

SONG SHARING IN THE NORTHERN HOUSE WREN
(Troglodytes aedon parkmanii)

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ABSTRACT

This work provides an initial characterization of song sharing among males in the Northern House Wren (*Troglodytes aedon parkmanii*). A sample of 21 different males was studied at two different locations across two breeding seasons in southern Alberta, Canada. In total, 35,067 songs were analyzed to assess patterns of song sharing among males within and between study sites and in returning males between years. Virtually all syllable types (n=27) were shared among males. However, they were used to create very large repertoires of mostly unique song types. Absolute levels of song sharing among males was low but song sharing was higher among neighbouring males and decreased with increasing distance between males and across study sites. These patterns are discussed as they relate to important issues in the process of song learning, in the functions of large song repertoires in mate attraction and territory defense, and in the potential formation of dialects in this species.

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Chapter 1

An Introduction to the Mechanistic, Functional, and Evolutionary Significance of Bird Song

Birdsong is amongst the most melodious, complex sounds in the natural environment. It is this quality of birdsong that has inspired some of the greatest poets and song writers alike. The complexity of birdsong has also evoked the curiosity of many great scientific minds, including that of Charles Darwin. In his work *On the Origin of Species by Mean of Natural Selection* (Darwin, 1859), Darwin introduced the idea of sexual selection and in future work, *The Descent of Man, and Selection in Relation to Sex* (Darwin, 1871), provided a comprehensive account of his theory of sexual selection.

He suggested that sexual selection is mediated by male-male competition and female mate choice. He discussed at length the courtship of birds and noted that female birds seem to have preferences for particular males. Many passages in the *Descent of Man* (1871) addressed this issue with Darwin asserting that mate choice may be the result of the male's ability to "charm and excite the female (p. 421)". As males are the predominate singers and sing most during the breeding season, he concluded that this must be the mechanism by which females are making mate choices. Although Darwin lacked any direct evidence that this was in fact the case in his time, a large body of research now suggests that male birdsong functions in two main ways both to attract and stimulate females and to repel rival males (Catchpole, 1989; Highsmith, 1989; Morse, 1970).

1.1 General Function of Bird Song in Mate Attraction

One can often catch a glimpse into the function of behaviour if the outcome of the behaviour proves to be beneficial to the organism (Catchpole, 1973). Field experiments and observation of the courtship of birds suggest that the function of male bird song is, in part, to attract a female mate (Catchpole, 1973; Kroodsma & Byers, 1991; Searcy & Andersson, 1986). If male song functions to attract a female mate, it can be supposed that males will sing at a higher rate when unpaired, and decrease singing upon pairing. To study this, observational field research is conducted where male bird song is recorded when a male is unpaired and subsequently paired with a female. It has been found that males do indeed sing at a markedly higher rate when unpaired and, upon pairing, cease to sing, or sing at a much lower rate. This has been demonstrated across a variety of species. Furthermore, Highsmith (1989) found that Golden Winged Warblers (*Vermivora chrysoptera*) also sing different song types when consorting with females using 'song type I' prior to pairing and then reducing the production of this song type after pairing.

Other research has corroborated this phenomenon, and in addition, found that the removal of the mated female restores singing to pre-pairing levels in diverse species, including White Throated Sparrows (*Zonotrichia albicollis*) (Wasserman, 1977), Sedge Warblers (*Acrocephalus schoenobaenus*) Reed Warblers (*Acrocephalus scirpaceus*) (Catchpole, 1973), and Starlings (*Sturnus vulgaris*) (Cuthill & Hindmarsh, 1985). The fact that males cease singing upon pairing, and resume singing if their mate is removed, provides strong evidence that song functions to attract a mate (Eriksson & Wallin, 1986).

The natural corollary is to test whether females are, in fact, attracted to male song *per se*. Here, a variety of indirect measures are used to assess female preference for male song, such as, approaching speakers playing song and engaging in additional copulation solicitation displays. For example, King & West (1977), raised Brown-headed Cow Birds

(*Molohrus ater*) in the laboratory in complete auditory and visual isolation from other cowbirds. When the female reached 8 months of age, she was exposed to recordings of male-cowbirds courtship songs and to songs of other species. They found that the female cowbirds displayed copulation solicitation displays only to the recordings of songs of male cowbirds. Similar preferences for own species songs have been obtained with female Sedge Warblers (*Acrocephalus schoenobaenus*) and female Song Sparrows (*Melospiza melodia*) (Catchpole, Dittami, & Leisler, 1984; Searcy & Marler, 1981).

Additional evidence supporting the mate attraction function of song comes from experiments in which loudspeakers and stuffed birds were placed next to nesting boxes containing traps designed to capture females who entered the territory (Erikson and Wallin (1986). In this experiment, significantly more females were trapped at nest boxes that broadcast conspecific song as compared to silent nest boxes.

Taken together, a variety of forms of evidence suggest that male song plays a role in attracting female mates and that females attend to male song when selecting mates.

1.2 General Function of Bird Song in Territory Defence

A second proposed function of male song is in competition between males, particularly in establishing and maintaining territories. Research has shown elevated levels of singing during territorial encounters between males in several species, including: Willow Warblers (*Phylloscopus trochilus*) (Järvi, Radesäter, & Jakobsson, 1980), Plain Titmice (*Parus inornatus*) (Johnson, 1987), House Wrens (*Troglodytes aedon*) (Johnson & Kermott, 1989, 1991), Reed Warblers (*Acrocephalus scirpaceus*) (Catchpole, 1973), and Yellow Warblers (*Dendroica pelechia*) (Morse, 1966). Research has also shown that neighbouring males respond aggressively to experimental playback

of song from other conspecific males, sometimes even approaching and attacking the playback speaker in species such as the Sedge Warbler (*Acrocephalus schoenobaenus*) (Catchpole, 1977), American Redstart (*Setophaga ruticilla*) (Ickes & Ficken, 1970) and Trials Flycatchers (*Euphidonax Traillii*) (Stein, 1963). Additional studies have shown that, in some species, males sing different songs during agonistic encounters. For example, Jarvi et al (1980), found that male Willow Warblers (*Phylloscopus trochilus*) produce a specific song type in agonistic encounters with rival males and, when exposed to playback of this song type, a listening male is more likely to retreat than when exposed to other song types.

Finally, male removal experiments have been conducted to test the role that song, by itself, plays in mediating territorial conflict. In this paradigm, a male is removed from his territory and replaced with a playback speaker that either continues to broadcast his song or that is not activated and remains silent. Experiments like this conducted on a variety of species, including White Throated Sparrows (*Zonotrichia albicollis*), Thrush Nightingales (*Luscinia luscinia*) (Falls, 1988) and Great Tits (*Parus major*) (Krebs, Ashcroft, & Webber, 1978) show that the song itself is sufficient to reduce territorial intrusions.

1.3 Song Matching and Territory Defence

One proposed way males can reduce the costs associated with aggressive interaction with territorial neighbours is to address one another indirectly with their songs in a phenomenon termed ‘song matching’. As the name suggests, song matching occurs when one male responds to the singing of a territorial neighbour by singing the same type of song in reply (Beecher & Brenowitz, 2005). Song matching is argued to be a tactic for

directing one's song at a specific rival. The phenomenon has been demonstrated in several species, including Song Sparrows (*Melospiza melodia*) (Anderson, Searcy, & Nowicki, 2005; Beecher, Campbell, & Nordby, 2000), Great Tits (*Parus major*) (Falls, Krebs, & McGregor, 1982) and Indigo Buntings (*Passerina cyanea*) (Payne, 1982).

However, there is some debate concerning how best to characterize the detailed function of this phenomenon, that is, to understand more clearly exactly how song matching works to adjudicate territorial competition. One proposal is that song matching qualifies as an unfakeable index of a male's quality (Smith & Harper, 1995) the honesty of which is guaranteed by the constraint of whether or not the male is able to match a rival's songs. Alternatively, others have proposed that song matching is a conventional signal of aggressive intent (Krebs, Ashcroft & Orsdol, 1981) the honesty of which is guaranteed by the ability to repel whatever physical attack ensues by matching and escalating aggression (Vehrencamp, 2001). Still others have proposed that song matching is a performance signal that reliably signals a male's quality because it allows listeners to gauge which of two males sings the better version of a particular song (Louge & Forstmeier, 2008).

1.4 Song Complexity

The general mate attraction function of male song is well-established. However, it is less clear exactly how song functions to attract female mates. Put differently, what are the features of male singing that females find attractive? In particular, what accounts for the great variety of songs by different species? In some species, males sing only one or a few simple songs. In other species, males possess large repertoires of sometimes long and complex songs. What accounts for this variety? Why have some species developed a

large and complex repertoire of songs to accomplish what other species accomplish with one or a few simple songs? In fact, the issue of song complexity has become a major focus of research in the evolution of birdsong.

The current consensus is that complex song advertises male quality at multiple levels (Brenowitz & Beecher, 2005; Gil & Gahr, 2002; Sakata & Vehrencamp, 2012) because song is a complex motor act that requires integration of multiple motor systems as well as specialized neurocognitive circuits to learn, remember and reproduce a large repertoire of different songs.

A variety of evidence supports this general hypothesis. For example, it has been shown that females prefer males with larger song repertoires (Searcy & Yasukawa, 1995) and that choosing males with larger repertoires brings direct benefits to females as males with larger repertoires are often older more experienced males, hold higher quality territories, and can invest more in offspring care (Catchpole, 1996).

In fact, large song repertoires and complex song patterns are often held to be the vocal equivalent of the “peacock’s tail” (Catchpole, 1987), i.e., they have been produced by sexual selection for extreme forms. Such extreme traits are thought to be adaptive because the costs associated with their elaboration are more than compensated by the benefits received in mating. Large song repertoires, like the peacock’s tail, are thus thought to be honest indicators of male quality (*sensu* (Zahavi, 1975).

A related hypothesis is that elaborated male traits advertise a male’s good genes and that it pays females to attend to such traits because they procure better genes for their offspring as a result. There is a variety of evidence consistent with this proposal. For example, females have been shown to select mating partners on the basis of genetic

heterozygosity which confers fitness advantages to their offspring (Keller & Waller, 2002). Furthermore, Foerster et al (2003) found that, in socially monogamous Blue Tits (*Parus caeruleus*), females pursued extra-pair copulations because this increased the heterozygosity of her offspring and resulted in higher reproductive success. Importantly, heterozygosity in socially monogamous birds has been shown to be correlated with other sexually selected traits such as song repertoire size (Marshall, Buchanan, & Catchpole, 2003).

1.5 Female Preference for Complex Song

Many field studies confirm female preferences for larger repertoire size. Male Song Sparrows (*Melospiza melodia*) with larger song repertoires were more likely to mate during their first year as they were more likely to pair with newly settled females. Furthermore, females who mated with males with a larger repertoire were more likely to breed earlier (Reid et al., 2004). In addition, song repertoire size in the Great Reed Warbler (*Acrocephalus arundinaceus*) correlated positively with the likelihood that a male would obtain another mate (extra pair fertilization) and when comparing his repertoire with the mated cuckolded pair-male, his repertoire size was always larger (Hasselquist, Bensch, & Von Schantz, 1996). Lamp & Esmark (2003) also provided further support in the Pied Flycatcher (*Ficedula hypoleuca*), with females of this species showing a preference for more complex song, evidenced by larger repertoire size and song versatility in paired males when compared to unpaired males. Laboratory studies also confirm this female preference for large repertoire size in Yellowhammers (*Emberiza citronella*) (Baker, Bjerke, Lampe, & Espmark, 1987), and female Great Tits (*Parus major*) (Baker, Bjerke, Lampe, & Espmark, 1986).

Most of the studies focus on female preference for large repertoires. One area of research that is particularly lacking is the extent to which large repertoires might be meaningful to same sex competitors. A study conducted by Leitao, ten Cate, & Riebel (2006), compared the responses of males (in the field) and females (in the laboratory using operant preference with song as a reinforcer) to songs with equal duration but which varied in the number of trill phrases. Both the males and females showed stronger responses to the songs with greater number of trills, suggesting that females may not be the only ones driving song complexity.

At the same time, however, there are other studies that report different findings, even within the same species, with some females preferring larger repertoires and others showing no preference (see review (Byers & Kroodsma, 2009). Forstmeier & Leisler (2004) conducted research on the Great Reed Warbler (*Acrocephalus arundinaceus*) which is a species commonly cited in support of a female preference for large song repertoires (Catchpole, 1986). These authors found that previous supportive data was confounded and potentially attributable not to song complexity *per se* but to variation in male age and territory quality. That is, females preferred older males who also had better territories and more complex songs compared to younger males making it difficult to know which is the causal factor in the preference (Forstmeier & Leisler, 2004).

In a similar vein, Howard (1974) found a correlation between male repertoire size and female preference that disappeared when territory quality was controlled. Yasukawa (1981) also found a female preference for large song repertoires in Red-winged Blackbirds (*Agelaius phoeniceus*) that disappeared when male age was controlled for.

Further, Krebs (1978) found no preference for complex song repertoires in the Great Tit (*Parus major*).

Ultimately, studies simply showing a preference for song complexity without controlling a variety of confounding factors do not provide unequivocal evidence that it is song itself, as opposed to some other trait of males, that is influencing female mate choice (Reid, et al., 2004). Overall, then, the current evidence in support of a female preference for large song repertoires is mixed and often confounded by other factors (Byers & Kroodsma, 2009). Further research on female preference for complex song is warranted with a focus on separating out confounding variables such as male age and territory quality.

1.6 Origins of Variable/complex Song

An additional important question concerning song variability is the mechanism by which variability is acquired and maintained. Some possibilities are revealed through study of the song learning process in different species which points to different patterns and styles of learning that ultimately lead to either variable song or not (Brenowitz & Beecher, 2005).

Differences exist on many dimensions of song learning, including: whether song is learned only once during an early sensitive period in life (so called, closed-ended learners), as exemplified by the Zebra Finch (*Taeniopygia guttata*), or whether new songs can be learned throughout life (open-ended learners), such as in the European Starling (*Sturnis vulgaris*) (Mountjoy & Lemon, 1995); whether birds learn songs by copying complete song types of conspecific males (Zebra Finch) (*Taeniopygia guttata*), or by improvising a set of novel song types from a set of learned song elements, as in the Sedge

Wren (*Cistothorus platensis*) (Kroodsma & Verner, 1978). Which song learning process is favored in a particular species may reflect additional functional pressures. For example, for species that engage in song matching as a way of mediating territorial competition, it is functionally important to be an 'open-ended learner' to allow the addition of new songs sung by new male neighbours from year-to-year.

An additional important source of song variability comes from errors in the process of copying songs during song learning (Marler & Slabbekoorn, 2004). With time, errors can accumulate in local populations causing 'drift' in the song types produced by males in different areas. When such differences become entrenched, they are often referred to as 'dialects' on analogy to regional variation in human languages.

1.7 Local Dialects, Population Sub-structuring and Speciation

Song dialects represent regional variation in song types produced by different populations of males. This process can have important consequences for genetic sub-structuring of populations and perhaps ultimately for speciation because, as already emphasized, song plays a prominent role in mate selection. If females have a preference for the local dialect they find themselves in, then the song differences between regions can become effective barriers to gene flow. This process has been proposed to be a possible route to speciation (Marler & Tamura, 1962).

Dialect variation in song has been documented in a variety of species, but most notably in White-crowned Sparrows (*Zonotrichia leucophrys*) studied by Peter Marler in the San Francisco Bay area (Marler & Tamura, 1962). White-crowned Sparrows in this region consist of three populations with a greater heterogeneity in song patterns between compared to within populations. The effect of this variation on female mating

preferences has not been studied in this population of White-crowned Sparrows but has in others which has confirmed a female preference for local dialects over foreign ones (Baker, 1983; Baker, Spitler-Nabors, & Bradley, 1981; MacDougall-Shackleton & MacDougall-Shackleton, 2001).

The territorial response of males to local versus foreign dialects has also been tested and, like females, males have been found to respond more strongly to local dialects (e.g., Darwins' finches (Ratcliffe & Grant, 1985), and White-crowned Sparrows (Milligan & Verner, 1971).

In sum, dialect variation in songs has important evolutionary implications as a possible route to speciation. Indeed, some have argued that it is specifically the capacity for song learning, and with it the capacity for geographical variation in song (dialects), that explains the tremendous diversity of songbird species (Baker, 1983). Although this assertion remains debated, it does highlight the importance of better understanding the origin and maintenance of song variation within and between populations. And one obvious index of such variation is the degree to which males within and between populations share songs.

1.8 Song Sharing and Song Development

The extent to which males share songs can also depend on details of the song learning process and how that integrates with other important life history factors such as migration behavior. For example, the song learning strategy employed by species might vary as a function of whether the species is migratory or sedentary (non-migratory). In sedentary species of populations, sexually mature males in a given area may often share songs because they have learned from other males in their natal community and, because

the birds do not migrate, the composition of the male population is relatively stable across years. In contrast, in migratory species or populations, where lifespans are generally shorter and over-winter survival worse, the turnover of males in breeding populations is higher. Hence, there may be more pressure for males to be able to add songs that match the songs of new neighbours each year and drop others that do not match.

Nelson and Marler (1994) have outlined a model to account for these processes. They argue that the song learning process has two stages. The first stage happens during the bird's natal year, when songs are memorized early in development by listening to songs of other males in the local population. The second stage ensues during the first breeding season when these young males are now mature and males must establish their own territory. During this stage, referred to as selective attrition, males must select those songs from the broader set they heard in their first natal year a subset that will make up their final repertoire.

Their song choice is shaped by counter-singing interactions with neighbouring males, as a male attempts to match the songs of his new neighbours. This process involves pruning songs from a larger repertoire of those heard the year before to converge on a set needed to interact with local neighbours. This process is usually employed to explain species of birds that are referred to as 'closed' or 'age-limited' learners.

The model can be extended to account for migratory males that, from year-to-year, may settle next to a male with whom they do not share songs. In this case, the male would have to modify his songs to match those of his new neighbour. Marler and Nelson suggest that, in this case, the male may combine elements from his original plastic

repertoire of songs to create songs that match his present neighbour to the best of his ability. This process would then exemplify a more ‘open-ended’ learning strategy. In either case, the extent to which a male can match the song of his neighbours has implications for his ability to acquire and maintain a territory as well as attract a mate.

1.9 Song Sharing: Mate Attraction and Territory Defence

Both the size of a male’s song repertoire and the ability to match songs are factors that may play an important role in acquiring a territory, defending it and attracting a mate. Thus, to acquire and maintain a territory a male needs to efficiently address rival, neighbouring males. And, as noted above, one way to do this is via counter-singing and song matching. Furthermore, males with the largest song repertoires may be more effective competitors in such neighbour competition precisely because they can match the songs of a larger number of rivals so as to escalate aggression with them or avoiding matching (by singing non-overlapping song types) to reduce aggression (Vehrencamp, 2001).

Following from this, females (and other males) may attend to such counter-singing contests between rival males and glean valuable information on male quality that assists them in their mate choice (and male avoidance) decisions (Logue & Forstmeier, 2008), a phenomenon sometimes referred to as ‘eavesdropping’ (Mennill, Ratcliffe, & Boag, 2002). That is, from vocal duels between males, both females in the area and other males may learn things about the quality of rival singing males. For example, they may attend to whether a male matches or does not match the song of his rival when counter-singing. Vehrencamp (2001), argues that all males have the potential to match the song of their neighbours but they will only do so if they perceive that they can withstand a

physical attack by their opponent. Hence, matching is regarded as more threatening than non-matching when counter-singing. She thus believes that matching conveys short-term information about aggressive intention while non-matching is signaling submission. The honesty of this dynamic is maintained by receiver retaliation or punishment. If a male matches the song of a neighbour then he must be able to withstand a subsequent attack prompted by matching.

At the same time, when rival males match songs, this provides other listeners an opportunity to make refined comparisons of the quality of the song renditions produced by two counter-singing males, in this way learning something additional about potential variation in their quality based on how well they sing the same songs (Logue & Forstmeier, 2008). This hypothesis predicts that fit males benefit from matching because it displays to eavesdroppers their ability to outperform a rival male. In contrast, low quality males should avoid matching or being matched. Hence, they should produce songs that other males do not produce to preclude detailed comparisons of variation in the quality of song renditions. This process of avoiding matching may select for increased song complexity, paradoxically, by forcing less fit males to produce more novel songs to avoid being matched by other males. These other males, in turn, then attempt to match the song types of less fit males to demonstrate their superior quality, which selects for less fit males who develop even more novel songs, and the system continues to ratchet up. In this way, large, complex song repertoires may result from the song matching competition that mediates male-male territorial rivalry but then also provides an opportunity for females to glean information about male quality in the process thereby also mediating mate choice.

1.10 Summary

In general bird song has two main functions: to attract a mate and to defend a territory. A puzzle arises when song repertoires become highly variable and complex. Why do some species use only a few songs to attract a mate and defend a territory while other species use a multitude of songs to accomplish the very same thing? Also, what are the origins of variable song? Does variability stem simply from the copying errors that arise naturally through the process of cultural transmission of song, or through a more active process of song improvisation? While it is argued that song complexity may be attractive to females, research is lacking on the function of song complexity in male competition. One way in which males can address one another is through a process of song matching, but this phenomenon has primarily been studied in species with small repertoire size. Few studies (Price & Yuan, 2011) have investigated song matching in species with large repertoire sizes, where it may be more challenging to match a particular song type. In this case, the ability to match songs in the service of male-male competition may also indicate features of male quality relevant in female mating decisions. Hence, the phenomenon of song sharing has implications for many important dimensions of the life-history and evolution of songbirds.

1.11 Thesis Objective

The objective of this thesis is limited to providing an initial characterization of the extent and patterns of song sharing among males in two populations of the Northern House Wren (*Troglodytes aedon*). Research on song sharing among males with large repertoires is lacking and this research will thus help fill an important gap as House Wrens are noted for having large, complex song repertoires (see below). Song sharing in

the Northern House Wren has not been studied systematically and a study of this sort has the potential to contribute to our understanding of the function of song sharing and its possible roles in mate attraction and male rivalry and also illuminate details of the song learning style of this species. The latter has implications for the possibility of regional dialects in this species which, in turn, has ramifications for the potential genetic sub-structuring of populations that is ultimately the basis for speciation. Hence, there are a variety of potential implications that flow from an analysis of song sharing.

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

The House Wren (*Troglodytes aedon*) has been the subject of many studies including comprehensive research on ecology, behaviour and taxonomy (Keith, 2004). The house Wren is a small (10 gram), active and insectivorous bird. It is a cavity nester and will nest in a variety of natural cavities including those produced by wood peckers but also crevices in trees or in artificial nestboxes. House Wrens are widely distributed from southern Canada to South America (Brumfield & Capparella, 1996). In fact, they have the widest distribution of any songbird in the Western Hemisphere. The species wide distribution is attributable no doubt to its ability to adapt to highly diverse habitats, including many types of disturbed habitats and areas used by humans. In general, house Wrens prefer open, sparse forests and forest edge habitats, which preference suggests a bias to boundary areas and disturbance. This preference accounts for their ability to thrive in many anthropogenically modified habitats including in cities and towns.

1.11.2 Taxonomy Uncertainties

Across its wide geographic range the taxonomic status of different populations of House Wrens is debated. Typically, House Wrens are divided into three groups that are

either full species or subspecies of the nominal *Troglodytes aedon*. The three groups are:

1. The Northern House Wren (*Troglodytes aedon aedon*) which breeds from Canada to southern United States and northern Mexico (California, Mexico);
2. The Brown Throated Wren (*Troglodytes a. brunneicollis*) which breeds from southeastern Arizona to Oaxaca and west-central Veracruz, Mexico, and;
3. the Southern House Wren (*Troglodytes a. musculus*) which breeds from eastern Oaxaca, Mexico to Tierra del Fuego, Chile (Brumfield & Capparella, 1996).

Although there is little morphological and plumage variation among these populations there are considerable behavioural and life history differences. For example, the Northern House Wren is migratory and shows appreciable levels of polygyny (Johnson & Albrecht, 1993; Johnson, Kermott, & Lein, 1993), and has large clutch sizes of 7-8 eggs. In contrast, the Southern House Wren is sedentary and is monogamous in year-round territories, with smaller clutch sizes of 4-5 eggs (LaBarbera, Lovette, & Llambías, 2012).

The dramatic behavioral and life-history differences between Northern and Southern House Wrens has prompted some researchers to question whether they are really part of the same species or should be elevated to their own species status. Elevating each to species status is suggested by some genetic work (Arguedas & Parker, 2000; Brumfield & Capparella, 1996). However, the lack of plumage or other morphological variation mitigates against. Overall, there is continuing uncertainty about the taxonomic status of House Wrens. Here, variable song patterns offers an important opportunity to resolve matters because song is important in mate attraction and territorial defence (Catchpole, 1989), and consequently also in species recognition. Hence, research on

patterns of song variation in Northern House Wrens may contribute to resolving taxonomic uncertainties.

1.11.3 Song variability in House Wrens

House Wrens are noted informally for their singing ability and are arguably among the finest and most voluble singers. Their effervescent song attracts many naturalists who casually note the Wren for having a variable, complex song. Only a handful of studies have been conducted to examine song organization in any detail. Kroodsma (1977) studied song organization in nine different species of Wren, including the House Wren, and found the song of all nine species to be complex with the House Wren toward the extreme end of complexity. Platt & Ficken (1987) also conducted research on song organization in the Northern House Wren (*Troglodytes aedon*) and reported several patterns of variable song organization.

The most comprehensive study to date is that by Rendall & Kaluthota (Kaluthota, 2013; 2013) which provided a detailed analysis of song organization and variability in Northern House Wrens (*Troglodytes aedon parkmanii*). That work confirmed that the songs of Northern House Wrens are indeed highly variable and complex. The research reported here builds on this recent study and provides a detailed analysis of patterns of song sharing in the same populations of birds. As emphasized earlier, song variability and complexity affords males increased opportunity to engage in complex vocal interactions. Hence, a detailed study of patterns of song sharing in these populations thus offers a natural opportunity to extend recent work on this species and contribute to a better understanding of the diverse possible mechanisms and functions of complex song in this and other songbird species.

Chapter 2

A Detailed Analysis of Song Sharing Patterns in the Northern House

Wren

Song sharing is a phenomenon in which males of a particular species in a local area may sing songs that have the same detailed (notes and syllable) structure. The phenomenon of song sharing bears on a number of important issues in the life-history and evolution of songbird species, including in the processes by which learned songs are acquired, in the functions of large song repertoires in mate attraction and territory defense, and in the potential formation of dialects that may create barriers to gene flow between populations and thus lead to speciation.

In an effort to contribute to these issues, the phenomenon of song sharing was studied in the Northern House Wren (*Troglodytes aedon parkmanii*). There has been no previous study of song sharing in this species, and only few studies of its pattern of singing in general (Kroodsma 1977; Platt & Ficken 1987; Johnson & Kermott 1991; Rendall & Kaluthota 2013), but the species is noted for producing large, complex repertoires of different song types which provide ample opportunities for song sharing among males. This chapter provides an initial characterization of song sharing among male House Wrens studied at two different studies across two breeding seasons in southern Alberta, Canada.

2.1 Materials and Methods

2.1.1 Study Site

Research was conducted over the course of two consecutive breeding seasons (2011-2012) at two field sites in the foothills of the Rocky Mountains of southwest Alberta, which represents a montane habitat at approximately 1200-1400m elevation. The characteristics of the habitat include a medley of open grasslands interposed by small stands of Aspen (*Populus tremuloides*) and occasional Douglas fir trees (*Pseudotsuga menziesii*).

One site was located in the Bob Creek Wildlands of the Whaleback region (Alberta Wildlife Management Unit 308) and the other was located approximately 35 km away on private lands in the Burmis-Lundbreck Corridor (Alberta WMU 302). These sites were strategically chosen for their similar montane habitat profiles to minimize the effects that variable ecologies can have on song structure.

2.1.2 Study Subjects

Research was conducted primarily between May and August which represented late spring and summer for this latitude. This time also represents the primary breeding season for the Northern House Wren with birds starting to arrive at the breeding grounds as early as the second week in May. Upon arrival, male House Wrens establish a territory and nest primarily in cavities previously excavated in aspen trees by woodpeckers. They sometimes also utilize natural cavities, hollows, or cracks in aspen and fir trees. Once they have established a territory and nest cavity, they devote a large portion of their time to singing to attract females who arrive shortly after.

A survey of the land was conducted to establish the location of the potential subjects. Male House Wrens were chosen based on behaviours that display commitment to a territory which include nest building, defending the territory from intruding males,

and singing from a few choice song posts. Once it was established that a male was committed to a territory, this male was then classified as a candidate for the study. In order to provide positive individual identification, each male was captured and marked.

Capture and marking was conducted using standard operating procedures. Males were captured in mist nets (2 ply, 30 mm mesh) as they moved around their territory naturally. House Wren song playbacks were sometimes employed 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 set of four color 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 Data Collection

Data collection for the remainder of the breeding season focused on recording songs. Song recording protocol included sampling males systematically at times during which the males were most actively singing. These times included early morning between 5:30am to noon and when the birds were unpaired. The duration of each recording session amounted to one hour sample times with each male on average recorded twice per week.

Prior to each recording session, the ID of the male was identified by the researcher via colored bands on the legs of the birds. Throughout the recording sessions notes on behaviours and breeding stage were also recorded. The confident nature of the House Wren allowed researchers to record within 5-10 meters resulting in high quality recordings. Recordings were made using digital recorders (Marantz PMD 660 and 670 and Sound Devices 702) and shotgun microphones (Sennheiser ME67 and MKH 816).

Additional recordings were captured using an automated and programmable recording device (Wildlife Acoustics SM2+) mounted in the male's territory, specifically on or close to the nest tree. These units were programmed to record for 30 minutes every hour on the hour between 5:00am and 9:00am. These recorders were generally left in a male's territory for four consecutive days with the ID of the bird being visually verified each day by researchers. Data were also collected on the general activities of the focal male, his female partner, and direct neighbours. Field recordings were transferred daily to computers for post processing with each recording assigned a unique filename and stored for subsequent analysis.

2.1.4 The Recording Sample

The recording sample for 2011 consisted of 24 banded males (Table 2.1). Of these, 15 males were recorded sufficiently to include in the final sample for song analysis which entailed a total of 15, 513 songs. The 2012 sample was made up of 29 new banded males, and 6 males who returned from the 2011 breeding season to yield a total sample of 35 males (Table 2.2). Of the 35 males in the 2012 sample, recordings were obtained from 33 of the males and yielded a song sample in excess of 100,000 songs. This sample was too large to analyse in its entirety for this work. Hence, for the purpose of this thesis, I

selected a subset of the males that included the 6 returnee males from 2011 to facilitate year-over-year comparisons in song repertoires and 6 of the new males from 2012. The recording sample for this group of 12 males from 2012 involved 19, 554 songs.

In summary, then, the 2011 sample consisted of 15,513 songs from 15 males and the 2012 sample consisted of 19,554 songs from 12 males. In total, the sample thus consisted of 35,067 songs from 21 different males, 6 of which were sample in both years and are, henceforth, referred to as ‘returnees’.

2.1.5 General Description of Song

House Wren song can easily be classified into discrete songs made up of a concatenation of notes that are organized into consistent syllables with two easily discernible sections, classified as introduction and main sections (Figure 2.1). The introduction section is made up of low amplitude, broadband notes that in general are harsh in structure. The main section, which follows immediately after the introduction section, is composed of louder tonal, frequency modulated notes. Notes and syllables were defined using conventional nomenclature. A note was defined as a continuous signal trace in the song spectrogram (no gap or break in the signal structure) and syllables were defined as regularly grouped combinations of notes (notes that always occurred together).

2.1.6 Main Section of Song

For this research the focus was on the main section of the song, sometimes referred to as the ‘terminal trill’ (Rendall & Kaluthota, 2013), as this portion of the song is louder and thus will transmit further in the service of addressing potential female mates

and competing neighbour males. In contrast, the low amplitude nature of the introduction section means that it is probably not heard by House Wrens who are not very close to the singer. The main portion of the song can be heard as far as 300 meters and arguably even further distances by the birds themselves. Territory size for this species is on average 50 meters, so the transmitting qualities of the main portion of the song are optimal for territorial interactions as well. These are all attributes of the main part of the song that make it optimal when investigating territorial interactions between males.

2.1.7 Song Analysis

Analysis of song recordings were conducted using Praat software (Boersma & Weenink, 2012). Analysis focused on segmenting individual songs and annotating their syllable content using an established note and syllable repertoire for this population (Kaluthota, 2013; Rendall & Kaluthota, 2013). Statistical analysis of song syllable content was conducted using IBM SPSS Statistics 20.

2.1.8 Syllable Repertoire Sharing

Previous work has shown that the syllable repertoire for this population is large (n=27 different types of syllable), but that most of these syllables are shared by all males in the population (Rendall & Kaluthota, 2013). Nevertheless, males differ in their relative production of different syllables (i.e., showing some favoritism for different syllables) and they combine syllables in novel ways to generate large repertoires of different song types that vary considerably among males (Rendall & Kaluthota, 2013).

Variation among males in their production of different syllable types (syllable type favoritism) was evaluated in pairwise fashion using a coefficient, or index, of compositional similarity, defined as

$$s=1-0.5*8|o_{ik}-o_{jk}|$$

where o_{ik} as the relative occurrence of syllable k (measured as the number of times when syllable k is detected in the song record/total number of syllables analyzed in the song record) in individual i , while o_{jk} is the relative occurrence of the same syllable in individual j (Garamszegi, Zsebők, & Török, 2012).

This index quantifies the degree of similarity (or difference) in relative syllable production between males. Index values range between 0 and 1, with 1 representing complete similarity in the pattern of syllable production between males.

To produce a visual representation of the patterns of syllable production similarity among males I used hierarchical clustering analysis. The technique is a variant application of common clustering analysis methods used in taxonomic analysis to evaluate similarities among populations or species based on morphological or other trait characteristics. In this case, it was used to group males together based on pairwise similarities in the relative rate of syllable production.

2.1.9 Song Types

Song types were defined as a unique sequence of different syllable types, ignoring variation in the number of times particular syllable types might be repeated within songs (Figure 2.1). I used a conservative definition of a song type match between males in which songs were considered to be the same (to match) only if the entire sequence of

syllables was the same (i.e., songs consisted of the same syllable types arranged in the same order). This is a conservative but conventional definition of matching song types used in many other studies (Hultsch & Todt, 1981; Molles & Vehrencamp, 1999; Price & Yuan, 2011).

2.1.10 Song Repertoire Sharing

The extent of song type sharing was measured in pairwise fashion (i.e., between pairs of males) and evaluated across the entire song repertoire using an index of repertoire sharing:

$$RS = Z / ((X + Y) - Z),$$

where X and Y are the total number of song types sung by male X and Y, and Z is the number of song types they share (Hultsch & Todt, 1981; Price & Yuan, 2011).

This song sharing index can vary between 0 and 1, where 0 indicates no songs in common and 1 indicates that all songs are shared. This equation controls for potential differences in the absolute size of song repertoires between males.

Sharing indices, so defined, were generated in three different ways to avoid additional potential biases in perceived sharing patterns. For example, previous work has already shown that many song types are entirely unique – sung by only one male and then only rarely (Rendall & Kaluthota, 2013). Hence, when the analysis focuses on the complete repertoire of songs sung by individual males, it reveals a very low absolute level of song sharing among males. However, males produce a smaller subset of their entire repertoire more commonly – i.e., their singing is focused on the regular production of a much smaller subset of the songs they are capable of producing (Rendall &

Kaluthota, 2013). It is possible, therefore, that much higher degrees of song sharing might be observed in the smaller ‘effective’ song repertoires of individual males.

To capture this possibility, I generated three different indices of song sharing: RSD1 calculates song sharing across the entire repertoire of song types for each male; RSD5 calculates song sharing using song types sung five times or more by each male (i.e., it excludes very rare song types sung only one or a few times); RSDCOM calculates song sharing using only ‘commonly produced songs’, which were defined as song types that accounted for more than 1% of a birds song output.

Using this index, song sharing was evaluated at 4 different levels: (1) between neighbouring males (defined by adjacent territorial boundaries); (2) between pairs of males within each of the two study sites (LF and WB); (3) between pairs of males across the two different study sites; (4) and within returnee males between their 2011 and 2012 song samples. The distance between birds was calculated as the linear distance between the centers of their respective territories established by GPS co-ordinates taken at the nest trees and based on a spherical earth model.

2.2 Results: Syllable Sharing

2.2.1 Cluster Analysis

To assess similarity in the syllable production patterns of different males in the sample, a hierarchical cluster analysis was conducted. This analysis grouped males based on similarity in the syllable production patterns. The analysis was conducted hierarchically by successive joining of males whose syllable production patterns were most similar to one another. This method allows visualization of syllable production similarities among males to see if males that are closer in proximity (ie: neighbours) also

cluster together in this analysis. The results are shown in Figure 2.2 and Figure 2.3 which summarize the patterns of similarity in syllable production among males in the 2011 and 2012 samples, respectively.

In general, the dendgrams show no obvious clustering of males based on proximity. In some cases, neighbouring males cluster near one another based on syllable production similarity, but in many other cases they do not. Overall, there is no clear evidence that the syllable production patterns of neighbouring males are more similar than are those of non-neighbours.

2.2.2 Syllable Sharing as a Function of Distance

The possibility of greater syllable sharing based on spatial proximity was tested in a second way by examining the relationship between syllable sharing and the physical distance among males derived from GPS location data. This relationship was examined within years but with the syllable sharing data collapsed across the two study sites using a simple linear regression. There was no relationship between the distance separating males and degree of syllable sharing for either the 2011 sample (Figure 2.4, $r^2=.033$, $p=.164$) or the 2012 sample (Figure 2.5, $r^2=.010$, $p=.585$). These outcomes largely corroborate the cluster analysis in confirming that, in general, males closer together did not show elevated rates of syllable sharing.

2.2.3 Syllable Sharing and Song Type Sharing

Similarities in singing patterns among males was also examined by evaluating the relationship between syllable sharing and song type sharing. This was tested using simple

linear regression to test whether males share more of their syllable repertoire also end up singing more of the same song types. There was a significant positive relationship between syllable sharing and song type sharing in the 2011 sample (Figure 2.6, $r^2=.239$, $p<.001$) but not in the 2012 sample (Figure 2.7, $r^2=.071$, $p=.1490$).

2.2.4 Syllable Sharing and Song Sharing Among Returnees

The relationship between syllable sharing and song sharing was further examined by focusing more specifically on the pattern for returnee males in the 2012 sample. This test serves as a baseline for comparison of syllable and song sharing among males because the degree to which males share syllables and song types with themselves from one year to the next helps to set the expectation for how much one should expect different males to share syllables and song types within years. Further, if males are adjusting their singing patterns to match songs of rival neighbouring males, then one would expect that their own repertoire of syllables and song types might change significantly from year-to-year in order to adjust to the different singing patterns of the new neighbours they have each year. Alternatively, if males are not matching their songs to those of neighbours, there would be less pressure to change syllable and song type repertoires from year-to-year. In fact, there was a significant positive relationship between syllable and song sharing for the returnee males (Figure 2.8, $R^2=.817$, $p=.013$) whereas there was no such relationship observed between syllable and song sharing among other males in the 2012 sample. In other words, a male's repertoire of syllables and songs were more similar across breeding seasons than they were to the syllable and song repertoires of other males.

2.3 Results: Song Sharing

2.3.1 Song Repertoire Overlap

To gain a better understanding of the magnitude of song type overlap in this population the percentage of shared song types between males was examined. The comparison of song repertoires among males of the 2011 sample revealed that of the 998 song types in the repertoires of 15 males, 76% (767) of these song types were unique (i.e., sung by only one male), whereas 23% (231) of song types were shared by one or more males. In the 2012 sample, there were 802 different song types recorded across the repertoires of 12 males and levels of song type sharing were slightly higher. Only 66% (535) of song types were unique and 33% (267) of song types were shared by one or more males. Collectively, over half the song types produced in both years were unique pointing to an absolutely low-level of song type sharing.

2.3.2 Song Type Sharing Within Sites

Although absolute levels of song sharing were low, in general, there may nevertheless be revealing patterns in song sharing for those songs that were shared. To test this possibility, song type sharing values were further evaluated using an independent-sample *t*-test to assess whether mean levels of song sharing differed between the 2011 and 2012 samples. Values for the coefficient of song sharing are provided in Table 2.3 through Table 2.8 for both 2011 and 2012 samples and including all three levels of repertoire sharing. Mean values for the coefficient of sharing within sites were significantly different between years (Figure 2.9; Table 2.9, Table 2.10) with higher

values in 2012 compared to 2011 (RSD1, $t(88)=7.75, p<0.001$; RSD5, $t(46) = 7.07, p<0.001$; and RSDCOM; $t(88)= 4.63, p<0.001$). This finding indicates that song type sharing was higher among males in 2012 than in 2011.

2.3.3 Song Sharing Between Sites

Song sharing values were also examined across the two study sites and compared to those observed within sites to test for greater song sharing within sites. An independent-sample t -test, yielded no significant differences in song sharing between the two sites for the 2011 sample (Figure 2.10, Table 2.11; RSD1, $t(103)=0.69, p=0.49$; RSD5, $t(103) = 1.11, p=0.27$ and RSDCOM; $t(103)= 0.20, p<0.001$), but a significant difference between sites for the 2012 sample (Figure 2.11, Table 2.11; RSD1, $t(64)= -2.7, p=0.009$; RSD5, $t(64) = -4.42, p<0.001$; and RSDCOM, $t(64)= -2.4, p<0.001$). These findings suggest that males were no more likely to share songs with other males who occupied the same study site compared to a different, distant study site in 2011 but they were more likely to share songs with other males occupying the same versus a distant site in 2012.

2.3.4 Song Sharing Between Neighbours

To examine whether neighbouring males (defined by adjacent territorial boundaries) shared songs at a greater level than non-neighbouring males, a Mann Whitney test was used to test differences in mean levels of sharing between the two groups (means and standard deviations reported in Table 2.12). Collapsed across the two breeding seasons and sites, neighbouring males shared significantly more song types than

did non-neighbouring males (Figure 2.12; RSD1, $U=115$, $p<001$; RSD5, $U=129$, $p=.002$; and RSDCOM; $U=193$, $p=.028$), suggesting that, although absolute levels of song sharing were low, neighbouring males nevertheless shared more song types than non-neighbours.

2.3.5 Song Sharing as a Function of Distance

To flesh-out the relationship between song sharing among neighbours, a follow-up analysis was conducted examining song sharing as a function of the linear distance between males using a simple linear regression. This analysis yielded no significant relationships for the 2011 sample at either site for any level of the birds repertoires (Table 2.13, Figure 2.13, Figure 2.14, Figure 2.15, and; Lundbreck Falls, RSD1, $R^2=0.002$, $p=0.741$, RSD5, $R^2=0.053$, $p=0.091$, RSDCOM, $R^2=0.016$, $p=0.351$), (Table 2.13, Figure 2.16, Figure 2.17, Figure 2.18, Whaleback; RSD1, $R^2=0.062$, $p=.634$, RSD5, $R^2=0.707$, $p=0.036$, RSDCOM, $R^2=0.002$, $p=0.933$).

There appears to be a significant negative relationship between repertoire sharing and distance using songs that are sung 5 times or more (RSD5) for the Whaleback site. However, there were very few points in this analysis (few males at this site) and so the result is regarded as highly unstable. This negative relationship also disappears when the data are collapsed across the two sites to increase the sample size and likely validity of the outcome (Table 2.13, Figure 2.19, Figure 2.20, Figure 2.21; RSD1, $R^2=0.00$, $p=0.894$, RSD5, $R^2=0.034$, $p=.153$, RSDCOM, $R^2=.010$, $p=.448$). These results suggest that there was no relationship in song sharing as a function of distance for males in the 2011 sample.

In contrast, in the 2012 sample, there were significant negative relationships between repertoire sharing values and the distance between males both for the Lundbreck Falls site (Table 2.14, Figure 2.22, Figure 2.23; RSD1, $R^2=0.261$, $p=0.018$, RSD5, $R^2=0.366$, $p=0.004$) and when the data were collapsed across the two sites (Table 2.14, Figure 2.24, Figure 2.25; RSD1, $R^2=0.199$, $p=0.012$, RSD5, $R^2=0.299$, $p=0.001$) at repertoire levels RSD1 and RSD5. These outcomes suggest that males who were closer in proximity shared more of their song repertoires. The relationship was not significant when focused only on commonly song type (RSDCOM) at the Lundbreck Falls site (Table 2.14, Figure 2.26; RSDCOM, $R^2=0.093$, $p=0.178$) and collapsed across the two sites (Table 2.14, Figure 2.27; RSDCOM, $R^2=0.067$, $p=0.160$) suggesting that song sharing is focused on less commonly produced song types.

The negative relationship between song sharing and distance at the Lundbreck Falls site may have been unduly affected by a few data points. For example, LF15 was a male who was considered part of the Lundbreck Falls population but was located much farther from the core of this site than the other males in this population. Hence, it is possible that that song sharing between this male and the other males at this site is skewing the broader pattern. Consequently, the analysis was re-run after removing this male from the sample. The negative relationship is weakened but remains nearly significant (Figure 2.28; RSD1, $R^2=0.237$, $p=0.06$). A second possibly anomaly concerns male LF02 who relatively low levels of song sharing with other males (mean = 0.13) compared to the average level of song sharing observed for other pairs of males (mean=0.23). Removal of LF02 from the sample further weakens the relationship which in fact becomes non-significant (Figure 2.29 $R^2=0.016$, $p=0.724$). Because the

relationship between distance and song sharing appears to be contingent on the inclusion of one or two specific males, the overall significant effects should be viewed with caution.

Focusing only on the Whaleback site, there was no relationship between repertoire sharing values and the distance between males at any level of the birds' repertoire (Table 2.14, Figure 2.30, Figure 2.31, Figure 2.32; RSD1, $R^2=0.008$, $p=0.824$, RSD5, $R^2=0.40$, $p=0.068$, RSDCOM, $R^2=0.008$, $p=0.814$). However, these findings should be viewed with caution given the comparatively small sample of males available at this site.

In summary, there was no relationship between distance and song type sharing values for the 2011 population at either site and collapsed across the sites. In 2012 a relationship existed between distance and song type sharing at repertoire levels RSD1 and RSD5 at the Lundbreck Falls site and collapsed across the two study sites. No relationship existed at the Whaleback site at song sharing levels RSD1 and RSD5. At both sites and collapsed across sites, no relationship existed at the level of RSDCOM.

2.3.6 Song Type Sharing Among Returnees

The level of song sharing within returnee males from one year to the next were compared, using a Kruskal-Wallis test, to sharing levels among males within year to test whether males share more song types with themselves than with other males (Figure 2.33). There was a significant difference in levels of song sharing between the two groups of males $X^2(2, N=96)=39.76$, $P<0.000$). Follow up Mann Whitney tests using the Bonferroni correction were conducted to evaluate the differences between the groups.

Returnee males shared more songs with themselves (RSD1; N=6, M=.19, SD=.08) than did males in general in the 2011 sample (RSD1; N=61, M=.10, SD=.05) but not those in the 2012 sample (RSD1; N=31, M=.20, SD=.06).

The level at which returnee males shared songs with themselves from year-to-year was compared to sharing values for other males who were or were not neighbours (Figure 2.34). There was a significant difference in mean sharing values between groups, $X^2(2, N=96) = 12.07, p=0.002$ returnee males show levels of self-sharing (RSD1; N=6, M=.19, SD=.08) approximately equal to those of neighbours (RSD1; N=8, M=.21, SD=.07) and significantly higher than those of non-neighbours (RSD1; N=82, M=.13, SD=.06).

2.4 Discussion

Results show that male House Wrens display very high levels of syllable sharing. Virtually all syllables in the population repertoire were produced by all males. Only a very few syllables were produced by only a small number of males. This finite repertoire of syllables was used to produce very large repertoires of songs for individual males. Such large song repertoires afforded males the opportunity to engage in complex vocal interactions including extensive song matching. However, the absolute level of song sharing among males was actually quite low because, in fact, the majority of each males' song repertoire was composed of song types that were unique and not shared, at least by the conservative definition of song sharing used here.

Nevertheless, more detailed analysis of the non-unique (i.e., shared) song types showed that males who were closer in proximity shared more song types, and that males shared more song types with other males in their own neighbourhood (study site). These

findings can shed some light on the major themes outlined at the beginning of this thesis related to: 1. the potential functions of song sharing in mate attraction and territory defense; 2. the likely learning style of the species, and: 3. the potential formation of regional song dialects. In what follows, I address each of these themes in turn.

2.4.1 What do patterns of song sharing suggest about the potential territory defence and mate attraction functions of song?

Song sharing differences existed between years, with males showing higher levels of song sharing in 2012 than in 2011. This pattern of differential sharing may reflect differences in the dispersion of males between years. In the 2011 breeding season, males were more widely dispersed with a mean distance of 0.88 km between males, compared to a mean distance of 0.76 between males in 2012. Because were more closely clustered in 2012 there may have been greater pressure for song sharing (and matching) between males in the service of both mate attraction and neighbour competition. As hypothesized by others, males in such a situation might benefit from greater song sharing and active song matching because it displays fitness qualities to eavesdropping males and females (Forstmeier & Leisler, 2004) as well as functioning to resolve territorial disputes (Vehrencamp, 2001).

In contrast, males were more widely dispersed in 2011 thereby reducing the pressure on or value in song sharing and active song matching because these males did not have to invest as much time defending their territory. Furthermore, to advertise fitness through song matching requires the existence of another male close in proximity.

The fact males in 2011, in general, had fewer close neighbours may have further reduced the utility of song matching.

Interestingly, in 2012, the songs shared among males tended not to be the commonly produced song types but rather song types that were less common in the population as a whole. This finding suggests that only a portion of a male's repertoire may be used to address neighbouring males.

Taken together, there was some evidence that neighbouring males were more likely to share songs and therefore that a process of song matching may have characterized at least some component of their singing activity. There are a variety of reasons offered to account for this kind of phenomenon as reviewed in the Introduction.

Briefly, research suggests that males benefit from sharing songs with neighbours because males that share few or no songs have more aggressive encounters and greater territory turn-over compared to males that share more songs (Wilson, Towner, & Vehrencamp, 2000). Such sharing of songs with neighbours has been shown to translate into direct fitness advantages (Beecher, et al., 2000; Payne, 1982). For instance, Indigo Buntings (*Passerina Cyanea*) that share songs with neighbours have higher reproductive success and sharing is also correlated with mating success in brown-headed cowbirds, possibly because males that are able to address neighbours directly via song sharing are more effective in managing and maintaining a territory.

As noted in the Introduction, it is also possible that song sharing plays a role in mate attraction by advertising a male's singing prowess, as higher quality males are those that can dynamically modify or improvise new song types to match songs produced by

other, neighbour males. Furthermore, the active process of song matching may allow further detailed comparisons of the fidelity of song renditions sung by competing males, allowing females to make refined quality comparisons among males. The analyses conducted here do not allow any clear test of this question. However, there some additional interesting patterns in the song sharing results that might bear on the issue.

In particular, the male, LF02, was unusual in showing very low levels of song sharing with himself between the 2011 and 2012 breeding seasons. This is in contrast to all the other returnee males that displayed relatively high levels of self-song-sharing across breeding seasons. LF02 was notable also in producing one of the largest most variable repertoires of songs and also in struggling to successfully pair or fledge chicks in both the 2011 and 2012 breeding seasons. Together, these findings might indicate that LF02 was a relative low quality male whose repertoire of songs was so large and variable within and between years specifically because he as attempting not to share or match songs with rival males (Logue & Forstmeier, 2008). This is hypothesized to be one route to increased song complexity as less fit males avoid matching songs to complicate the female's ability to assess males, because it is arguably more difficult to compare dissimilar signals (novel song types) than similar ones (matched song types).

2.4.2 What do patterns of syllable and song sharing suggest about the process of song learning?

The ability to share songs ultimately stems from the cultural transmission of song. Therefore, patterns of syllable and song sharing provide a window through which the processes of song learning and transmission can be examined.

2.4.3 Syllable Sharing versus Song Sharing

Sharing of song syllables may differ from sharing of song types, as males with very similar syllable repertoires might nevertheless use these common syllable repertoires to create very different repertoires of song types through a process of improvisation. A high degree of syllable sharing was found in this population of House Wrens, which is consistent with previous work on this species (Kaluthota, 2013; Platt & Ficken, 1987). In the 2011 population, 11 of the 27 syllable types were shared by all males in the sample, and the remainder were shared by at least 3 males. In the 2012 population, all males shared all but 4 of the 27 syllable types. From this set of common syllables, males generated very large repertoires of song types most of which were not shared.

This pattern of shared syllables but mostly unshared song types is interesting. It suggests that the syllable repertoire is acquired at a young age and becomes crystalized and unchanging. In this respect, House Wrens exemplify closed-ended learners. In contrast, the song type repertoire appears more open-ended in the sense that the males are using a static syllable repertoire to produce an almost infinite number of different song types through a process of improvisation.

In theory, with 27 syllable types and an average of 4 syllable types per song, males could produce up to 421,200 different song types. Although no male approached this number of song types (not even close), previous analyses have shown that individual males in this population did produce up to 194 different song types with no evidence that they were reaching a ceiling (Rendall & Kaluthota, 2013). Hence, in their song repertoires, House Wrens appear to be more open-ended. This juxtaposition of closed-

ended learning for syllables and open-ended song repertoires may not indicate that males are in fact ‘learning’ new song types from year-to-year (or even within years) so much as ‘improvising’ new song types from their standard set of common syllable types. Hence, they may not be ‘open-ended’ in same sense that some other species (e.g., starlings) are that appear truly to learn new song types – as whole song types – from one year to the next.

These findings also have implications for the potential targets of selection on song traits. The fact that differences among males were not expressed on the level of syllables but rather at the level of song types, may indicate that selection is acting more on the latter component of songs (Grießmann & Naguib, 2002). Sexually selected traits should vary among individuals, so it is possible that song repertoires in House Wrens are under the pressure of sexual selection, more so than syllable types, as it is the song repertoires that are highly variable among males.

2.4.4 What do patterns of song sharing suggest about the formation of dialects?

The extent of song sharing in a population can provide insight into the song development process of a species, as well as the development of song variation. Furthermore, a greater understanding of how song variation develops could lead to further knowledge on the function of song variation. As just noted, the large and highly variable song repertoires of the Northern House Wren seem to arise through a process of improvisation which may be functional in allowing males to interact with other males and females through the species very wide geographic range. The song improvisation process

may also lead to the formation of local song dialects as a by-product as males modify their song repertoires to match songs produced by other males in the local populations where they settle and breed.

In the study sample, there were differences in the number of songs shared by males across the two study sites, with greater levels of song sharing observed among males within as compared to between sites. This finding may be consistent with the existence of a type of dialect, formed through a process of improvisation. These “dialects” may not be formed in the conventional way through the accumulation of errors during the learning of whole song types, but rather as a result of improvising song types that match those of other males in the local population from a set of common syllable types. Such dialects, if they should be conceived as such, would also not be static in the same ways as canonical dialects but rather potentially yearly as new males enter the population. The dialect formation process may also differ in as much as it might not be the young males driving the formation of dialects through errors in the song learning process, but rather older males driving the formation of dialects as young, naïve males attempt to sing songs produced by older mature returning males.

Table 2.1: Males banded in the 2011 breeding season at Lundbreck falls site and Whaleback site (males utilized in this sample denoted by *).

Bird ID	Recording Data
HWLF1101	No
*HWLF1102	Yes
*HWLF1104	Yes
HWLF1105	No
*HWLF1106	Yes
*HWLF1108	Yes
*HWLF1109	Yes
*HWLF1110	Yes
*HWLF1111	Yes
*HWLF1112	Yes
*HWLF1113	Yes
*HWLF1114	Yes
*HWLF1115	Yes
*HWWB1101	Yes
*HWWB1102	Yes
HWWB1103	No
HWWB1104	No
*HWWB1105	Yes
HWWB1106	No
*HWWB1108	Yes
HWWB1109	No
HWWB1110	No
HWWB1111	No
HWWB1112	No

Table 2.2: Males banded in the 2012 breeding season at Lundbreck falls site and Whaleback site (males utilized in this sample denoted by *).

Bird ID	Recording Data
HWLF1220	Yes
*HWLF1221	Yes
*HWLF1222	Yes
HWLF1224	No
HWLF1225	Yes
HWLF1226	Yes
HWLF1227	Yes
HWLF1228	Yes
HWLF1229	No
HWLF1230	Yes
HWLF1231	Yes
*HWLF1232	Yes
HWLF1233	Yes
HWLF1234	Yes
HWLF1235	Yes
HWLF1236	Yes
HWLF1237	Yes
HWLF1238	Yes
HWLF1239	Yes
*HWLF1108	Yes
*HWLF1112	Yes
*HWLF1115	Yes
*HWLF1102	Yes
HWWB1213	Yes
HWWB1214	Yes
*HWWB1215	Yes
*HWWB1216	Yes
*HWWB1217	Yes
HWWB1219	Yes
HWWB1220	Yes
HWWB1221	Yes
HWWB1223	Yes
HWWB1224	Yes
*HWWB1105	Yes
*HWWB1101	Yes

Table 2.3: Number of song types shared (above diagonal) and calculated values of repertoire sharing for all song types produced at least once by each male (RSD1) for the 2011 sample.

	LF02	LF04	LF06	LF08	LF09	LF10	LF11	LF12	LF13	LF14	LF15	WB01	WB02	WB05	WB08
LF02	X	5	6	9	14	5	5	5	9	9	5	6	3	4	3
LF04	0.02	X	20	21	21	15	15	17	19	18	15	19	16	14	13
LF06	0.02	0.15	X	33	20	25	27	24	27	25	38	28	23	16	12
LF08	0.03	0.13	0.16	X	20	22	32	27	26	33	32	29	26	19	15
LF09	0.06	0.17	0.11	0.10	X	17	20	11	24	24	17	21	14	18	12
LF10	0.02	0.11	0.14	0.11	0.10	X	27	11	19	27	33	19	19	11	5
LF11	0.02	0.09	0.12	0.13	0.09	0.13	X	20	20	28	32	25	29	22	8
LF12	0.02	0.25	0.20	0.19	0.09	0.09	0.13	X	18	14	20	16	15	10	11
LF13	0.03	0.10	0.11	0.09	0.10	0.08	0.07	0.09	X	38	26	22	18	16	18
LF14	0.03	0.08	0.09	0.11	0.09	0.10	0.09	0.06	0.12	X	30	35	31	30	17
LF15	0.02	0.10	0.20	0.15	0.09	0.18	0.14	0.15	0.10	0.11	X	25	25	18	10
WB01	0.02	0.14	0.15	0.14	0.12	0.10	0.11	0.13	0.09	0.13	0.13	X	26	27	15
WB02	0.01	0.15	0.14	0.14	0.09	0.12	0.15	0.15	0.08	0.13	0.15	0.17	X	25	14
WB05	0.02	0.12	0.09	0.10	0.11	0.07	0.11	0.09	0.07	0.12	0.10	0.17	0.19	X	17
WB08	0.01	0.14	0.08	0.09	0.09	0.03	0.04	0.13	0.09	0.07	0.06	0.10	0.12	0.14	X

Table 2.4: Number of song types shared (above diagonal) and calculated values of repertoire sharing for all song types produced at least once by each male (RSD1) for the 2012 sample.

	LF02	LF08	LF12	LF15	LF21	LF22	LF32	WB01	WB05	WB15	WB16	WB17
LF02	X	52	40	40	79	56	46	40	63	21	33	21
LF08	0.14	X	63	43	80	70	57	57	62	27	29	23
LF12	0.11	0.36	X	30	64	55	47	42	53	25	26	20
LF15	0.11	0.21	0.15	X	53	40	31	32	41	15	23	15
LF21	0.16	0.25	0.20	0.16	X	79	68	69	81	29	34	25
LF22	0.15	0.34	0.27	0.18	0.23	X	62	60	65	24	33	27
LF32	0.12	0.28	0.24	0.14	0.20	0.29	X	54	57	22	30	20
WB01	0.10	0.27	0.21	0.14	0.21	0.27	0.26	X	65	30	32	27
WB05	0.15	0.23	0.20	0.15	0.21	0.23	0.21	0.24	X	30	50	33
WB15	0.06	0.16	0.17	0.09	0.09	0.13	0.13	0.18	0.13	X	17	18
WB16	0.10	0.17	0.17	0.14	0.11	0.18	0.17	0.18	0.23	0.15	X	18
WB17	0.06	0.15	0.15	0.10	0.08	0.16	0.13	0.18	0.15	0.22	0.19	X

Table 2.5: Number of song types shared (above diagonal) and calculated values of repertoire sharing for all song types produced at least five times by each male (RSD5) for the 2011 sample.

	LF02	LF04	LF06	LF08	LF09	LF10	LF11	LF12	LF13	LF14	LF15	WB1	WB02	WB05	WB08
LF02	x	1	1	1	2	2	2	1	2	2	1	1	1	0	1
LF04	0.02	x	3	6	3	4	2	2	3	5	4	7	3	1	3
LF06	0.01	0.07	x	13	6	6	7	7	8	7	13	10	5	5	3
LF08	0.01	0.10	0.18	x	8	6	10	10	8	13	13	12	7	6	6
LF09	0.03	0.09	0.13	0.12	x	7	7	4	7	10	6	4	2	1	3
LF10	0.03	0.12	0.12	0.08	0.18	x	6	3	5	8	11	6	2	2	3
LF11	0.02	0.04	0.11	0.12	0.14	0.11	x	3	4	9	11	6	6	3	3
LF12	0.02	0.07	0.17	0.16	0.11	0.08	0.06	x	4	5	4	5	3	3	3
LF13	0.02	0.06	0.13	0.09	0.13	0.08	0.05	0.07	x	10	9	7	6	4	5
LF14	0.02	0.06	0.07	0.11	0.12	0.09	0.09	0.06	0.10	x	14	12	9	6	5
LF15	0.01	0.08	0.22	0.15	0.11	0.20	0.16	0.07	0.12	0.14	x	10	10	6	5
WB01	0.01	0.16	0.17	0.15	0.07	0.11	0.09	0.10	0.10	0.12	0.14	x	5	5	6
WB02	0.01	0.09	0.10	0.10	0.05	0.04	0.11	0.08	0.11	0.10	0.18	0.09	x	7	4
WB05	0.00	0.03	0.10	0.08	0.02	0.04	0.05	0.08	0.07	0.07	0.10	0.09	0.18	x	4
WB08	0.02	0.13	0.07	0.10	0.10	0.09	0.06	0.11	0.10	0.06	0.10	0.13	0.13	0.12	x

Table 2.6: Number of song types shared (above diagonal) and calculated values of repertoire sharing for all song types produced at least five times by each male (RSD5) for the 2012 sample.

	LF02	LF08	LF12	LF15	LF21	LF22	LF32	WB01	WB05	WB15	WB16	WB17
LF02	X	19	23	10	20	33	19	16	27	7	5	8
LF08	0.16	X	23	17	35	30	19	22	22	7	10	7
LF12	0.23	0.29	X	10	27	22	15	18	19	7	9	6
LF15	0.09	0.20	0.14	X	20	17	12	12	17	2	9	6
LF21	0.14	0.32	0.27	0.19	X	33	22	22	29	6	12	6
LF22	0.33	0.37	0.31	0.23	0.33	X	19	16	24	7	9	10
LF32	0.18	0.22	0.21	0.17	0.21	0.25	X	16	17	4	7	4
WB01	0.12	0.22	0.20	0.13	0.18	0.16	0.17	X	27	6	9	10
WB05	0.21	0.19	0.19	0.17	0.22	0.23	0.17	0.24	X	7	17	13
WB15	0.08	0.11	0.15	0.04	0.07	0.13	0.08	0.09	0.09	X	5	4
WB16	0.05	0.14	0.16	0.17	0.13	0.14	0.12	0.12	0.21	0.17	X	8
WB17	0.09	0.10	0.11	0.12	0.06	0.17	0.07	0.14	0.16	0.16	0.08	X

Table 2.7: Number of song types shared (above diagonal) and calculated values of repertoire sharing for song types that comprise 1% of a males repertoire (RSDCOM) for the 2011 sample.

	LF02	LF04	LF06	LF08	LF09	LF10	LF11	LF12	LF13	LF14	LF15	WB01	WB02	WB05	WB08
LF02	X	.02	.02	.01	.02	.04	.05	.02	.04	.02	.01	.02	.01	.02	.02
LF04	0.02	X	.09	.16	.20	.15	.08	.08	.16	.15	.10	.15	.12	.09	.19
LF06	0.02	0.09	X	.19	.12	.13	.13	.10	.17	.10	.24	.15	.11	.13	.09
LF08	0.01	0.16	0.19	X	.17	.11	.10	.20	.16	.13	.18	.15	.15	.10	.12
LF09	0.02	0.2	0.12	0.17	X	.18	.15	.11	.17	.15	.11	.07	.08	.04	.07
LF10	0.04	0.15	0.13	0.11	0.18	X	.11	.07	.12	.13	.17	.13	.05	.08	.07
LF11	0.05	0.08	0.13	0.1	0.15	0.11	X	.09	.11	.10	.17	.13	.16	.07	.08
LF12	0.02	0.08	0.1	0.2	0.11	0.07	0.09	X	.11	.10	.09	.07	.08	.10	.14
LF13	0.04	0.16	0.17	0.16	0.17	0.12	0.11	0.11	X	.09	.10	.12	.08	.14	.13
LF14	0.02	0.15	0.1	0.13	0.15	0.13	0.1	0.1	0.09	X	.19	.13	.11	.08	.06
LF15	0.01	0.1	0.24	0.18	0.11	0.17	0.17	0.09	0.1	0.19	X	.17	.18	.12	.08
WB01	0.02	0.15	0.15	0.15	0.07	0.13	0.13	0.09	0.12	0.13	0.17	X	.13	.15	.17
WB02	0.02	0.12	0.11	0.15	0.08	0.05	0.16	0.08	0.08	0.11	0.18	0.13	X	.12	.18
WB05	0.02	0.09	0.13	0.18	0.04	0.08	0.07	0.1	0.14	0.08	0.12	0.15	0.18	X	.20
WB08	0.02	0.19	0.09	0.12	0.07	0.07	0.08	0.14	0.13	0.06	0.08	0.17	0.12	0.2	X

Table 2.8: Number of song types shared (above diagonal) and calculated values of repertoire sharing for song types that comprise 1% of the males repertoire (RSDCOM) for the 2012 sample.

	LF02	LF08	LF12	LF15	LF21	LF22	LF32	WB01	WB05	WB15	WB16	WB17
LF02	x	.05	.08	.14	.19	.12	.12	.01	.17	.07	.10	.06
LF08	0.05	x	.25	.18	.21	.24	.20	.14	.15	.14	.19	.13
LF12	0.08	0.25	x	.13	.25	.22	.21	.20	.13	.19	.22	.17
LF15	0.14	0.18	0.13	x	.19	.16	.14	.10	.16	.08	.17	.13
LF21	0.19	0.21	0.25	0.19	x	.33	.15	.13	.25	.10	.18	.14
LF22	0.12	0.24	0.22	0.16	0.33	x	.21	.20	.26	.12	.13	.23
LF32	0.12	0.2	0.21	0.14	0.15	0.21	x	.13	.14	.15	.17	.13
WB01	0.04	0.14	0.2	0.1	0.13	0.2	0.13	x	.18	.20	.13	.21
WB05	0.17	0.15	0.13	0.16	0.25	0.26	0.14	0.18	x	.17	.17	.18
WB15	0.07	0.14	0.19	0.08	0.1	0.12	0.15	0.2	0.17	x	.15	.17
WB16	0.1	0.19	0.22	0.17	0.18	0.13	0.17	0.13	0.17	0.15	x	.20
WB17	0.06	0.13	0.17	0.13	0.14	0.23	0.13	0.21	0.18	0.17	0.2	x

Table 2.9: Mean repertoire sharing values for the 2011 sites

Site	Sharing Value	Mean	Standard Deviation	Pairwise Comparisons
Lundbreck Falls	RSD1	.10	.05	55
Lundbreck Falls	RSD5	.09	.05	55
Lundbreck Falls	RSDCOM	.12	.06	55
Lundbreck Falls	SSD	.69	.07	55
Whaleback	RSD1	.15	.03	6
Whaleback	RSD5	.12	.03	6
Whaleback	RSDCOM	.16	.02	6
Whaleback	SSD	.76	.05	6
Lundbreck Falls/Whaleback (Within site)	RSD1	.10	.05	61
Lundbreck Falls/Whaleback (Within site)	RSD5	.09	.05	61
Lundbreck Falls/Whaleback (Within site)	RSDCOM	.12	.05	61
Between site	RSD1	.15	.04	44
Between site	RSD5	.18	.04	44
Between Site	RSDCOM	.19	.04	44

Table 2.10: Mean repertoire sharing values for the 2012 sites

Site	Sharing Value	Mean	Standard Deviation	Pairwise Comparisons
Lundbreck Falls	RSD1	.21	.07	21
Lundbreck Falls	RSD5	.23	.07	21
Lundbreck Falls	RSDCOM	.18	.06	21
Lundbreck Falls	SSD1	.80	.04	21
Whaleback	RSD1	.19	.03	10
Whaleback	RSD5	.16	.05	10
Whaleback	RSDCOM	.18	.02	10
Whaleback	SSD1	.80	.04	10
Returnee Males	RSD1	.19	.08	6
Returnee Males	SSD1	.79	.07	6
Lundbreck Falls/Whaleback (Within site)	RSD1	.20	.06	31
Lundbreck Falls/Whaleback (Within site)	RSD5	.21	.08	31
Lundbreck Falls/Whaleback (Within site)	RSDCOM	.18	.05	31
Between site	RSD1	.16	.05	35
Between site	RSD5	.14	.05	35
Between site	RSDCOM	.15	.04	35

Table 2.11: Mean repertoire sharing values within sites and between sites for the 2011 and 2012 sites

Sample	Sharing Value	Group	Mean	Std. Deviation	n
2011	RSD1	Between site	.09	.04	61
		Within site	.10	.05	44
2011	RSD5	Between site	.08	.04	61
		Within site	.09	.05	44
2011	RSDCOM	Between site	.10	.04	61
		Within site	.12	.05	44
2012	RSD1	Between site	.16	.05	35
		Within site	.20	.06	31
2012	RSD5	Between site	.13	.05	35
		Within site	.21	.07	31
2012	RSDCOM	Between site	.15	.04	35
		Within site	.18	.05	31

Table 2.12: Mean repertoire sharing values for neighbouring and non-neighbouring males collapsed across the 2011/2012 breeding seasons and sites.

Sharing Value	Group	Mean	Std. Deviation	n
RSD1	Neighbouring	.21	.07	8
RSD5	Neighbouring	.37	.09	8
RSDCOM	Neighbouring	.24	.04	8
RSD1	Non-neighbouring	.13	.06	82
RSD5	Non-neighbouring	.12	.07	82
RSDCOM	Non-neighbouring	.14	.06	82

Table 2.13: Simple regression values for the 2011 Lundbreck Falls and Whaleback sites and collapsed across the two sites.

Site	Sharing Value	R²	<i>p</i>	Beta
Lundbreck Falls	RSD1	.002	.741	.046
Lundbreck Falls	RSD5	.053	.091	.230
Lundbreck Falls	RSDCOM	.016	.351	.128
Whaleback	RSD1	.062	.634	.249
Whaleback	RSD5	.707	.036	-.841
Whaleback	RSDCOM	.002	.933	.045
Lundbreck Falls & Whaleback	RSD1	0	.894	.017
Lundbreck Falls & Whaleback	RSD5	.034	.153	.185
Lundbreck Falls & Whaleback	RSDCOM	.010	.448	.099

Table 2.14: Simple regression values for the 2012 Lundbreck Falls and Whaleback sites and collapsed across the two sites.

Site	Sharing Value	R^2	p	Beta
Lundbreck Falls	RSD1	.261	.018*	-.511
Lundbreck Falls	RSD5	.366	.004*	-.605
Lundbreck Falls	RSDCOM	.093	.179	-.305
Whaleback	RSD1	.008	.824	-.087
Whaleback	RSD5	.400	.068	-.632
Whaleback	RSDCOM	.008	.814	.092
Lundbreck Falls & Whaleback	RSD1	.199	.012*	-.446
Lundbreck Falls & Whaleback	RSD5	.299	.001*	-.547
Lundbreck Falls & Whaleback	RSDCOM	.067	.16	-.258

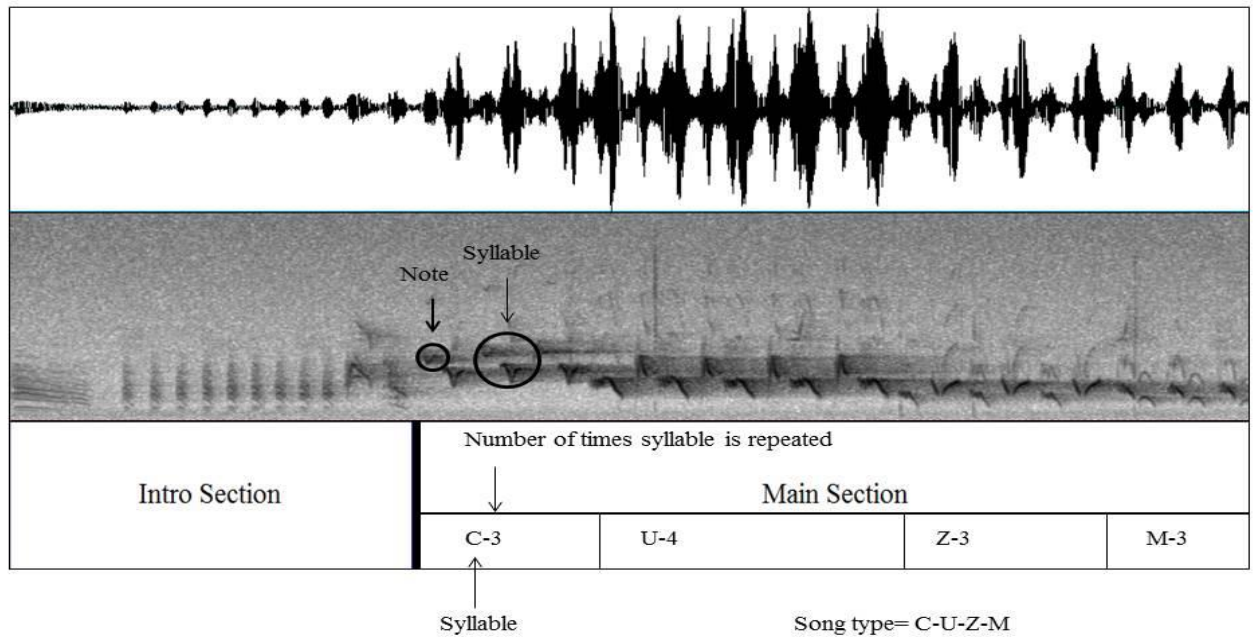


Figure 2.1: A song of male House Wren showing waveform and spectrogram. Introduction (intro) section consists softer lower frequency, broadband signals. The main section consists of louder high frequency, tonal signals. Notes (continuous signal trace) and syllables (regularly grouped combinations of notes) are exemplified here as well as the sequence of syllables that make up a song type.

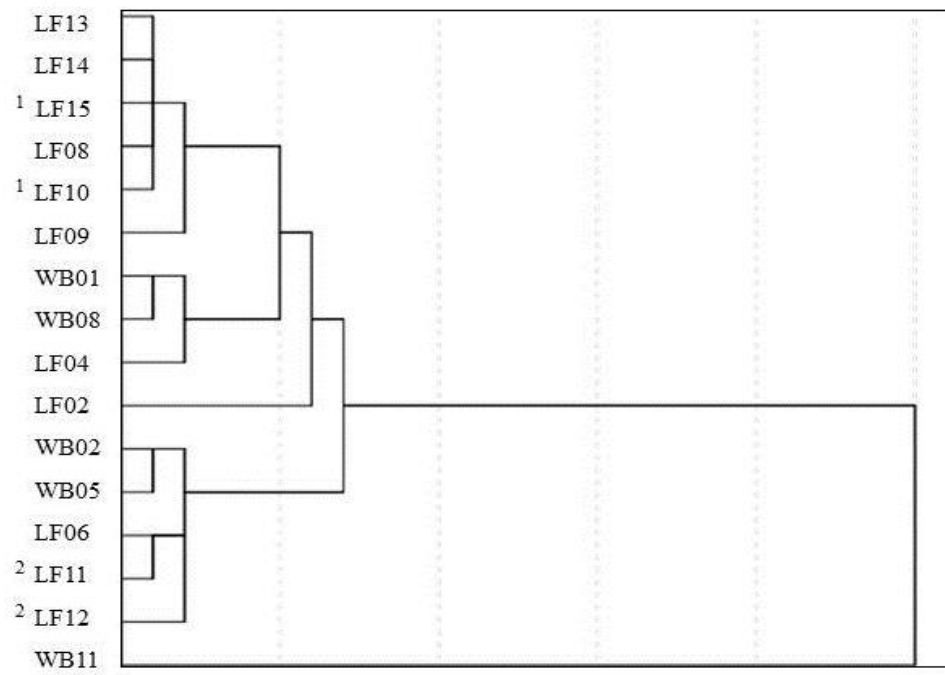


Figure 2.2: Hierarchical classification of all 2011 males (neighbouring males denoted by matching numbers) based on syllable composition similarities of their repertoires.

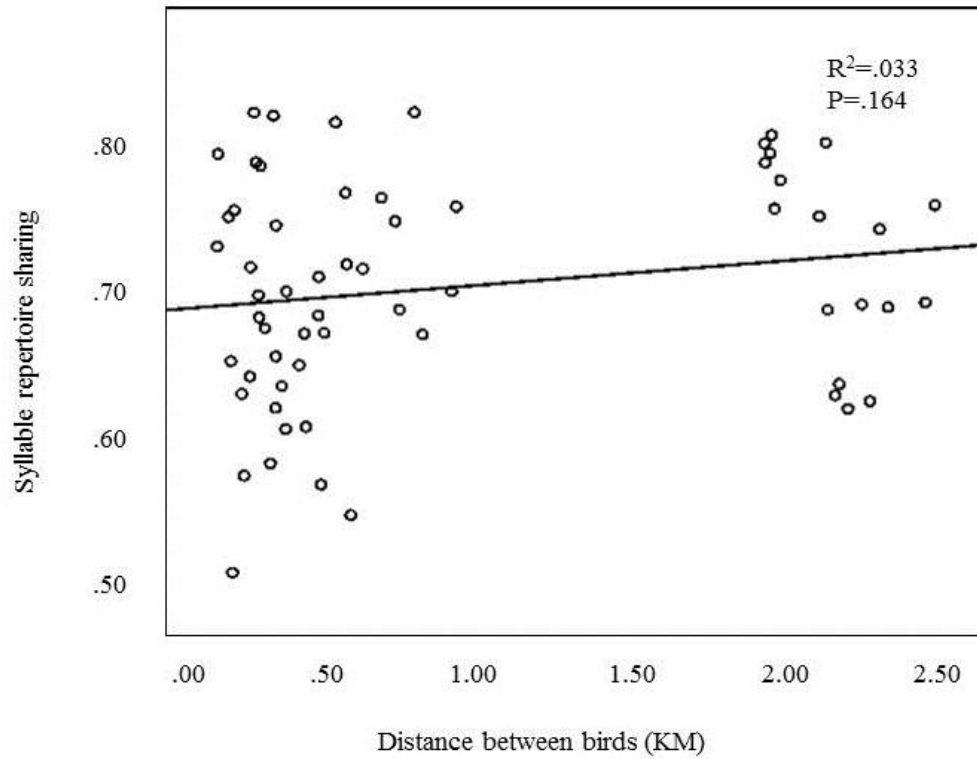


Figure 2.4: Relationship between syllable repertoire sharing values and the physical distance between males calculated using the bird's entire repertoire of songs (RSD1) and collapsed across the 2011 Lundbreck Falls and Whaleback sites.

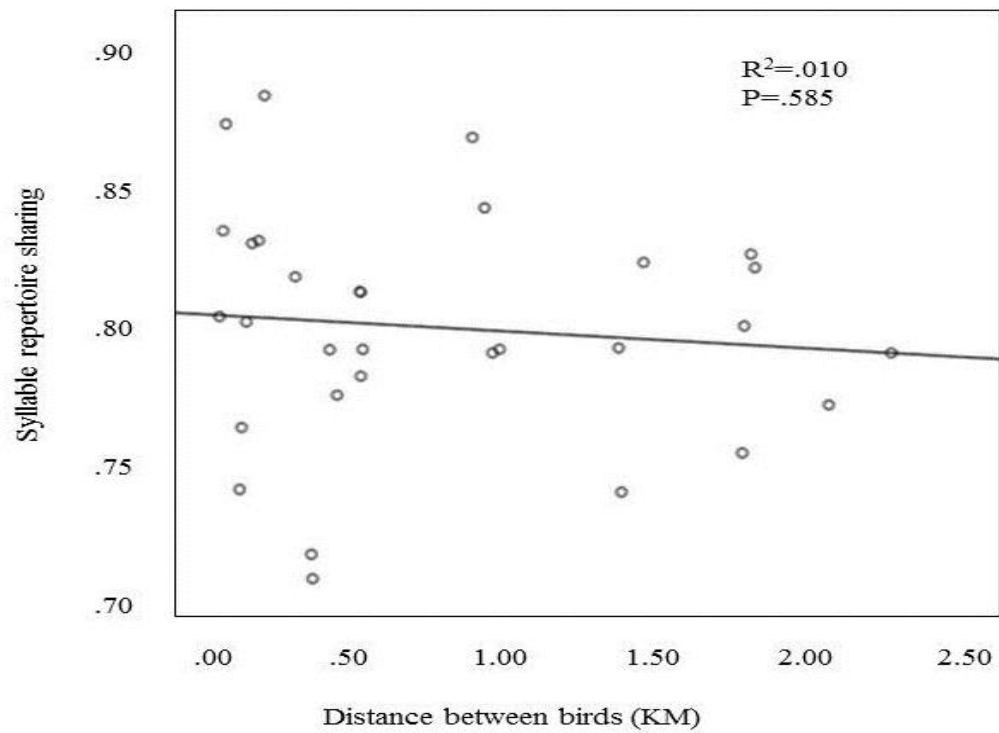


Figure 2.5: Relationship between syllable repertoire sharing values and the physical distance between males calculated using the bird's entire repertoire of songs (RSD1) and collapsed across the 2012 Lundbreck Falls and Whaleback sites.

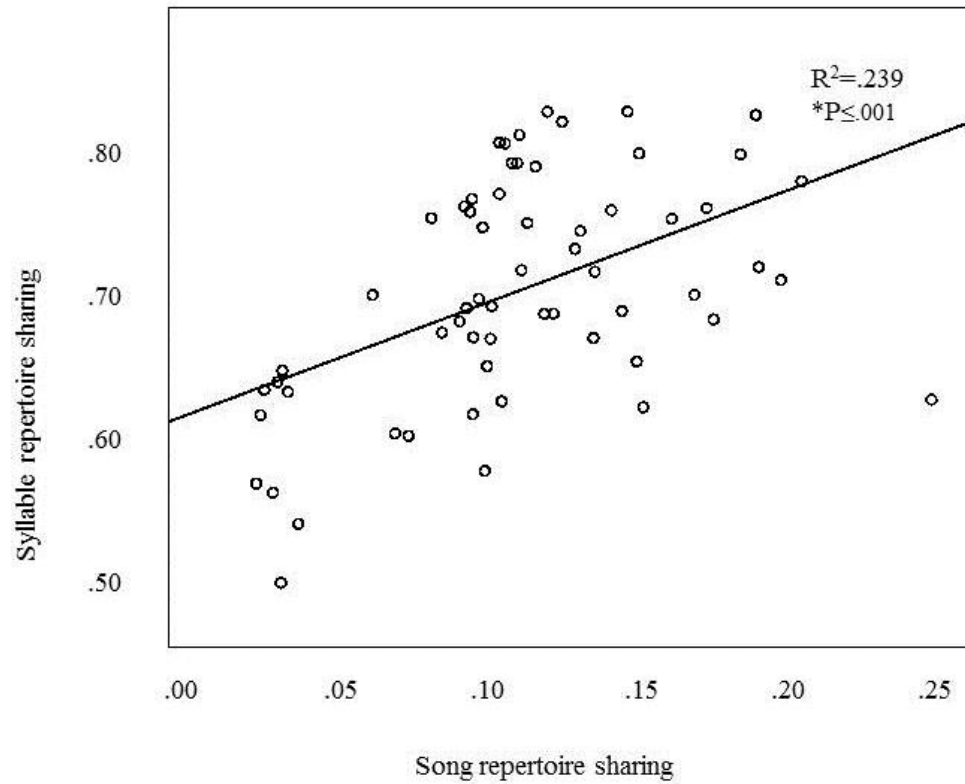


Figure 2.6: Relationship between syllable repertoire sharing values and song repertoire sharing values calculated using the bird's entire repertoire of songs (RSD1) and collapsed across the 2011 Lundbreck Falls and Whaleback sites.

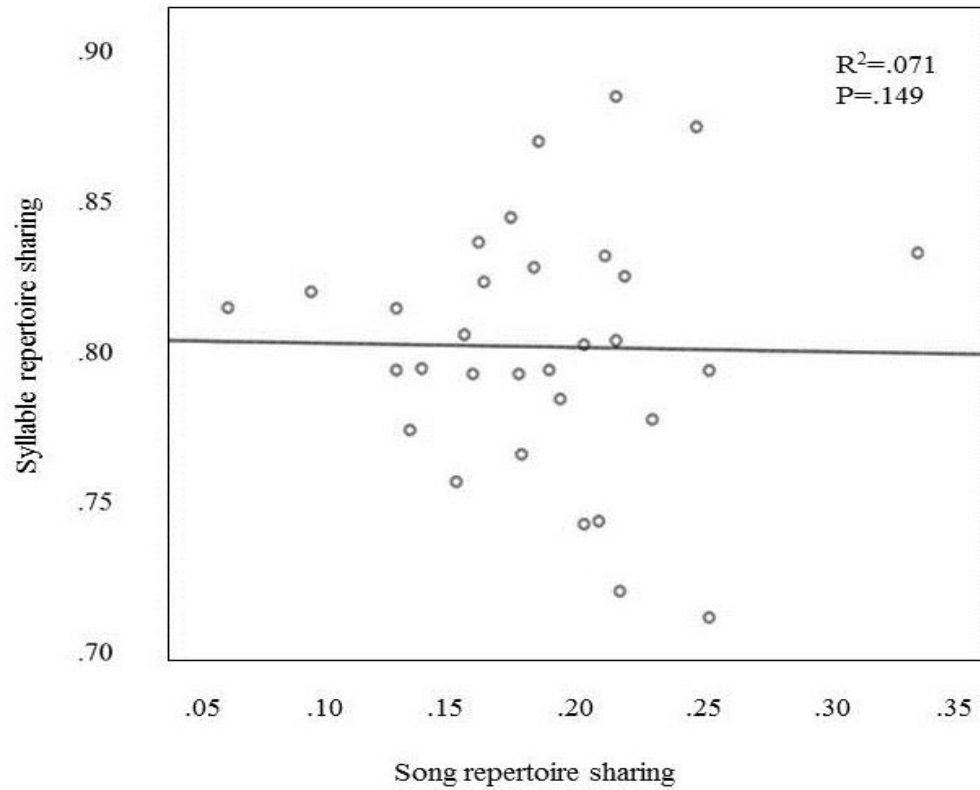


Figure 2.7: Relationship between syllable repertoire sharing values and song repertoire sharing values calculated using the birds's entire repertoire of songs (RSD1) and collapsed across the 2012 Lundbreck Falls and Whaleback sites.

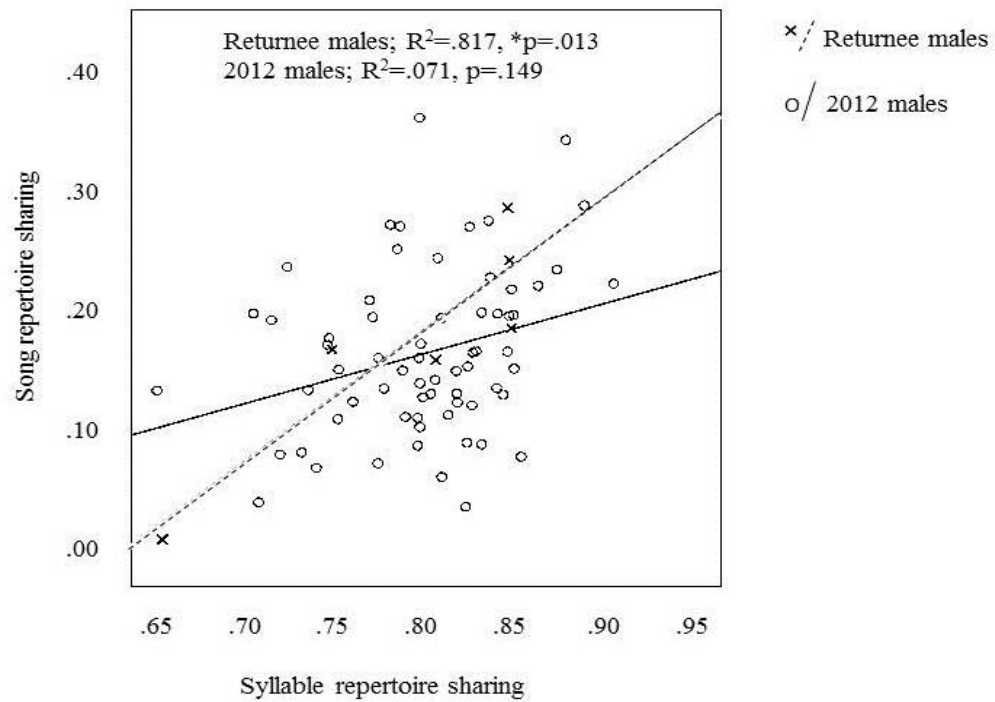


Figure 2.8: Relationship between syllable repertoire sharing values and song repertoire sharing values calculated using the birds's entire repertoire of songs (RSD1) and collapsed across the 2012 Lundbreck Falls and Whaleback sites and compared with the values for returnee males.

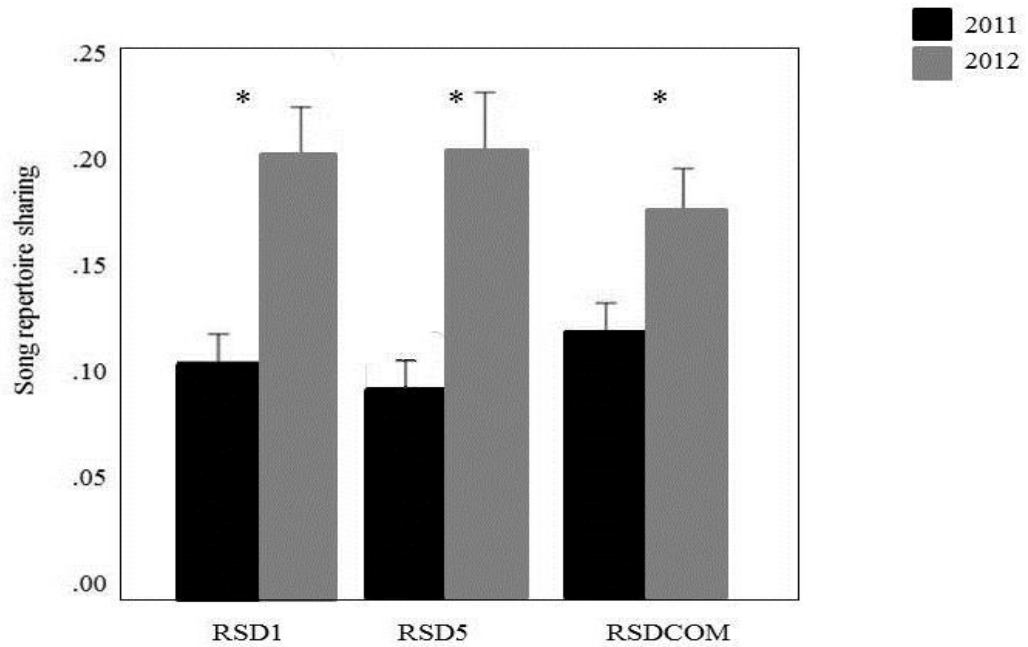


Figure 2.9: Mean (95%CI) repertoire sharing values, at all levels of the bird's repertoire, for the 2011 and 2012 populations, collapsed across sites.

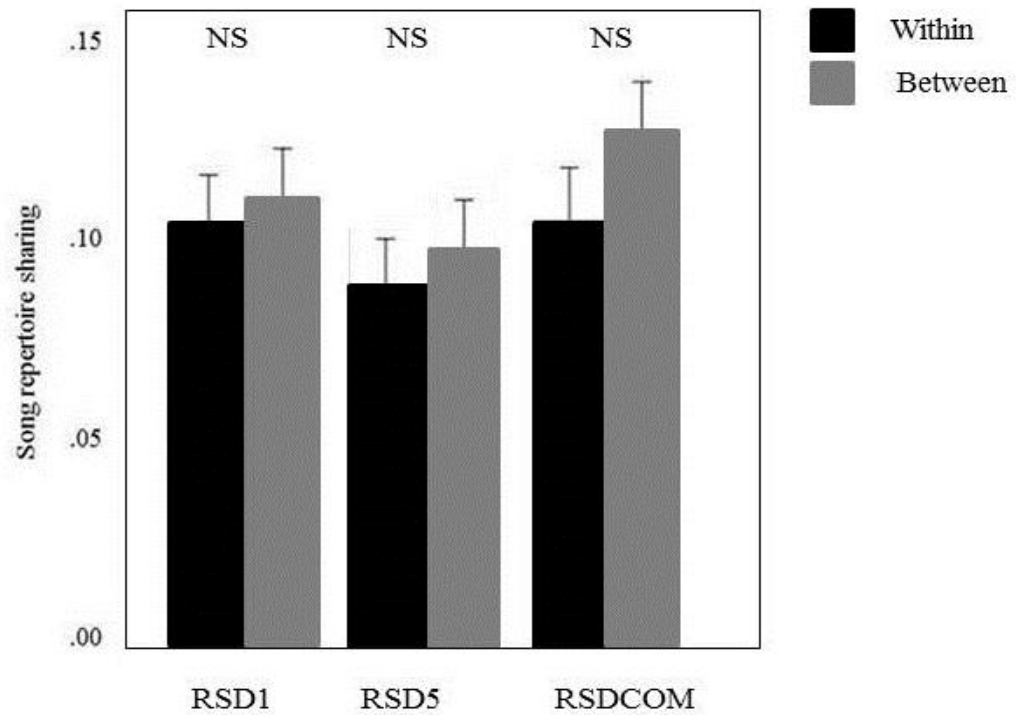


Figure 2.10: Mean (95% CI) repertoire sharing values, at all levels of the bird's repertoire, for 2011, comparing the relationship between repertoire sharing values within sites and between sites.

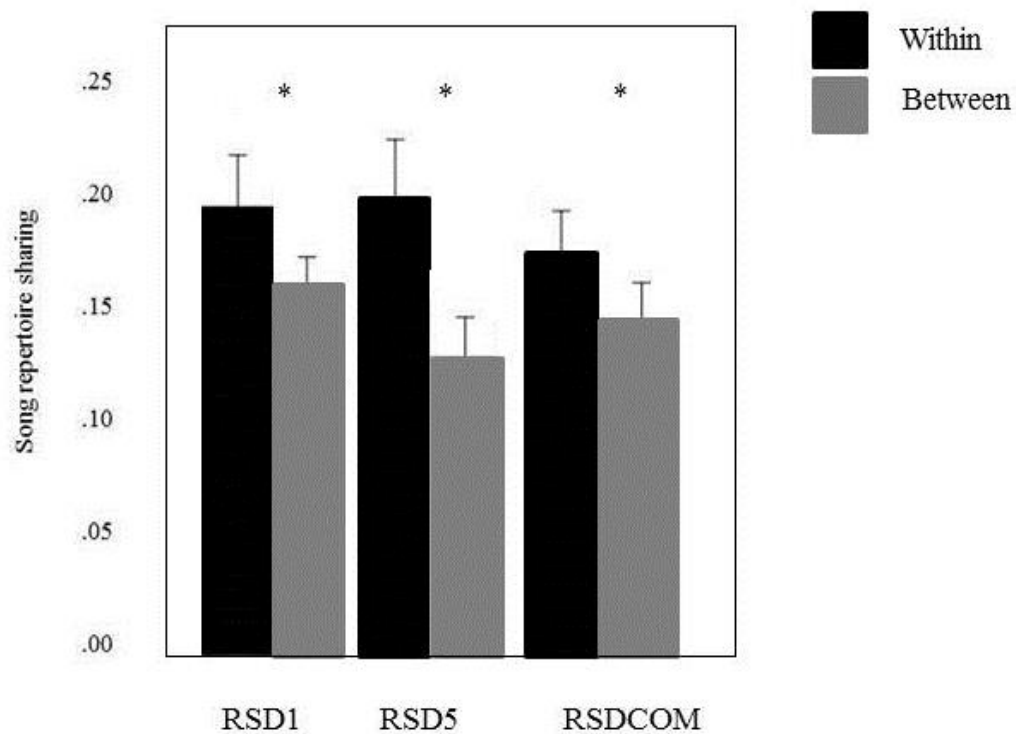


Figure 2.11: Mean (95% CI) repertoire sharing values, at all levels of the bird's repertoire, for 2012, comparing the relationship between repertoire sharing values within sites and between sites.

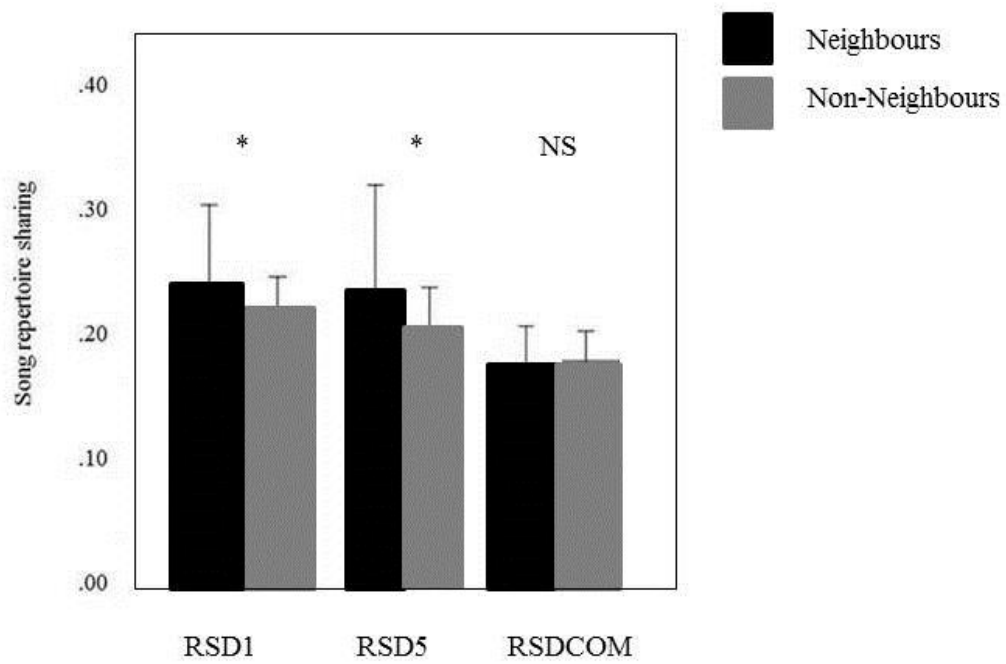


Figure 2.12: Mean (95% CI) repertoire sharing values, calculated at all levels of the bird's repertoires, between neighbouring and non-neighbouring males, collapsed across years and sites.

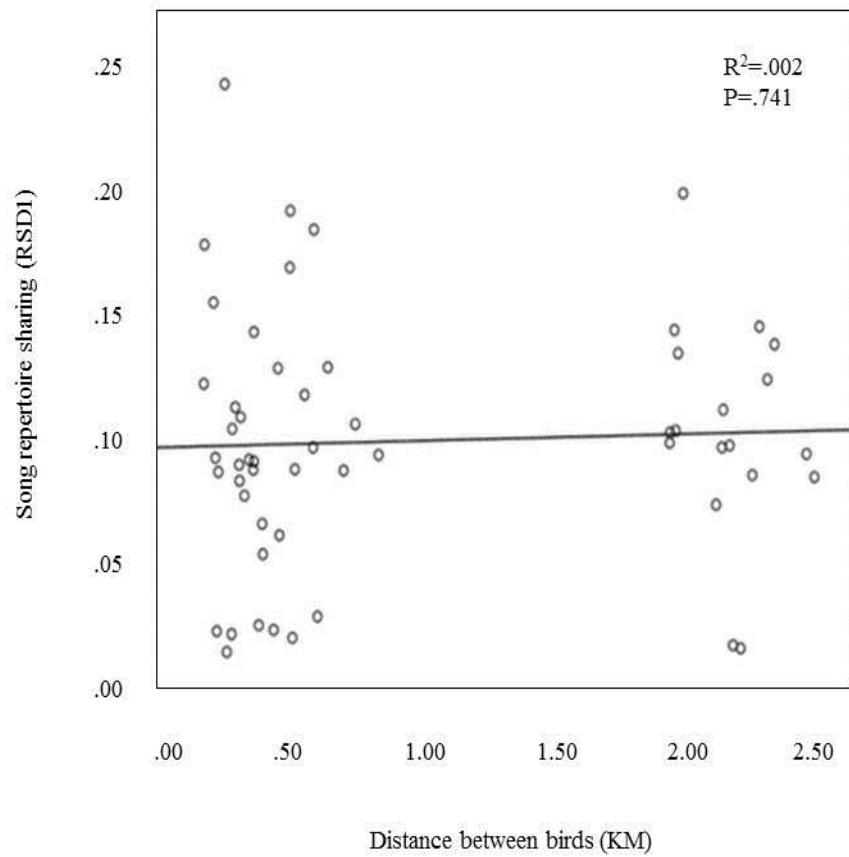


Figure 2.13: Relationship between song repertoire sharing values and the physical distance between males calculated using the bird's entire repertoire of songs (RSD1) for the 2011 Lundbreck Falls population.

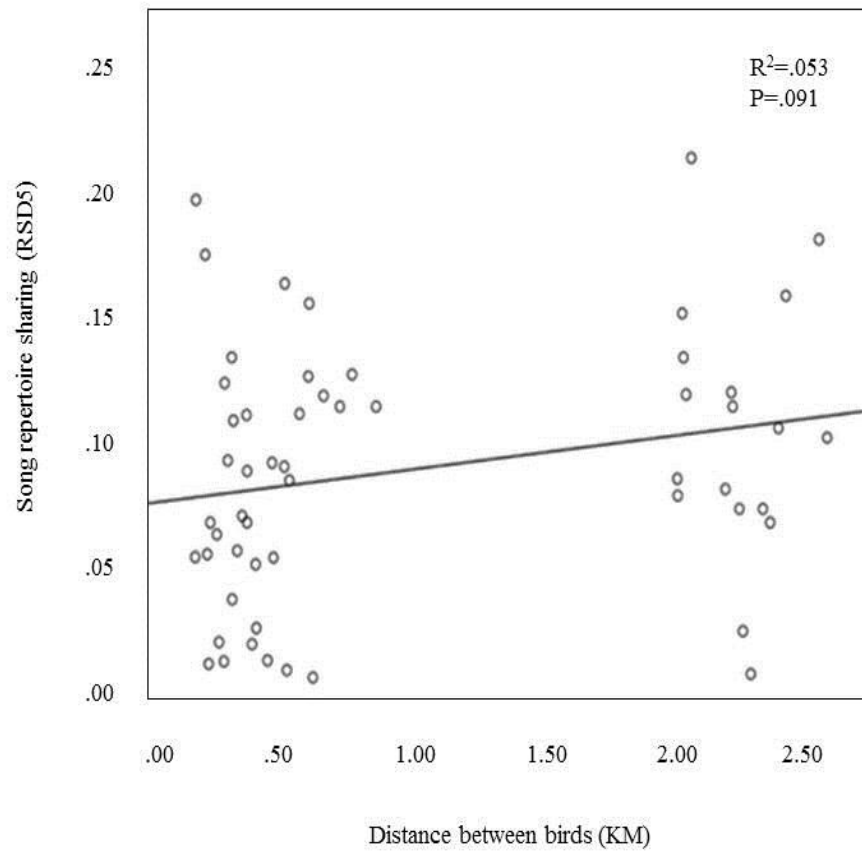


Figure 2.14: Relationship between song repertoire sharing values and the physical distance between males calculated using songs that are sung five times or more (RSD5) for the 2011 Lundbreck Falls site.

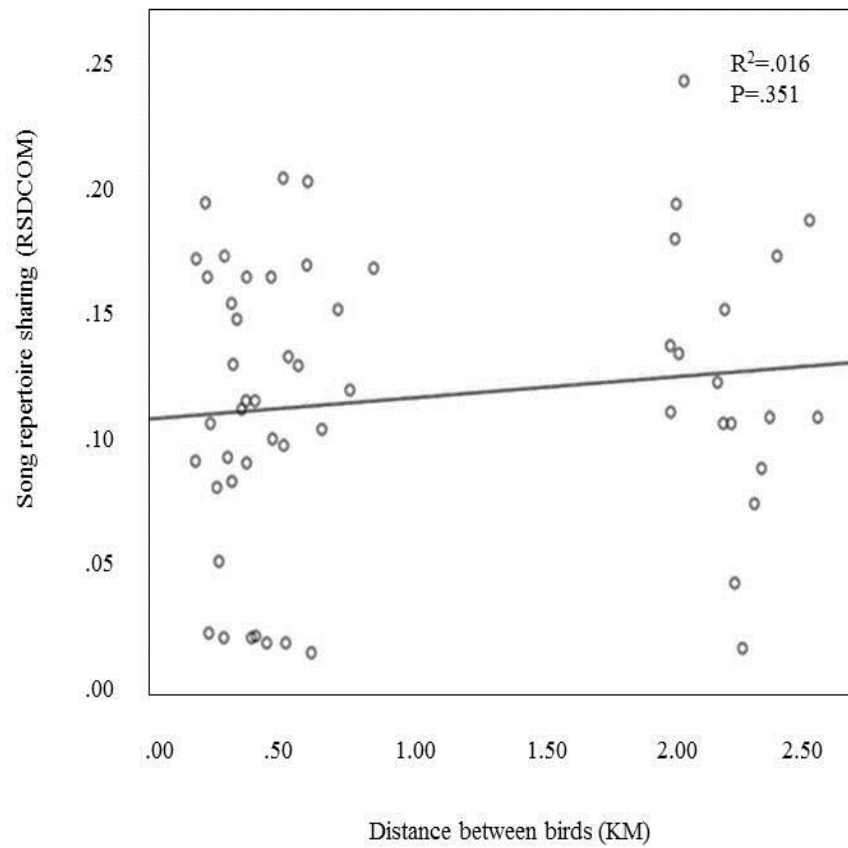


Figure 2.15: Relationship between song repertoire sharing values and the physical distance between males calculated using songs that comprise more than 1% of the bird's song repertoire (RSDCOM) for the 2011 Lundbreck Falls population.

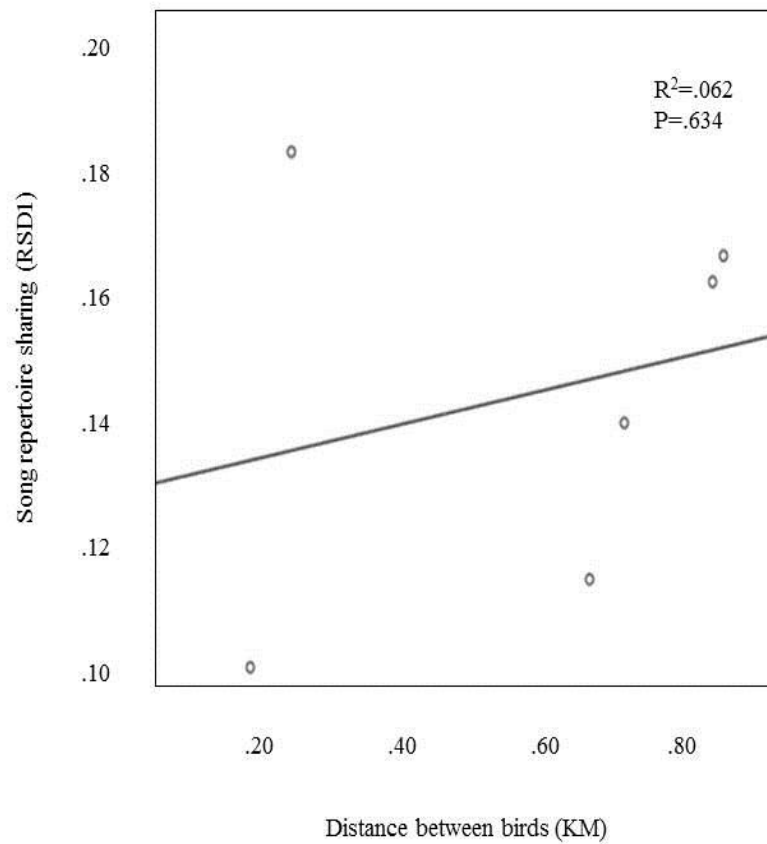


Figure 2.16: Relationship between song repertoire sharing values and the physical distance between males calculated using the bird's entire repertoire of songs (RSD1) for the 2011 Whaleback site.

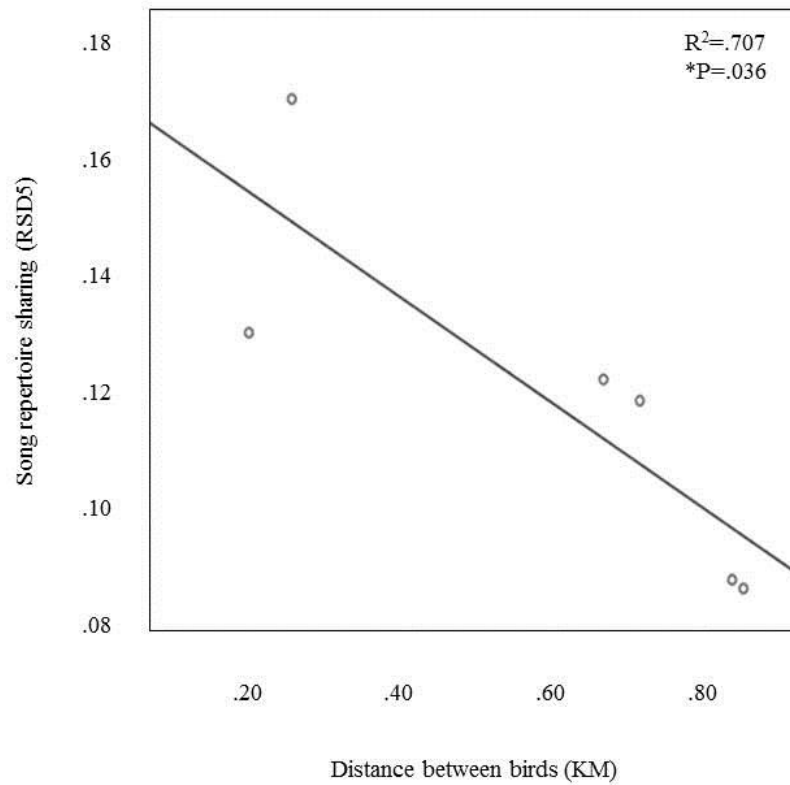


Figure 2.17: Relationship between song repertoire sharing values and the physical distance between males calculated using songs that are sung five times or more (RSD5) for the 2011 Whaleback site.

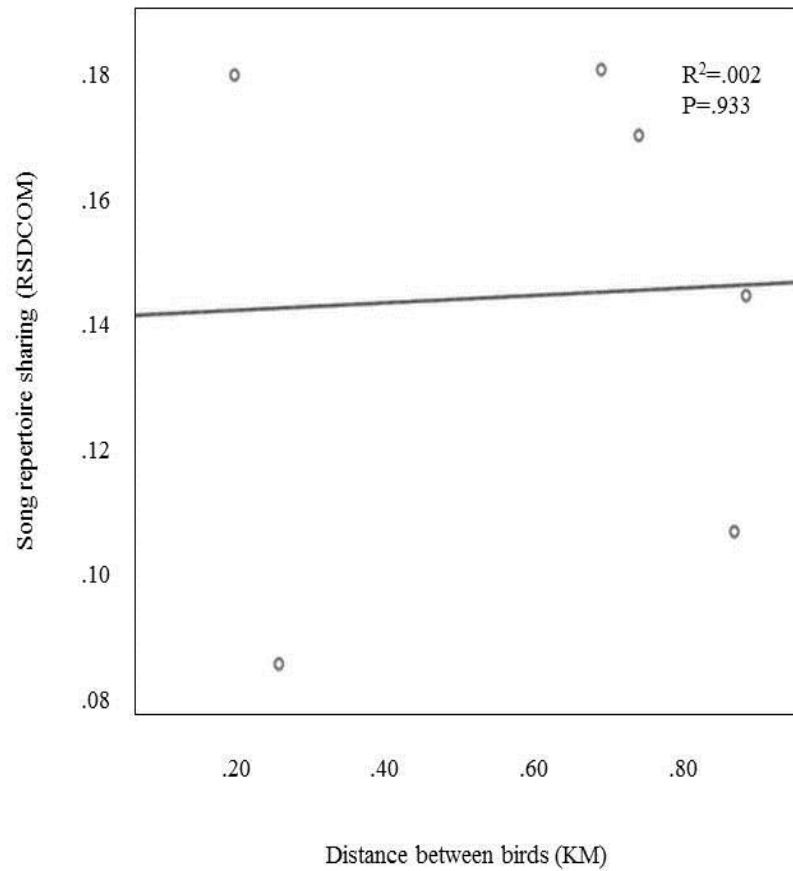


Figure 2.18: Relationship between song repertoire sharing values and the physical distance between males calculated using songs that comprise more than 1% of the bird's song repertoire (RSDCOM) for the 2011 Whaleback site.

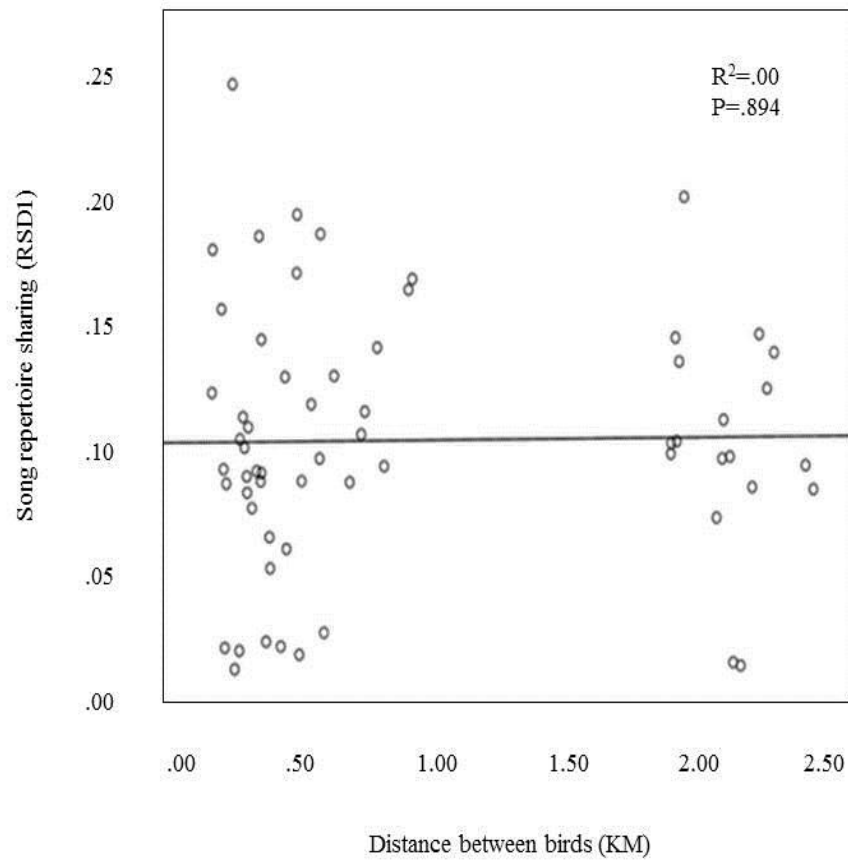


Figure 2.19: Relationship between song repertoire sharing values and the physical distance between males calculated using the bird's entire repertoire of songs (RSD1) collapsed across the 2011 Lundbreck Falls and Whaleback sites.

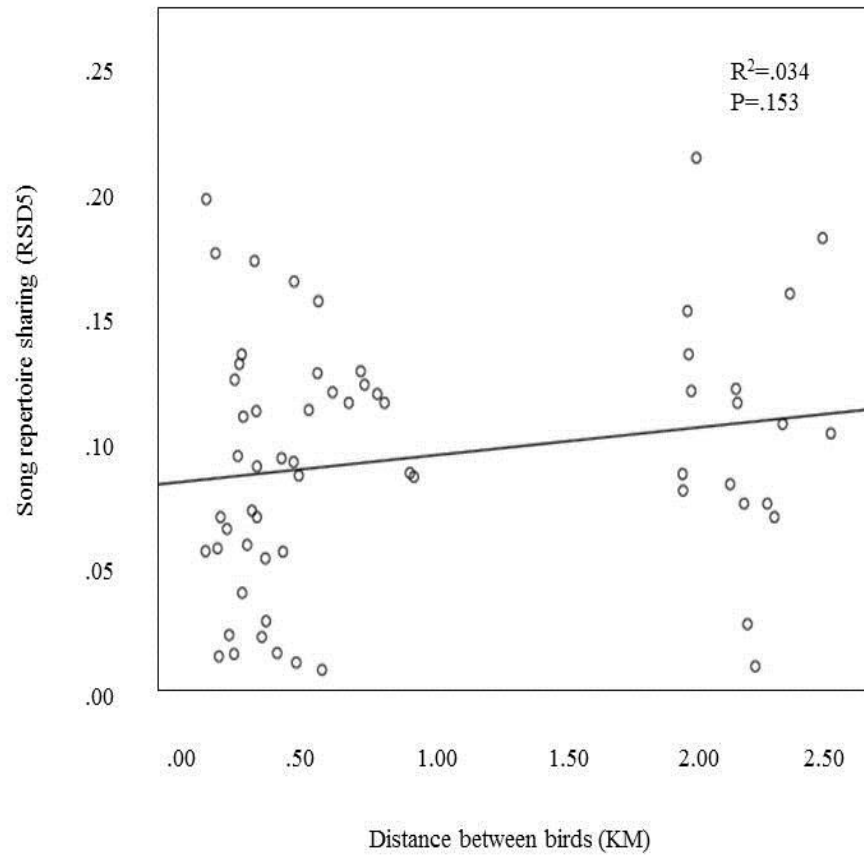


Figure 2.20: Relationship between song repertoire sharing values and the physical distance between males calculated using songs that are sung five times or more (RSD5) collapsed across the 2011 Lundbreck Falls and Whaleback sites.

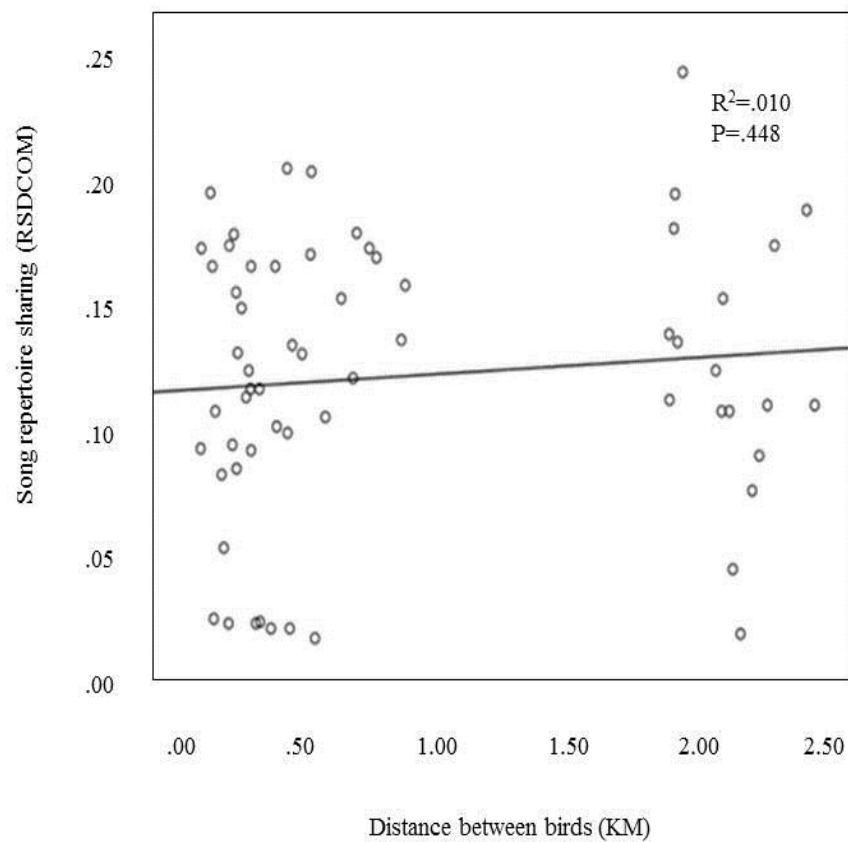


Figure 2.21: Relationship between song repertoire sharing values and the physical distance between males calculated using songs that comprise more than 1% of the bird's song repertoire (RSDCOM) collapsed across the 2011 Lundbreck Falls and Whaleback sites.

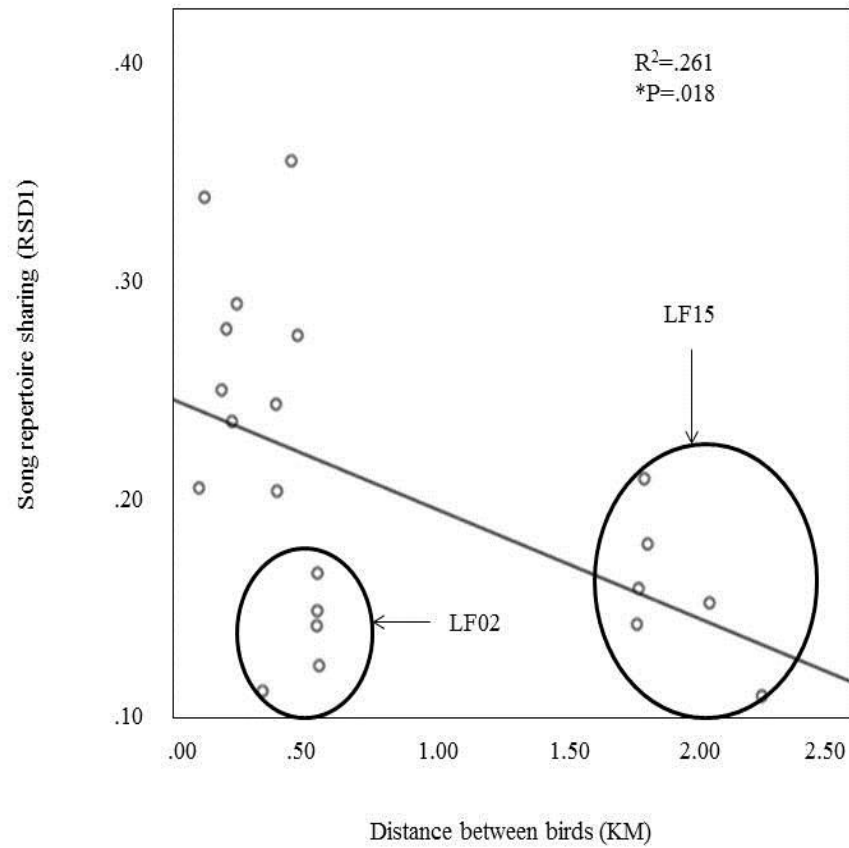


Figure 2.22: Relationship between song repertoire sharing values and the physical distance between males calculated using the bird's entire repertoire of songs (RSD1) for the 2012 Lundbreck Falls site.

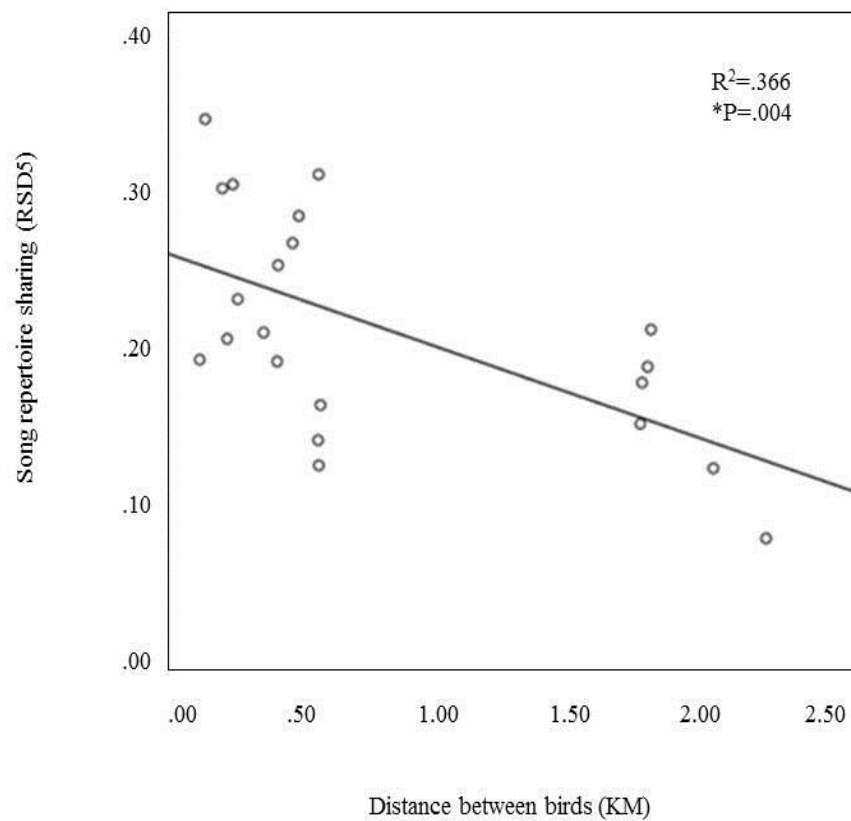


Figure 2.23: Relationship between song repertoire sharing values and the physical distance between males calculated using songs that are sung five times or more (RSD5) for the 2012 Lundbreck Falls site.

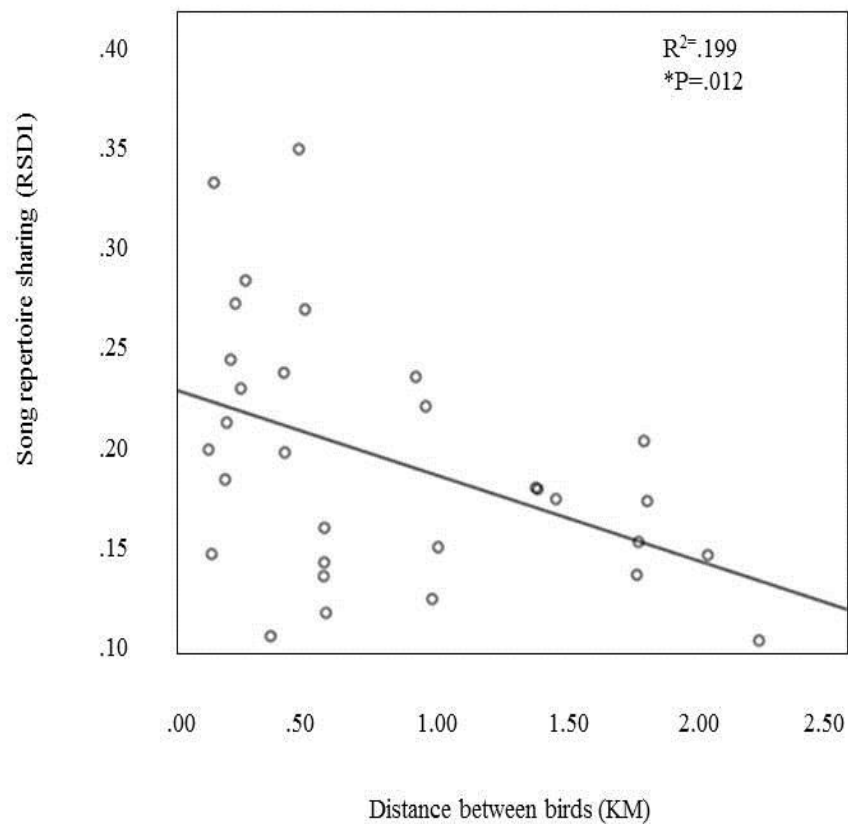


Figure 2.24: Relationship between song repertoire sharing values and the physical distance between males calculated using the bird's entire repertoire of songs (RSD1) collapsed across the 2012 Lundbreck Falls and Whaleback sites.

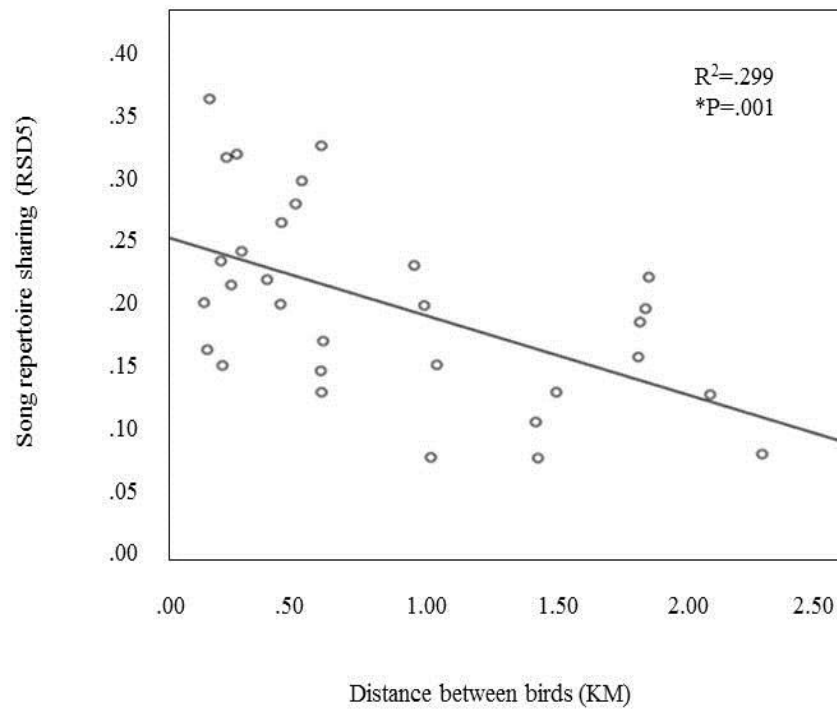


Figure 2.25: Relationship between song repertoire sharing values and the physical distance between males calculated using songs that are sung five times or more (RSD5) collapsed across the 2012 Lundbreck Falls and Whaleback sites.

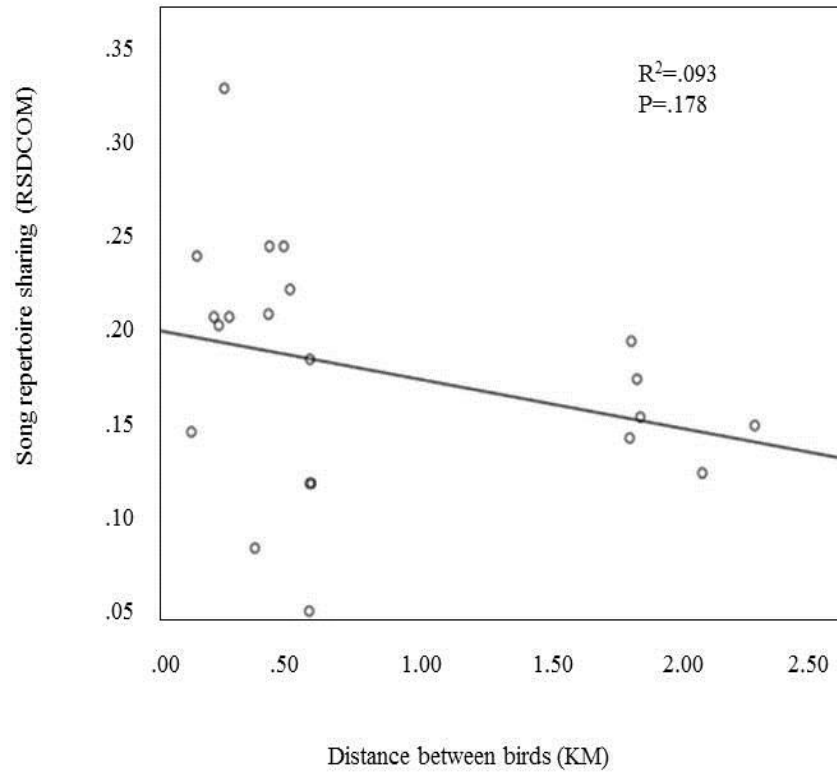


Figure 2.26: Relationship between song repertoire sharing values and the physical distance between males calculated using songs that comprise more than 1% of the bird's song repertoire (RSDCOM) for the 2012 Lundbreck Falls site.

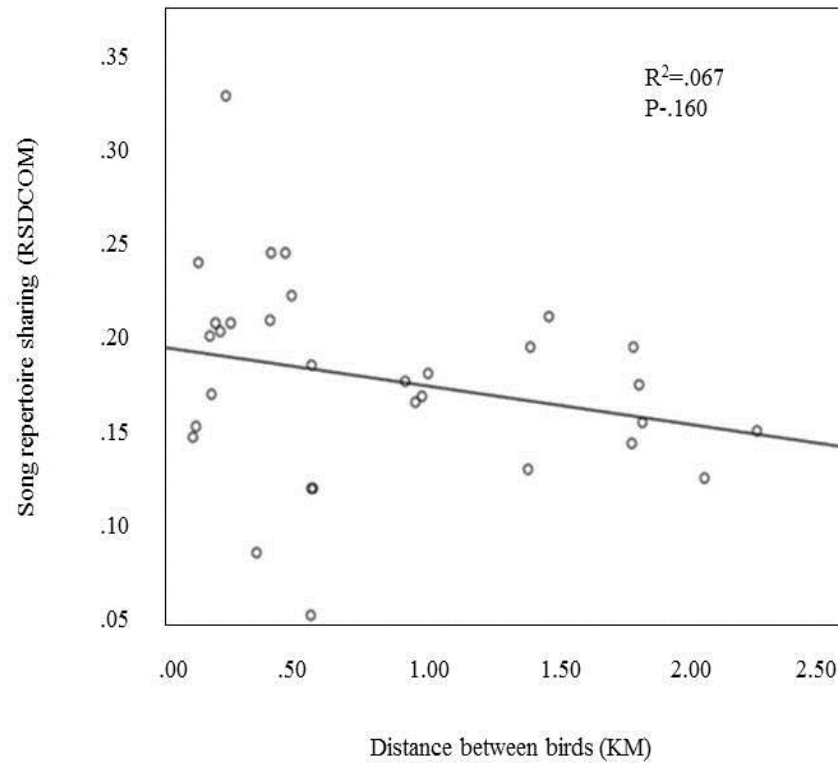


Figure 2.27: Relationship between song repertoire sharing values and the physical distance between males calculated using songs that comprise more than 1% of the bird's song repertoire (RSDCOM) collapsed across the 2012 Lundbreck Falls and Whaleback sites.

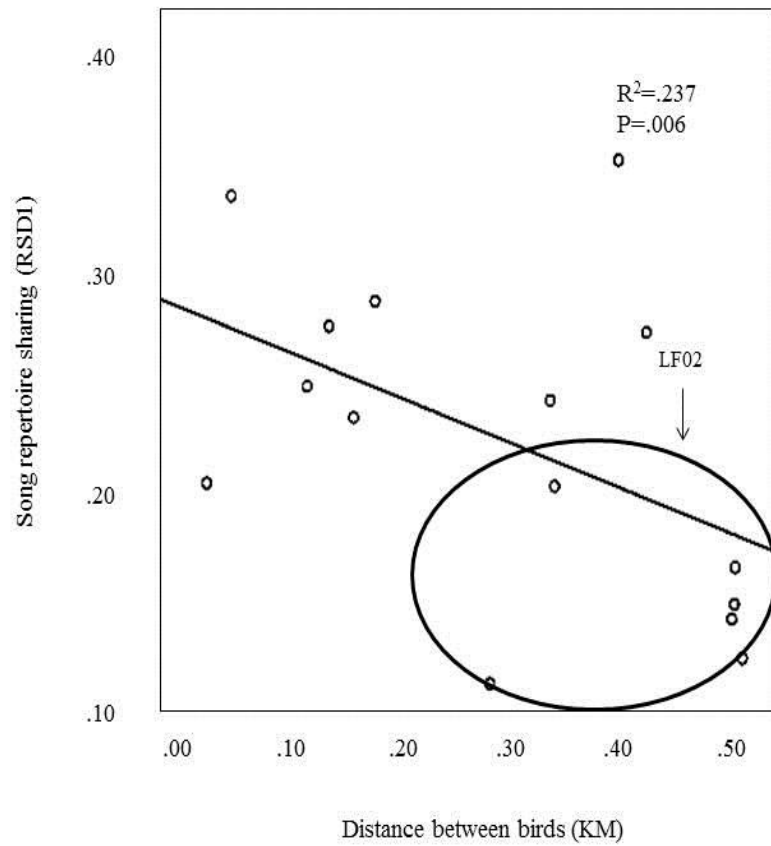


Figure 2.28: Relationship between song repertoire sharing values and the physical distance between males calculated using the bird's entire repertoire of songs (RSD1) for the 2012 Lundbreck Falls site excluding LF15.

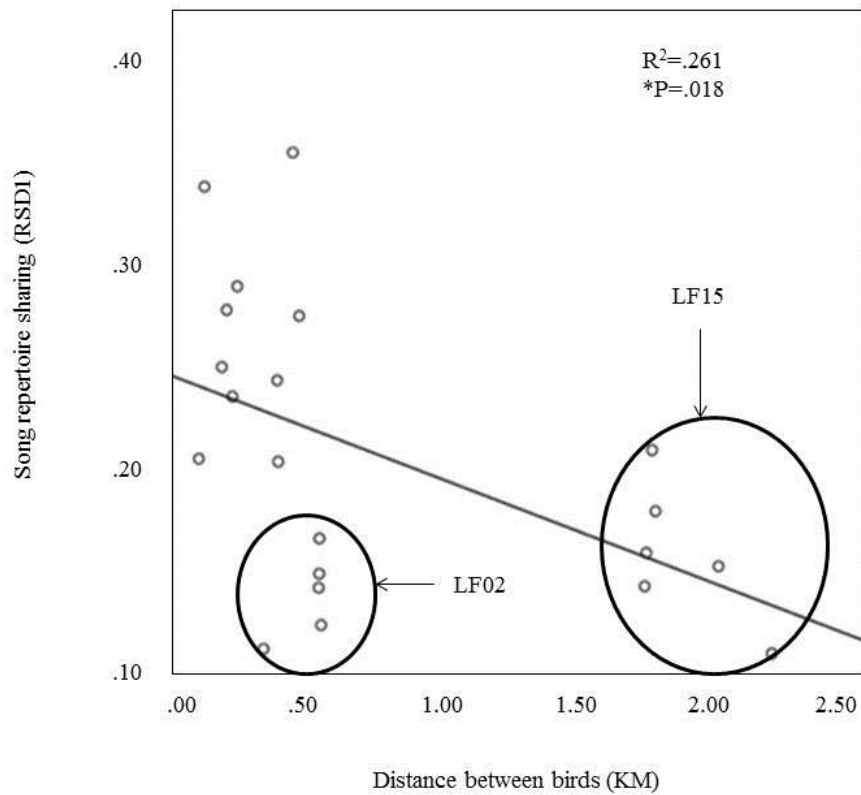


Figure 2.29: Relationship between song repertoire sharing values and the physical distance between males calculated using the bird's entire repertoire of songs (RSD1) for the 2012 Lundbreck Falls site, excluding LF15 and LF02.

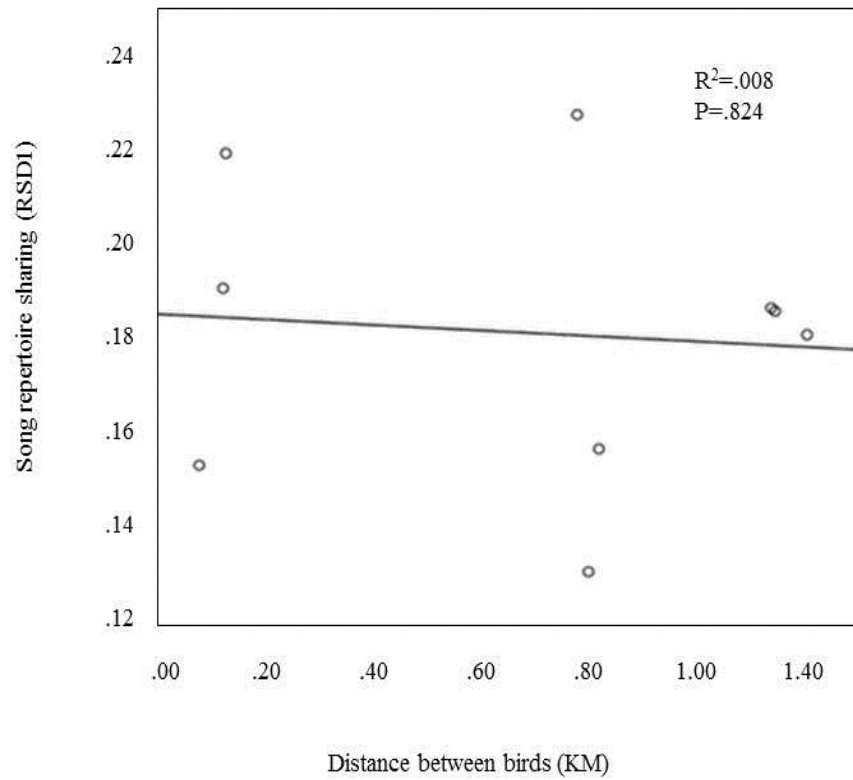


Figure 2.30: Relationship between song repertoire sharing values and the physical distance between males calculated using the bird's entire repertoire of songs (RSD1) for the 2012 Whaleback site

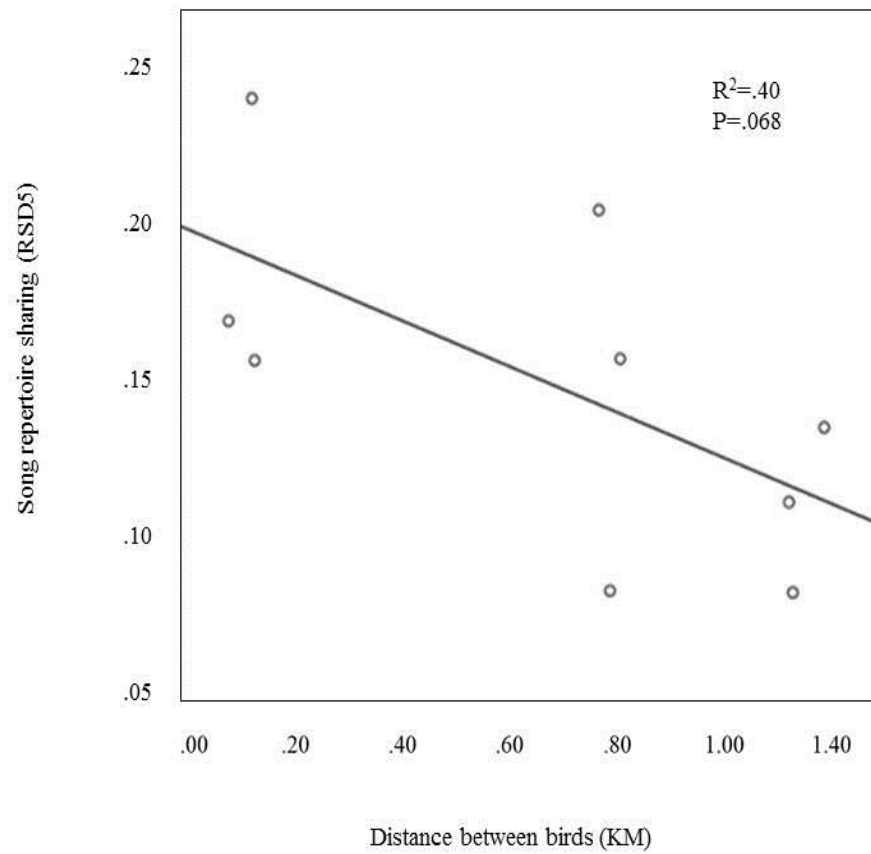


Figure 2.31: Relationship between song repertoire sharing values and the physical distance between males calculated using songs that are sung five times or more (RSD5) for the 2012 Whaleback site.

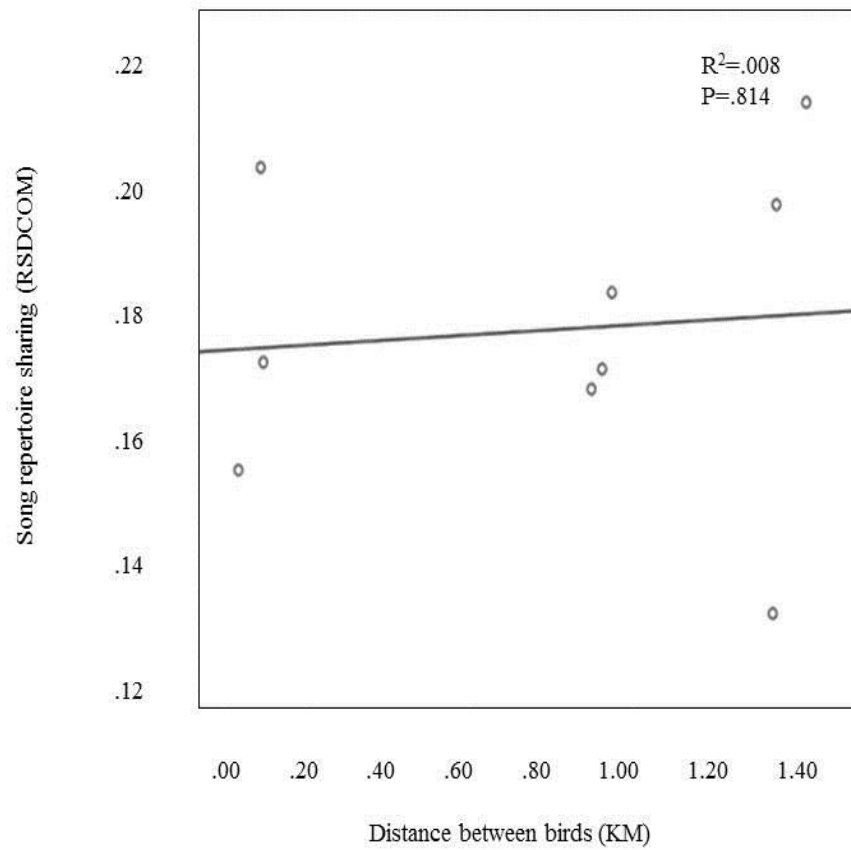


Figure 2.32: Relationship between song repertoire sharing values and the physical distance between males calculated using songs that comprise more than 1% of the bird's song repertoire (RSDCOM) for the 2012 Whaleback site.

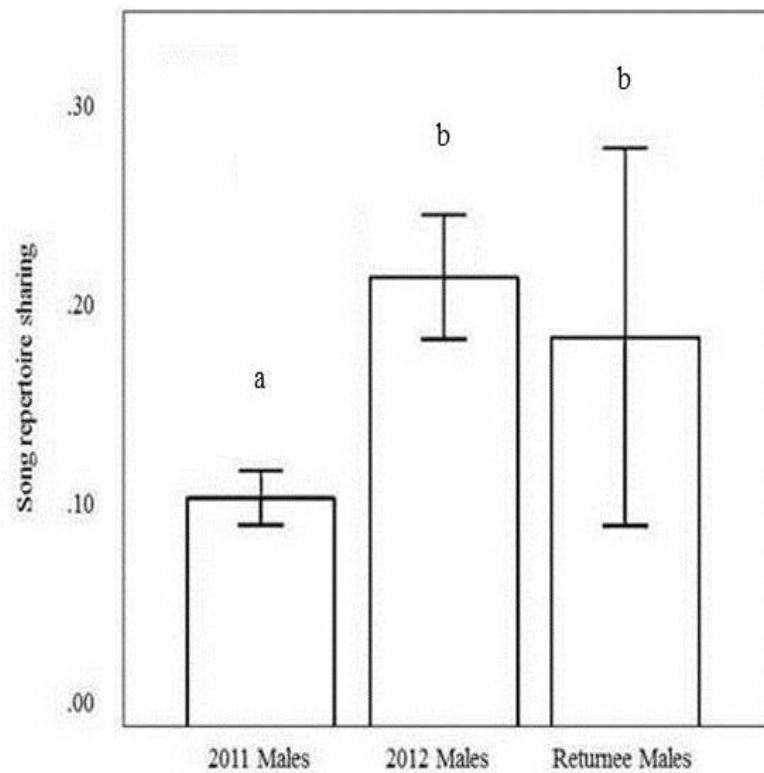


Figure 2.33: Song type repertoire sharing values calculated using the bird's entire repertoire of songs (RSD1), compared between years within the same birds to sharing values between birds within the same breeding season.

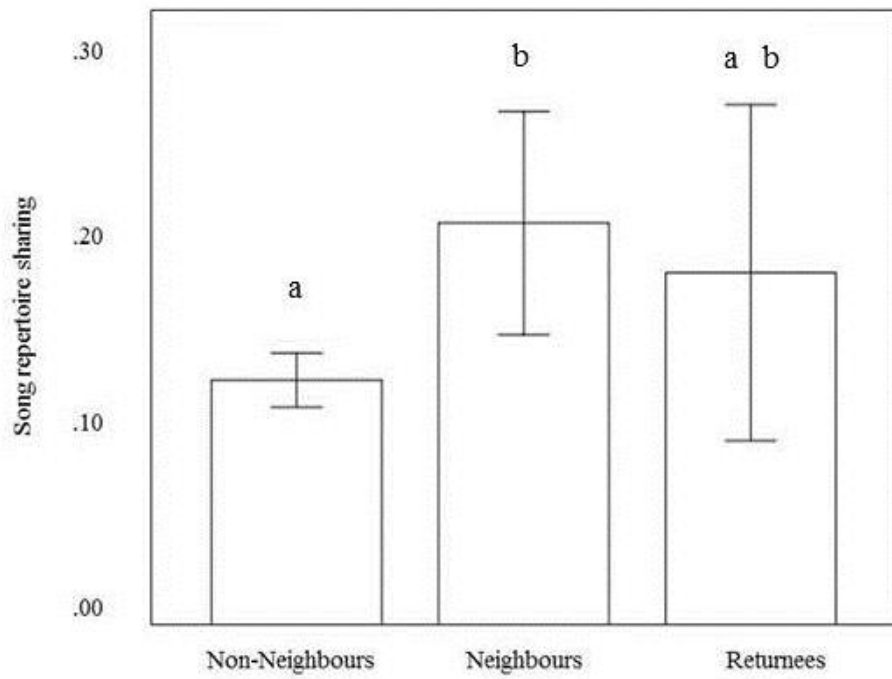


Figure 2.34: Song type repertoire sharing values calculated using the bird's entire repertoire of songs (RSD1), compared between years within the same birds to sharing values between neighbouring and non-neighbouring males.

Chapter 3

General Discussion

The goal of this thesis was to explore the basic spatial patterns of song sharing, thereby provide the foundation for subsequent detailed testing of a variety of hypotheses concerning the functions of complex song. As with any research, the present work involved many strengths but also some important limitations and weaknesses that should be considered in future studies.

3.1 Research Strengths

3.1.1 Sample Size

One considerable strength of the current work is simply its sample size which involved an unprecedentedly large number of song recordings ($n=35,067$) and a large number of males ($n=21$). By comparison, most other studies of song sharing have used comparatively small samples. For example, Comocho-Schlenker, Courvoisier, & Aubin (2011), conducted a similar study of song sharing in the Winter Wren (*Troglodytes troglodytes*) and utilized three pairs of neighbouring males and only 336 songs. Catchpole & Rowell (1993), studying song sharing in the European Wren (*Troglodytes troglodytes*), had a larger sample of males ($n=13$) and a larger sample of songs ($n=1,533$). However, neither study even approaches the sample collected and analysed here. Such a large sample is important in as much as both the reliability and the validity of the results of any kind of study hinge heavily on the size and richness of the sample used.

3.1.2 Sampling Males in their Natural Environment

Another important strength of the current study was its use of birds nesting in natural cavities. This was an unusual choice because most researchers studying cavity nesting birds provide artificial nest boxes, which the birds prefer. However, the use of nest boxes may affect behavior in a variety of ways germane to the phenomenon of song sharing studied here. For example, some cavity nesters, including the House Wren are known to prefer nest boxes, which have also been shown to support improved breeding outcomes. Further, nest boxes may facilitate higher levels of polygyny if their placement allows males to defend more than one box better than they could dispersed natural cavities. And these effects, in turn, may affect levels of song sharing. For example, the increased availability of suitable cavities through nest boxes might lead to less vigorous male-male competition and thereby reduced pressures on song sharing either in territory competition or mate attraction compared to the natural condition. Hence, in studying birds nesting in natural cavities, the findings reported here might have greater ecological validity than a substantial amount of work conducted previously. In short, we may be able more certain that the levels of song sharing observed here are a better reflection of the male's natural behaviour.

3.2 Research Weaknesses and Limitations

3.2.1 Research Design: Natural Cavities versus Nest Boxes

As just noted, nest boxes represent a contrived environment that may reduce ecological validity. However, at the same time, the use of nest boxes could also be

advantageous in some ways. For example, if the density of nest boxes were systematically controlled and manipulated it provide a degree of control over the dispersion of males and with it the intensity of the pressures for song matching in the service of mate attraction and territory defense. In this way, using nest boxes might allow a more controlled, experimental test of the pressures affecting song sharing than is possible in the unmanipulated natural condition.

3.2.2 Song Sharing Computations

Another limitation of the current work concerns the analyses used to evaluate levels of song sharing among males. These did not involve establishing levels of song sharing among males that would be expected just by chance. This is a challenging issue, because it is not immediately obvious how to establish ‘chance’ levels of sharing. However, one method used in other studies involves a permutation method (Grießmann & Naguib, 2002). Permutation methods compute all the possible ways that a set of scores can be arranged, in this case how many times males will share songs if all songs and all males are randomly shuffled. This permutation method of song- and male-shuffling involves establishing a distribution of possible song sharing levels for the sample involved, to which the actual levels of song sharing can be compared. In other words, it generates a unique sampling distribution – that represents the null hypothesis – that is specific to the sample of data collected, rather than being a generic distribution based on a variety of sampling assumptions that are made in typical parametric and non-parametric statistics.

One problem with permutation methods is that they are time consuming and computationally intensive. Indeed, most previous work using permutation methods have

involved species with small to moderate size repertoires ($n < 40$) (Camocho-Schlenker, et al., 2011; Griebmann & Naguib, 2002; Hultsch & Todt, 1981). The method becomes cumbersome when dealing with species that have very large repertoires. Hence, studies of song sharing involving species with relatively large repertoires generally do not employ a method of permutation (Hultsch & Todt, 1981; Price & Yuan, 2011). Nevertheless, future work might profit from attempts to use permutation methods for species with large song repertoires, such as the House Wren.

3.2.3 Definition of Song Matching

A further possibly limitation of the current work was its use of a very conservative definition of song sharing limited to strict matching in the sequence of syllable types. This conservative approach was adopted very deliberately – to be conservative – because there is no general consensus in the literature of what constitutes a song type match. Some researchers have used the conservative definition used here (Catchpole & Rowell, 1993), while others have scored a match if song types did not differ in more than two basic song components (syllables) (Griebmann & Naguib, 2002), and still others have used more liberal definitions and characterized songs as belonging to the same type when they differed on no more than three of the ten elements in the first two sections of the song (Hultsch & Todt, 1981).

In many respects, such variability in the definition of what constitutes the ‘same’ song type is understandable given the tremendous variety that exists in the syllable and song repertoires of different species. However, it does create a potential problem in cross-species comparison. For example, had a more liberal definition of song sharing been used

in the current work – say, requiring matching on only two of the four syllable types that characterized the average song – then levels of song sharing among males in the current work would have been dramatically higher. Whether or not that kind of difference in the absolute level of song sharing is reported is meaningful to the birds themselves, it would certainly complicate comparisons with absolute levels of song sharing reported in other species. Given the discrepancies in how song sharing has been calculated in past work, perhaps the simplest conclusion to draw is that comparisons across species should not focus on differences in the absolute levels of sharing reported but rather only differences (and similarities) in the relative levels of sharing observed among classes of males (e.g., neighbours versus non-neighbours). Such comparisons of relative differences in song sharing among categories of individuals should often remain valid independently of differences in the methods used to compute absolute levels of sharing.

3.2.4 Real-time Song Matching

This thesis provided the necessary first step needed to move in additional focused tests of the function of song sharing and song matching. In this respect, future work could profit from two additional types of study. First, observational approaches could be used that employ a method of time-synchronized recordings to capture simultaneously the song production of multiple males in a local area. By synchronizing the recordings of multiple males one could evaluate patterns in their production of particular song types to test whether some males (e.g., neighbours) are more likely than others (e.g., non-neighbours) to be singing the same song types at the same time. Second, an even more direct approach would dynamic interactive playbacks to measure directly how individual

males respond to simulations of rival males singing songs that either match or do not match the subjects' own songs. This would be an even more direct way to evaluate whether males do in fact adjust their own real-time singing to match (or not match) songs of rival males in this species.

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