coupled with female preferences for dialect variants, might actually accelerate the rate of speciation in songbirds (Lachlan and Servedio 2004).

1.5 Summary

The phenomenon of variable song in songbirds bears on a number of important mechanistic, functional and evolutionary issues. Variable song may arise largely through details of the song learning process, although it remains unclear whether such variation is driven primarily by mistakes in the song copying process or some more active process of innovation or improvisation. It is also unclear why such processes might be more common, or at least more commonly preserved, in some species more than others, such that some species sing relatively simple songs across wide geographic scale while others sing far more variable songs with consistent regional differentiation. Further, although there are intuitive hypotheses to account for the function of song variability in important social contexts, such as mate attraction and territory defense, the evidence to date for either function remains mixed. Finally, while it has long been mooted that variable song might facilitate speciation in songbirds and help to account for their tremendous world-wide diversity, clear cases where variable learned song is implicated in speciation are rare.

1.6 Thesis Objectives

The objective of this thesis is to provide the first characterization of song organization and variation in the Northern House Wren (*Troglodytes aedon*). The song of this species has not been studied systematically, but it has the potential to contribute to

our understanding of many of the functional, mechanistic, and evolutionary issues just reviewed. None of these issues will be targeted specifically for study in this thesis, however. Instead, the objective is simply to provide a detailed description of the singing style and patterns of song variability found in House Wrens as the necessary first step in designing and conducting more focused studies of these other issues.

1.6.1 Study Species: The Northern House Wren (*Troglodytes aedon*)

House Wrens are one of the most ubiquitous and widely distributed songbirds in the Western Hemisphere. They have the greatest latitudinal breeding range of all passerine birds, from 58^0 N of Canada to 55^0 S in Tierra del Fuego (Brewer 2001). Its resident distribution range is roughly estimated as 25.7 million square kilometers (BirdLife International 2012) and its population size is estimated as 50-100 million mature individuals and therefore categorized as `Least Concern` (LC) in the red-listing process (BirdLife International 2012).

A large part of their extensive distribution can be attributed to having very broad habitat tolerances. House Wrens live in almost every habitat type across the Americas, including tropical dry forests, temperate forests, plantations, arable lands, urban areas, etc. One subspecies, *T.a. cobbi,* is even adapted to extreme conditions in coastal habitats of Argentina where it forages among seaweeds and tidal shores and nests in tussock grasses. The House Wren's wide distribution includes wide elevation tolerance as well, ranging from sea level to about 4000 m (Kroodsma and Brewer 2005). In general, House Wrens prefer open or sparse forests and they therefore readily inhabit disturbed edge

habitats close to human settlements. The latter tolerance probably accounts for their slight or statistically insignificant population increases in the last 40 years (Butcher and Niven 2007), as natural habitats in the Americas have been altered by human expansion, urbanization and industrialization.

1.6.2 Taxonomy Uncertainties

Importantly, across this tremendous range, the number of species and subspecies of House Wrens is currently debated. Indeed, even the higher level taxonomy of the *Troglodytes* was unclear until recently. Historically, the family Troglodytidae was placed under several families such as Timalidae (Babblers and Parrotbills) and Turdidae (Thrushes), due to lack of understanding of its relationship with other groups (Kroodsma and Brewer 2005). It is now largely accepted as a cohesive monophyletic group (Kroodsma and Brewer 2005). However, relationships and placement of Troglodytidae relative to other families is still debated (Barker 2004). Also, relationships among genera within the family are still uncertain (Rice et al. 1999, Brumfield and Capparella 1996, Gomez et al. 2005).

This taxonomic uncertainty extends to relationships within the House Wren group itself. Brumfield and Capparella (1996) proposed that House Wrens distributed across the Americas comprise three species, the Northern House Wren (*Troglodytes aedon)* in North America, the Southern House Wren (*Troglodytes musculus*) in southern Central America and South America and the Brown-throated Wren (*Troglodytes brunneicollis*) in Mexico and northern Central America, a classification that contradicted the classic taxonomy of

Sibley and Monroe (1990, 1993). Gomez et al. (2005) endorses this classification. Woods (1993) proposed to elevate the Cobb's Wren subspecies of the Falklands Island (*T. a. cobbi*) to species status, while Brewer (2001) and Kroodsma and Brewer (2005) treated mainland forms *musculus*, *brunneicollis*, and other island forms *beani*, *cobbi* and *tanneri* as separate species. However, the ruling authority, the South American Classification Committee (SACC) (Remsen et al. 2012) treats all these as subspecies of *T. aedon*, until more concrete evidence of species differences is obtained. Because many of the taxonomic issues are unresolved, conventional agreement is to consider the populations in three groups (AOU 1998) that includes at least 31 subspecies across North and South Americas. It includes, the Northern House Wren populations with two subspecies, *T. aedon* and *parkmanii*, which range in Eastern and Western North America respectively. A second group, the *brunneicollis* group, has three subspecies, breeding primarily in montane habitats of Central America and Mexico. The third and largest group, the *musculus* group, contains subspecies resident from Southern Mexico to Central and South America. Brewer (2001) includes 23 subspecies under the *musculus* group, while Kroodsma and Brewer (2005) include 25 subspecies under the *musculus* group.

In short, there is considerable taxonomic uncertainty not only about the broader taxonomic association of the *Troglodytes* to other passerines, but to the species and subspecies affinity of populations within the House Wren complex in particular. The latter uncertainty reflects lack of focused study, but also the fact that, across their entire broad range, there are relatively few differences among populations of House Wrens in obvious external characters such as size, morphology and plumage. There are, however,

some basic differences in behavior and life-history. For example, Northern House Wrens are almost exclusively migratory, actively polygynous and have large clutches of 7-8 eggs, while Southern House Wrens are almost exclusively sedentary in year-round monogamous pairs and have smaller clutches of 4-5 eggs. To date, there have been no systematic studies of song in any of these populations, much less any comparative research on song variation across populations. Hence, the extent to which song variation might illuminate any of the taxonomic issues in this group is unclear.

1.6.3 Song Variability in House Wrens

The members of the family Troglodytidae are considered to be some of the finest singers among all bird species, with many wren species noted for their relatively variable and complex songs. Although the song of the House Wren has not been studied in detail, it is known casually for also having variable and complex song. Because the species is highly vocal during the breeding season, it attracts many observers. Hence, many of these descriptions are based on naturalists` accounts of the species. There are only a few studies that have tried to examine and document song organization and complexity in the species, and these were relatively short studies with small samples (Kroodsma 1977, Platt and Ficken 1987). Nevertheless, on this basis of his analysis, Kroodsma (1977) rated song complexity in the House Wren as one of the most complex of temperate wren species, second only to the Winter Wren (*Troglodytes troglodytes*).

Taken together, the House Wren is an excellent model species for studying song variability. It is a member of a family of birds (Troglodytidae) noted for complex song

and, even with this group, is thought to be one of the most complex singers. It is widely distributed with uncertain taxonomic affinities, leaving considerable potential for analyses of song to contribute to resolving species and subspecies relationships of diverse populations. Given its wide distribution and capacity for variable song, it is also well suited for studying the mechanisms by which geographic variation in songs (dialects) arise and are maintained and whether and how they contribute to geographic substructuring of populations, and ultimately possibly to speciation. Although the latter issues will not be addressed systematically in this thesis, they will be revisited and discussed again briefly in a final chapter following Chapter 2, which provides a detailed analysis of song organization and variability in two populations of Northern House Wrens studied in southwest Alberta.

Chapter 2

A Detailed Analysis of Song Organization and Variability in the Northern House

Wren

The diversity of bird species and the diversity of their songs are related themes in evolutionary research because the songs of each species are unique and because songs are important to the breeding behavior of species via their role in species recognition and mate choice. Hence, a common assumption is that the evolution of species is naturally linked to the evolution of song patterns. The critical question then becomes, how and why does such variation arise and evolve, and thereby facilitate and sustain the evolution of species?

This question has been studied thoroughly, at multiple different levels, and a variety of causal processes are implicated. For example, song is proposed to play an important role in mate attraction and in territory defense, and thus to affect the breeding dynamics of males and females alike. Variable, or complex, songs in particular are hypothesized to be functional in each of these contexts in very specific ways (e.g. Krebs 1977, Sakata & Vehrencamp 2012). Variation in song is also variously hypothesized to arise and be maintained for specific functional reasons related to local mate choice benefits, or to be simply an artifact of the song-learning process that may nevertheless be perpetuated and affect species' evolution by virtue of the way song patterns (dialects) are 'culturally' transmitted (Marler & Tamura 1965, Catchpole & Slater 2008).

As reviewed in the previous chapter, there is evidence in support of all of these causal influences on song variation, but also evidence inconsistent with them. The various evolutionary and cultural pressures involved in creating and sustaining song variation remains a central theme in evolutionary biology. The necessary first step in addressing these issues for any species is a thorough description of patterns of song organization and variability in the species. In this chapter, an attempt is made to provide a characterization of song organization and variability in the Northern House Wren (*Troglodytes aedon*), a species noted for complex song, but for which detailed characterizations of song patterns have not been undertaken. This characterization of species song is an important prerequisite to more focused studies of how variable in song arises and is sustained in this species, with potential implications for the broader evolutionary and cultural roles of variable song patterns in birds generally.

2.1 Materials and Methods

2.1.1 Study Sites

Research was conducted at two field sites in the foothills of the Rocky Mountains of southwest Alberta (Figure 2.1). One site was located in the Bob Creek Wildlands Park of the Whaleback region (Alberta Wildlife Management Unit 308) and the other was located on private lands in the Burmis-Lundbreck Corridor (Alberta WMU 302). The two sites were separated by approximately 50 km, but both were in montane habitat at approximately 1200-1400 m elevation where the vegetation is a mosaic of open grasslands punctuated by small stands of aspen (*Populus tremuloides*) and occasional Douglas fir trees (*Pseudotsuga menziesii*). In these habitats, House Wrens nest primarily

in cavities previously excavated in aspen trees by Woodpeckers, but will also utilize other natural cavities, hollows, or cracks in aspen and fir trees. The two study sites were specifically chosen for their similar montane habitat profiles to minimize the effects that variable ecologies can have on song structure (Morton 1975).

2.1.2 Study Subjects

House Wrens arrive in southern Alberta in the middle of May and males immediately begin to establish territories, identify and prepare nest cavities and sing to attract females who arrive shortly after males. Initial surveys were conducted to identify candidate males that might be suitable subjects of study because they showed signs of having committed to remaining in the area. Candidate males were then captured and marked to allow reliable individual identification. Capture and marking was conducted using standard operating procedures. Briefly, males were captured in mist nets (2 ply, 30 mm mesh) as they moved around their territory naturally. In some cases, song was played to facilitate capture. Upon capture, each male was weighed and a number of additional body measurements were taken using calipers and wing rulers (e.g., beak length, width, and depth, wing length, tarsus length, tail length). A blood sample was taken for future genetic work, and a set of four bands was then applied on each male, two bands on each leg. These included a uniquely numbered federal band applied to the left leg and three additional color bands that were applied in unique color combinations to facilitate subsequent identification at a distance, one on the left leg and two on the right leg. Birds were released immediately after this processing, which was conducted as quickly as possible (typically less than 10 minutes) to minimize stress to the bird.

2.1.3 Song Recording

Marked males were then sampled regularly for the remainder of the breeding season with a focus on recording song. To this end, males were sampled systematically at times of day and at breeding stages throughout the season when they were most actively singing. Sampling thus focused on males that were actively courting females and singing to do so and emphasized the early morning hours from around 5:30 am to noon. Recording was done in one-hour samples and an effort was made to sample each male at least twice per week. House Wren males are confident and are not disturbed by human presence. So, it was possible to approach the birds very closely (3-5 m) and thereby obtain high-quality recordings without influencing their normal behavior. Focal birds were confirmed for each sample, by identification of colored lag bands, prior to recording. Recordings were made using digital recorders (Marantz PMD 660 and 670) and shotgun microphones (Sennheiser ME67 and MKH 816). Additional data were collected on the general activities of the focal male, his female partner, and direct neighbors.

2.1.4 Song Analysis

Field recordings were transferred daily to computer for post processing. Each recording was assigned a unique file name and stored for subsequent analysis. Analysis of songs was conducted using Praat software (Boersma & Weenink 2011). The first step in analysis was to develop a catalog of all notes and syllables produced by the species. Conventional nomenclature and definitions were used, with notes defined as continuous signal traces in the song spectrogram (i.e. no gaps in the signal structure) and syllables

defined as regularly grouped combinations of notes (i.e. notes that always occurred together). In defining notes and syllables, attention was paid only to global patterns in the spectral shape of signals ignoring minor differences in frequency range – i.e. whether notes were shifted up or down in frequency. To facilitate note and syllable delineation, a different sample of 2,500 songs recorded in the previous year (2010) from a sample of 10 birds was used. Notes and syllables developed from this sample were cross-referenced and confirmed in the 2011 sample that is the focus of this work.

After establishing the note and syllable repertoire for the study populations, song analysis focused on segmenting individual songs and annotating their syllable content. Additional basic data were gathered concerning the duration of individual songs and the intervals between them. The resulting data were extracted from annotated song files and exported to a database to generate collated reports of song patterns for subsequent descriptive and analytic statistics. All statistics were performed in SPSS.

2.2 Results

2.2.1 General Features of Singing Behavior

Male House Wrens sang most vigorously early in the breeding season, immediately on arrival on the breeding grounds, as they established territories and attempted to attract a female to settle with them. At this time, males produced songs in protracted bouts that could last for 30 minutes or more of continuous singing with very short intervals between successive songs (i.e., 8-12 songs/minute and upwards of 500 songs/hour). Most males continued to sing as their female partners completed construction of the nest, but then curtailed their singing prior to egg-laying. Some males resumed singing again later, after their female mates had begun incubating eggs, possibly in an attempt to attract a second female. Some males also resumed vigorous singing later in the season after fledging chicks from their first nest, once again in an attempt to attract another female mate with which to undertake a second nest. Regardless of the breeding stage, males were most active singing in the early morning hours from just before sunrise until mid-day. Males sang much less in the afternoon, and there was no systematic resumption of singing in the evening as there can be in some other passerine species.

Males were also predictable in singing from one or a few specific locations within their territories. For most males, preferred locations were directly adjacent to the nest cavity, sometimes on a branch of the same tree next to the nest or on a branch of a neighboring tree with direct visual access to the nest cavity. Males sometimes also sang from a few other locations within their territories, at times moving to and singing near their boundaries with neighboring males.

2.2.2 Global Song Structure

In House Wrens, song can be partitioned into two very discrete sections, which are readily distinguished both by ear and by inspection of spectrograms. The first section is a rapid concatenation of low-amplitude, broadband notes that are generally either harsh (noisy) in structure or sometimes involve a harmonic series. In contrast, the second following section is composed of relatively loud, tonal, frequency-modulated notes. For this analysis, the first section is designated as the 'Introduction section' of the song and the second section is designated as the 'Main section' of the song (Figure 2.2). Canonical songs contain both sections. In the present sample of 15,608 songs, 93.53% contained both an Introduction and Main section as just described. However, there were sometimes deviations from this pattern. For example, males occasionally produced songs lacking an Introduction section. The sample contained 758 songs (4.8%) of this kind across all birds. Similarly, males sometimes produced only the Introduction section (i.e., no Main section). This was even rarer, with only 262 such songs (1.66%) recorded in this sample. Additional deviations involved cases where males produced songs containing two Main sections separated by a very brief interval. Again this was quite rare.

The Introduction section of the song, containing only low-amplitude components, is difficult to hear beyond a few meters. It is therefore unlikely to transmit any great distance and be heard and interpretable to birds even in neighboring territories. In contrast, the Main component of the song is much louder and transmits a considerable distance. It can often be heard by human listeners at more than 300 m and possibly at even greater distances by the birds themselves. Individual male territories average

approximately 50 m in diameter; hence the main portion of House Wren songs has an effective range of several territories. Given the much greater transmission capacity of the main portion of House Wren songs, further detailed analyses of song organization and variability concentrated on this section of the song.

2.2.3 General Temporal Characteristics of Song

Table 2.1 presents data on four general temporal characteristics of song, namely the total song duration, the duration of the Introduction section of the song, the duration of the Main section of the song, and the duration of the interval between successive songs in a bout.

Across all birds, mean song duration was 2.16 seconds. The Introduction section of the song was generally shorter (0.90 s) than the Main section of the song (1.32 s). The mean interval between songs was 5.82 seconds. There was considerable variation between males in each of these parameters, with some males singing longer songs and concatenating them together more rapidly (i.e., shorter intervals between songs). However, some of this variation among males might have been spurious, reflecting variation in how males sing in different breeding stages, which were not sampled entirely equally for all males. Unfortunately, the sampling regimen did not permit further analysis of consistent differences in singing patterns at different breeding stages.

Nevertheless, there were several consistent relationships among these temporal parameters. There was a strong positive correlation between duration of the Introduction

section of the song and total song duration (Pearson r=0.952, p<0.01; Figure 2.3). Likewise, there was a strong positive correlation between the duration of the Main section of the song and total song duration (Pearson r=0.875, p<0.01; Figure 2.4). These two relationships seem obvious, given that total song duration is dependent upon the duration of both the Introduction and the Main sections of the song. However, there was also a strong positive correlation between the duration of the Introduction section and the duration of the Main section (Pearson r=0.715, p<0.01) indicating that the duration of these two sections do not trade-off against one another, but rather varied in unison and mutually reinforced variation in overall song length (Figure 2.5).

At the same time, there was a significant negative relationship between total song duration and the duration of the interval between successive songs (Pearson r=-0.737, p<0.01). In other words, when males sang longer songs they also concatenated them together more rapidly, thus confirming the subjective impression in the field of increased vigor in singing (Figure 2.6).

2.2.4 Bout Size

There was considerable variation in the length of singing bouts, ranging from very short bouts composed of only a single song to very long bouts containing up to 259 songs (mean 21.6 songs/bout). Figure 2.7 provides a frequency distribution of the size of singing bouts. Once again, there was considerable variation among males (Figure 2.8), some of which also probably reflects variability in the breeding stages sampled for

different males as males tended to sing longer bouts of more closely spaced songs when actively courting females than at other stages of the breeding cycle.

2.2.5 Duty Cycle

Variation among males in singing activity is captured in an additional derivative variable, labelled 'duty cycle' which calculates the proportion of singing time actually devoted to song as follows:

Duty cycle = Sum song duration/ (sum song duration + sum interval duration)

A higher duty cycle indicates greater singing effort per unit time. The mean duty cycle for males in these populations was 0.30 (i.e., 30% active singing), with considerable variation among males (Figure 2.9) again likely attributable in part to variation in breeding stages sampled.

2.2.6 Detailed Song Structure

The Main section of House Wren song contains 1- 25 syllables (mean 10.49) as a concatenation of 1-9 different syllable types (Mean=3.88) each syllable type repeated 1-16 times (Mean=2.7) before switching to the next type. The syllable repertoire for the population is largish, with 27 different syllable types represented. Most syllables could be produced in different frequency ranges – they could be shifted upward or downward in frequency – and this depended in part on their placement within a song, as most songs showed a tendency for the frequency of syllables to decrease from beginning to end.

These different syllables were constructed of a repertoire of 22 different notes. The repertoire of notes and syllables is illustrated in Figure 2.10, and additional details of syllables, and their constituent note structures, are given in the table 2.2.

Some syllables were formed from a single note (e.g., AI, S, D), while others were comprised of the regular combination of two (AG, M, C) or three notes (F, AD). Some syllables generally only occurred at the beginning (e.g., AI, AM, BG, BH, BI, BJ) or end of songs (e.g., N), while others generally occurred in the middle (e.g., D, F, L, T). Still others were more flexible and could occur in various places (e.g., C, E, M, G, U, Z).

In general, males were all capable of producing the same syllables. The total syllable repertoire for the population was 27 syllables and the mean for individual birds was 21.6 (Figure 2.11, Table 2.3). A few birds produced substantially fewer syllables, but this probably reflected variable sampling effort that resulted in an underestimate of their full syllable repertoires. The fact that most males produced most of the syllables suggests that 27 probably represent an upper limit to the current syllable repertoire for this population.

At the same time, there was again considerable variation among males in the use of particular syllables. For example, some syllables (e.g., U) were very common, occurred in all birds, and were used frequently by all of them (Figure 2.12). In contrast, other syllables were relatively rare (e.g., BF) and were produced by only a few birds and then only rarely.

Figure 2.13 illustrates the time course over which syllable types were revealed in a male's singing behaviour. The figure illustrates that most birds revealed their full syllable repertoire within the first 300-400 songs they sang. The fact that the syllable accumulation levels off for all birds also suggests that there is a ceiling to the syllable repertoire for these populations. It is important to note, however, that there is once again considerable variation in the rate at which males revealed syllables in successive songs. Focusing on the first 200 songs recorded from each male, there were considerable differences among males in the slopes of the syllable accumulation curves, suggesting that some males more than others were singing with more syllable variety over short intervals (Figure 2.14).

2.2.7 Syllable Transition Patterns

Table 2.4 provides a matrix of all possible transitions between adjacent syllable types within the Main section of songs, where the values in individual cells in the matrix quantify the frequency of particular syllable type transitions. For this analysis, transitions to the same syllable type (i.e., repetitions of same syllable type before switching types) were ignored. The matrix clearly shows that syllable type transitions are not random. For example, some syllable type transitions were very common (e.g., AE-AD; D-E; E-F; F-G;), while others were much rarer (e.g., AE-F; D-AD; L-E), and many possible syllable type transitions never occurred at all (cell values of zero). Furthermore, some syllables could transition to one of many other syllable types. For example, syllable AG could be followed by 20 other syllable types. In contrast, other syllable types could be followed by only one or a few other syllable types. For example, syllable F could be followed by 5

other syllable types, but effectively was followed by only one (G) with any frequency. These patterns indicate extensive constraints on the variety of syllable type transitions that occur.

To further quantify syllable type transition patterns, the transition probabilities were recalculated based on the total transition universe (i.e. considering all the transitions that occurred in the sample excluding same syllable repetitions). These transition possibilities are shown per 1000 transitions in Table 2.5. This table emphasizes the extent to which only a relatively small number of all possible transitions actually occur with any frequency.

These two matrices confirm additional patterns of syllable organization noted earlier in Table 2.2, namely that some syllables (e.g., AI, S, AM, and K) occurred primarily only at the beginning of the Main section of the song, while other syllables (e.g., N, Z) tended to occur at the end of the Main section of the song. Some common syllables (e.g., G and M) could occur at almost any place in the song.

2.2.8 Basic Song Variability Measures

Table 2.6 provides additional measures of song variability for this sample. These are the number of syllables and syllable types produced per song and the ratio of syllable types to syllables in each song, the latter characterizing the general syllable diversity or versatility of songs (SVI, Song Versatility Index). The rate of production of syllables and syllable types are also given. The mean number of syllables produced in a song ranged

between 8.96 and 12.89 for different males, averaging 10.49 across all males, while the number of syllable types produced in a song ranged between 2.92 and 4.74, averaging 3.88 across males. The SVI for different males ranged between 0.32 and 0.46 and averaged 0.39 across males. Syllable production and syllable type production rates were fairly consistent across males and averaged 7.98 syllables per second and 3.12 syllable types per second, respectively.

There was a very strong positive relationship between the number of syllables produced in a song and the Main duration of the song (Pearson r=0.956, p<0.01), indicating that as males added syllables to their songs, they did not increase the rate of syllable production per se, but rather simply extended the length of their songs (Figure 2.15). In contrast, there was no relationship between the duration of the main section of the song and the number of syllable types produced (Pearson r=0.376, p=0.168) (Figure 2.16). This reveals that, as songs increased via the production of additional syllables, they did so by the repetition of the same syllable types rather than by the addition of more different types of syllables. In other words, when males sang longer songs, they tended to repeat the same syllable types rather than adding new ones. This fact is confirmed in the SVI, which shows a significant negative correlation with the duration of the Main section of the song (Pearson r= 0.634, p=0.05; Figure 2.17), indicating that, as songs got longer, the diversity of their syllable content decreased.

There was a significant positive correlation between the syllable repertoire of individual males and the mean number of syllable types contained their songs (Pearson r=

0.548, p=0.05). Birds with larger syllable repertoires sang songs containing more different syllable types (Figure 2.18). However, these relationships could also be affected in part by variation of overall sampling effort for different males and also in the particular breeding stages that were sampled for each.

There was a significant positive relationship between the size of a male's repertoire of different song types (defined below) and the size of his syllable repertoire (Figure 2.19). Males with a larger syllable repertoire also had a larger repertoire of different song types (Pearson r=0.674, p<0.01). However, once again, this relationship might be attributable in part to variation in sampling effort across males.

2.2.9 Song Types

A song type was defined as a unique sequence of syllable types, ignoring variation in the number of times particular syllable types might be repeated within a song. The only exception to this rule involved cases where the same syllable type was repeated in a song, but separated by another different syllable type, which happened only very rarely. There was considerable diversity in the song types produced by males in this population with fully 996 different song types sung in the total sample of 15,608 song recordings. There was considerable variation in song type diversity across birds, with the song type repertoire of individual males ranging from a low of 38 different song types to a high of 196, and averaging 109 different song types across all males (Figure 2.20).

Once again, some of this variation in males could be attributed to variation in sampling effort. Those males with relatively small song repertoires were males for which there was a smaller overall recording sample. This relationship is evident in Figure 2.21 which illustrates the time course of introduction of new song types into the singing activity of individual males. This figure clearly shows that males for which the sample of song recordings were large were also those for which the repertoire of song types was large, while males for which the sample of song recordings was relatively small also showed much smaller song type repertoires. However, the figure also shows that, for all males, regardless of song sample size, novel song types are continuously introduced over time, and the slope of the song type accumulation functions for individual males shows little sign of levelling off. For example, male HWLF1114 had the largest song sample with nearly 3,500 songs recorded. This male also had the largest repertoire of different song types at 196. However, even with such a large repertoire of different song types, the song type accumulation function for this male does not reach an asymptote but continues to rise (Figure 2.21).

Although males had very large repertoires of different song types, they sung most of them only rarely. In fact, of the 996 different song types in the sample, fully 427 (42.8%) were sung only once. In fact, only 56 different song types (5.6%) were sung more than 50 times.

2.2.10 Song Type Transitions

Focusing on this sample of 56 common song types, a song type transition matrix was constructed, exactly analogous to the syllable type transition matrix presented earlier, to quantify the frequency of transitions among different song types in adjacent positions in the sequence of songs in a bout. Even limiting the analysis to this set of only 56 common song types, the resulting matrix is too large to display (56 x 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 song types was to the same song type. Of the total 7,975 transitions between songs that occurred in our sample, 6707 (84.1%) were repetitions of the same song type. Only 1268 transitions (15.9%) involved switching to a different song type. And many of these latter transitions were between song types that differed by only a single syllable type. Hence, successive songs in a bout of singing 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 (Figure 2.22). As a result, over long bouts of singing, the syllable content of songs tend to change very gradually. Only rarely did males switch song types more abruptly to something very different. These two styles of song type switching (gradual versus abrupt) are illustrated graphically in Figure 2.23.

2.2.11 Song Templates

Combining data on common song types and syllable type transitions frequencies, a set of song templates was constructed for this population. For this analysis, the number of syllable types was restricted to four, the average number of syllable types observed in

songs of this population. Song templates were seeded with the most common starting

syllable types which were C, AG, AI, AM and S, which 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 possibility of 30%.

Figure 2.24 illustrates the possible song templates that can be constructed from

these five syllable seeds. Figure 2.24a shows that, when starting from syllable C, there

are two main routes that can be followed, the first involving a transition to syllable U

(which occurs 55% of the time) and the second a transition to syllable D (which occurs

34% of the time). Following syllable U, there are also two possibilities for the next

transition, either to syllable E (58% of the time) or to Syllable Z (37% of the time). From

syllable D, there is only one subsequent pathway, which is to syllable E (69% of the

time). From each of the three possible syllables in the third syllable position, there is only

one common pathway to the fourth syllable. Hence, starting from syllable C, there are

three major song templates possible, namely C.U.E.F, C.U.Z.M and C.D.E.F.

Figures 2.24b-e trace out possible song templates seeded with syllables AG, AI,

AM and S, respectively. Songs starting from AG, AI, and AM can yield only two

different song types each (AG.L.M.E; AG.Z.M.E; AI.AD.R.U; AI.AD.G.N; AM.U.E.F;

AM.U.Z.M); while songs seeded with syllable S leads to only one song template

(S.T.M.E). Indeed, most of these song templates correspond to the most frequently

observed song types in the sample of recorded songs.

2.3 Discussion

There are few previous studies of song organization in House Wrens and only two allow meaningful comparisons with the present work. One previous study was by Kroodsma (1977) who compared several basic features of song organization in nine different species of North American Wrens, including House Wrens. No detailed information was provided about the number of males recorded or the overall sampling effort involved for House Wren songs in this study and the characterizations of song provided are therefore very general. A second, more detailed study was by Platt and Ficken (1987) which involved a sample of 1,993 songs recorded from four male House Wrens in Wisconsin. Although both previous studies are limited in their samples and the number of song features reported, they nevertheless allow some broad comparisons with the current work and, in general, the patterns observed in these previous studies accord well with those observed in the current work.

Kroodsma (1977) suggested that House Wrens have a finite syllable repertoire, but that syllables can be recombined in varied ways to create a much larger song type repertoire, a basic pattern confirmed in the present work. Kroodsma also suggested that House Wrens typically repeat the same song type many times within bouts before switching, rather than switching between different song types in rapid succession. He characterized these two singing patterns as involving either 'eventual' variety or 'immediate' variety in singing in virtue of the different rate at which males reveal to listeners the various song types in their repertoire. Hence, Kroodsma suggested that House Wrens sing with eventual variety and here again, his general characterization was

confirmed in the present work, as males in southwest Alberta did tend to repeat song types many times before switching.

More detailed comparisons with the work of Platt and Ficken (1987) are possible. They noted that House Wren song consists of two sections, namely an Introduction and a Main section (what they termed the Terminal section), where the Introduction section was reported to be relatively low amplitude compared to the Main Section, and, these general structural differences in song were confirmed in the present work. Mirroring the current work, Platt and Ficken (1987) also focused their analyses of songs on the Main (or Terminal) section of the song, and found that the mean duration of this section was 1.25 seconds, which is similar to the 1.32 seconds observed in the present work for House Wrens in Alberta. The syllable constitution of songs in Wisconsin was also similar to that in Alberta. Platt and Ficken (1987) reported a mean of 11.49 syllables per song with a range of 3-22 syllables in Wisconsin, while the present work found a mean of 10.49 syllables per song with a range of 1-25 syllables in Alberta. The mean number of syllable types per song was somewhat smaller in Wisconsin, averaging 2.9 (range 1-6), compared to 3.88 (range 1-9) in Alberta.

The overall syllable repertoires of the two populations are also very similar. Thus, Platt and Ficken (1987) documented a total of 26 syllable types in the Wisconsin sample based on 1,993 songs from four males. The present sample for Alberta birds was substantially larger encompassing 15,608 songs from 15 males, yet documented a very similar population syllable repertoire of 27 syllable types. The consistency in the size of

the syllable repertoires in the two populations, despite the large differences in sampling effort and males studied, strongly suggests that there is an upper limit (ceiling) to the syllable repertoire in this species, and that it is probably close to 26 or 27. This point is further corroborated by the syllable accumulation data reported in the present study (Figure 2.13) where all birds showed a levelling off in the introduction of new syllable types to their repertoires within the first few hundred songs recorded. The syllable repertoire levelled-off in this fashion for all birds, regardless of sampling effort and the number of songs ultimately recorded from them. For example, the largest recording sample in the present work was for HWLF1114 from whom 3,500 songs were recorded. Although this male was sampled on many days and produced a large sample of song for analysis, he nevertheless showed the same pattern of reaching a syllable type ceiling within the first few hundred songs, after which no new syllable types were introduced despite extensive subsequent recording. Hence, the consistent syllable type repertoire limit of 26-27 obtained in both Wisconsin and Alberta is not likely to be an artefact of sampling effort. Additional recording of individual males seems unlikely to reveal an even larger syllable repertoire. On the contrary, there appears to be some constraints on the size of the syllable repertoire. Exactly what those constraints are for House Wrens, and why they should yield such a consistent limit across populations is unknown and should be taken up in a future study. Nevertheless, a finite syllable repertoire is a common feature of song in songbirds, even for those with largish repertoires and varied singing habits (Catchpole 1976, Eens 1997).

A detailed comparison of syllable types produced in Wisconsin versus Alberta is not really possible both because the spectrograms published in Platt & Ficken (1987) are of relatively poor quality and they lacked either time or frequency scales. Crude comparisons of the overall shapes of syllables in the two populations suggest that some of those produced in Wisconsin are very similar to those found in Alberta. However, many syllable types appear to be very different, which suggests that different House Wren populations diverge, at least to some degree, in the structure of their notes and syllables. Geographic differentiation of note and syllable forms is also a common pattern among broadly distributed songbird species (Bitterbaum and Baptista 1979, Lemon 1966, Baptista 1977).

Platt and Ficken (1987) reported a relatively high degree of syllable type sharing among the individual males in their sample, which is consistent with the present work. However, they also found that 12 of the 26 syllable types were unique to specific individuals, which was something not replicated in the current work. In Alberta, a few syllable types were quite rare (BG, BH, BI) and were shared by only a few males, but 11 syllable types were shared by all 15 males in the sample, and all other syllable types were shared by at least 3 males. Hence, there seems to be a difference in the degree of syllable type sharing in Wisconsin versus Alberta. However, caution is needed in interpreting this difference because it seems possible that the greater degree of syllable uniqueness in the Wisconsin sample may simply be an artefact of having sampled only 4 males compared to the 15 males sampled in Alberta. This is an important issue to resolve with future

detailed study of populations in Alberta and elsewhere to establish if the apparent

difference in rates of syllable sharing among males within populations is real or not.

Platt and Ficken (1987) also reported very low song type sharing. Out of the total

song type repertoire of 130 for their sample, 120 song types were unique to particular

individuals; hence only 8% of the song types were shared among males. This is a pattern

that was replicated in the larger Alberta sample, which involved a total of 996 different

song types across the entire sample of 15 males. Only a single song type was shared by

all 15 males, while 14 song types (1.4%) were shared by 10 or more males. 231 song

types (23.12%) were shared by at least two males, but 765 song types (76.8%) were

completely unique to particular males. Hence, the results for both populations are

consistent and indicate that, while there are a few common song types that can be shared

widely by many males, most song types in fact are not shared, but rather are unique to

particular males. Thus, males in the two populations appear to be consistent in using a

finite number of syllable types to construct a much larger repertoire of different and

mostly unique song types.

As a consequence, having a largish, but ultimately limited, number of syllable

types does not impose any very serious limit on the range of song type diversity. In

principle, with a repertoire of 27 different types of syllables that are used to construct

songs composed of, on average, four different syllable types, males could conceivably

produce up to 421,200 different song types. This assumes that there are no constraints on

the transitions between successive syllable types within a song – i.e., that any syllable

type can precede or follow any other syllable type. In fact, however, there do appear to be constraints on the transitions between adjacent syllable types within songs, as clearly shown in the syllable transition matrix reported here for the songs of all Alberta males (Table 2.4). This matrix of the actual transitions observed among syllable types in the complete sample of songs shows that the syllable transitions are not equi-probable. Instead, some syllable type transitions were very common, while others were quite rare. And many possible transitions among syllable types never occurred at all. Indeed, of the 702 pairwise syllable type transitions that are possible for the 27 different syllable types (excluding self-syllable transitions), fully 403 (60.3%) never occurred. It is obviously possible that an even larger sample, involving many more males, would show that some of the syllable transitions that were not observed in the present sample nevertheless can occur in other males. Nevertheless, the fact that more than half of all the possible syllable type transitions never occurred in the present sample, suggests that there may be constraints on the kinds of syllables that can precede and follow one another, which would then also limit the ultimate range of song diversity that is possible.

This point is further buttressed by the present song template analysis. Thus, when song templates were constructed based on the most common syllable transition probabilities observed in the present song sample to try to develop potential 'rules' of song construction, only a very small number of song construction paths were actually followed by singing males. Overall, there were only 10 common pathways followed to generate the average 4-syllable type song (Figure 2.24), and some of these pathways were relatively subtle variants of one another (e.g., C.U.E.F and C.U.Z.M, see Figure 2.24a).

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Further, many additional song types were relatively straightforward modifications of one of these 10 common pathways. For example, one song template was the C.U.E.F song type. This template was the profile for producing several common variants varying 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). One interpretation of this finding is that the birds may be following certain 'rules' when creating song types, which are clearly not a random concatenation of syllable types. An alternative, non-exclusive possibility, is that this regularity in song construction is pointing to some constraint on the flexibility of song construction. It is not clear what such constraints might be (but see below), but there certainly appears to be some limitation on the kinds of syllable types that can precede or follow one another.

This outcome has obvious implications for the diversity of different song types that are possible. Thus, although the sample of 996 different song types recorded in the present sample probably does not represent anything like the upper limit of song type variety for the species, it is likely also the case that the upper limit of actual song type is nowhere even close to the theoretical limit of 421,200.

Some additional observations of song structure patterning might shed some light on possible constraints on syllable transitions and song construction. In general, the frequency of successive syllables within songs descends from beginning to end. In other words, the Main section of the song tends to start with syllable types of relatively high frequency and end with syllable types of relatively low frequency. Some syllable types can vary in frequency depending on their place within the song. That is, the same syllable

type can be made with a relatively high frequency profile if it appears at the beginning of the song or with a relatively low frequency profile if it appears at the end of the song. Syllables like this include M, G, and U. However, other syllable types do not show this flexibility. For example, the syllables AM, AG, T, and S tend to be produced only at a relatively high frequency and also to occur only at the beginning of songs, while the syllable N tends to be produced only at a relatively low frequency and also occurs only at the end of the song. Hence, it seems that differences in the frequency profile of different syllable types (and in the flexibility of these frequency profiles) may be one factor constraining the types of syllables that can precede or follow one another, thereby also imposing some limits on song type diversity.

A further constraint on song diversity appears to lie in the number of different syllable types that can be included in a song. In the present sample, this number ranged from 1 to 9, with an average of four different syllable types in a song. The wide range here suggests that males are able to increase or decrease the number of syllable types they include in their songs. However, this ability seems to be limited as confirmed by the relationships observed between the duration of the Main section of the song and the number of syllables versus syllable types it contained. Although the number of syllables per song was strongly and positively correlated with the duration of the Main section of the song, there was no similar correlation between this duration and the number of syllable types produced. Hence, males typically lengthened their songs not by including more syllable types in their songs, but by increasing the number of repetitions of the same

syllable types. This outcome therefore also points to there being constraints on the number and diversity of syllable type combinations that are possible for the birds.

There may also be constraints on song diversity at other levels. For example, the overall song type repertoire for this Alberta population was large (996 different song types) and the repertoires of individual males were therefore also large (100 – 200 song types). However, many of these song types were sung only a handful of times. Indeed, many were sung only once or twice. Thus, while each male produced, on average, 109 different song types, all of them actually had a much smaller 'effective' repertoire of only about 25 song types that they sung with any regularity. Therefore, while male House Wrens are obviously capable of considerable song type diversity, this diversity potential seems not to be very fully realized or exploited because all males regularly sing only a fraction of all the song types they are demonstrably capable of. This result points to the possibility of some additional constraint on the number of song types that can be effectively maintained in a male's current 'production' repertoire.

At the same time, though, even with a smaller repertoire of 25 common song types, males could be capable of quite diverse singing patterns. For example, with a repertoire of 25 different songs that can be sung, individual bouts of singing could still be quite diverse, composed of a complex mixing of these 25 different songs. And, yet, in general, bouts of singing did not display such variety. Most bouts of singing contained only a very small number of different song types, each song type being repeated several times (sometimes many, many times) before switching. Indeed, by far the majority of

'transitions' (84%) between adjacent songs within a bout were to the same song (i.e., successive songs did not change in their syllable type sequence). When males did change the type of song they sung within a bout, the change was most often to a very similar song type, usually differing by only one syllable type. Hence, songs within a bout changed very slowly and incrementally. Only rarely were more abrupt changes to completely different types of song observed within singing bouts. As a result, in general, within bouts, the singing pattern was quite repetitive and not obviously diverse at all. As noted earlier, this pattern accords with Kroodsma's (1977) characterization of the House Wren as a species that sings with 'eventual' rather than 'immediate' variety. But it highlights important questions to be addressed with future work. For example, if song diversity (song complexity) is a sexually selected trait, as often hypothesized (Buchanan and Catchpole 1977, Searcy and Marler 1984, Hasselquist 1998), that is valued by females for the cues it provides to male quality, and male House Wrens are capable of producing a great variety of different songs, then why are they not producing this variety with any regularity? And why are they not revealing the variety they are capable of producing more immediately? Why are bouts of singing relatively monotonous by comparison to how diverse they could be?

One possibility here is that, in House Wrens, females assess male quality not based on variety alone, but on some combination of variety and consistency. That is, females are focused on how consistently males can produce (and reproduce) the same songs time-after-time, and for how many different types of song they can do this. This kind of assessment pattern would represent a combination of the singing and assessment

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patterns observed in some species that focus on variety and produce many different song types and other species that focus on consistency and generally produce only one or a few song types (Buchanan and Catchpole 1997, Catchpole 1980, 1983, Botero et al. 2009, Garamszegi et al. 2007, Rivera-Gutierrez et al. 2011, Rivera-Gutierrez et al. 2012). In effect, House Wrens might be combining these two patterns, focusing on both consistency and variety. This is an intriguing, but speculative, hypothesis that warrants future focused investigation.

In a related vein, another relationship worth pursuing in future work was that between the syllable and song type diversity of different males in the sample. In the present sample, there was a significant positive correlation between the size of the syllable type and song type repertoires of different males. Males with larger syllable type repertoires also had larger song type repertoires. This is a particularly intriguing relationship pointing to the possibility of individual-specific constraints on syllable and song diversity. That is, some males may be more capable songsters than others, which would also be relevant to theories of song complexity based on sexually selected differences in male quality. However, once again, caution is warranted in drawing any such inference from the present work because the sampling effort varied considerably across males and because there was also considerable variation in the breeding stages at which different males were recorded. For example, some males were sampled very early in the season while still actively courting females, while others were sampled primarily only after they had paired. And, of course, singing behavior can vary substantially between courting and paired males, not only in the volume of song produced, but also

potentially in its relative complexity (Johnson and Kermott 1991a, Espmark and Lampe 1993). For instance, three birds in the sample (HWLF 1104, HWLF 1112 and HWWB 1108) were already paired when song recording commenced. Hence, the sample does not contain recordings from these males during their early season courtship stage. At the same time, because paired males sing less vigorously, the overall sample of songs for these birds is relatively small. It is probably no coincidence then that these three males placed at the low end of both syllable type and song type diversity (Figure 2.19). As a result, the values for these males probably underestimate their true syllable and song type repertoires. Unfortunately, the overall sample is too heterogeneous to allow systematic testing of the influence of breeding stage and sample size on the syllable type and song type repertoires obtained for different males. However, because the syllable and song type repertoires may have been underestimated for some males, the apparent relationship between low syllable type diversity and low song type diversity (and between high syllable type diversity and high song type diversity) may be illusory.

Figure 2.1: The location of two field sites in the foothills of the Canadian Rockies, in the

Bob Creek Wildlands and near Lundbreck Falls, Alberta. (Map source: Google Earth)
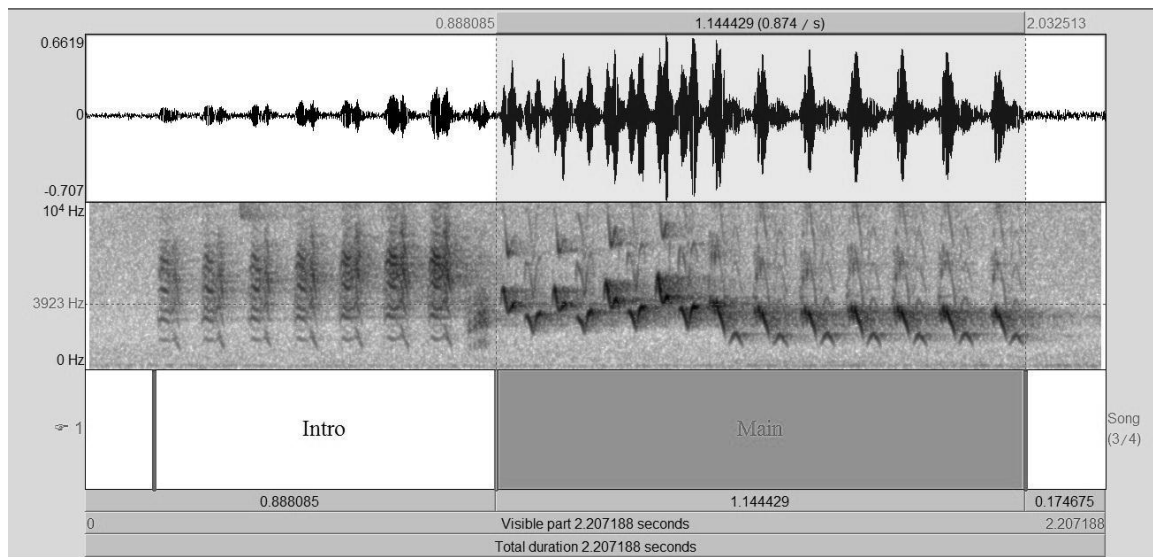
Figure 2.2: A typical song of a male House Wren. Top panel shows the sound waveform and the middle panel a spectrogram of the frequency structure of the song. The lower panel demarcates the Introduction section of the song consisting of low-amplitude broadband notes, and the Main section of the song consisting of louder, tonal and frequency-modulated notes.

Table 2.1: Mean duration of different temporal features of song.

Bird name	Introduction Duration (s)	Main Duration (s)	Song Duration (s)	Interval Duration (s)
HWLF1102	0.93	1.51	2.43	5.42
HWLF1104	0.62	1.19	1.70	8.66
HWLF1106	0.87	1.18	2.02	7.52
HWLF1108	0.72	1.22	1.77	6.05
HWLF1109	0.66	1.16	1.81	7.41
HWLF1110	0.89	1.20	2.06	6.44
HWLF1111	1.09	1.50	2.59	4.07
HWLF1112	0.94	1.20	2.10	6.48
HWLF1113	1.13	1.31	2.43	2.74
HWLF1114	1.01	1.34	2.34	3.58
HWLF1115	1.22	1.65	2.87	4.61
HWWB1101	1.00	1.42	2.41	4.14
HWWB1102	0.78	1.18	1.87	6.88
HWWB1105	0.89	1.48	2.23	7.27
HWWB1108	0.71	1.24	1.81	6.06
Mean	**0.90**	**1.32**	**2.16**	**5.82**
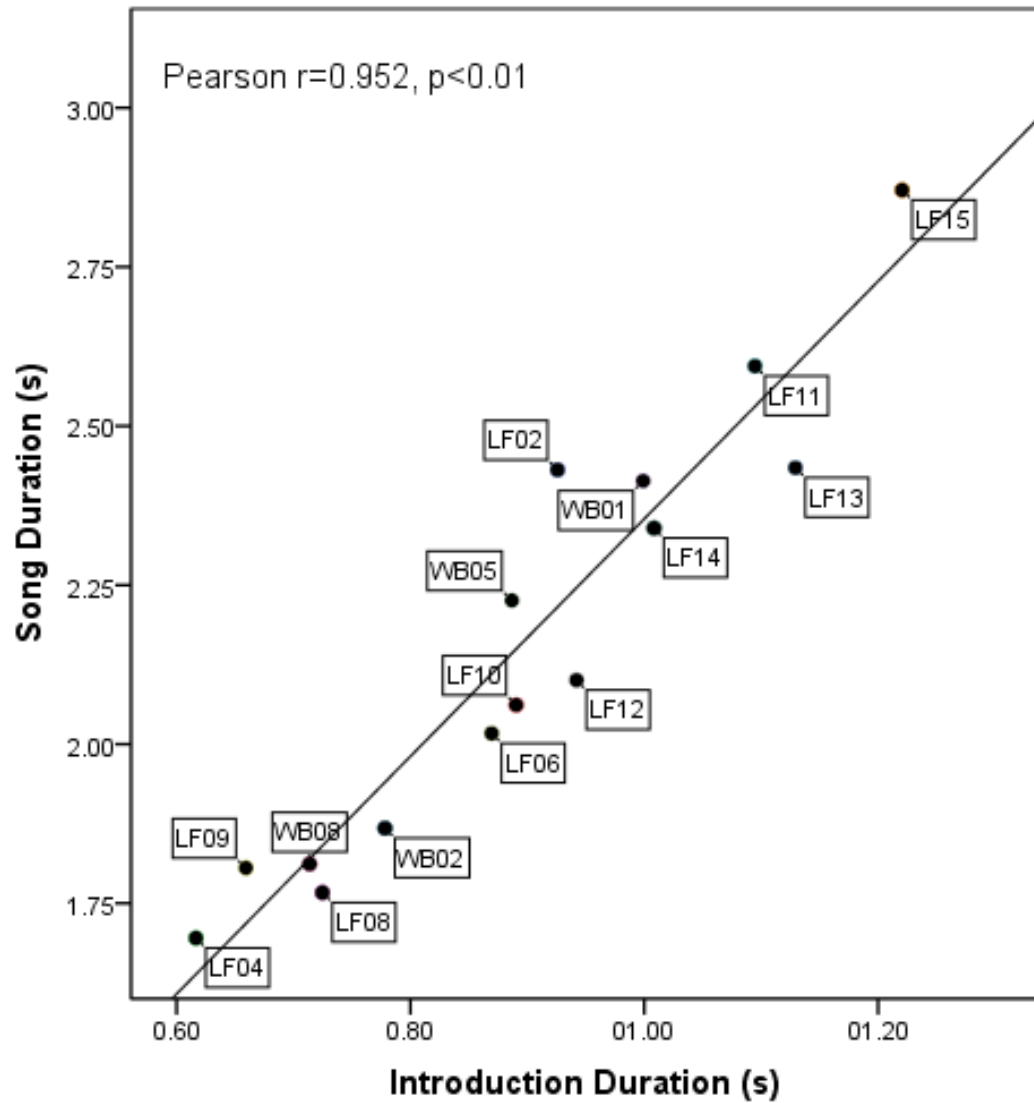
Figure 2.3: Relationship between the duration of the introduction section of the song and the duration of the entire song (Intro + Main). Individual points represent different males whose labels have been abbreviated (e.g. LF02=HWLF1102).
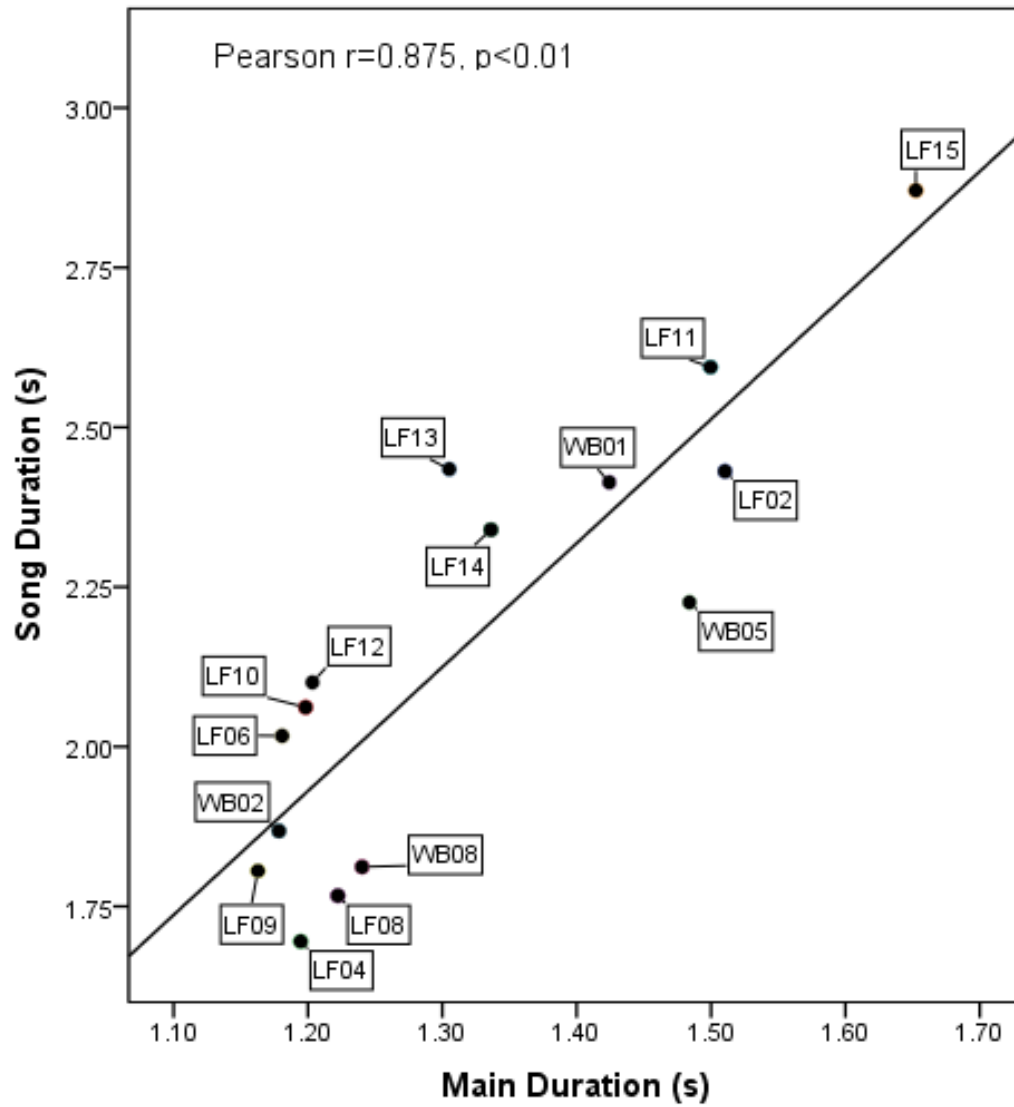
Figure 2.4: Relationship between the duration of the main section of the song and the duration of the entire Song (Intro + Main).
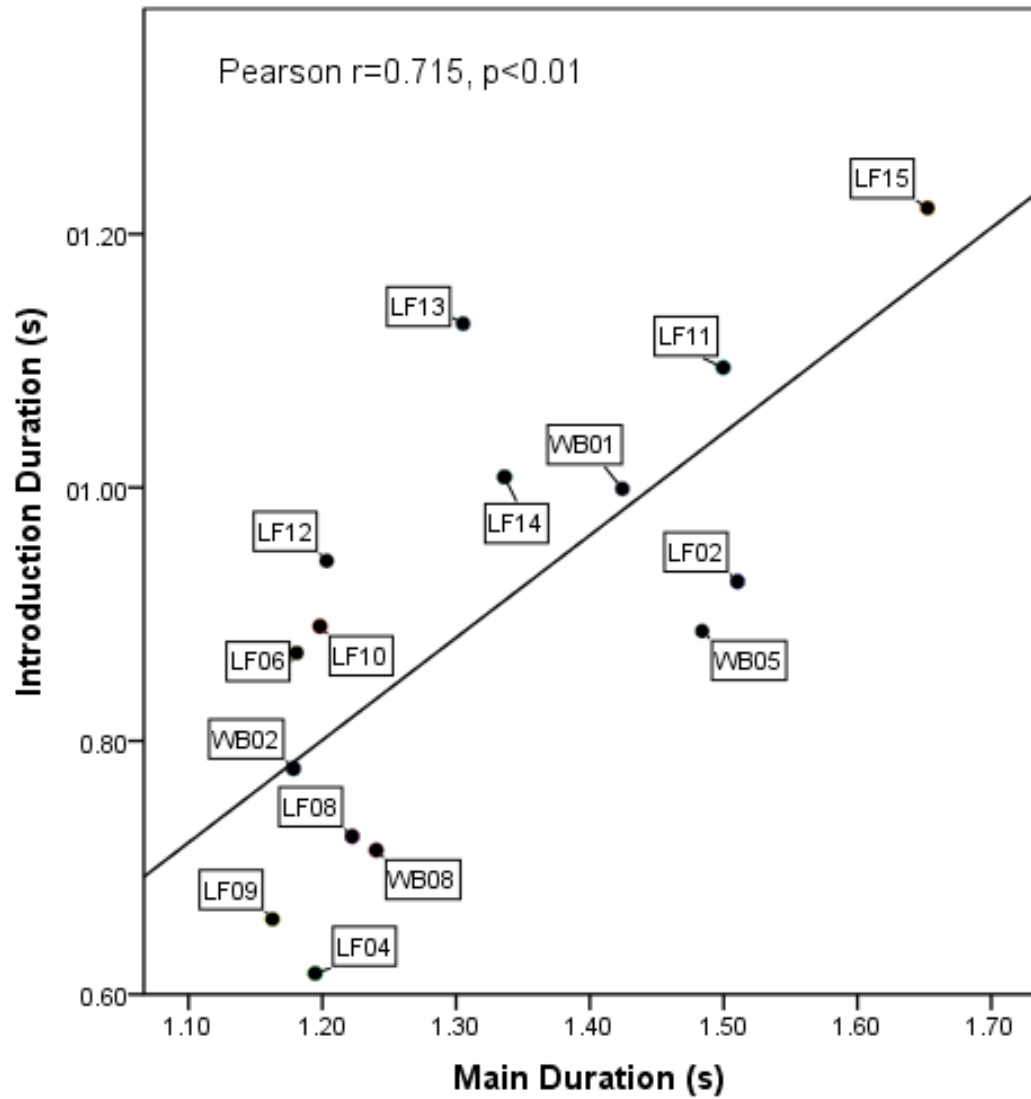
Figure 2.5: Relationship between the duration of the main section of the song and the duration of the introduction section of the song.
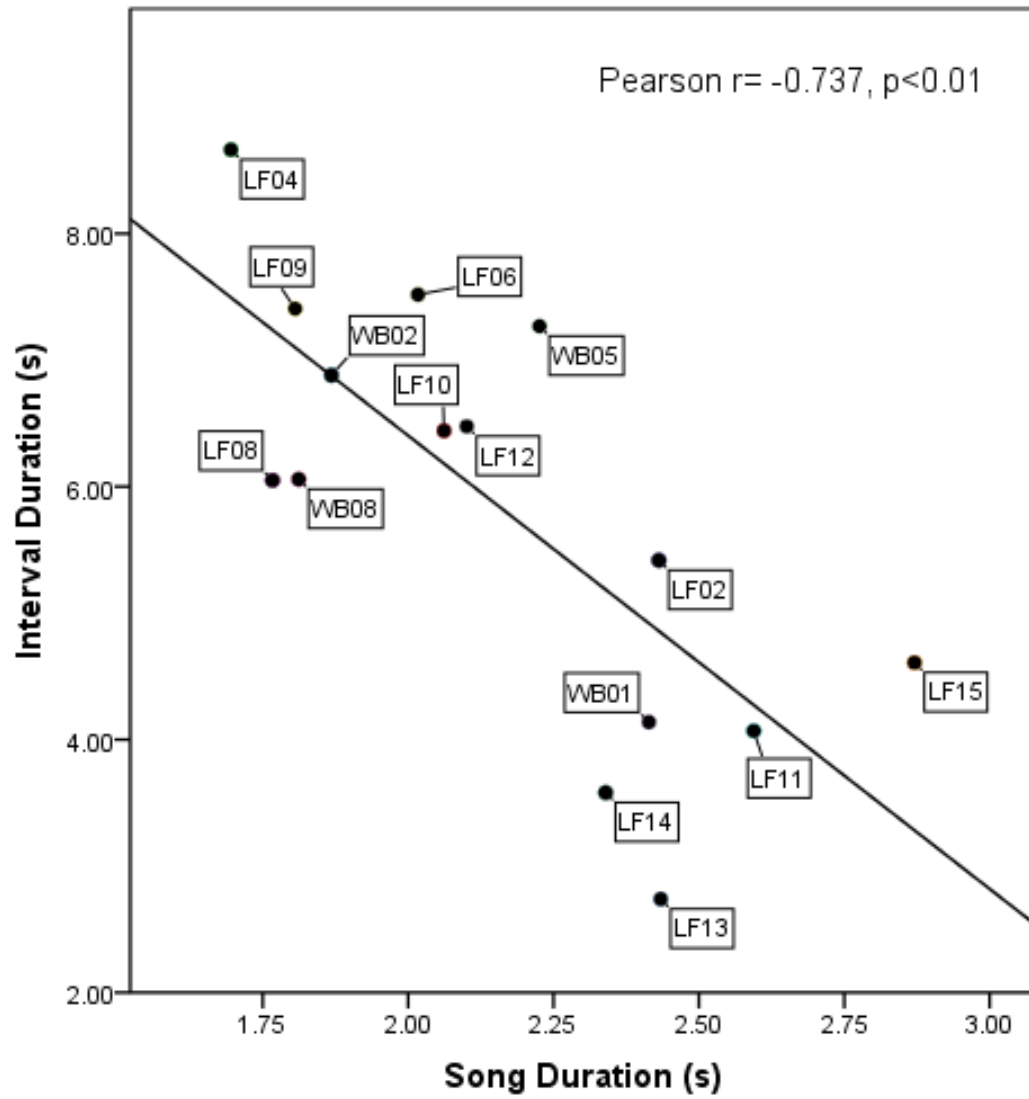
Figure 2.6: Relationship between the duration of the entire song and the duration of the interval between successive songs.
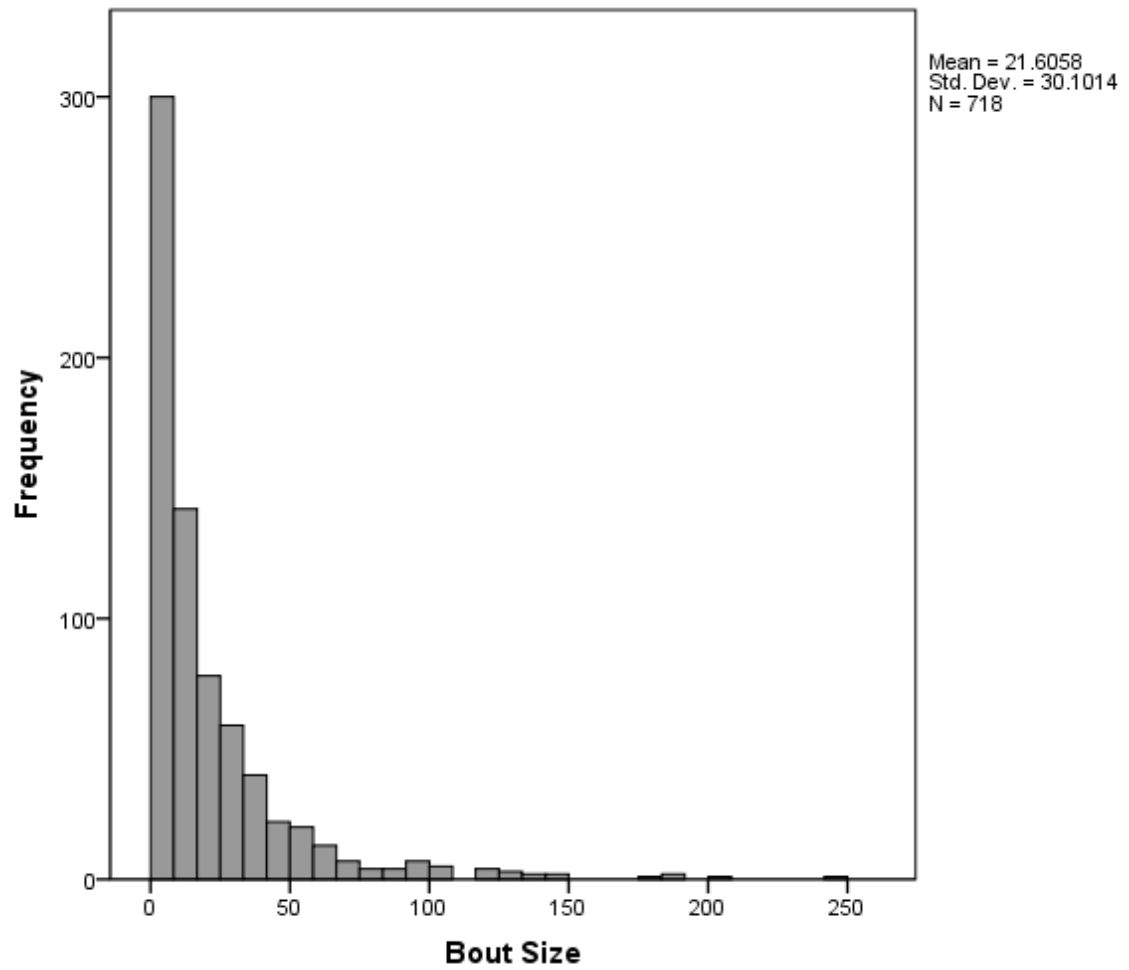
Figure 2.7: Frequency distribution of the number of songs in bouts of singing.
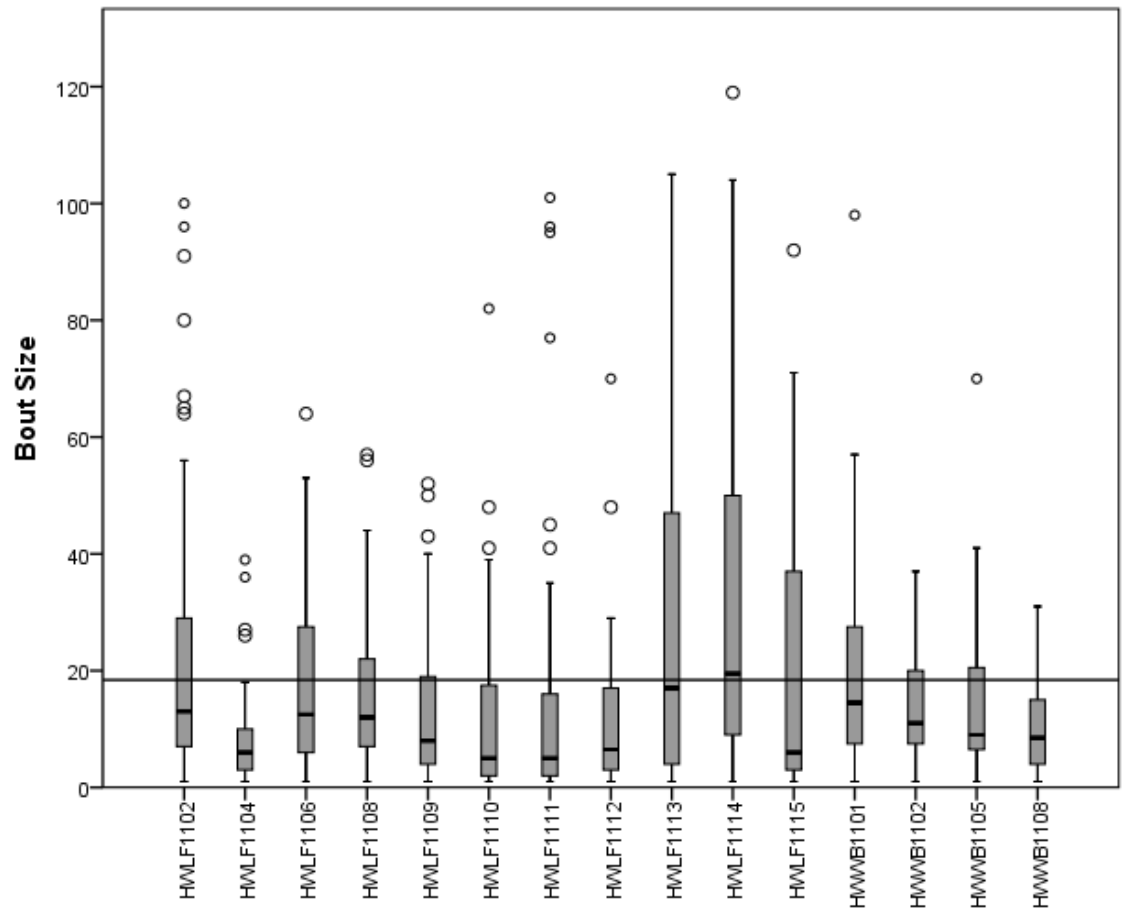
Figure 2.8: Box and whisker plot illustrating individual variation in the size of singing bouts. For each male, box boundaries represent the inter-quartile range and the solid line within each box represents the median. (Sixteen song bouts that had more than 120 songs were excluded from this graphic to facilitate better visualization of results.)
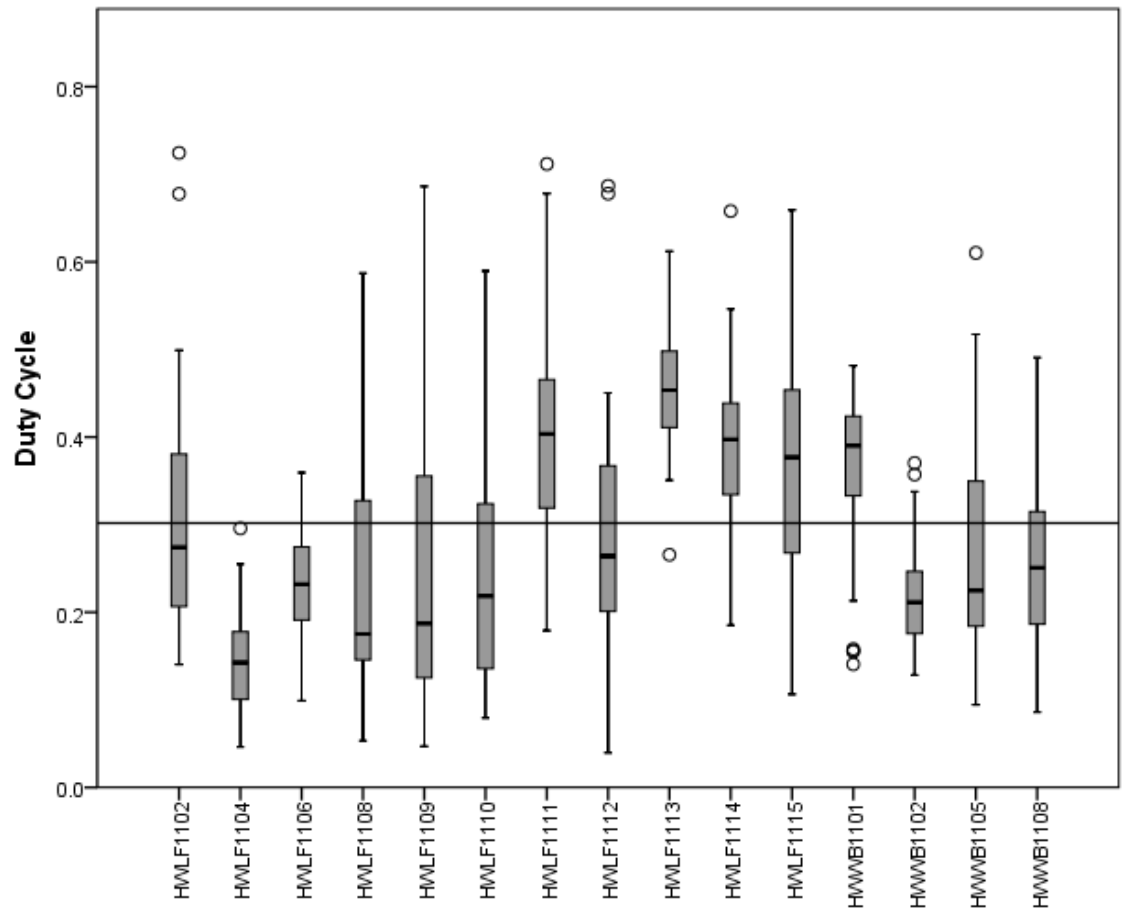
Figure 2.9: Box and whisker plot illustrating individual variation in the duty cycle of singing. Duty cycle is defined as the amount of time spent singing as a fraction of total song bout duration. The horizontal line represents the mean value across all males (0.3).
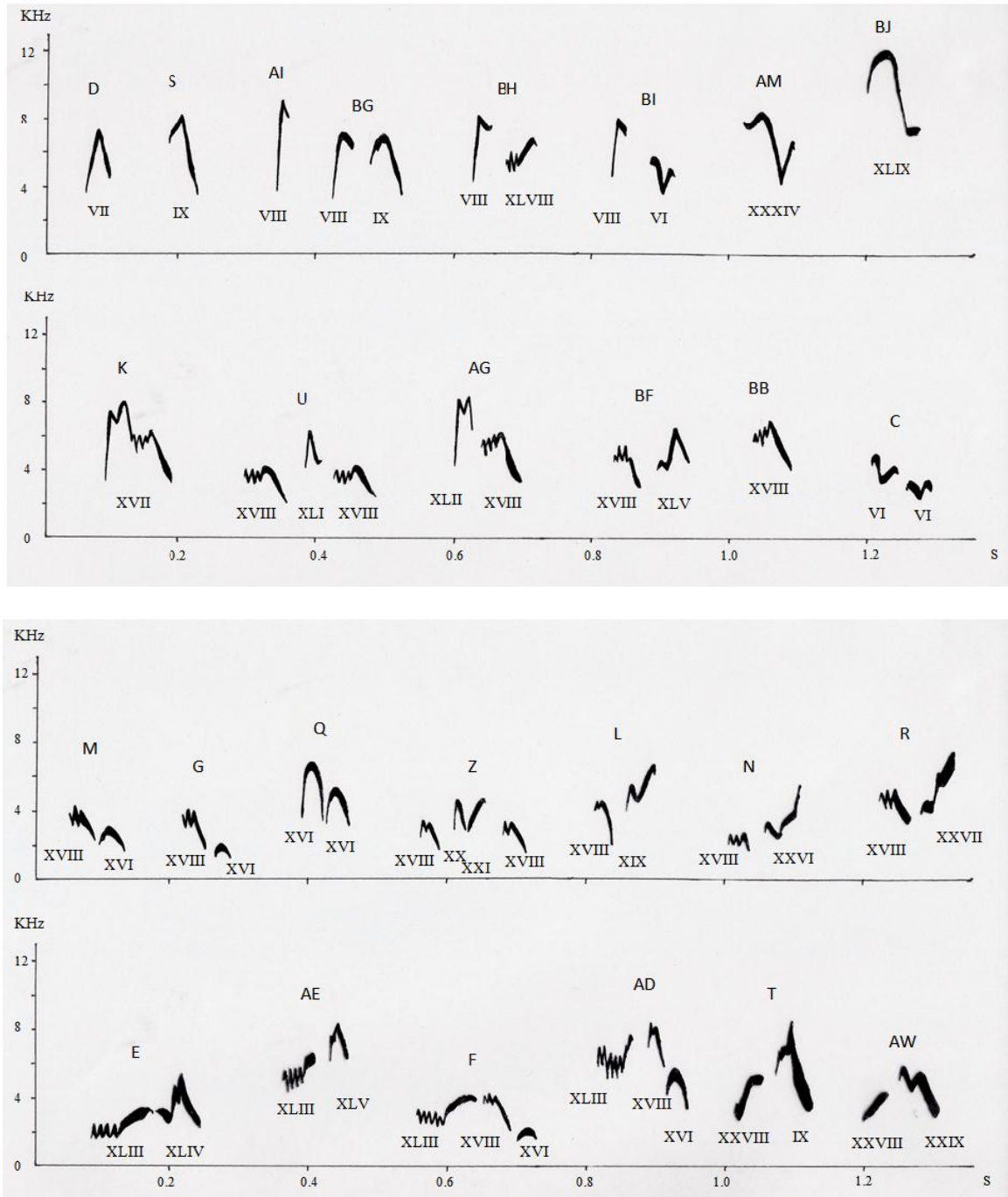
Figure 2.10: Complete note and syllable repertoire for the study population. (Notes are given in Roman numerals, syllables in letters.)

Table 2.2: Catalogue of notes and syllables.

Syllable	Number of notes	Notes	Placement*
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
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

*Placement indicates where each syllable usually occurs within the main section of the song.
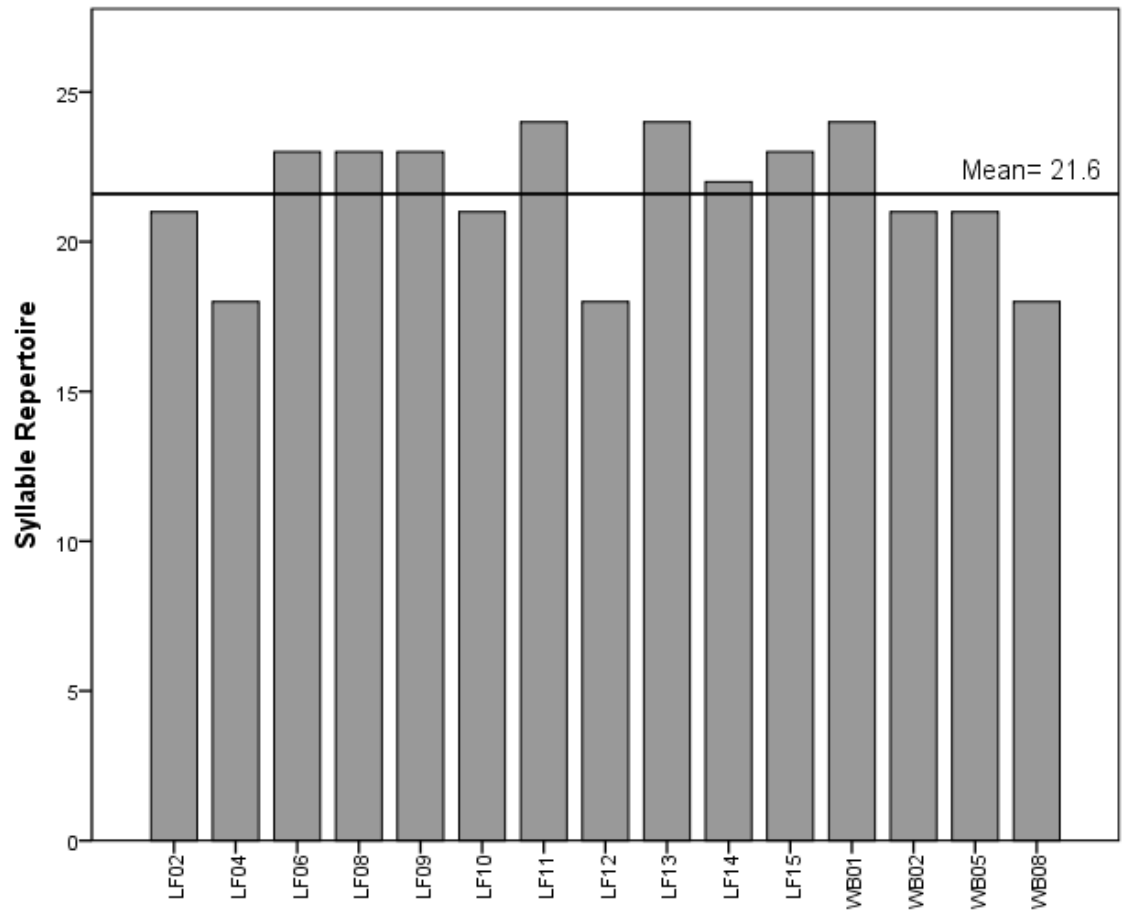
Figure 2.11: Histogram showing variation in the size of the syllable repertoire of each

male.

Table 2.3: Detailed syllable repertoires for individual males.

	HWLF1102	HWLF1104	HWLF1106	HWLF1108	HWLF1109	HWLF1110	HWLF1111	HWLF1112	HWLF1113	HWLF1114	HWLF1115	HWWB1101	HWWB1102	HWWB1105	HWWB1108
AD	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
AE	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
AG	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
AI	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
AM		x	x	x			x	x	x		x	x	x	x	x
AW	x		x	x	x	x	x	x	x	x	x	x	x	x	
BB	x		x	x	x	x	x		x	x	x	x			x
BF	x			x	x		x		x			x			
BG	x								x			x			
BH			x		x				x	x				x	
BI	x								x	x		x			
BJ			x	x			x				x				
C	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
D	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
E	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
F	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
G	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
K			x		x	x	x				x		x		
L	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
M	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
N		x	x	x	x	x	x	x	x	x	x	x	x	x	x
Q	x		x	x	x	x	x	x	x	x	x	x	x	x	
R	x	x	x	x	x	x	x	x		x	x	x	x	x	x
S	x	x		x	x	x	x		x	x	x	x	x	x	x
T	x	x	x	x	x	x	x		x	x	x	x	x	x	x
U	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Z		x	x	x	x	x	x	x	x	x	x	x	x	x	x
Total	**21**	**18**	**23**	**23**	**23**	**21**	**24**	**18**	**24**	**22**	**23**	**24**	**21**	**21**	**18**

X denotes the presence of syllables

HWLF1102
n=1767, Syllable types=21

HWLF1104
n=324, Syllable types=18

HWLF1106
n=891, Syllable types=23

HWLF1108
n=1456, Syllable types=23

HWLF1109
n=641, Syllable types=23

HWLF1110
n=581, Syllable types=21

HWLF1111
n=1354, Syllable types=24

HWLF1112
n=558, Syllable types=18

HWLF1113
n=1404, Syllable types=24

HWLF1114
n=3528, Syllable types=22
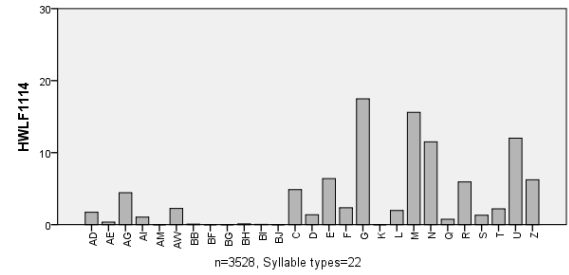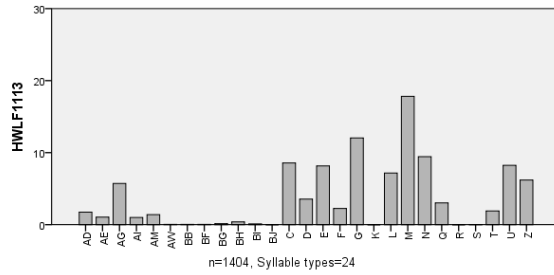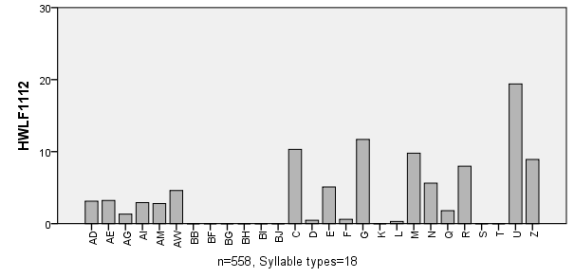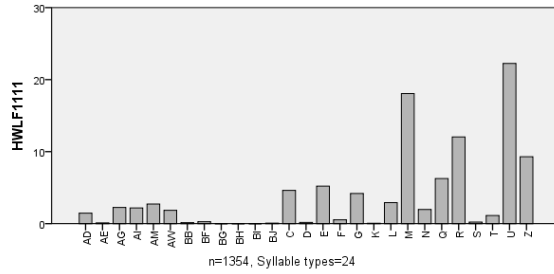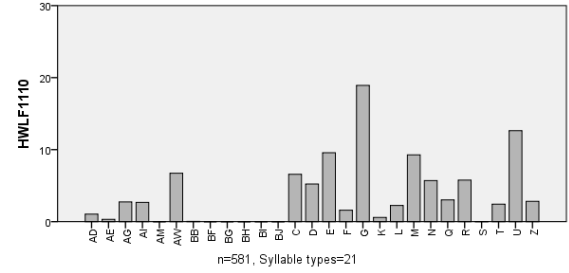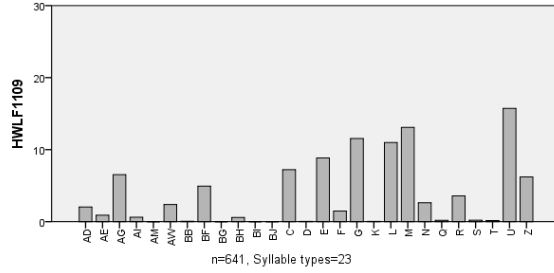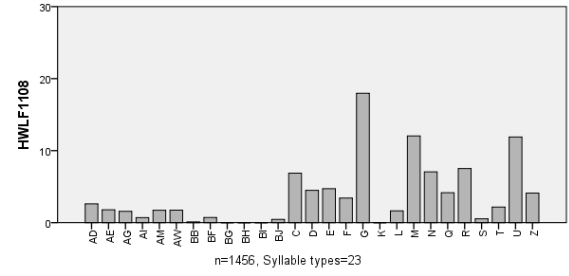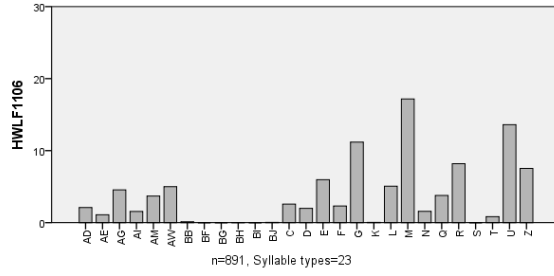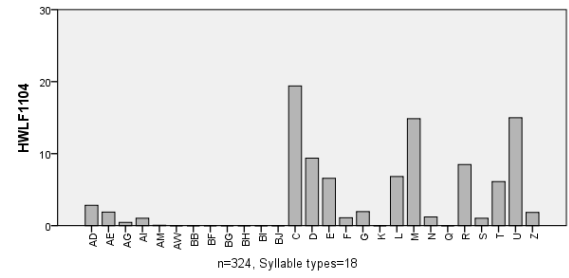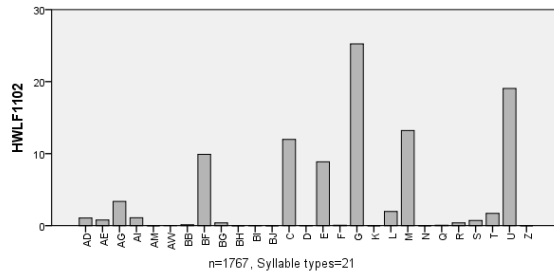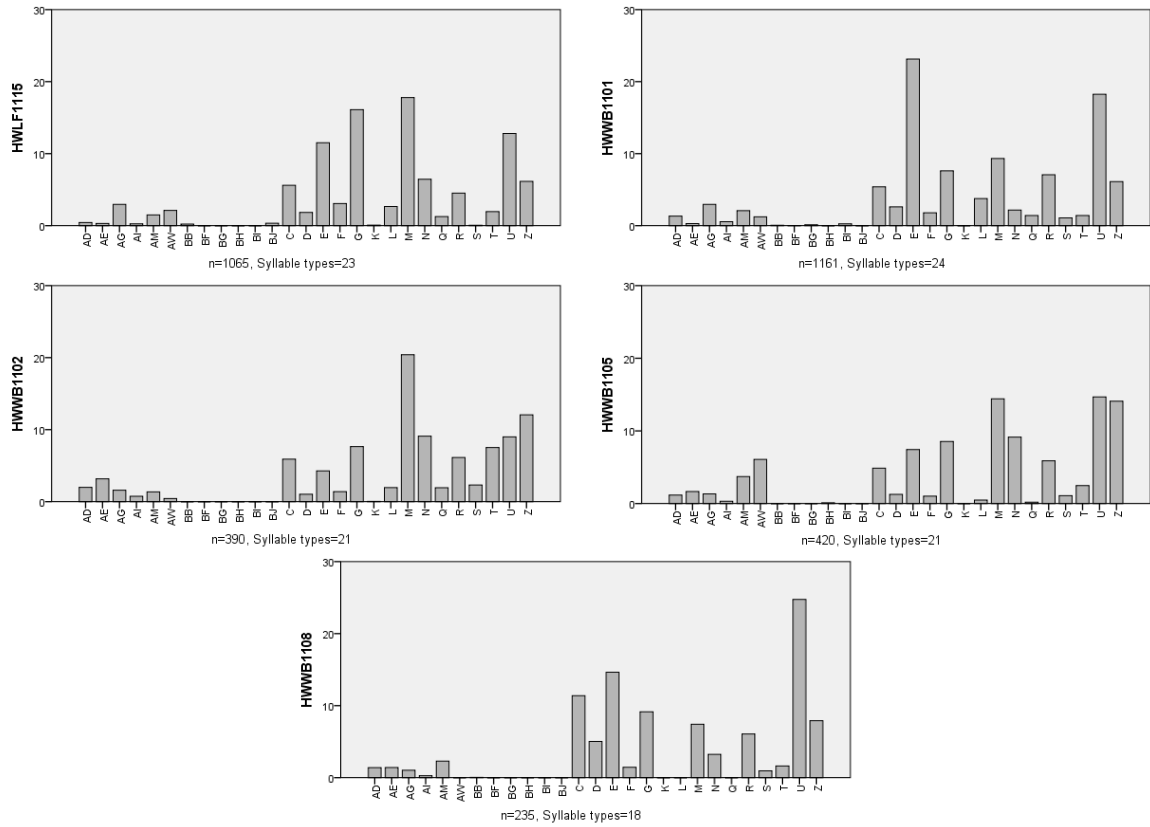
Figure 2.12: Frequency distribution of syllable type production for individual males.

Each panel represents a different male. The X-axis lists the different syllable types for the

entire population and the Y-axis shows the production of particular syllable types as a

percentage of a male's total song sample. The song sample (n) for each male is given.
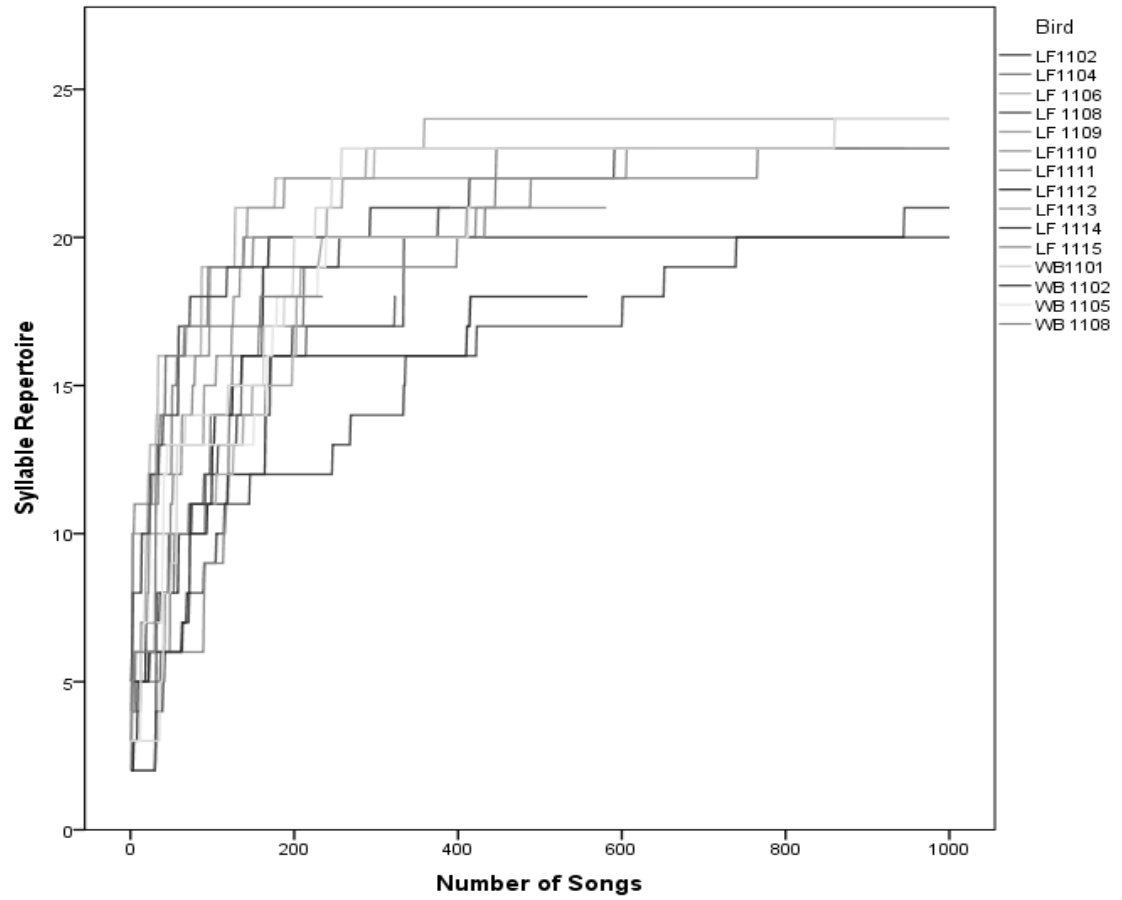
Figure 2.13: Syllable accumulation functions for individual males. Plot illustrates the rate at which new syllable types in each male's repertoire are revealed in successive song recordings from them.

Figure 2.14: Syllable accumulation functions for individual males for the first 200 songs recorded. Plot illustrates the rate at which new syllable types in each male's repertoire are revealed within the first 200 song recordings from them.

Table 2.4: Syllable transition matrix

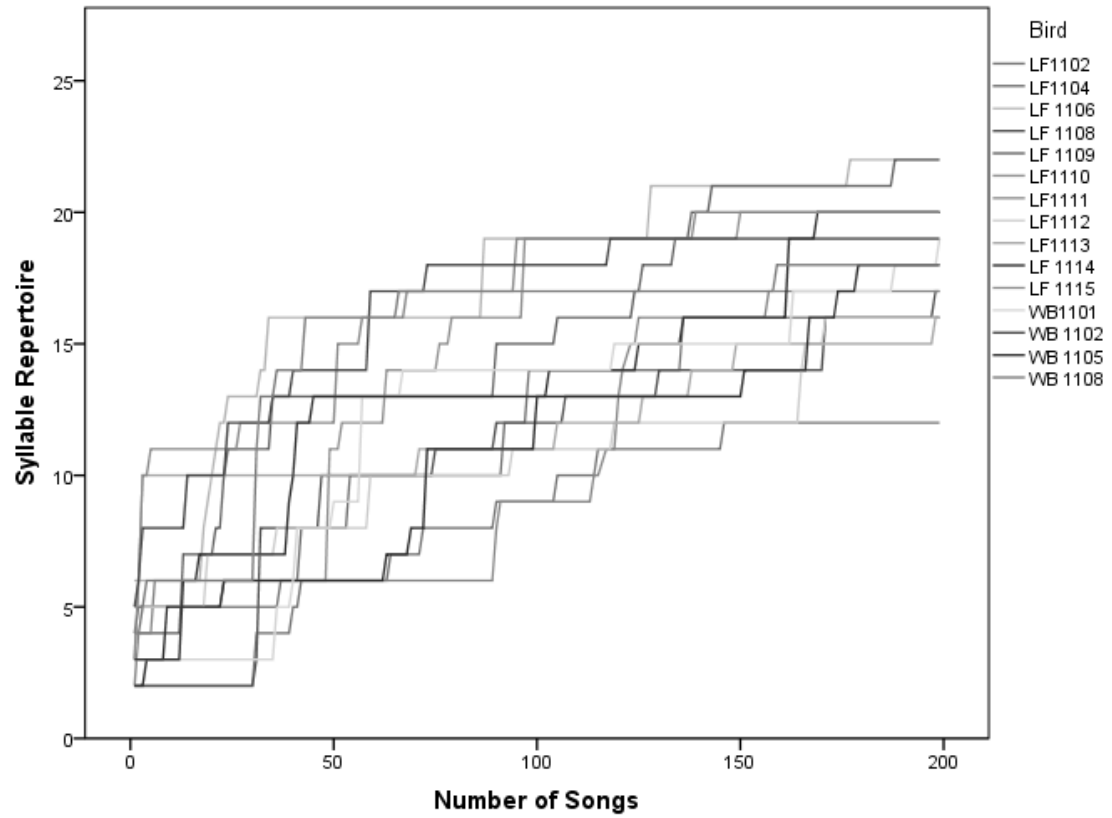|	AD	AE	AG	AI	AM	AW	BB	BF	BG	BH	BI	BJ	C	D	E	F	G	K	L	M	N	Q	R	S	T	U	Z
AD		0.07						0.52									42.59			3.82	2.40	5.99	43.60				1.01
AE	87.53								0.35					0.09	1.22	2.62	1.22		0.09	2.79		1.92	2.01	0.09	0.09		
AG	0.03	2.59		0.12	0.03	0.12	0.06	3.41		0.03	0.09		0.09		5.15		0.00		46.54	0.18		0.21	8.12	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	18.85	0.26		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		3.28											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	

Legend: 0% | <20% | 20-40% | 40-60% | 60-80% | 80-100%

Values represent probability of transition from one syllable type to another, where the preceding syllable is listed in rows and the following syllable is listed in columns. Probability values are calculated within rows and show the likelihood of transition from the listed preceding syllable to all possible following syllables.

Table 2.5: Syllable transition matrix based on total possible transition universe.

	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		0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	24.3	0.0	0.0	2.2	1.4	3.4	24.9	0.0	0.0	0.0	0.6
AE	21.4		0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.3	0.0	0.0	0.7	0.0	0.5	0.5	0.0	0.0	0.0	0.0
AG	0.0	1.9		0.1	0.0	0.1	0.0	2.5	0.0	0.0	0.1	0.0	0.1	0.0	3.7	0.0	0.0	0.0	33.8	0.1	0.0	0.1	5.9	0.1	1.1	0.1	22.8
AI	14.4	3.3	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	1.3	0.0	0.0	0.0	1.9	3.9	0.0	8.6	5.5	0.0	0.2	0.5	0.0
AM	0.1	0.7	0.0	0.0		0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	6.2	0.0	0.0	0.0	27.8	0.0
AW	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.2	0.4	0.0
BB	0.0	0.1	1.8	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
BF	0.7	0.1	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.1	0.0	0.0	1.5	0.0	0.0	0.1	0.0	0.0	5.0	0.0
BG	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.2	0.1	0.0	0.1	0.0	0.5	0.0	0.0	0.0
BH	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
BI	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0
BJ	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.0	0.2	0.0
C	0.1	0.1	0.1	0.0	0.3	1.1	0.0	0.0	0.0	0.0	0.0	0.0		30.3	1.3	0.1	4.9	0.0	0.0	1.5	0.0	0.1	0.0	0.0	0.0	48.0	0.0
D	4.8	0.9	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.4		22.1	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
E	10.1	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		58.6	12.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
F	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		54.6	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
G	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.6	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0		0.0	0.0	0.3	43.3	0.0	4.4	0.0	0.0	0.1	0.5
K	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0		0.4	0.0	0.0	0.0	0.5	0.0	0.0	0.1	0.0
L	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		37.4	0.1	1.2	0.0	0.0	0.0	2.7	0.0
M	0.0	0.1	0.0	0.0	0.3	2.2	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	52.0	0.1	0.1	0.0	0.0		13.9	0.1	9.7	0.0	0.0	0.1	0.1
N	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	2.3	0.0
Q	0.0	6.7	0.0	0.0	0.0	8.4	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.2	0.6	1.5		10.8	0.0	8.9	0.0	1.7
R	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.0	0.0	0.9	0.0	0.0		0.0	0.0	47.7	0.1
S	0.4	1.8	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.5		18.9	0.0	0.0
T	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.4	7.5	0.0	0.0	21.4	0.0	1.0	0.0	0.0		0.6	0.0
U	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.1	0.0	46.1	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.1	0.4	0.0		29.6
Z	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	2.7	0.0	0.1	46.6	0.0	0.0	0.1	0.0	0.0	0.1	

Probability values are calculated across the entire matrix representing all syllable transitions in the database. Values are shown per 1000 transitions, with cells over 5 highlighted.

Table 2.6: Mean values for various measures of song variability.

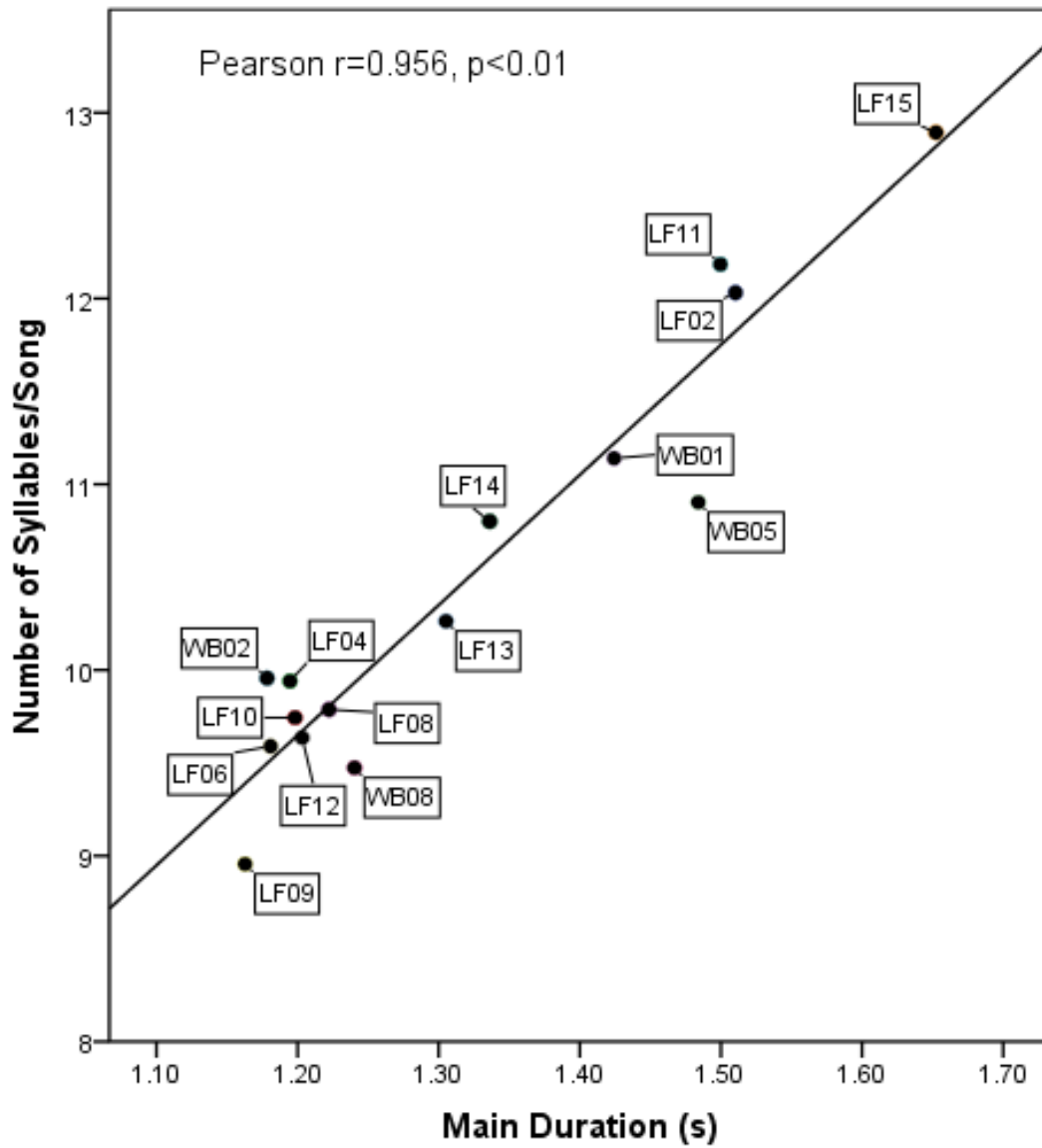|	Number of Syllable Types	Number of Syllables	SVI	Syllable Production Rate	Syllable Type Production Rate
HWLF 1102	3.73	12.03	0.32	8.03	2.53
HWLF 1104	2.92	9.94	0.35	8.38	2.89
HWLF 1106	4.18	9.59	0.46	8.14	3.67
HWLF 1108	4.2	9.79	0.45	7.99	3.6
HWLF 1109	3.31	8.96	0.39	7.73	2.96
HWLF 1110	4.16	9.74	0.44	8.22	3.6
HWLF 1111	3.94	12.18	0.33	8.14	2.69
HWLF 1112	3.71	9.64	0.44	8.04	3.57
HWLF 1113	3.99	10.26	0.4	7.87	3.14
HWLF 1114	4.25	10.8	0.4	8.08	3.23
HWLF 1115	4.74	12.89	0.38	7.83	2.99
HWWB 1101	3.89	11.14	0.36	7.86	2.88
HWWB 1102	3.94	9.96	0.41	8.43	3.49
HWWB 1105	3.57	10.9	0.34	7.31	2.5
HWWB 1108	3.67	9.47	0.4	7.66	3.1
Mean	**3.88**	**10.49**	**0.39**	**7.98**	**3.12**

SVI = Number of Syllable Types/ Number of Syllables

Figure 2.15: Relationship between the duration of the main section of the song and the number of syllables produced per song. Values plotted represent the means for individual males.
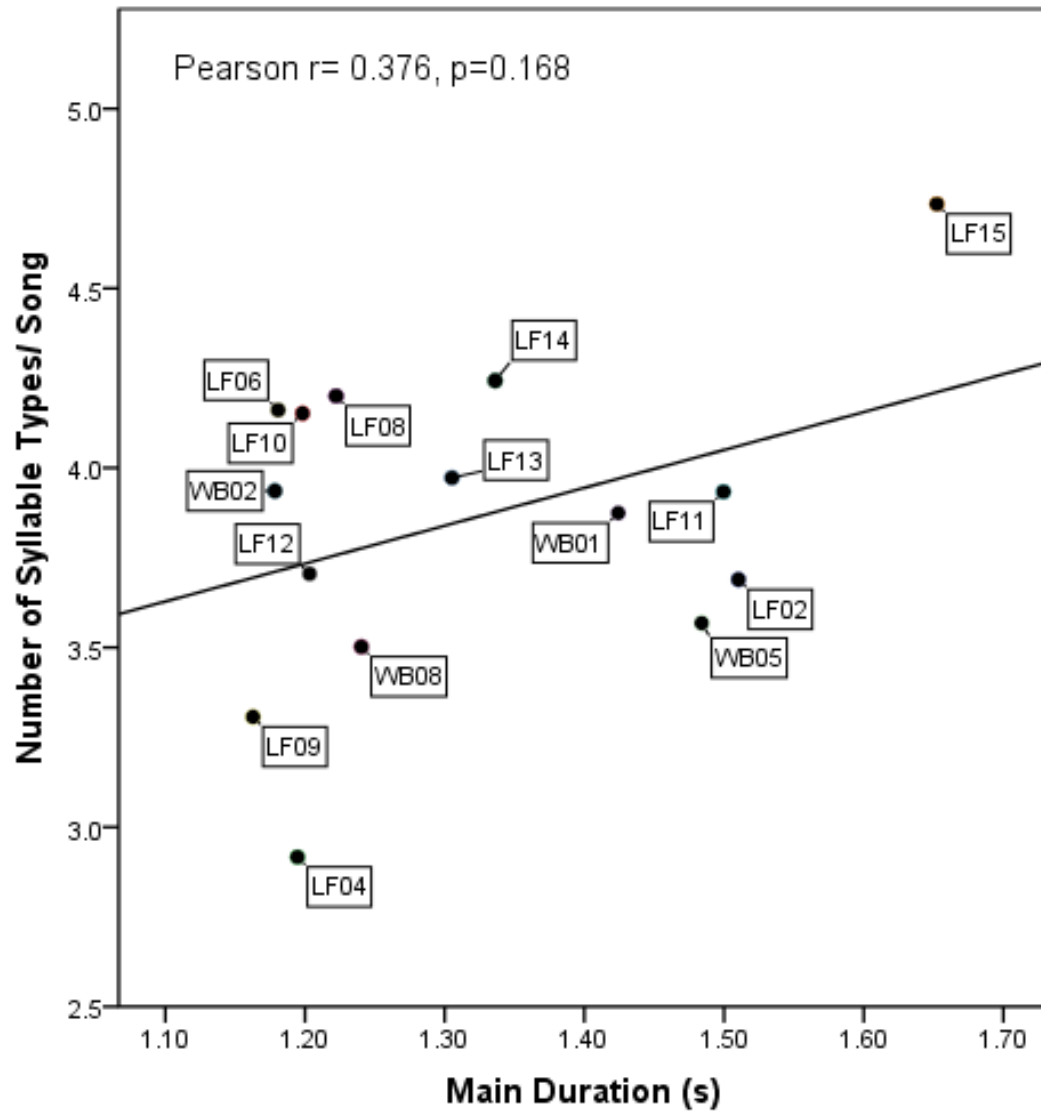
Figure 2.16: Relationship between the duration of the main section of the song and the number of syllable types produced per song. Values plotted represent the means for individual males.
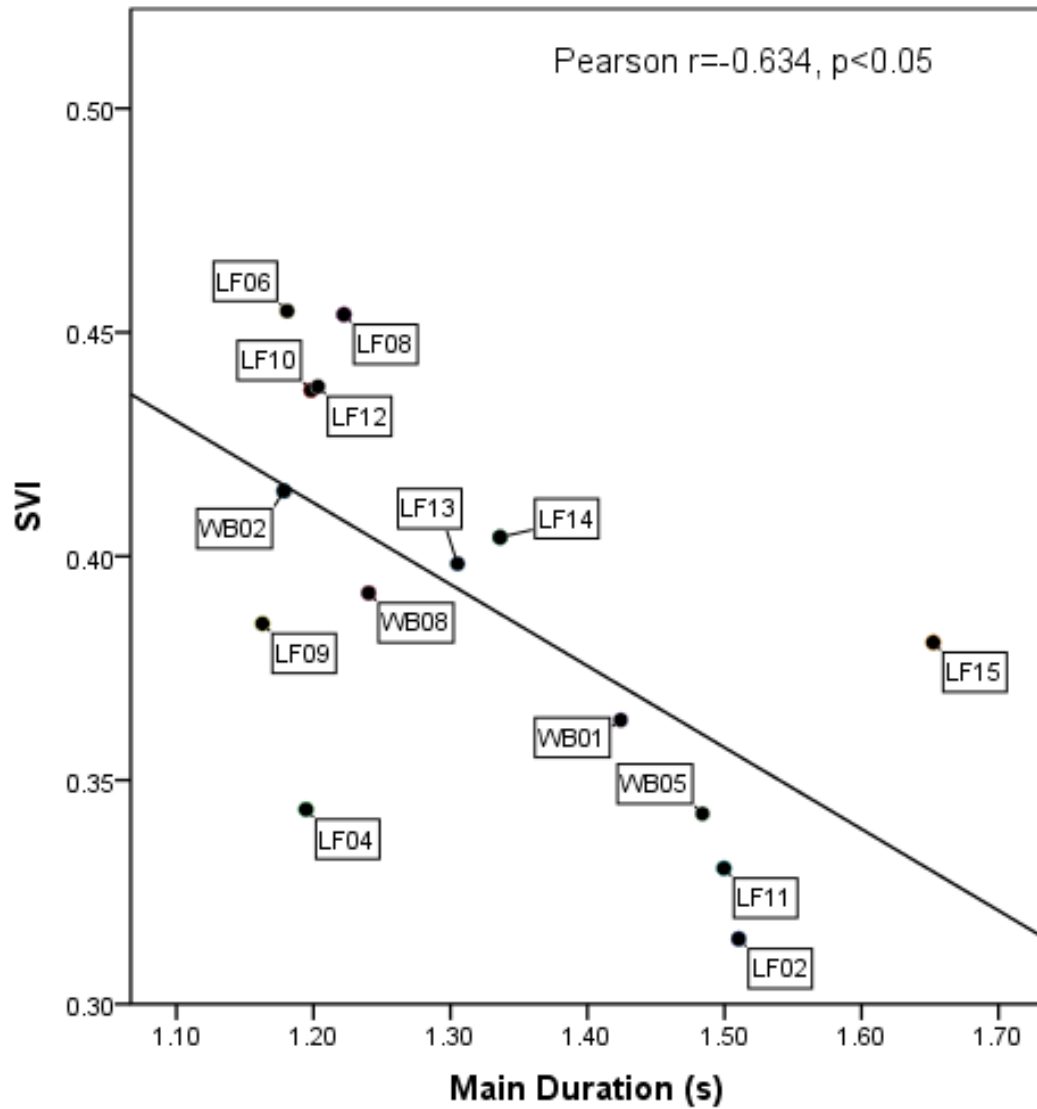
Figure 2.17: Relationship between the duration of the main section of the song and the SVI index. The SVI index measures the relative diversity, or heterogeneity, of the syllable content of songs. Values plotted represent the means for individual males.
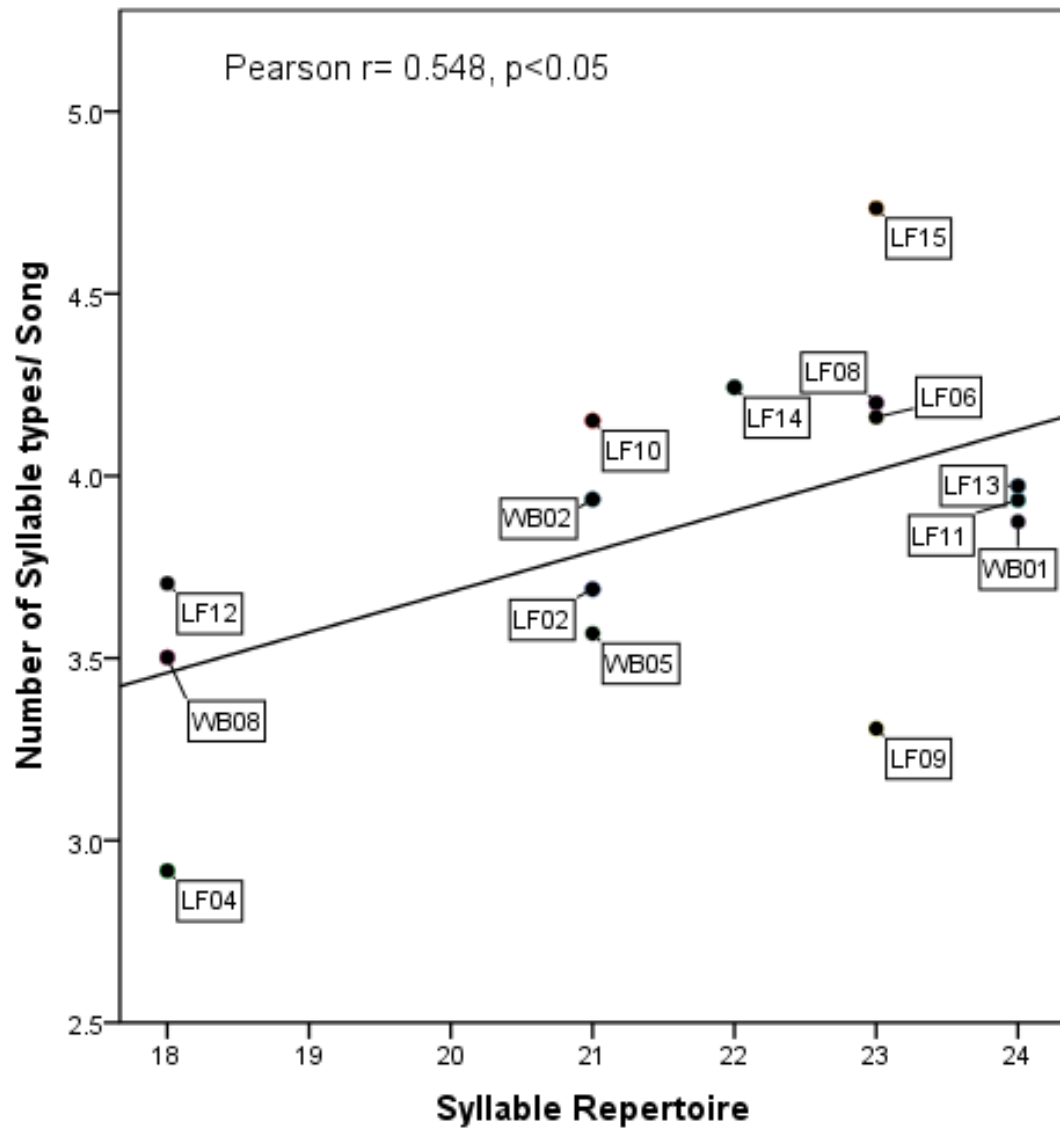
Figure 2.18: Relationship between the size of the syllable repertoire of individual males

and the mean number of syllables they produce per song.

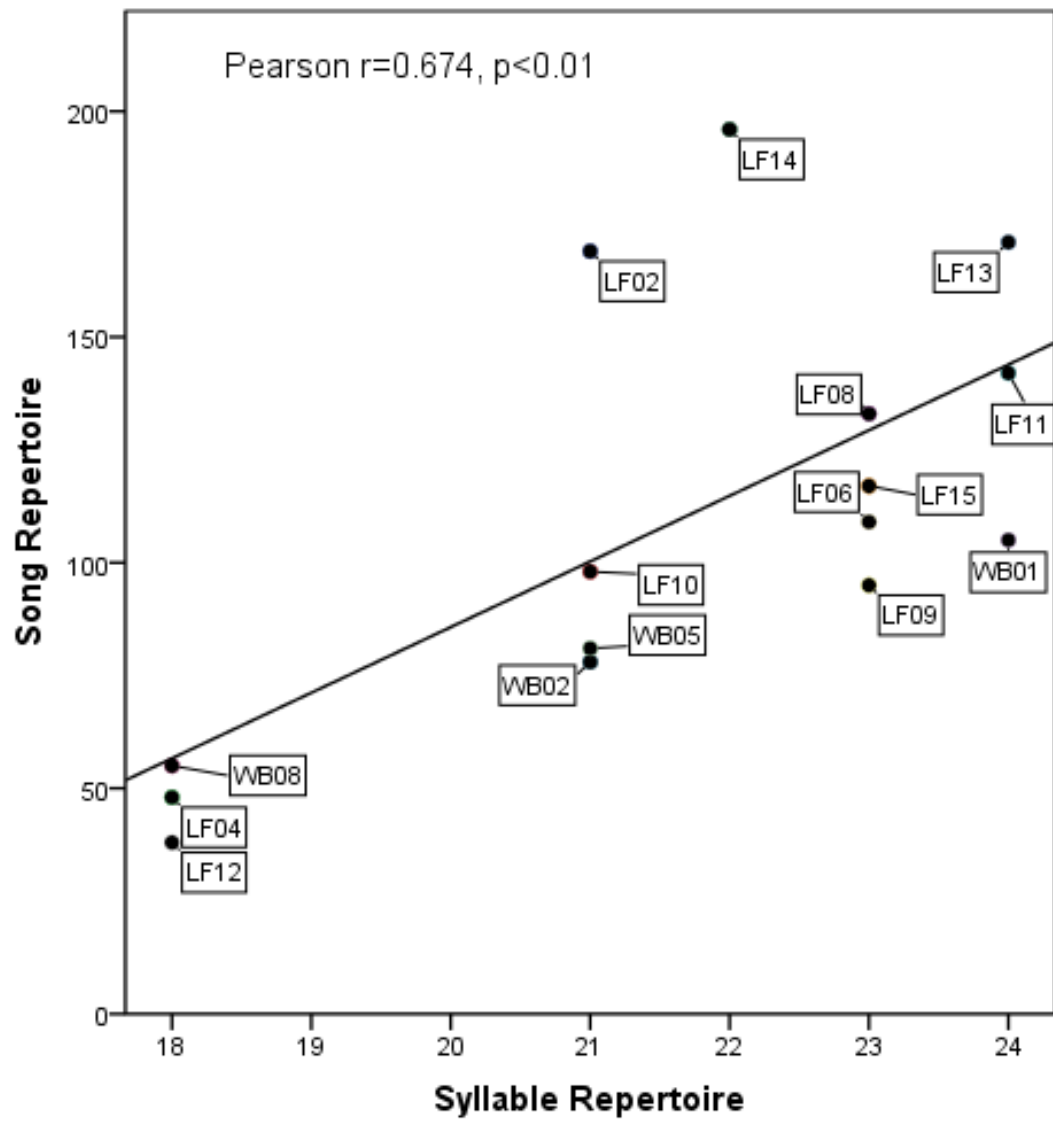Figure 2.19: Relationship between the size of the syllable and song repertoires of
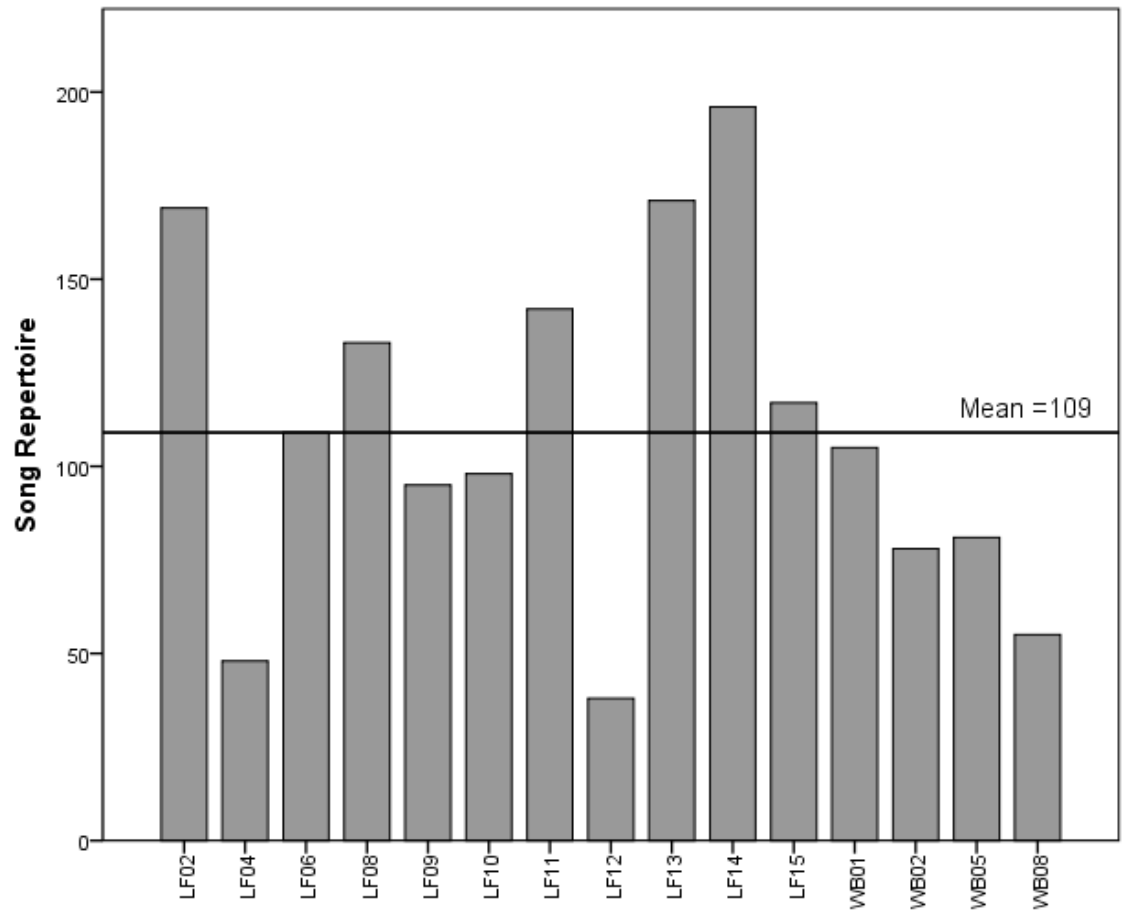
individual males.

Figure 2.20: Histogram showing variation in the size of the song repertoires of individual
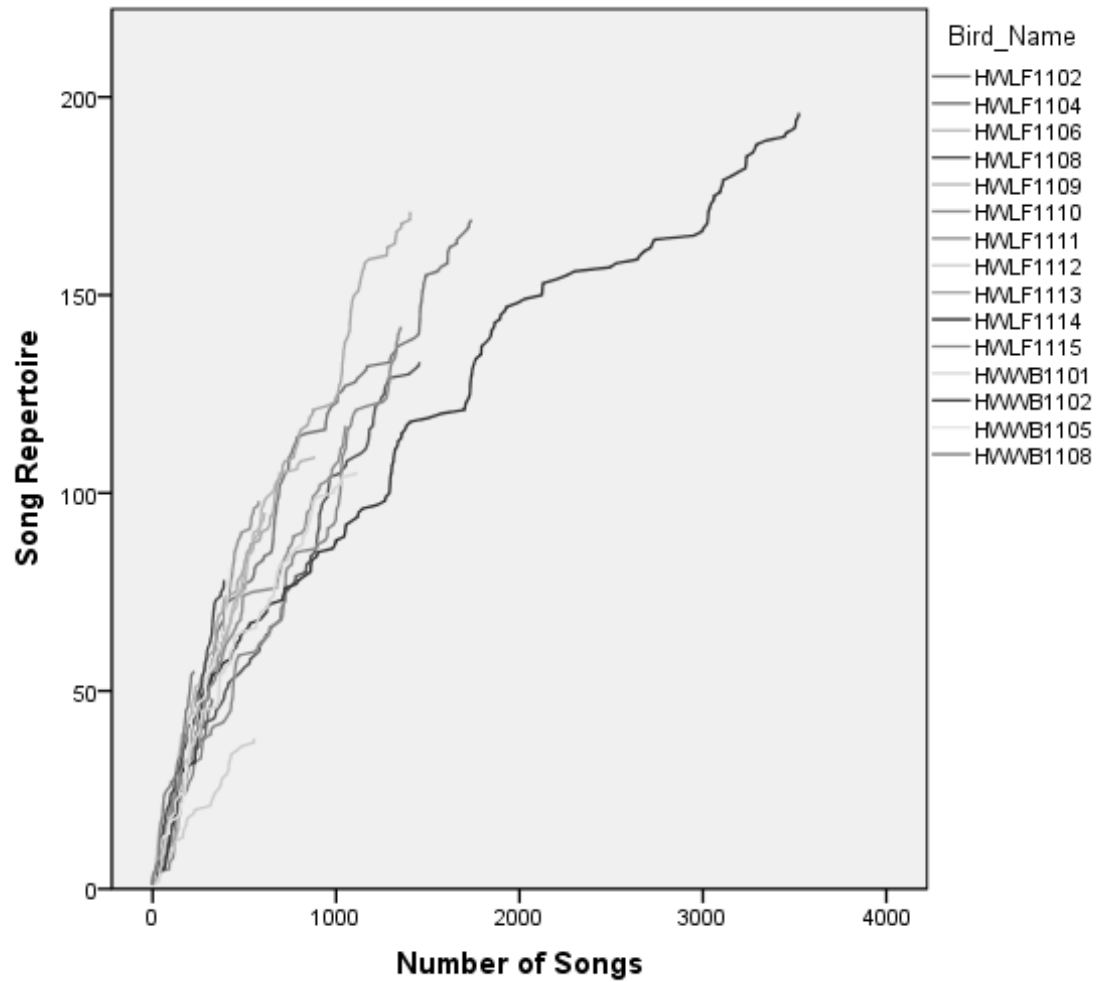
males.

Figure 2.21: Song type accumulation functions for individual males. Plot illustrates the

rate at which new song types in each male's repertoire are revealed in successive song

recordings from them.
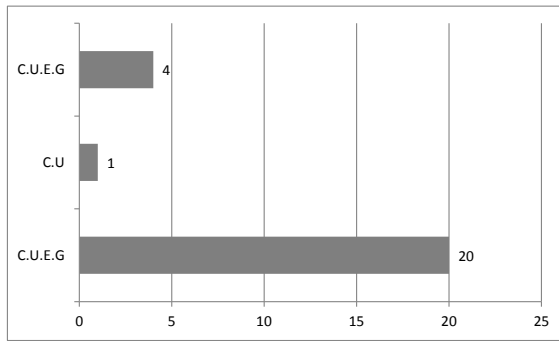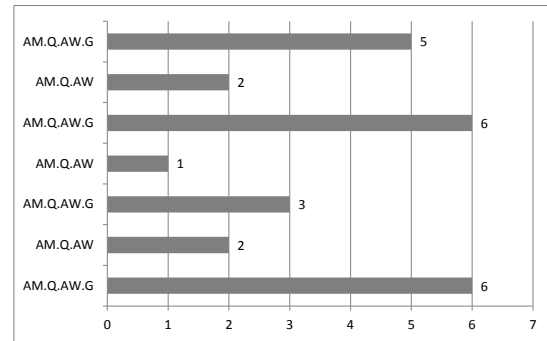
Figure 2.22a   Figure 2.22b

Figure 2.22: Examples of the typical song delivery style. Each panel represents a bout of

25 songs. The size of each bar (and the number to the right of each bar) represents the

number of times the same song type is repeated within a singing bout before switching to

a different song type. In 2.22a, the male starts with the song type C.U.E.G. and, after 4

repetitions, switches to the song type C.U. for one song, thereby dropping 2 syllable

types. He then switches back to C.U.E.G. and repeats this song type 20 times. In 2.22b,

the male also sings only two very similar song types (AM.Q.AW.G and AM.Q.AW), and

switches back-and-forth between them several times after only a few repetitions of each.
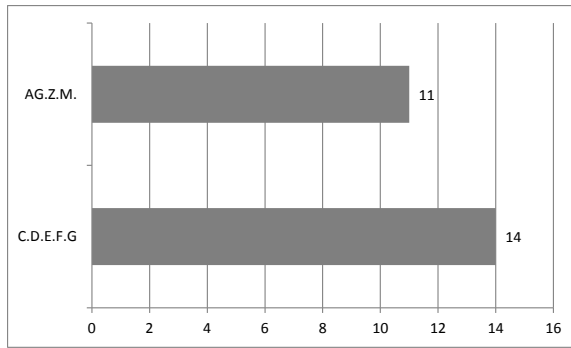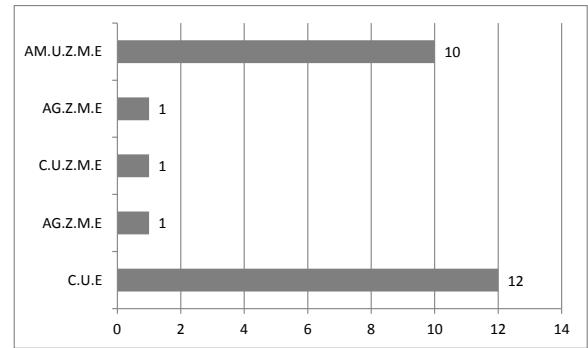
Figure 2.23a   Figure 2.23b

Figure 2.23: Examples of rarer song delivery styles that involve either abrupt or gradual

changes to very different song types. In 2.23a, the male starts with the song type

AG.Z.M. and repeats it 11 times. He then switches abruptly to a very different song type,

C.D.E.F.G. with no intermediate forms, and then repeats this new song type 14 times. In

2.23b, the transition to different song types is more gradual and involves intermediate

song types that successively add or delete syllable types.
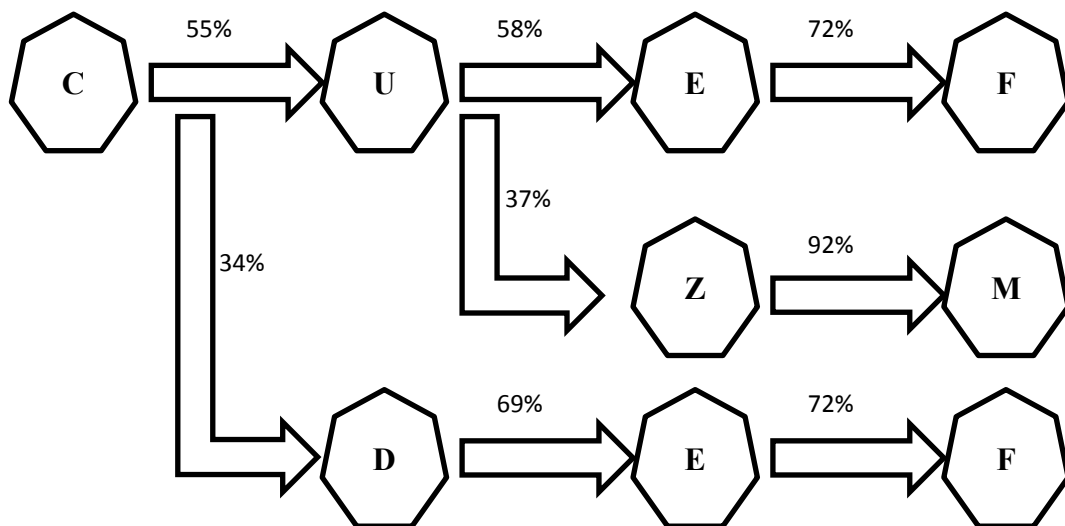
Figure 2.24a:
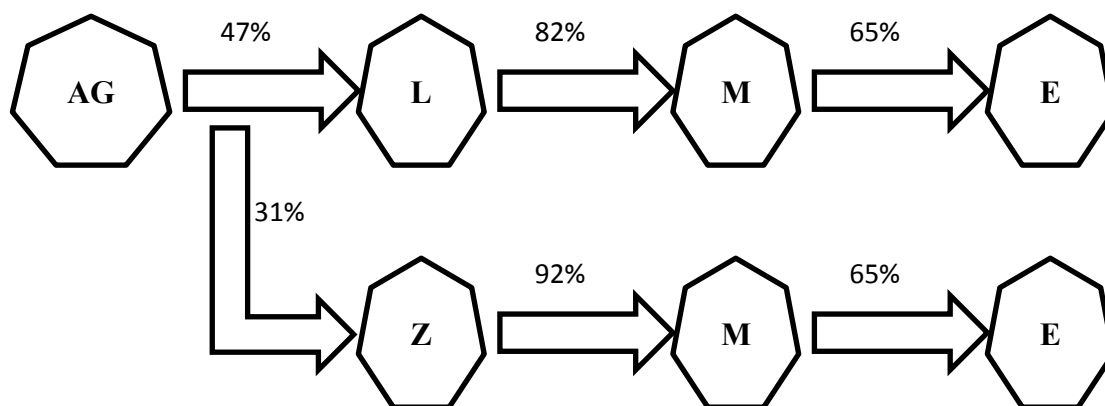
Figure 2.24b
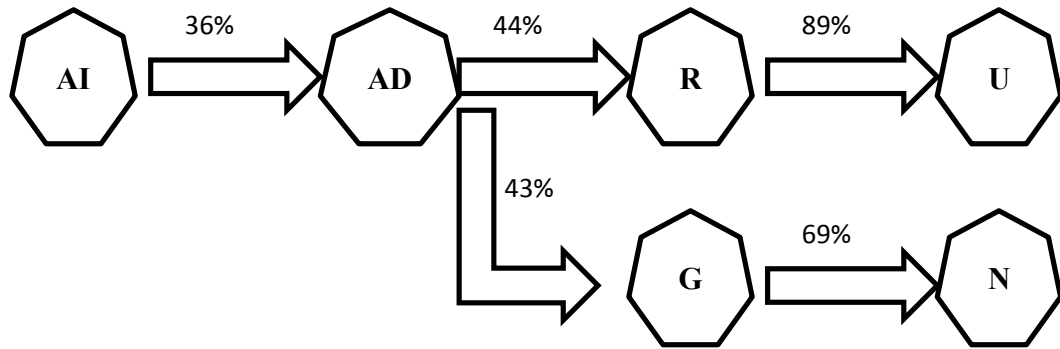
Figure 2.24c
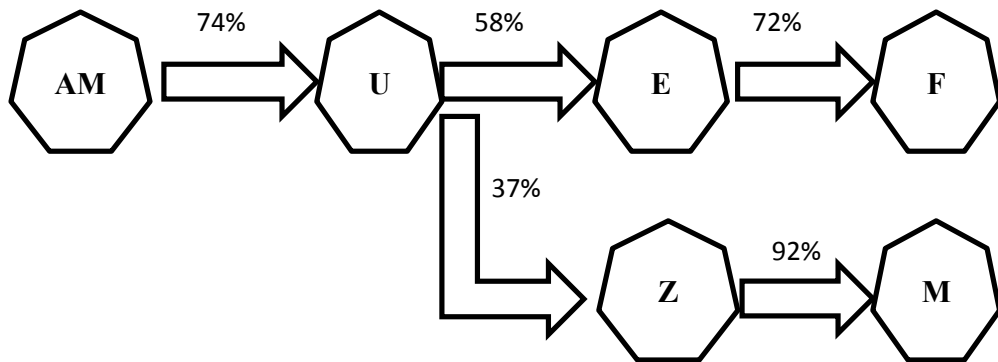
Figure 2.24d
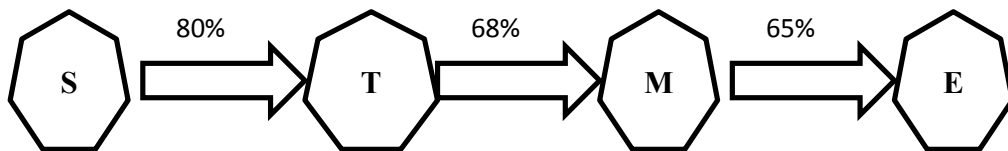
Figure 2.24e

Figure 2.24: Song templates created from the five most common seed syllables.

Each syllable after the seed syllable is based on the probability that it follows the syllable

before it. Percentages shown represent these transition probabilities based on the actual

syllable transitions observed in the entire song sample.

Chapter 3

A General Discussion of Song Variability in Northern House Wrens

The goal of this thesis was to provide an initial characterization of song organization in the Northern House Wren and further to provide some characterization of the patterns of song variability within and between males. Neither issue has been addressed systematically in previous research on this species. Hence, until now there has been no comprehensive description of the song patterns of the Northern House Wren. Furthermore, a clearer understanding of general song organization and patterns of song variability are important prerequisites for more focused studies addressing the specific behavioral functions of song and the role that variability in particular may play in mediating these functions.

For example, as outlined in the opening Chapter, one important general focus in bird song research is the role that male song plays in attracting female mates and coordinating territorial relationships with male neighbors, and there are many hypotheses concerning how both functions may be accomplished by song. A further focus of evolutionarily oriented research concerns if and how regional variation in song patterns (dialects), affect breeding behavior and contribute to genetic sub-structuring of populations ultimately potentially influencing the process of speciation. This thesis cannot credibly address any of these functional issues in detail, some of which are proposed to be taken up in greater detail in a subsequent thesis. Nevertheless, some of the results of this thesis do bear on these important behavioral and evolutionary issues.

Therefore, in what follows, each will be discussed briefly in the light of results of the present thesis that may have some relevance to them.

3.1 The Functions of Song and Song Variability in Mate Attraction

By far the most common proposed function of song for most songbird species is attracting female mates, and there is considerable evidence in support of this hypothesis, as reviewed in Chapter 1. Further, in some species, it is proposed that having a large song repertoire is also particularly functional in this respect, because large song repertoires are thought to be more difficult to produce and maintain than small song repertoires and they therefore reveal important aspects of male quality to which females should be attentive. There is also some support for this hypothesis (Catchpole 1980, 1987, Sakata & Vehrencamp 2012). Although the function of song in mate attraction was not formally tested in this thesis, a number of observations nevertheless suggest that, as in other species, song plays a role in mate attraction in House Wrens as well.

For example, male House Wrens generally sang at high intensity in the first days after arriving on the spring breeding grounds. Long song bouts with short intervals between songs were characteristics of this style of singing. Further, males generally continued to sing at high intensity like this until paired with a female. Males who remained unpaired for an extended period continued to sing at high intensity. Specific examples include male HWLF 1113 who failed to pair with a female in the first week of the season and who sung continuously during this period, and male HWLF 1114 who appeared on the study site later in the season, without a mate, and sung continuously at

high intensity for many days until he finally paired. Both birds were characterized by the largest sample of recorded songs (high song output) and had large song repertoires compared to the other birds.

In addition, when males were actively seeking a female mate early in the breeding season, they were often visited by one or more females over the course of several hours or a couple of days. These females moved around the male's territory and inspected the various potential nest cavities it contained, seemingly evaluating the breeding potential of the territory. During these female visits, males sang at notably higher intensity – longer song bouts, often with virtually no intervals between successive songs. Once paired, however, male singing intensity decreased noticeably.

Taken together, this basic pattern of general high intensity singing early in the season when males were single and especially also acute bouts of high intensity singing during active visits by prospective female mates, coupled with much lower intensity singing once paired with a female, is entirely consistent with the hypothesis that part of the function of song is to attract a female mate.

At later stages of the breeding cycle, the pattern of singing changed, in ways that were also consistent with a mate attraction function. Thus, after female mates laid eggs, male singing intensity was generally reduced. During the incubation period, some males became very quiet, and hardly sang at all. However, other males increased their rate of singing again. However, when they did, they tended to sing away from the original nest

cavity where the current female mate was incubating eggs, and from a more remote

location in their territory where there was another suitable nest cavity that could be

occupied by a second female. Indeed, other females were observed to visit such

'secondary' cavities whereupon males showed even higher intensity singing, as just noted

above when visited by a first prospective mate. These observations are consistent with

reports of attempted (and successful) polygyny in this species elsewhere (Johnson et al.

1993, Johnson and Kermott 1991b).Finally, in the last stages of breeding, when nests

reached the fledgling stage, most males spent a considerable portion of their time

provisioning chicks, alongside their female mates. And, at this stage, males generally did

not sing much.

Overall, then, the variable singing profile of male House Wrens across the

breeding cycle is consistent with the hypothesis that at least part of the function of song is

to attract female mates, sometimes more than one. These observations are in accordance

with those of Johnson and Kermott (1991a) who also found that the song output of male

House Wrens, measured as the number of songs produced per hour, varied in different

breeding stages and was highest in the premating period and declined thereafter. Johnson

and Kermott (1991a) likewise noted that males sometimes resumed high intensity singing

later in the breeding cycle to attract a second mate.

Having a large song repertoire may further contribute to mate attraction, as

reviewed in Chapter 1. The fact that House Wrens can produce quite large song

repertoires might be evidence in support of this hypothesis. However, there are some

aspects of House Wren song organization, song delivery and song repertoire size and use that are puzzling and possibly inconsistent with this proposal. For example, male House Wrens sang with 'eventual' not 'immediate' variety (Kroodsma 1977). Thus, within song bouts, they tended to sing the same song type over-and-over many times before switching to a different song type. And when they switched, they tended to switch to a song type very close the one they had just finished singing. Furthermore, although males all had sizeable repertoires of different song types (on average more than 100 song types per male), they tended to sing only a fraction of these with any regularity. Most of the song types they were capable of singing were, in fact, sung very rarely.

Collectively, these observations appear inconsistent with impressing potential female mates with the variability of one's song repertoire, because a female would have to listen for a long time in order to hear a male's full repertoire, or even a large portion of it. Indeed, producing many repetitions of the same song type over-and-over actually seems to be concealing one's singing prowess more than revealing it. By contrast, switching song types rapidly – singing with immediate variety – seems far more consistent with revealing one's prowess for song variety. Hence, this aspect of House Wren song represents a puzzle and suggests that females might use traits other than song repertoire size *per se* in evaluating potential mates based on their singing.

One possibility here is that females attend both to potential variability in song types, but also to the consistency with which males can sing them. Hence, they may prefer males that can sing some variety of different song types, but who can also sing

each one with high fidelity. If so, this might explain the pattern of male singing wherein males do sing several different song types over the course of several minutes, but they do so by repeating each song type many, many times possibly demonstrating their ability to sing each of several song types over-and-over without errors or deviations.

This possibility remains speculative, but should be taken up in future research. If the hypothesis is true, then an important potential corollary is that some of the large repertoire of different song types produced by males are, not deliberate variants produced as part of demonstrating a capacity for variable singing, but rather are mistakes in song production. This possibility might help to make sense of the different song types sung by males in the study population that were only ever produced once or twice by a given male. This is an admittedly speculative suggestion at this point but it yields an interesting and completely novel prediction *vis a vis* the mate attraction function of variable song, namely, that better quality males actually should produce smaller rather than larger song repertoires because they make fewer mistakes.

These conjectures point to the possibility that male House Wrens are striking a balance between female preferences for consistency and their preferences also for variability. These are generally conceived of as competing and mutually exclusive pressures on song production. That is, species are generally thought either to focus on consistency in song production, and thus converge on one or a few simple song types best suited to demonstrating high fidelity repeatability, or to focus on variability and diversify singing to produce large repertoires of different song types. Perhaps female House Wrens

have some balanced preference for both traits and male House Wrens, in turn, are pressured to produce songs that display both variability and repeatability.

An additional possibility worth addressing in future research is that females assess male song based on other detailed aspects of song structure rather than simply on song repertoire size alone. For example, females may be attending to specific parameters, such as peak frequency, frequency bandwidth, trill rate, or the 'bandwidth/ trill rate trade-off' that is proposed to represent a general motoric constraint on song production in songbird species generally (Podos 1996, Podos et al. 2004). An additional related possibility is that females attend to details of song structure related to the syllable sequences themselves.

For example, the syllable transition analysis undertaken here revealed that transitions between some syllable types were quite common while transitions between other syllable types were quite rare or never occurred. This pattern may indicate that some transitions are simply easier – from a motor production standpoint – while others are much harder, a possibility similar in principle to Podos' proposed bandwidth/trill-rate trade-off. If so, then males that are able to produce more 'difficult' transitions, even rarely, might be more attractive to female mates. This raises the possibility that, some of the very rare song types produced by males are not mistakes so much as males attempting especially difficult syllable transitions, which they attempt only rarely. Alternatively, these too might be mistakes, made in the process of 'experimenting' with novel difficult transitions. Both possibilities should be addressed in future work based on more detailed

characterization of the motoric requirements involved in producing different syllable types and transitions between them.

3.2 The Functions of Song and Song Variability in Territory Defense

A second major proposed function both of song and of variability in song is in territory defense, and there is evidence in support of both ideas in some species, as reviewed in Chapter 1. Some aspects of male House Wren song are also consistent with these ideas, but other aspects of House Wren song are not entirely consistent with them. Thus, at the beginning of the breeding cycle, males defended their territories vigorously. Males generally sang primarily from one or a few locations very close to the nest tree. However, males also occasionally went to the edge of their territory and sang from there. Further, if a neighboring male approached and sang close to the edge of its territory, the resident male would often fly directly toward it and sing from the edge of its own territory. During such close encounters with neighbors or intruders, males sang at a high rate with very short intervals between songs. They would sometimes also chase and attack intruders. Similar observations were made of male House Wrens by Johnson and Kermott (1991a) and the pattern of elevated singing in the context of aggressive interactions with neighbors is obviously wholly consistent with a territorial function of song.

Furthermore, as noted earlier, singing intensity decreased at later stages of the breeding cycle, especially when the eggs had hatched and the male and female were feeding nestlings. At this stage, males seemed not to consider singing by neighbor males

to be a threat unless the neighbor actually approached the nest site. It was observed that some neighboring males, who were still not paired late in the season, did try to invade the territories of males who already had nestlings in their nests. At this stage, the latter, successful males were confined to a much smaller portion of their original territory possibly because there were sufficient insect resources near the nest to provision the chicks. However, it is also possible that the shrinking of territory size was, in part, a product of the reduced singing of these males. Whether cause or effect, this additional pattern of male House Wren singing – reduced song and reduced territorial sensitivity at later breeding stages – also points to a territorial function of song. However, what is far less clear, is whether the territorial function of song is influenced by the particular songs that are sung, or the variability observed in the song repertoire, or whether the fact of singing is by itself what is most functional.

Some of the results of this thesis may also support the hypothesis that larger song repertoires play a role in territory defense. Thus, males for which the largest samples of song were recorded were those recorded at the earliest breeding stages when males were first arriving on the breeding grounds and establishing territories. These males also showed some of the largest song repertoires. Hence, it is possible that some part of these large repertoires was attributable to their function in active territory establishment and defense early in the season. Of course, this was the stage at which males were also actively courting females, so the effects of these two different functions of song and song variability are perfectly confounded at this stage of the breeding cycle.

Studies that suggest that having a large repertoire is functional in territory defense often emphasize the importance of being able to match the songs of neighbors (Vehrencamp 2001, Molles and Vehrencamp 2001). This is because song matching, and avoiding song matching, are hypothesized to be ways that neighboring males can, respectively, escalate or de-escalate aggression with neighbors. In order to match song types sung by neighbors, males must be able to produce those song types and switch to them dynamically during the course of a bout of territorial singing. Hence, having a large and flexible song repertoire is hypothesized to be important and allow males greater ability in song matching.

No data were collected for this thesis concerning dynamic song type matching during bouts of territorial singing with neighbors; hence, it is not possible to evaluate the extent to which song matching occur in House Wrens. However, some more general patterns in the song repertoires of males in the sample suggest that it may not be occurring. Specifically, the observation that males in the sample generally shared very few song types and instead tended to produce unique song types, suggests that, all else equal, song type matching in the strictest sense is not occurring. That is, males are probably not generally matching the complete syllable sequence (i.e., full song type) of neighbor male songs. Of course, it is also possible that, in territorial contests, males may match only a portion of the song that a rival male sings, and this may be sufficient to influence territorial relations. Unfortunately, there seems to be no current consensus in the literature concerning how much of a song type must be matched between neighbors in

order for it to be considered a match, the criterion often varying between studies (Beecher 2000, Catchpole and Slater 2008, Hughes et al. 1998).

A further way in which song is thought to be involved in territory defense is by reducing potential habituation by listeners to repeated songs, thereby, reducing a male's ability to habituate to the effects of his neighbor's repeated singing (Krebs 1976, 1977; Dong and Clayton 2009, Searcy et al. 1994). In this situation, long bouts of variable song should be more distracting than long bouts of the same song type. In the present work, however, male House Wrens tended to repeat song types many times within bouts with only gradual incremental changes in the song types sung. That is, they sang with relatively little short-term variety. On the surface of it, then, this pattern of singing is not at all consistent with the anti-habituation effects proposed for variable song in territory defense. At the same time, though, there was considerable variation in the number of times particular syllable types were repeated within singing bouts, even when the same overall song type was being sung. In other words, successive songs in a bout were often of the same general song type (the sequence of distinct syllable types was the same), but the number of repetitions of each syllable type often varied. So, perhaps it is possible that variation in syllable repetition of this sort, from song-to-song, is sufficient to preclude habituation in the manner proposed. Ultimately, it is difficult to know, *prima facie* without systematic study and experimentation, which of the two forms of variation is most functional in promoting anti-habituation effects.

A classic variant of the anti-habituation hypothesis for song variability in territory defense is labeled the 'Beau Geste' hypothesis (Krebs 1977). The idea is that, when facing an enemy of unknown strength it is functional to make yourself seem as intimidating as possible. One way to do this is to produce sounds that exaggerate the size of your own contingent; in this case, producing song that exaggerates the number of rivals that your enemy is facing. This may be affected by producing highly variable song that misleads newcomers into interpreting the area to be more densely populated than it actually is. A number of findings of singing by male House Wrens are inconsistent with this idea. First, if established males are to effectively mislead newcomers about the number of males in the area, they would be expected to regularly sing from multiple locations within their territories, and rapidly move between them, thereby singing in each of many different locations simulating multiple different singers. As noted earlier, male House Wrens tended not to do this. Instead, they tended to sing primarily from only one or a few relatively central locations next to the nest tree and only occasionally did they go to the boundaries of their territories to sing.

Further, if established males are to mislead newcomers about the number of males present, they should switch rapidly between different song types, as they move around to different locations, to more effectively simulate different males singing different songs. Here again, as noted several times already, male House Wrens tended not to sing in this fashion. Rather, they tended to sing the same song type repeatedly many times before switching.

On the surface of it, then, neither feature of male House Wren song is consistent with their being a role of song variability in mediating territorial relationships. Although male House Wrens can produce a large variety of different song types, they seem not to use their repertoire of variable song types in ways consistent with the anti-habituation or Beau Geste hypotheses of territory defense. Platt and Ficken (1987) similarly rejected these ideas for House Wrens based on their observations of male singing behavior.

3.3 Song Variability and the Song Learning Process

A great deal of the variety in song patterns across songbird species can be attributed to the fact that songs are learned, by imitation of the song of adult singers. Copying errors in this learning process can introduce novel variation, as can a tendency to improvise new song elements, or variants on existing elements. In many well-studied songbird species, the song learning and improvisation process is confined to a very early period post-fledging (often called a 'sensitive period') and additional learning and improvisation in adult-hood is limited (Konishi 1965, Marler and Tamura 1964, Marler 1997, Nordby et al. 2001). This is often taken to be the canonical song-learning processes and species characterized by this pattern of song learning are often referred to as 'closed' learners. In contrast, some other species are noted for their ability to continue to learn and improvise new song material later as adults (Baptista and Petrinovich 1984, Baptista and Morton 1988, Payne 1985, Todt and Geberzahn 2003). Still others appear to be able to learn new song material continuously throughout adulthood, thereby allowing them to modify their songs from year-to-year. Such species are often therefore referred to as 'open-ended' learners.

Unfortunately, virtually nothing is known about the song learning and improvisation process in House Wrens. Kroodsma (1974) suggested for a congeneric species, the Bewick's Wren, that song learning follows the traditional closed learner pattern with a sensitive period within the first three months of life and little modification thereafter. The Bewick's Wren is characterized by songs that are regarded as less variable or complex than those of House Wrens, and it is not clear whether they are a good model for the process of song learning in House Wrens. There is very little in the results of this thesis that can credibly adjudicate the matter or specifically illuminate the song learning process in House Wrens and how it might contribute to the additional variability (complexity) of song in this species. However, a few observations are nevertheless worth noting for their potential relevance to this issue.

For example, young House Wrens seem to have relatively little opportunity to learn song in their first year after fledging because, by the time they have fledged the nest, there are very few other males, including their father, that are actively singing. The only exceptions were rare cases where an adult male was courting a second female on his territory when his first nest fledged and equally rare cases where there was a single male in the local area actively courting his first female mate at very late stages of the breeding season when chicks from a neighboring nest were fledging. There were only two such exceptional cases observed during the 2011 breeding season. As a result, it would seem that most fledglings have limited opportunity to hear songs of adult males of their species after fledging the nest. Hence, most of the song exposure young birds get and from which they have to learn song patterns might come at even earlier life stages, perhaps as

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nestlings in the nest, or possibly even earlier at the egg stage. However, there is no evidence for song learning before 10 days of age (Marler 1970, Petrinovich 1985).

At the same time, fledglings were capable of producing song-like signals (sub-song) that bore a clear resemblance to adult song only a few days after they fledged the nest. Taken together, the juxtaposition of these two observations suggests that young House Wrens might learn the local repertoire of syllables very early, either while still in the nest or in the first few days after fledging. Of course, it is also possible that first year birds are exposed to song on the wintering grounds and that this over-winter song exposure is critical in song learning. It is generally assumed that, for most songbirds, very little singing occurs over winter, but this assumption has seldom been systematically confirmed. Nevertheless, if it were true that young House Wrens got considerable song exposure over winter, which was critical to them in the song learning process, then one would expect much greater variety among males in their syllable repertoires as migrants from various locations almost certainly mix liberally in wintering areas. Hence, first year males would be exposed to many more syllable types on the wintering grounds than just those sung by males in their natal populations. The fact that adult males in the Alberta populations studied all sang almost the identical set of syllables suggests that winter season song exposure is unlikely, or at least unlikely to affect the songs that first year birds learn and later produce.

The fact that all adult males sang the same repertoire of syllable types also suggests that improvisation is not a major element of the song learning and production

process. If it were, one would expect much greater differences among the syllable repertoires of different males. There were some rare syllable types (e.g., BF, BG, BH, BI) produced by only few males. And it is possible that these do, in fact, point to some degree of improvisation. It is also possible that these rare syllable types simply represent infrequent 'mistakes' in the normal copying process associated with song learning. For example, the relatively rare BH syllable is, quite similar to the more common AG syllable, while the BJ syllable is quite close to the AM syllable. Hence, it is possible that these three rare syllable types are novel variants arising by copying errors. In contrast, the rare BI syllable appears to be a re-combination of notes involved in two other syllables, namely the single note involved in the AI syllable and the repeated note that appears in the C syllable. Hence, the rare BI syllable points to some potential improvisation, or at least flexibility, in the construction of syllables from constituent notes. Otherwise, the consistency in the form of syllables across males, and the consistency in the repertoire of syllables they produce, both suggest that the song learning process is canonical and not open-ended and that it targets the memory and production of whole syllables rather than constituent notes.

At the same time, however, House Wrens clearly show a more open-ended capacity for recombining a core set of shared syllables into a much larger set of song types that differ among males. Hence, it may be at this level – the level of song type construction – where House Wrens show a capacity for improvisation. Because the sample studied here involved only a single year of song production, it is not known whether individual males sing the same (though unique to themselves) songs from year-

to-year, or whether each male has the capacity to produce new songs (from the same fixed set of syllables) in successive years. Given that other males do not generally share most songs, such a capacity for change year-on-year, if it exists, seems more likely to be indicative of ongoing song improvisation than of continued learning of novel songs from other males.

Overall all, then, it seems House Wrens may conform in part to the canonical, closed-learning pattern of song learning typical of many songbird species from which they acquire their repertoire of syllables. However, they also seem to have some more open-ended production capacities perhaps largely due to improvisation, from which they generate a large repertoire of mostly novel songs from their fixed syllable repertoires. Whether or not such improvisation capacities continue throughout adulthood is unclear, and both inferences are speculative. Nevertheless, they bear centrally on important issues in the organization and plasticity of song patterns in songbirds and on the underlying neural machinery responsible for plastic song perception and production, and these are core focuses of contemporary songbird research. Hence, the issues should be taken-up in greater detail in future work to help illuminate the potential plasticity of song learning and production in House Wrens.

3.4 Song Variability, Local Dialects, Speciation and Taxonomy

Given the above noted patterns of song learning and improvisation for House Wrens, an important corollary is that there is likely to be geographic variation in song organization and structure – i.e., dialects – as have been described for many other

songbird species. The fact that the syllable repertoire did not differ appreciably between the two Alberta study sites sampled in the present work (separated by approximately 45km), suggests that dialect variation is unlikely over very short distances, even though dialect variation can occur over such distances in other species (e.g., Marler and Tamura 1964). However, comparison of the syllable repertoires of males in Alberta with those in Wisconsin, the latter described by Platt and Ficken (1987), indicates that there is indeed geographic variation in song patterns of the sort considered as dialects over much wider distances at least.

The likelihood of dialect variation across broad geographic scales in House Wrens is increased by the fact that House Wrens are extremely widely distributed across North, Central and South America; hence, there may be many categorizable dialect differences across this range. This potential is further magnified in House Wrens because they also have very broad habitat tolerances and thus inhabit a tremendous variety of habitats across this wide range. Such habitat variation magnifies the potential for dialect variation because habitat structure has an important influence on sound transmission which, in turn, imposes important pressures on optimal song structures of populations occupying different habitats. Indeed, variable habitat acoustics contribute to population differences in song structures in songbirds (Morton 1975, Wiley 1991, Slabbekoorn & Smith 2002b, Patten et al. 2004).

These issues have important taxonomic implications for House Wrens because dialect differences have long been mooted to have an influence on population segregation

given that song plays a central role in female mate choice and selection in many species (Marler & Tamura 1964, Baker & Cunningham 1985, Irwin 2000). If females choose mates based partly on song, and they prefer males that sing local as opposed to foreign dialects, as has been shown for some other species (MacDougall-Shackleton & MacDougall-Shackleton 2001, Hernandez et al. 2009), then there is the potential for considerable genetic sub-structuring of House Wren populations across the Americas.

Further, because genetic sub-structuring of populations is a prerequisite to speciation, the potential for dialect variation in House Wrens has direct implications for the taxonomic status of these populations. Currently, House Wren taxonomy is debated, with from one to three species (and many subspecies) mooted (Brumfield & Capparella 1996, Barker 2004, Kroodsma & Brewer 2005) and considerable debate about the validity of any of the current taxonomies. To date, no systematic analyses have taken account of song as a potential character in species assessments, even though there is good reason to think it may be central in breeding segregation in songbirds generally.

If indeed there are geographic dialects in House Wrens, as seems likely, then it is a very good opportunity to study the population dynamics of the species and potentially help resolve many taxonomic issues for the House Wren species group as a whole. Further, because the role of song in the speciation process generally remains uncertain and debated (Price 2008), despite long-term assumptions that it might contribute to the tremendous evolutionary diversification of songbirds (Baker & Cunningham 1985), such

research also has broader implications for our understanding of the evolution of species generally.

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