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Duet Codes and Answering Rules in the Rufous-and-White Wren (*Thryophilus Rufalbus*)

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**DUET CODES AND ANSWERING RULES IN THE RUFOUS-AND-WHITE
WREN (*THRYOPHILUS RUFALBUS*)**

by

ANNEKA ELEANOR OSMUN

A Thesis
Submitted to the Faculty of Graduate Studies
through Biological Sciences
in Partial Fulfillment of the Requirements for
the Degree of Master of Science at the
University of Windsor

Windsor, Ontario, Canada

2010

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Duet codes and answering rules in the Rufous-and-white Wren (*Thryothorus rufalbus*)

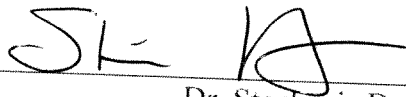
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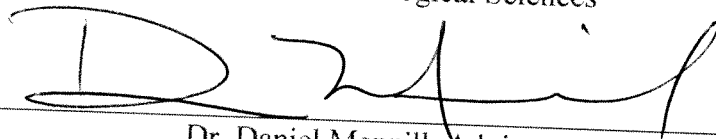
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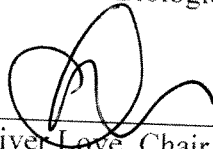
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Declaration of Co-Authorship

I. Co-Authorship Declaration

I hereby declare that this thesis incorporates material that is result of joint research, as follows:

I am sole author of Chapter 1 and am the principle author of the data chapter, Chapter 2. I acknowledge the input of my supervisor Dr. Daniel Mennill who funded this research, shared ideas for research design, statistical analyses and writing, and collected the historical data on which the thesis is based.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-author(s) to include the above material(s) in my thesis.

I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work.

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I declare that this is a true copy of my thesis, including any final revisions, as approved by my thesis committee and the Graduate Studies office, and that this thesis has not been submitted for a higher degree to any other University or Institution. The chapters are presented in manuscript format for peer-reviewed publication.

Abstract

In many tropical birds, breeding partners combine their songs in coordinated vocal duets. In species that have song repertoires, duetting birds may follow answering rules where they combine particular songs from their repertoire with particular songs in their partner's repertoires. These associations are called duet codes. I explored the answering rules and duet codes of Rufous-and-white Wrens (*Thryophilus rufalbus*), a Neotropical duetting songbird. I analysed over 5,000 duets recorded over seven years from a colour-banded population of Rufous-and-white Wrens. I found that pairs follow duet codes, and their answering rules remain consistent between years and partnerships. I found that females adhere more strongly to answering rules than males. Different pairs of Rufous-and-white Wrens followed the same answering rules. My findings enhance our understanding of duet function, communication in tropical animals, and the evolution of song repertoires.

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Chapter 1

General introduction

Mulder et al. 2003, Seddon et al. 2002, Sonnenschein and Reyer 1983). The mate guarding function of female song has been demonstrated through the presentation of playback of male and female songs; females react more aggressively towards playback of female solo stimuli (Koloff 2010, Mennill and Vehrencamp 2008, Marshall-Ball et al. 2006, Seddon et al. 2002). Resident females may perceive intruder females as more of a threat than intruder males because of the potential of usurpation of their position in the pair bond or for extra-pair copulations with their mate (Hall 2004).

Avian duetting

In species where both males and females sing, songs are often coordinated into joint acoustic displays known as duets (e.g. Figure 1.1; Hall 2004). Duetting behaviour is widespread and has evolved independently across several avian taxonomic groups (Hall 2004). Given the repeated evolution of this behaviour, selection for duetting is thought to be strong (Hall 2004). The life history characteristics that are associated with the evolution of duetting are still debated, although several life history traits linked with the tropics seem to be associated with the evolution of female song: year-round territoriality, breeding synchrony, lack of migration, monogamy, and dispersed nest sites (Hall 2009, Price 2009, Price et al. 2009). In duetting species, long term monogamy and year-round territoriality appear to be common (Hall 2009, Slater and Mann 2004).

The focus of my thesis is not on duet function, but on the mechanics of song type choice within the duets of a Neotropical wren. Nevertheless, it is worthwhile to briefly discuss the function of duetting behaviour. The adaptive significance of duets is understood to vary both within and between species. Many hypotheses have been proposed, and few are mutually exclusive. The original opinion of many scientists (e.g.

Thorpe 1963) was that duetting is a cooperative behaviour between the sexes where both members contribute to duets to achieve a common goal (Hall 2004). This line of thinking has produced at least three hypotheses for the function of duets:

Hypothesis 1: Maintaining contact hypothesis. Duets are used by pair members to locate one another, often in dense vegetation (Mennill and Vehrencamp 2008, Logue 2007a).

Hypothesis 2: Reproductive synchrony hypothesis. Duets are used to coordinate breeding activities (Dilger 1953). Singing certain types of duets or changing the level of duet output can signal different stages of the breeding cycle to a partner (Topp and Mennill 2008, Sonnenschein and Reyer 1983).

Hypothesis 3: Joint resource defence hypothesis. Pair members perform duets to maintain or defend territories from conspecific intruders (Mennill 2006, Grafe et al. 2004, Hall 2000).

More recently, an alternative idea has emerged, suggesting that duets may not be cooperative endeavours, but that each sex might duet to further their own agenda (Levin 1996a). Several hypotheses focus on the conflict-based, non-cooperative nature of duets. This line of thinking has produced at least two additional hypotheses for the function of duets:

Hypothesis 4: Mate or paternity guarding hypothesis. Duets are used to advertise a partner's mated status to other birds or to monitor a potentially promiscuous partner. Mate-guarding has been demonstrated through acoustic playback studies where birds were more aggressive toward same-sex solo stimuli (Mennill and Vehrencamp 2008, Marshall-Ball et al. 2006, Grafe and Bitz 2004b).

Hypothesis 5: Signalling commitment or pair-bond maintenance hypothesis.

Duets are used to monitor commitment of a partner in terms of the energy they devote to duetting. Both partners signal willingness to invest in the pair bond through duetting (Marshall-Ball et al. 2006, Hall 2004, Hall 2000).

It is widely accepted that duets serve several functions and that species can duet for many different purposes. For example, previous work shows that Rufous-and-white Wren (*Thryophilus rufalbus*) duets play an important role in territory defence, maintaining contact, synchronizing breeding and acoustic mate-guarding (Mennill and Vehrencamp 2008, Topp and Mennill 2008, Mennill 2006). Plain Wrens (*Cantorchilus modestus*) use duets for joint territory defence and mate guarding and also for pair-bond maintenance (Marshall-Ball et al. 2006). Slate-coloured Boubous duet to achieve breeding synchrony and to defend a territory (Sonnenschein and Reyer 1983). Species may have a variety of different motives for duetting with their partners, and the duets themselves can carry several different messages.

Repertoires

Some bird species can only sing one type of song (Catchpole and Slater 2008). In many species, however, each individual has a library of song types called a “repertoire”. Repertoire sizes can vary within and between species. Repertoires can be as small as two songs, as in some Great Tits, or as large as 1500, as in some Brown Thrashers (*Toxostoma rufum*; Catchpole and Slater 2008). The function of repertoires is a longstanding topic of interest in behavioural ecology and ornithology. Research has shown that different songs in a repertoire may serve different functions. Some warbler

species, for example, have different song types for advertising location, breeding status, propensity for movement and aggression (Staicer et al. 2006, Byers 1996).

Most research on repertoires focuses on the idea that birds use their repertoires in mate attraction and male-male aggression. Studies on the importance of repertoires in mate attraction demonstrate that larger repertoires are more attractive to females. Both Great Tit (Baker et al. 1986) and Song Sparrow (*Melospiza melodia*) females prefer males with larger repertoires over males with smaller repertoires (Searcy 1984). Female Song Sparrows even prefer larger repertoire sizes than those that exist in nature, suggesting an open-ended preference (Searcy 1984). Studies on the importance of repertoires for male competition highlight their use in song matching and countersinging. Birds share song types in their repertoires to escalate or de-escalate singing contests. Birds signal escalation by singing the same songs as their rivals and signal de-escalation by choosing to sing different songs than their rivals (Burt et al. 2001). Although the importance of repertoires for mate attraction and male-male aggression in temperate male birds is well-described, repertoires in tropical, duetting birds are poorly studied and such research may result in new discoveries in animal communication.

Duet codes and answering rules

Some duetting birds use repertoires in a novel way: to create duet codes. Duet codes arise when two birds combine songs in their repertoires non-randomly to create duets (Logue 2006). Duet codes are comprised of “answering rules,” cognitive rules for combining song types from one individual’s repertoire with particular song types from their partner’s repertoire (Hall 2009). The specific combinations of duets created by

answering rules are known as duet types. Collectively, the answering rules for a pair of birds constitute their duet code (Figure 1.2).

To date, duet codes have been reported in 13 species of birds (Table 2.1; reviewed in Logue 2006). A variety of duetting birds that use repertoires also have duet codes, suggesting that there may be strong and widespread selection for answering rules and duet codes in duetting birds. It is worthwhile to note that duet codes have been found in species distributed across several families (Artamidae, Cinclosomatidae, Dicruridae, Malaconotidae, Monarchidae, Passeridae, Timaliidae, Troglodytidae; Logue 2006), demonstrating that the evolutionary pressure to combine songs according to duet codes is widespread (Mann et al. 2009, Logue 2006). In most species, we have a very rudimentary understanding and incomplete description of duet codes, and consequently further work characterizing duet codes is an important line of investigation.

Depending on the species, duet codes can be unique to pairs or they can be shared across an entire population (Figure 1.3). Population-wide duet codes occur when every pair in the population shares the same answering rules. The function of population-wide duet codes has not been thoroughly examined, yet there is evidence to suggest that different duet types may be used to convey different messages. Grafe and Bitz (2004a) discovered that one of the duet types of the Tropical Boubou (*Laniarus aethiopicus*) is used as a post-encounter display. The closely related Slate-coloured Boubou uses specific duet types for territorial defence and to coordinate breeding activities (Sonnenschein and Reyer 1983). It has been proposed that population-wide duet types may aid in countersinging (Beecher et al. 2000). Eastern Whipbirds (*Psophodes olivaceus*) use their

population-wide duet code for this purpose, where rival pairs of birds sing back and forth with the same duet type (Rogers et al. 2006).

Pair-specific duet codes occur when each pair in the population follows its own set of answering rules. Each pair will consequently exhibit its own duet code and produce different duet types than other pairs in the population. Several species of duetting birds have been found to have pair-specific duet codes including Plain Wrens (Marshall-Ball and Slater 2008), Australian Magpie-larks (Hall 2006), Black-bellied Wrens (Logue 2006), White-browed Sparrow Weavers (*Plocepasser mahali*; Voigt et al. 2006), Bay Wrens (*Cantorchilus nigricapillus*; Levin 1996a), Australian Magpies (*Cracticus tibicen*; Brown and Farabaugh 1991), and African Drongos (*Dicrurus adsimilis*; Wickler 1976). Pair-specific duet codes have been suggested to require partner-directed learning (Wickler 1980), and the development of a pair-specific duet code may be an important part of partnership formation in duetting birds (Hall 2000), although this idea is controversial (Levin 1996a).

For birds with pair-specific duet codes, one sex often determines the answering rules. In Black-bellied Wrens, for example, females always follow the same answering rules even if they change breeding partners; males vary their answering rules with different females (Logue 2007). Thus females in Black-bellied Wrens will always follow the same duet codes whereas male duet codes will change with their breeding partner. In Bay Wrens, the opposite pattern occurs where males follow the same duet code with different breeding partners; females vary their duet code if they change breeding partners. Males show consistent duet codes regardless of the female they are paired with (Levin 1996a). Consequently, in addition to thinking of such duet codes as “pair-specific”, it is

also useful to think of them as “individual-specific” duet codes because it is individuals who determine the answering rules (Logue 2006).

Very few studies have focused on careful descriptions of answering rules and duet codes. In most of the cases presented in table 2.1, the description is anecdotal or based on a small analysis. For example, in Wickler’s (1976) study of African Drongos, he states that “different pairs sing different duets”, yet no data or statistical analyses were presented to support this claim. This highlights the need for rigorous statistical tests and observations to learn more about answering rules and duet codes in duetting birds.

The functions of duet codes and answering rules

Very few studies have tested hypotheses for the function or importance of answering rules and duet codes. It is uncertain whether duet codes are used for intra or inter-pair communication or both (Farabaugh 1982). Duet codes may be a refined form of intra-pair communication. For example, birds may assess partner commitment by their ability to learn or adhere strongly to answering rules (Wickler 1980). In this case, answering rules are predicted to take time to learn and should become stronger the longer the pair is together (Wickler 1980, Thorpe 1963). Evidence for this idea comes from a study of White-browed Sparrow Weavers: birds match their duet repertoires with their partners, eventually losing songs from their repertoires that aren’t important in duet codes (Voigt et al. 2006). The Weavers’ repertoires become more similar the longer the pair is together, indicating a possible pair commitment function to duet codes in the species (Voigt et al. 2006). Other species, however, appear to need little time to learn duet codes. In an extreme case, Bay Wrens have been shown to learn their partner’s answering rules within days of pairing without an extended period of learning (Levin 1996a). This

indicates that duet codes may have little to do with signalling pair commitment through partner directed learning in Bay Wrens.

Variation in duet behaviour, either in terms of variation in adherence to duet codes or variation in duet song output, may be important in communicating changes to an animal's breeding partner (e.g. signalling readiness to breed in Slate-coloured Boubous; Sonnenschein and Reyer 1983). With respect to duet output, both Rufous-and-white Wrens and Barred Antshrikes (*Thamnophilus doliatus*) increase duet output at the onset of the breeding season (Koloff 2010, Topp and Mennill 2008). With respect to answering rules and duet codes, birds may do something similar and choose specific duet types to signal breeding activity. Slate-coloured Boubous, for example, increase the output of a particular duet type prior to the reproductive season as a mechanism for synchronizing the breeding activities between males and females of a pair (Sonnenschein and Reyer 1983).

An alternative explanation for the function of duet codes is that they may be useful for revealing individual or pair identity. If duet codes are distinctive to an individual or pair, duet codes may be used to identify either one's mate, or one's neighbours (Logue 2006). In areas where visual identification is difficult (e.g. dense tropical forests) a bird could aurally distinguish between their breeding partner and a territorial intruder by listening to whether the bird answers their song according to the pair's duet code. This may be especially important in sexually monomorphic species living in visually occluded environments, where it may be challenging to rapidly distinguish between an animal's breeding partner and a territorial intruder (Logue 2006). The idea that answering rules and duet codes are important in distinguishing between individuals is relatively new and is known as the Identity Hypothesis (Logue 2006). This

hypothesis has been explored in a single species, the Black-bellied Wren, where Logue (2006) suggests that individual-specific duet codes are used by pairs to identify each other in a “complex acoustic environment”.

Although the roles of duet codes in intra-pair communication have been explored in some detail, the role of duet codes in inter-pair communication has received little attention. Duet codes may be used by pairs to determine the threat level of another pair of birds. Territorial birds might listen to how closely a rival pair adheres to a duet code, and use this information to assess the threat level posed by those birds (Rogers 2005, Grafe and Bitz 2004b). Duet code adherence may improve the longer a pair is together, or may indicate the strength of a pair bond (Marshall-Ball et al. 2006). Consequently, if a pair has strong duet code adherence, they may be better able to defend or usurp a territory, and consequently pose more of a threat (Rogers 2005, Grafe and Bitz 2004b). Birds may use this information to determine the likelihood of winning aggressive contests against rival pairs.

If the sexes have different agendas while duetting (e.g. conflict-based rather than cooperative duet functions) this may be reflected in their duet codes. A strong adherence to the duet code between pair members may indicate a greater investment in a partnership (Marshall-ball et al. 2006). Several studies reveal that one sex often adheres to duet codes more closely than the other sex. For example, in Black-bellied Wrens and Eastern Whipbirds, females follow answering rules more closely than their male partners (Logue 2007, Rogers 2005). As mentioned previously, one sex often controls the duet code and dictates the answering rules in the partnership (Logue 2006, Levin 1996a). Whether rules are followed or dictated by an individual, may determine which pair member has more

invested in duetting and is an interesting new avenue to explore in the study of duetting species.

It is possible that duet codes are not adaptive, or that they are epiphenomena, and arise because of other associated behaviours. Duet codes could arise if some outside cues influence song choices of both pair members simultaneously. For example, both duet partners might select songs from their repertoire in accordance with an external cue, or duet partners might send other signals that cue their partner into singing a particular song (Logue 2006). Alternatively, pairs may cycle through their repertoires in synchrony with one another, so that certain songs are consistently sung together in duets simply by virtue of the internal singing rhythms of each bird (Logue 2006). Although these non-adaptive explanations are important to consider when studying duet codes, many non-adaptive explanations can be ruled out with some observation of birds' duetting behaviour. In terms of birds coordinating their songs based on external visual cues or visual signals from their partner, many birds duet with each other from variable distances, where visual contact is not possible (e.g. Mennill and Vehrencamp 2008, Logue 2007a). This would make it difficult for birds to follow a common visual cue to determine their song choices. Repertoire cycling in phase with a partner would also be an unlikely explanation for duet codes whenever partners have different repertoire sizes, different song rates, and when recordings are taken over extended periods (e.g. Mennill and Vehrencamp 2005, Mann et al. 2003, Sonnenschein and Reyer 1983). Taken together, there is little compelling evidence that these non-adaptive ideas can explain answering rules or duet codes across species.

Study species and site

My thesis focuses on answering rules and duet codes in Rufous-and-white Wrens. Rufous-and-white Wrens are Neotropical songbirds known for their clear flute-like songs which they combine to create duets (Figure 1.4; Mennill and Vehrencamp 2005). These resident birds are found living throughout much of Central America and northwestern South America, particularly along the Pacific coast of Central America, eastern Colombia, and northwestern Venezuela (Mennill and Vehrencamp 2005). My study population lives in Sector Santa Rosa of the Guanacaste Conservation Area in northwestern Costa Rica. This population has been studied in detail by Dr. Daniel Mennill, myself, and other students, since 2003. Rufous-and-white Wrens were formally in the genus *Thryothorus*. Mann et al. (2009) propose that they should be placed in the genus *Thryophilus* based on molecular and song form data. I refer to Rufous-and-white Wrens as well as other former *Thryothorus* wrens according to the genii suggested by Mann et al. (2009).

Rufous-and-white Wrens are an insectivorous species that is sexually monomorphic in plumage, although males are slightly larger and heavier than females (Mennill and Vehrencamp 2005). Rufous-and-white Wren territories are large (3.3 ± 0.3 acres or $13497 \pm 1043 \text{ m}^2$) and pairs defend them from adjacent territory holders (Mennill and Vehrencamp 2008). Their breeding season begins with nest building in April and early May, and birds lay their first clutch with the onset of the first rains of the year in mid-May (Topp and Mennill 2008). The breeding season continues during the first portion of the rainy season, until at least August (Topp and Mennill 2008). Both males and females contribute to building closed nests with a tubular entrance (Stiles and Skutch

1989). The birds in my study site preferentially nest in Bullhorn Acacia trees (*Acacia collinsii*) but will occasionally nest in other vegetation as well (pers.obs.). Birds live multiple years and often remain pair-bonded throughout the entire year. Although they breed monogamously, Rufous-and-White Wrens may have multiple mates over the course of their life (pers. obs.). Females lay three to four greenish-blue eggs per nesting attempt and can have several nesting attempts in one breeding season (Stiles and Skutch 1989, pers. obs.). Only females incubate the eggs but both sexes usually provision nestlings (Mennill and Vehrencamp 2005). Preliminary analyses indicate that although they follow a monogamous pattern of social mating, they follow a promiscuous genetic mating strategy, where a small number of nests contain one or two offspring that are unrelated to their social father (S. Douglas, pers. comm.).

Both male and female Rufous-and-white Wrens sing and both sexes have discrete and individually distinctive song types (Mennill and Vehrencamp 2005). The average male repertoire size is approximately 11 song types, while females have a smaller average repertoire of approximately 9 song types (Mennill and Vehrencamp 2005). Although their songs are individually distinctive at a fine-structural level, there are twelve song types that are particularly common in my study population (see Chapter 2, Fig. 2.1). Songs in most birds' repertoires can be classified as one of these population-level song types with a high degree of accuracy (shown with canonical discriminant analysis assigning songs into their population level song type categories with 94% accuracy, Barker 2008). Rufous-and-white Wrens share large portions of their repertoires with other nearby conspecifics, with particularly high sharing among neighbours (Mennill and Vehrencamp 2005). Males share more song types with other males than females share with other females (Mennill

and Vehrencamp 2005). Even though females tend to have more unique song types and less sharing than males, there is still a relatively high degree of sharing among females. There is also a significant amount of song sharing between the sexes (Mennill and Vehrencamp 2005), which is unique for duetting tropical wrens (Mann et al. 2009).

Both sexes of Rufous-and-white Wrens create duets by responding to their partner's song. Duets are created when male and female song types overlap or occur within one second of each other. Although the majority of duets in this species are created by two songs, Rufous-and-white Wrens sometimes have more complex duets where a string of songs are sung by males and females (Mennill and Vehrencamp 2005). Duets are created by the second individual who sings, turning their partner's solo song into a duet (Hall 2004).

Several studies have explored the function of duets in Rufous-and-white Wrens. Since the sexes create duets at equivalent levels during the pre-breeding season, they likely serve a cooperative function at this stage, likely for joint territory defence (Topp and Mennill 2008). Duets are most common before nest building and following predation events, when nesting is attempted again (Topp and Mennill 2008). This seems to indicate that duets are also used cooperatively to coordinate breeding activities. Males tend to answer more female songs when females are fertile indicating that duetting at this time may serve an additional function of mate-guarding by males (Topp and Mennill 2008). A playback study by Mennill (2006) showed that male Rufous-and-white Wrens, when presented with stereo duet playback, were more aggressive towards the speaker broadcasting male song than the speaker broadcasting female song, offering further support for a mate-guarding function of duets for males. Females, on the other hand, were

equally aggressive toward both speakers and would often follow the male (Mennill 2006). This may indicate that males use duets for mate or paternity-guarding as they find intruder males more threatening than intruder females. In a study that used an eight-channel acoustic location system to track birds' movements, birds were found to move closer to each other following duets, offering support for the maintaining contact hypothesis (Mennill & Vehrencamp 2008). Various studies of Rufous-and-white Wrens demonstrate that duets serve various functions depending on the context: duets are used in aggressive interactions with territorial rivals, to synchronize activities during the breeding season, to find a partner when separated and for mate-guarding a fertile partner.

Rufous-and-white Wrens are an excellent species in which to study duet codes. They have discrete song types that are easily identified and categorized. Although individuals share song types in the population they are individually identifiable by subtle differences in frequency and other fine structural characteristics (Mennill and Vehrencamp 2005). A high song sharing rate means that it is easy to compare the use of song types between pairs (Barker 2008). A preliminary analysis indicated that these wrens exhibit answering rules and duet codes (Mennill & Vehrencamp 2005), but these features had not been explored in detail. My study population has been monitored annually since 2003 (I collected data in both 2008 and 2009). This collection of recordings is the largest single-population dataset in the history of duet research. One unique aspect of this dataset is that several long-lived birds have been recorded performing duets over multiple years and with multiple breeding partners, providing the first ever opportunity to explore how duets change over time and with different breeding partners.

Summary and thesis goals

North Temperate Zone birds have been studied extensively and the functions of their songs are relatively well-known, unlike lesser-studied tropical species. Tropical birds live in a radically different environment and exhibit several unique life-history traits that influence their singing behaviours. For example, longer breeding seasons and year-round territoriality are common in tropical birds, and are associated with sex role convergence. In this environment, females are more likely to sing and pairs are more likely to perform coordinated vocal duets. In birds that both perform duets and possess song repertoires, breeding partners may exhibit a duet code, where pairs combine song types from their repertoires non-randomly into duets. The association of particular song types with specific song types from a partner are called “answering rules”. Considered together, all of the answering rules for a pair are called a “duet code”. Duet codes have been found in a variety of avian families. This indicates that selection on duetting birds to create answering rules is high. The dynamics and function of duet codes are still a mystery. It may function for mate recognition, particularly during territorial contests where visibility is low and birds are monomorphic. It may also synchronize breeding activities or be used to monitor commitment to the pair bond. Duet codes are a relatively new topic in the study of duetting birds. Describing the form and function of duet codes in duetting birds is a unique way to learn more about inter and intra-pair communication as well as increase our understanding of duetting and tropical birds.

In this thesis I explore the answering rules and duet codes of Rufous-and-white Wrens through detailed, multi-year analyses. I analyse whether pairs follow a duet code and how strongly they adhere to their answering rules. I determine if duet codes change

through years of partnership or after partner changes. I calculate duet code adherence for males and females to determine if the sexes follow answering rules differently. I perform population-level analyses to determine if Rufous-and-white Wrens have a pair-specific or population-wide duet code. My research offers insight into the ecology and evolution of communication in tropical birds by providing a rigorous description of duet codes in a population studied over a seven year period. My research stands out as being the largest scale analysis of duet codes to date.

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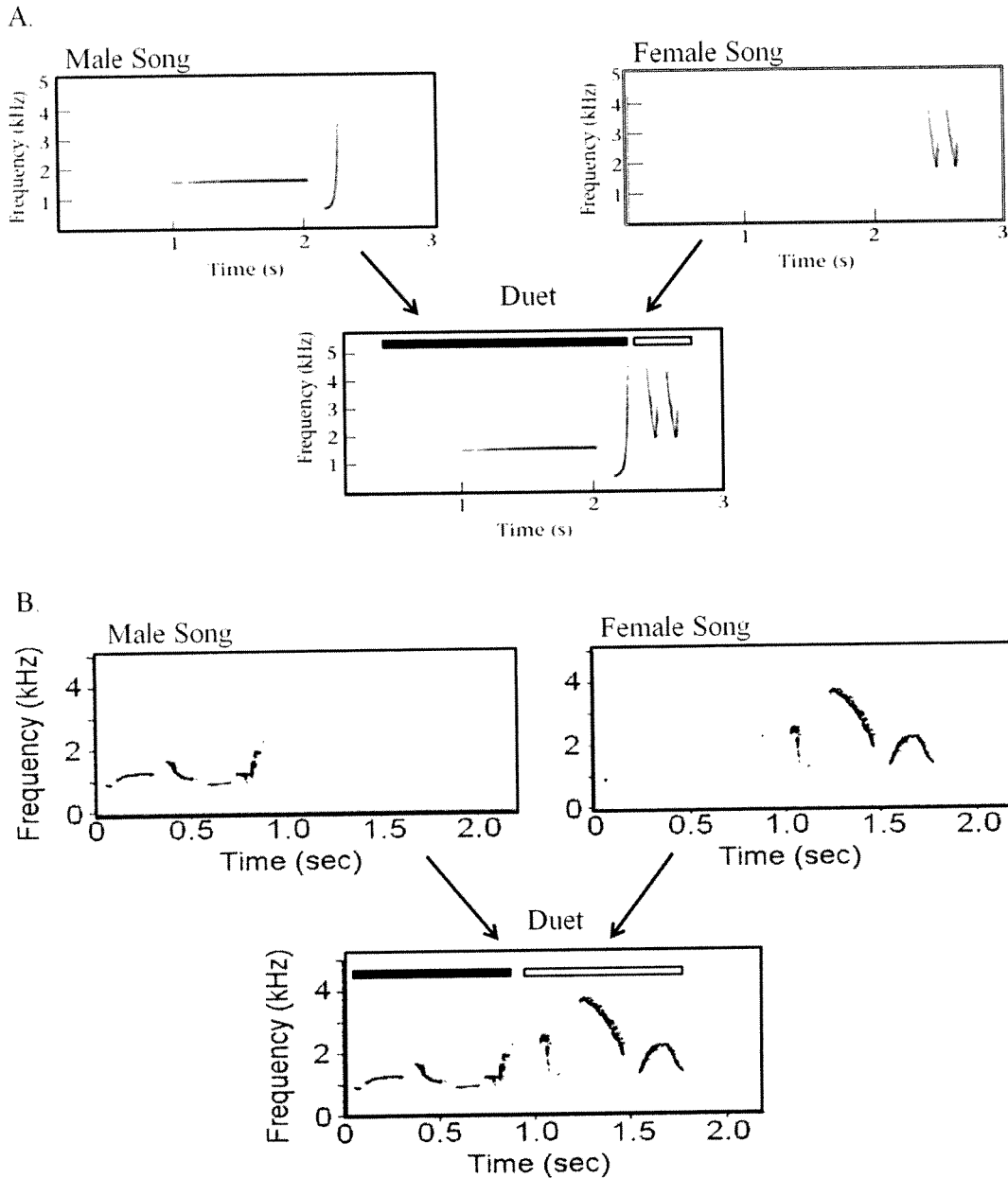


Figure 1.1. Examples of duets of (A) Eastern Whipbirds (taken from Rogers et al. 2006) and (B) Black-bellied Wrens (taken from Logue 2006). Duets are represented in sound spectrograms showing a male and female solo song and how they are combined into a duet. Male songs are indicated by black bars and females songs are indicated by white bars. Eastern Whipbirds (Family: Cinclosomatidae) and Black-bellied Wrens (Family: Troglodytidae) are found in two different families on different continents yet both exhibit similar duetting behaviour.

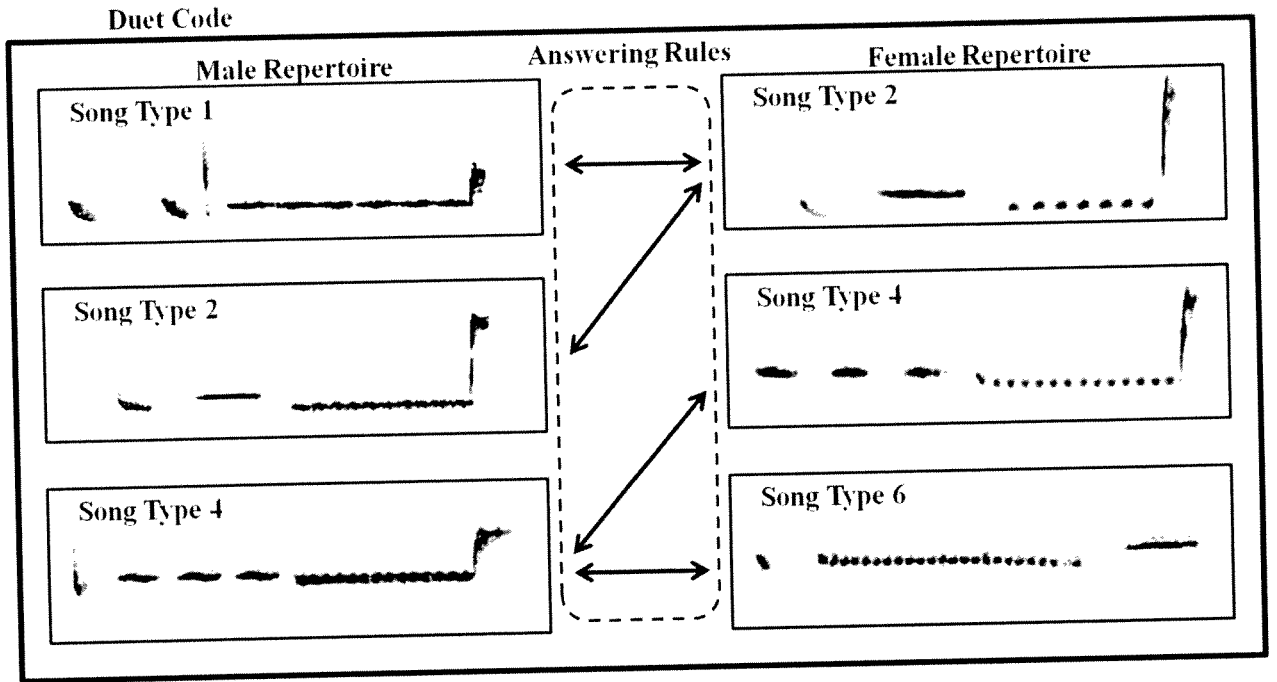


Figure 1.2. An example of a hypothetical duet code for a pair of Rufous-and-white Wrens. Both males and females have repertoires of song types, represented here as spectrograms of three male song types on the left, and three female song types on the right. Answering rules are represented by arrows connecting male and female song types. In this hypothetical example, when the male sings song type 1, the female is likely to respond with her song type 2; when the female sings her song type 2 the male is likely to respond with either his song type 1 or song type 2. The entire set of answering rules comprise the duet code for this pair.

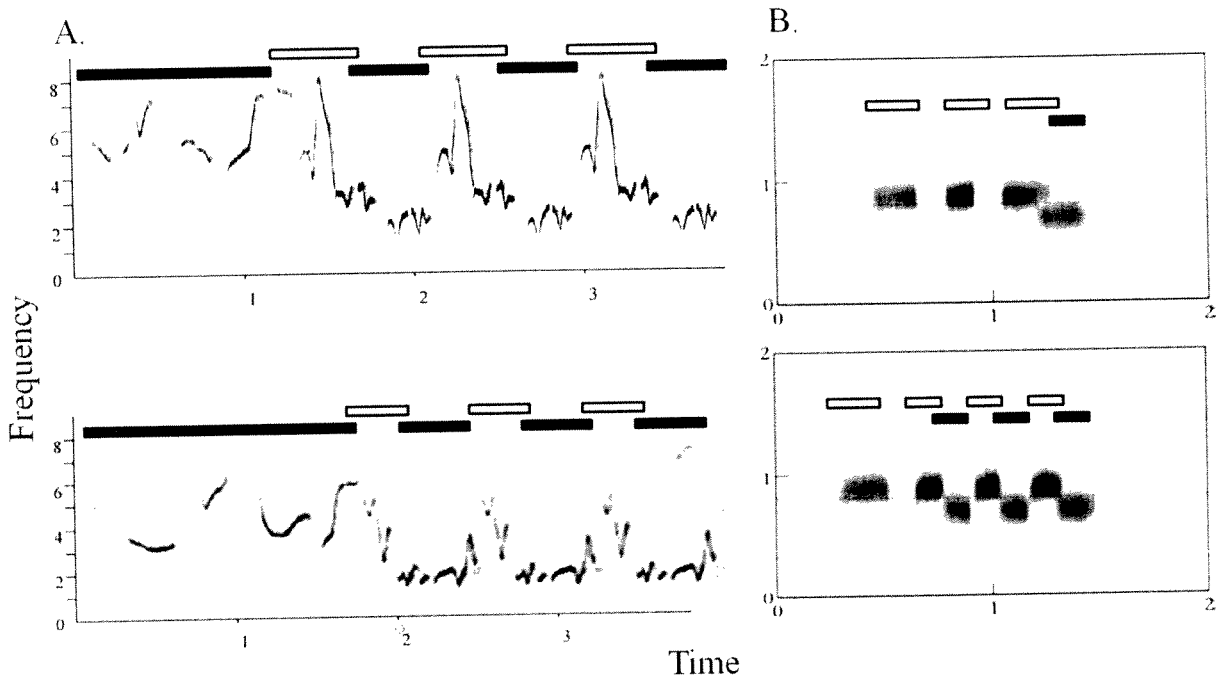


Figure 1.3. (A) Two Plain Wren duets (taken from Marshall-Ball and Slater 2008, Mann et al. 2003) and (B) two Tropical Boubou duets (taken from Grafe et al. 2004). Male contributions to the duets are indicated by black bars and female contributions are indicated by white bars. Plain Wren duets are pair-specific; the two duet types represented here will only be found in one pair in the population. Tropical Boubous have population-wide duet codes; the two duets types represented here will be found in most pairs in the population.

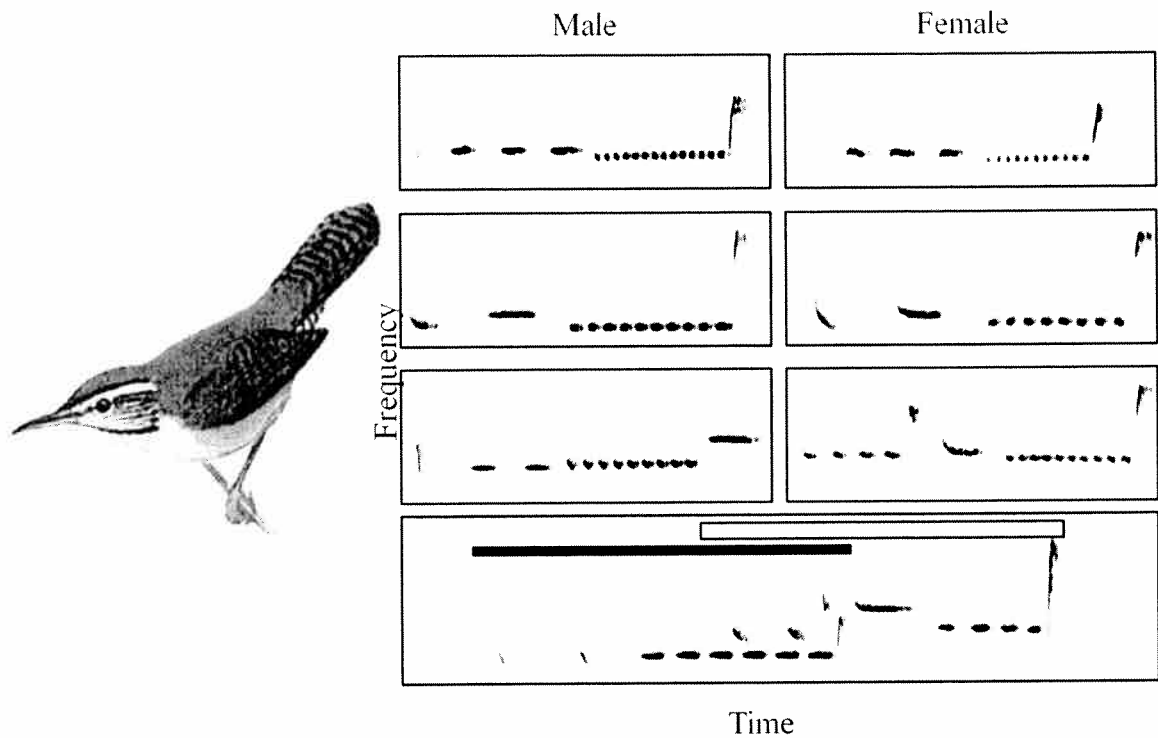


Figure 1.4. A plate of a Rufous-and-white Wren (illustrated by Dana Gardner; taken from Stiles and Skutch 1989) and spectrograms of male and female Rufous-and-white Wren song types. Both males and females are similar in colour and size. The top two rows of spectrograms show male and female representations of two population-level song classes. The third row shows male and female songs that are different song classes. The bottom spectrogram is a female-created duet.

Chapter 2

Duet codes and answering rules in the Rufous-and-white Wren (*Thryophilus rufalbus*)

Chapter Summary

Duets occur when members of a mated pair coordinate their songs with a high degree of temporal precision. Several species of duetting birds have song repertoires and follow answering rules, where they answer particular song types of their partner with specific song types in their own repertoire. All the associations together constitute a pair's duet code. In this study, I analyse the duet codes and answering rules of Rufous-and-white Wrens (*Thryophilus rufalbus*). I analyze over 5,000 duets collected from 113 pairs of birds recorded over a seven year period in Costa Rica. I found that pairs of Rufous-and-white Wrens follow duet codes. Duet code adherence (the strictness with which birds follow answering rules) was higher in females than males, indicating that females follow answering rules more strongly than males. The answering rules of long-term pairs do not change across years of pairing. Birds do not change their duet codes with breeding partners; their answering rules remain the same when birds change partners, a pattern that is true for both males and females. The answering rules of males and females within a pair are equivalent. Taken together, our data suggest that Rufous-and-white Wrens follow a population-wide duet code, where all individuals in the population have the same answering rules that they use to combine song types into duets. This detailed long-term study of duet codes reveals a novel use of song repertoires in duetting, tropical birds, which enhances our understanding of the ecology and evolution of bird song.

Introduction

Most research on bird song has focused on male behaviour and the importance of male song for both mate attraction and territorial defence (Catchpole and Slater 2008). These studies have focused on bird species in the North Temperate Zone where males are the primary singers and song is concentrated during a short breeding period. Tropical environments are different from the North Temperate Zone environment in a number of ways including low seasonal variability and high nest predation rates (Slater and Mann 2004, Martin 1996). These factors are thought to be associated with sex role convergence in both behaviour and morphology, where the roles of males and females are more similar (Slater and Mann 2004). A common example of sex role convergence is the presence of female song in the tropics; although largely absent from North Temperate Zone ecosystems, female song is quite common south of the Tropic of Cancer. The high incidence of female song in tropical and South Temperate Zone ecosystems means that these birds engage in different communication behaviours than their temperate counterparts.

Duets are acoustic displays created when two birds (usually members of a mated pair) coordinate their songs into complex vocal displays (Hall 2004, Farabaugh 1982). Duets can serve both cooperative and conflict-based functions (Hall 2004). Cooperative functions of duets occur when pair members have a similar objective in performing a duet. Examples of cooperative functions are performing duets to defend a territory against a rival pair or to locate a partner in dense vegetation (Hall and Peters 2008, Mennill and Vehrencamp 2008, Logue 2007a, Molles and Waas 2006, Logue and Gammon 2004). Conflict-based duet functions occur when pair members' agendas differ from each other.

Examples of conflict-based functions of duets are performing a duet to advertise one's level of commitment or mated status to prevent desertion or extra-pair mating (Mennill 2006, Seddon and Tobias 2006, Mulder et al. 2003, Levin 1996b). Cooperative and conflict-based functions of duets are not mutually exclusive and species often duet for several different reasons (Hall 2009).

Some species of duetting birds have song repertoires. A repertoire is a bird's "vocabulary" of song types, and studies of both temperate and tropical birds reveal that it is common for birds to have a number of song variants that they learn early in life and sing throughout their life (Catchpole and Slater 2008). Some duetting birds combine songs types in their repertoires non-randomly into duets (reviewed in Logue 2006). These non-random associations are called "answering rules" (Hall 2009). All of a pair's answering rules combined are known as the pair's "duet code" (Logue 2007b, Logue 2006) and the specific combinations of song types created by answering rules are called "duet types" (Hall 2009). Duet codes are a relatively new discovery in duetting bird behaviour. To date, thirteen species distributed across several families have been found to follow answering rules (Table 2.1; Logue 2006). Answering rules and duet codes can be either population-wide or pair-specific. For example, Tropical Boubous (*Laniarius aethiopicus*) and Eastern Whipbirds (*Psophodes olivaceus*) have population wide duet codes. All the pairs of Tropical Boubous in a population share the same 12 duet types (Grafe and Bitz 2004b) while Eastern Whipbirds share most of their duet types with other pairs (Rogers 2005).

The majority of duetting birds studied to date, however, have pair-specific or individual-specific duet codes, where answering rules are particular to each pair or each

bird (Australian Magpie-larks, *Grallina cyanoleuca*; Hall 2006, Black-bellied Wrens, *Pheugopedius fasciatoventris*; Logue 2006, Plain Wrens, *Cantorchilus modestus*; Mann et al. 2003, Bay Wrens, *Cantorchilus nigricapillus*; Levin 1996a, Australian Magpies, *Cracticus tibicen*; Brown and Farabaugh 1991, African Drongos, *Dicrurus adsimilis*; Wickler 1976). With pair-specific or individual-specific duet codes, usually one sex determines the duet code of the pair and this often varies by species. Bay Wren males determine the duet codes and this is evident when looking at duets following changes in partnership; regardless of who the male pairs with, his answering rules remain the same (Levin 1996a). Females, on the other hand, have new duet codes each time they pair with a new male (Levin 1996a). In contrast, the reverse situation occurs in Black-bellied Wrens where females determine the duet code. In both Bay Wrens and Black-bellied Wrens, birds follow individual-specific duet codes, where the answering rules are created by one partner and where the duet codes vary from one pair to the next (Logue 2006). In addition, birds may vary in how closely they follow answering rules (known as duet code adherence). For example, in Black-bellied Wrens, females follow answering rules 100 percent of the time, while males vary in how often they adhere to answering rules (Logue 2007b).

The function of answering rules and duet codes is not well understood. Duet codes may function in intra-pair communication. Before pairing, signals between males and females often communicate fitness or willingness to breed (Marks et al. 2010, Ballentine et al. 2004, Searcy and Yasukawa 1996, Catchpole 1987). Once paired, however, efficient intra-pair communication may be crucial for coordinated territory defence (Hall and Magrath 2007, Logue 2006), to deter predators (Bossema and Benus 1985), to coordinate

breeding activities (Sonnenschein and Reyer 1983) or to maintain the pair bond (Hall and Peters 2008). The difficulty in studying intra-pair communication, at least in vocal signals in birds, is that in many bird species females do not sing (Catchpole and Slater 2008). In tropical duetting species, however, females do sing and offer an excellent opportunity to study intra-pair communication in regards to vocal signals (Slater and Mann 2004, Langmore 1998). Pairs may use duet codes specifically to communicate to their partners. For example, a high level of duet code adherence may indicate a strong commitment to the pair bond (Wickler 1980). Pairs may judge their partner based on how quickly they learn duet codes or how strongly they follow answering rules. Additionally, following the correct answering rules may communicate identity to a partner (Logue 2006). Using answering rules for identification may be useful in dense vegetation where visual identification is difficult, especially during highly aggressive territorial interactions (Logue 2006). As well, certain duet types or changes in answering rules or duet codes may signal breeding stage or other states of motivation (Sonnenschein and Reyer 1983). For example, Slate-coloured Boubous (*Laniarus funebris*) use a particular duet type to synchronize breeding (Sonnenschein and Reyer 1983).

Alternatively, duet codes may be important in inter-pair communication. A lot of research has focused on male-male communication, particularly in temperate birds. Very little has focused on communication between pairs of mated birds, even though duetting birds have been documented to engage in bouts of counter-duetting with rival pairs (Rogers et al. 2006). For solo-singing birds, there are many species where birds share song-types (Beecher et al. 2000, Krebs et al. 1981, Lemon 1968) and sing these song types during interactions with rivals to communicate aggression (Vehrencamp 2001). By

singing a song type that a rival bird is singing, a bird can escalate a contest. A bird can also de-escalate a contest by singing a different song than the rival is singing (Burt et al. 2001). Duetting birds match songs in similar ways to solo-singing birds (Marshall-Ball et al. 2006, Molles and Waas 2006). However, it is possible for females to also match song types and for pairs to match duet types. Birds with pair-specific duet codes are unlikely to match duet types simply because they do not share duet types in common with other members of the population (e.g. Plain Wrens; Marshall-Ball and Slater 2008). Eastern Whipbirds, on the other hand, have a population-wide duet code and use their population-shared duet types for matching in territorial interactions (Rogers et al. 2006). Males and females song type match with rivals using solo and duet song. It is still uncertain whether duet type matching signals aggression in a similar fashion to solo singing birds in this species (Rogers et al. 2006).

Duetting birds may also use duets to advertise mated status and pair coordination to rivals (Hall and Magrath 2007, Hall 2004). Duets that are precise and highly coordinated in Magpie-larks are more threatening to intruders because they indicate a more synchronized pair, and therefore a stronger pair bond (Hall and Magrath 2007). Birds could also use adherence to answering rules to judge the threat level of rival pairs (Hall and Magrath 2007, Marshall-Ball et al. 2006, Grafe and Bitz 2004b).

The objective of this study is to describe the answering rules and duet codes of the Rufous-and-white Wren (*Thryophilus rufalbus*, formerly *Thryothorus rufalbus*, see Mann et al. 2009). Both males and females of this species sing and have repertoires of discrete song types (Mennill & Vehrencamp 2005). They combine these song types into duets and use them for territorial interactions, breeding synchrony, mate guarding and to maintain

contact with a partner (Mennill and Vehrencamp 2008, Topp and Mennill 2008). By analyzing thousands of duets from 113 breeding pairs recorded over a seven year period, I address the following questions: (1) Do Rufous-and-white Wrens follow a duet code and how strongly do they adhere to it? (2) Do duet codes and duet code adherence change over the length of the partnership? (3) Do duet codes change with changes in partnership? and (4) Do Rufous-and-white Wrens have population-wide or pair-specific duet codes? This is the first study of duet codes to span multiple years and changes in partnership.

Methods

General field methods

My study was performed in Sector Santa Rosa of the Guanacaste Conservation Area, Costa Rica (10°40'N, 85°30'W). The Guanacaste Conservation Area holds the world's largest remaining stand of Neotropical dry forest, which ranks among the most threatened ecosystems on Earth (Janzen 1988). Santa Rosa contains a mosaic of mature forest and regenerating forest; the study population of Rufous-and-white Wrens inhabit the mature humid forest in the area. Rufous-and-white Wrens are Neotropical duetting songbirds that generally form socially monogamous pairs that hold year round territories (Mennill and Vehrencamp 2005).

Recording methods

For this study, I used recordings collected from a colour-banded population of Rufous-and-white Wrens over seven years (2003-2009). During this period, wrens were sampled using both focal and automated recordings. Most focal recordings were conducted between 0500 and 0900h when song output is highest (Mennill and

Vehrencamp 2005). During focal recordings, pairs of birds were followed and recorded at close distances with a directional microphone (Sennheiser ME66/K6, ME67/K6 or MKH-70) attached to a Marantz digital recorder (model PMD-660 or PMD-670). During each recording, the birds' behaviour and colour-bands were described whenever possible and territory boundaries were estimated. In addition, birds were sampled using two different passive and automated recording techniques. In 2003 and 2004, an eight-channel acoustic location system was used which sampled duets from birds as they moved around their territories (details in Mennill and Vehrencamp 2008, Mennill et al. 2006). In 2006 through 2009, birds were sampled with single-channel automated recording units consisting of an omnidirectional microphone (Sennheiser ME62/K6) attached to a Marantz digital recorder (PMD-670) powered by a sealed lead-acid battery; microphones were positioned at the centre of birds' breeding territories and were mounted atop a three metre wooden pole (details in Hill et al. 2006).

Sound Analysis

I analyzed recordings with Syrinx-PC sound analysis software (John Burt, Seattle, Washington). Syrinx-PC provides a visual representation of sound as a spectrogram and allows users to isolate and categorize recorded sounds. I annotated songs in the recordings and categorized them based on which bird was singing, the song type, and whether it was a duet or solo. I classified songs as duets if male and female songs overlapped or were sung within 1 second of each other (following Mennill and Vehrencamp 2005). I classified duets as either male-created or female-created. Male-created duets occurred when males sang second, effectively turning the females solo song into a duet.

Alternatively, female-created duets occurred when females sang second, turning the male's solo song into a duet (Hall 2004).

Both male and female Rufous-and-white Wrens sing and have repertoires of song types. On average, males in the study population have 11 song types and females have nine song types in their repertoires (Mennill and Vehrencamp 2005). Although songs are individually distinctive, most songs can be classified as one of 12 song classes (Figure 2.1). Every song in each bird's repertoire was labelled as one of these 12 song classes. I classified each song within each bird's repertoire by visually comparing spectrograms to templates. A few songs did not fit any of these twelve common song types and were labelled as "other" and included in the analysis as a thirteenth category. Such song types were rare: on average, only 24% of males had one or more songs classified as "other", and only 26% of females had one or more songs classified as "other". Out of all the duets sampled in the recordings only 1.8% included a song classified as "other". By classifying songs according to population-level song types, I was able to compare duet codes between pairs, between years, and between the sexes.

In Rufous-and-white Wrens, birds routinely sing a particular duet combination several times before switching to another duet type (i.e. singing with eventual variety). It is common in duet studies to only include the first duet sung in the series, to ensure that data are independent (Logue 2006, Mann et al. 2003). I removed repeated duets from the analysis to avoid including repeated instances of the same duet; when duets were given as a string of duets of the same song types, I included only the first example and excluded the repeats from the analysis.

Analyses of duet codes

I organized duets into three datasets for analysis. I analysed all duets recorded, regardless of whether the male or female sang first (dataset 1). Previous research in this species has found that the sexes vary in how often they create duets (i.e. in how often they sing in response to their partner's song, turning their partner's song from a solo into a duet; Mennill and Vehrencamp 2005). Therefore, I also separately analysed all male-created duets (dataset 2), and all female-created duets (dataset 3).

I analysed a total of 5,326 duets recorded from 113 different pairs, recorded over a seven year period (1,524 male-created duets; 3,802 female-created duets). To test whether pairs of Rufous-and-white Wrens follow duet codes, I arranged the data into duet matrices with male song types along the left side of the matrix and female song types along the top of the matrix (Figure 2.2). I created separate matrices for each pair. For pairs recorded in multiple years, I created a separate matrix for each year (for within-pair analyses) as well as a matrix containing all the duets ever recorded for the pair (for between-pair analyses). I also created a single matrix for all duets that I recorded across the entire seven-year study. If birds contribute songs randomly to duets (i.e. if this species does not have answering rules or duet codes), then all cells within such a matrix should have similar values. However, if birds follow answering rules – if there is a duet code – then some cells (i.e. song combinations) should occur significantly more often than expected by chance.

Statistical Analysis

Since duet codes have only recently been identified and examined in the literature, the proper statistical technique for determining if duet frequencies vary from chance levels is still under dispute. I used two different techniques to evaluate duet codes and answering rules: a Randomization Test and a G-test for Goodness-of-fit. Below I describe the two techniques.

Randomization Test

I used a Monte Carlo Randomization Test to evaluate whether certain male-female song combinations occur more often than expected by chance (Whitlock and Schluter 2009). To establish chance levels, for each pair, I shuffled all female song types so they were randomly paired with male song types. I used the PopTools subroutine called “Resample” (Hood 2003) to accomplish this resampling procedure in Microsoft Office Excel. I shuffled the duet data in this manner 10,000 times for each pair, generating 10,000 matrices where the male-female song type choices were randomly paired. I then compared the duet matrix for the original dataset against the 10,000 resampled matrices for each pair. For each matrix, I calculated a Chi-squared value by comparing the matrix to an expected matrix based on chance associations, to generate one Chi-square value for each matrix. I report the p-value as the number of randomized tests that had a Chi-square value greater than that of the original dataset divided by 10,000.

G-test for Goodness-of-fit

Most studies to date have not followed the Randomization Test approach, and have used a G-test for Goodness-of-fit to test for a duet code (Mennill and Vehrencamp

2005, Mann et al. 2003). To perform a G-test, duets are organized into a matrix where combinations of male and female song types are scored within the cells of the matrix (as in Figure 2.2). To evaluate whether any male-female song type combinations occur more often than would be expected by chance, a contingency table is created where the number of cells in the matrix that have counts of 1, 2, 3, 4 etc. duets are tallied. These observed numbers of combinations are then compared to the expected number of cells that should be found with 1, 2, 3, 4 etc. duets according to a Poisson distribution (Mann et al. 2003). A G-test for Goodness-of-fit is then performed on the contingency table (not the original duet matrix) and determines whether the observed results are significantly different from the Poisson-directed expected levels (Figure 2.3).

To determine whether the Randomization Test was comparable to previous studies, I compared the Randomization Test results to the G-test for Goodness-of-fit results of the all duets dataset (dataset 1) with a Spearman's rank correlation. I found that the two techniques were highly similar (Spearman: $\rho=0.44$, $p\leq 0.0001$, $n=113$). This indicates that the two tests produced similar results. However, I chose to use the Randomization Test for reasons explained in detail in the discussion.

I ran a Spearman's rank correlation to determine whether sample size (the number of duets) affected the outcome of the Randomization Test. This was done to explore whether non-significance in the duet code analysis was due to birds not following duet codes or if it was the influence of a small sample size (i.e. low statistical power). A significant similarity between sample size and the significance of the Randomization Tests across the 113 pairs would demonstrate that the Randomization Test is influenced by small sample sizes.

I define duet code adherence as the strictness with which an individual follows answering rules. To evaluate duet code adherence I compared male-created and female-created duet matrices of n=113 pairs,. In each row (for males) or column (for females) of each matrix, I calculated the number of “incorrect” answers after determining what the “correct” answer was (the song type combination in the row or column with the highest number of duets). I then summed all of the “incorrect” answers. The total number of duets in the matrix was then divided by the total number of incorrect answers from each row or column. I subtracted that number by one to get an adherence score. This score was a proportion representing how often a bird responded to a song with the correct answer. I compared the overall duet code adherence of males and females based on the male-created and female-created duet matrices using a Wilcoxon signed rank test to determine if there was a significant difference between male and female duet code adherence.

To determine if duet codes remain consistent across years in Rufous-and-white Wren pairs, I used Spearman’s rank correlation to compare similarity in duet codes over years. I compared the duet codes of 22 pairs of Rufous-and-white Wrens who had been paired for two or more years. For all Spearman’s rank correlations in this study, I compared how often all possible combinations of song types occurred while duetting by organizing the data from a duet matrix into a table (Figure 2.4). For this particular analysis I compared the number of times particular song type combinations occurred between years of partnership.

To determine whether duet code adherence became stronger the longer a pair was together I examined duets from pairs that were social partners for two years or more. Using the duet code adherence scores calculated in the previous analysis, I compared

male and female adherence to duet code during each stage of their partnership. I ran this analysis on 22 males and 22 females. Duet code adherence scores were compared between years using a non-parametric Kruskal-Wallis Test.

To determine whether duet codes changed when birds changed breeding partners I used Spearman's rank correlation on males who had paired with multiple females and females who had paired with multiple males. I ran this analysis on 21 males and 14 females. I ran Spearman's rank correlations to compare the duet codes of these pairs to determine similarity of their duet codes between different breeding partners. I compared the number of times combinations of song types were sung in duets between different breeding partners.

To determine if duet codes arise due to male or female answering rules, I selected the 50 pairs that had the highest number of duets ($n \geq 31$ duets) and I compared their male-created and female-created duets. Using Spearman's rank correlation, I ranked duet type occurrence to determine if the duet types of male-created and female-created duets were similar.

To compare the duet codes of individuals to determine whether there was a population-wide or pair-specific duet code, I created a matrix of all duets recorded in the entire population. This matrix included all 113 pairs and contained 5326 duets. I performed a Randomization Test to determine if a duet code could be found in the population-level matrix.

All analyses were performed in JMP 6.0 (SAS Institute, Cary, North Carolina). All values are shown as mean \pm standard error.

Results

Do Rufous-and-white Wrens adhere to duet codes?

For the duet code analysis performed on all duets, 50% of pairs exhibited a duet code (Randomization Test: $p \leq 0.048$, $n=56$, duets: 5-556) while 50% did not show significance (Randomization Test: $p \geq 0.063$, $n=57$, duets: 2-227). I also separated duets into whether they were created by the male responding to a female song, or a female responding to a male song. For the analysis of male-created duets, 58% of males followed a duet code (Randomization Test: $p \leq 0.038$, $n=65$, duets: 5-128) while 42% did not show significance (Randomization Test: $p \geq 0.056$, $n=48$, duets: 5-32). For female-created duets, 62% of females followed a duet code (Randomization Test: $p \leq 0.048$, $n=70$, duets: 5-428) while 38% showed no significance (Randomization Test: $p \geq 0.067$, $n=43$, duets: 5-70).

P-values in the Randomization Tests were significantly correlated with sample size (Spearman's: $\rho = -0.30$, $p = 0.0005$, $n = 113$). This indicates that the number of duets recorded had an effect on whether birds exhibited duet codes, and suggests that sample sizes of < 30 duets do not have sufficient power to detect duet codes. However, some pairs with large sample sizes did not show a significant result. This may be due to variation in how well birds adhere to duet codes. Certain pairs may adhere poorly to duet codes and this may influence certain pair traits (e.g. breeding synchrony, nest-building, likelihood of divorce). See discussion for further details.

How tightly do birds adhere to answering rules?

Rufous-and-white Wrens do not follow duet codes exclusively, and most pairs showed instances of alternative answers to their partner's song. For example, for the pair

in Figure 2.2, when the female sang song type 02 the male most often sang his song type 02, but occasionally sang 01, 06, 08, and 09. Males and females show different levels of duet code adherence. Male Rufous-and-white Wren's adhere to duet codes, on average, in $67 \pm 0.02\%$ of their duets whereas females adhere to duet codes, on average, in $78 \pm 0.02\%$ of their duets. Female duet code adherence was significantly higher than male duet code adherence (Wilcoxon's: $Z=1548.50$, $d.f.=112$, $p<0.0001$).

Do duet codes change between years?

I analysed 22 pairs of wrens that were recorded in more than one year. Seventeen of these pairs were paired for two years, and five of the pairs were paired for three or more years. Out of the 17 pairs that were paired for two years, 16 pairs showed significant similarity in their duet codes from one year to the next (All Spearman's $\rho \geq 0.18$, $p \leq 0.02$). Four of the five pairs that had been paired for three years or more showed significant similarity in their duet codes between all years (All Spearman's $\rho \geq 0.23$, $p \leq 0.002$). The one pair that didn't show significance had been paired for four years and in between their second and third year and their third and fourth year there was no significant similarity in their duet codes (All Spearman's $\rho \leq 0.092$, $p \geq 0.23$). This is probably due to a very low sample size (total duets=9) in their third year.

Does duet code adherence change between years?

The analysis of duet code adherence showed no significant changes in levels of duet code adherence with year of partnership. This was true for both males (Kruskall-Wallis: $X^2=2.21$, $d.f.=3$, $p=0.53$) and females (Kruskall-Wallis: $X^2=0.51$, $d.f.=3$, $p=0.92$). Therefore, pairs did not adhere more or less to duet codes as the length of their

partnership increased (average duet code adherence for first year= 0.63 ± 0.047 , $n=17$ pairs; average duet code adherence for second year= 0.64 ± 0.047 , $n=17$ pairs).

Do duet codes change with breeding partners?

Over the seven year study, there were 22 males that were recorded performing duets with multiple females, for a total of 53 different pairings and 31 partnership changes. Out of these 31 partner changes, 19 showed significant similarity in duet code between partner changes (61%, All Spearman's $\rho \geq 0.155$, $p \leq 0.04$). Therefore, males' duet codes do not typically change when the birds change breeding partners.

There were 14 females that I recorded performing duets with multiple males for a total of 34 different pairings and 20 partner changes. Out of these 20 partner changes, 17 showed significant similarity in duet code between partner changes (85%, All Spearman's $\rho \geq 0.19$, $p \leq 0.013$). Therefore, females' duet codes do not typically change when they change breeding partners.

Do duet codes arise due to male or female answering rules?

Male-created and female-created duets were compared across 50 pairs of birds with the highest number of duets using Spearman's rank correlation. Out of those 50 pairs, 48 showed significant similarity between male-created and female-created duets (96%, All Spearman's $\rho \geq 0.167$, $p \leq 0.03$). Therefore, males and females appear to follow the same answering rules.

Are duet codes pair-specific or population-wide?

Three population-level matrices were created: all duets (n=5,326 duets), all male-created duets (n=1,524 duets), and all female-created duets (n=3,802 duets). All three matrices showed a significant non-random association of song-types (Randomization Test, all duets: $p < 0.0001$; male-created duets: $p < 0.0001$; female-created duets: $p < 0.001$). This indicates that there is a population-wide duet code. Out of the ten most common duet types, five were created by males and females matching the same song class while 5 were created by combining different song classes the four most common in the population are shown in Figure 2.5).

Discussion

Analysis of 113 duetting pairs recorded over a seven year period reveal that Rufous-and-white Wrens follow a duet code. Evidence for duet codes was strong for pairs where I recorded many duets, whereas evidence was ambiguous for pairs where I recorded few duets. Rufous-and-white Wrens do not show changes in their duet codes the longer they are paired nor do their duet codes change when they change breeding partners. Males and females follow the same answering rules and the accumulated population-level duet matrices showed significant adherence to a duet code. All these factors indicate that Rufous-and-white Wrens are following a population-level duet code where all males and females in the population use similar answering rules when responding to their partner's songs.

I compared my preferred method of statistical analysis, the Randomization Test, to another commonly used method, G-test for Goodness-of-fit. I found that both the

Randomization Test and G-test for Goodness-of-fit produce similar results. However, in contrast to previous studies (Mennill and Vehrencamp 2005, Mann et al. 2003) I focus on the results of the Randomization Test because of the limitations of the G-test for Goodness-of-fit. G-tests for Goodness-of-fit are known to produce questionable results with small sample sizes; if expected cells in a contingency table fall below five, then a G-test for Goodness-of-fit can give inaccurate p-values (McDonald 2009, Zar 1974). Low sample sizes are common in field studies due to the challenges of data collection. My dataset had sample sizes that ranged from 5 to 500 duets per pair. The G-test for Goodness-of-fit did not have the flexibility I needed to test this wide range of sample sizes. In addition, the G-test for Goodness-of-fit does not take into account variation in the level of output for each song type sung by males and females. Birds preferentially sing particular song types that will appear in duets more often, and this may cause the G-test for Goodness-of-fit to identify duet codes when they may not exist. The Randomization Test is unaffected by small sample sizes and takes into account the variation in output of the individual song types when calculating duet codes. It is a preferable statistical test and should be used in future studies of duet codes.

Rufous-and-white Wren females adhere to duet codes significantly more strongly than males. Females also create the majority of duets (73%; Mennill and Vehrencamp 2005). This may indicate that females are more motivated to perform duets, and may also have more to gain from creating duets and following duet codes. Rufous-and-white Wrens show a similar pattern of duet code adherence to Black-bellied Wrens, as females in both species show stronger duet code adherence than males (Logue 2006). Black-bellied Wren females, however, show 100% duet code adherence (Logue 2006),

strikingly higher than Rufous-and-white Wren females (78%). It would be interesting to conduct a comparative study to determine what factors influence such differences in duet code adherence between congeneric wrens.

Duet code adherence may be used as an intra-pair signal. Strong adherence to a duet code may be indicative of commitment similar to duet precision and duet responsiveness (Hall and Magrath 2007, Hall 2000). Birds may use duet code adherence to judge their partner's commitment or assess whether or not they will be a devoted parent. Duet code adherence could then predict divorce, or effort placed in nest building or nestling feeding. White-browed Sparrow Weavers (*Plocepasser mahali*), for example, refine their duet codes by losing song components their partner doesn't have over years of pairing (Voigt et al. 2006). Similarly, Plain Wrens' duet code adherence gets stronger the longer they are paired (Marshall-Ball et al. 2006). This refinement may indicate that duet codes are an intra-pair signal of commitment. My analysis of Rufous-and-white Wren duet codes, however, demonstrates that duet code adherence does not change the longer a pair is together. This may be due to the population-wide duet code. Theoretically, individual-specific duet codes should take longer to learn at the beginning of new partnerships due to the individual-specific answering rules. Bay wrens, however, learn individual-specific duet codes over short periods (Levin 1996a). Since duet code adherence does not improve the longer a pair is together in Rufous-and-white Wrens, duet code learning may not require much time either. Since Rufous-and-white Wrens don't show significant changes in duet code adherence between years, it may indicate that duet codes are not used to communicate commitment in the species. However, meticulous

studies need to be conducted and recordings need to be collected at the onset of pairings to truly understand duet code learning and its relation to pair commitment.

Logue's (2006) Identity Hypothesis states that duet codes could be used for mate or pair identification, particularly for sexually monomorphic birds that live in thick vegetation where visual identification might be difficult. This hypothesis is typically associated with birds who follow pair or individual-specific duet codes and may not apply to population-wide duet codes; when duet codes are shared among all individuals, adherence to answering rules cannot reveal anything about partnership during aggressive interactions. It has been suggested, however, that even species with population-wide duet codes have pair-specific signatures within their duets (Grafe and Bitz 2004b). If this is the case, the identity hypothesis may still be a possibility for Rufous-and-white Wrens. More studies need to be done to determine if birds use duet codes for individual discrimination.

Alternatively, duet code adherence may be an inter-pair signal. A pair that has a strong duet code adherence may signal a strong pair bond, or longer length of partnership. Strong adherence may signal to other birds that a pair is more coordinated and thus more of a threat to intruders (Hall and Magrath 2007, Marshall-Ball et al. 2006, Rogers 2005, Grafe and Bitz 2004b). It would be interesting to determine whether pairs with stronger duet code adherence fare better in territorial interactions. If duet code adherence signals commitment, it may deter other birds from seeking copulations or attempting to usurp a pair member. Since Rufous-and-white Wren females adhere more strongly to the duet code than males, it may indicate that females find more advantages in advertising their mated status to other individuals. Mate guarding or prevention of mate usurpation may be a function of duet code adherence. Long term studies and acoustic playback experiments

may elucidate the functions of differences in duet code adherence both within and between species by comparing duet code adherence to rates of divorce, reproductive behaviours or likelihood of winning contests.

The population-wide duet code of Rufous-and-white Wrens may be used for song matching in aggressive interactions with other pairs of birds. Song type matching and countersinging are used in solo-singing male birds during song contests to communicate aggression or motivation (Burt et al. 2001, Beecher et al. 2000). Duetting species with population-wide duet codes use duet types in similar ways to song type matching in solo-singing birds. Eastern Whipbirds duet type match during aggressive interactions (Rogers et al. 2006) and Tropical Boubous are suspected of such behaviour (Grafe and Bitz 2004b). In Rufous-and-white Wrens, males share an average of six songs with other males and females share an average of two songs with other females (Mennill and Vehrencamp 2005). Sharing between birds becomes less likely as they become more distant geographically from each other (Mennill and Vehrencamp 2005). If songs are learned from neighbours, and particular areas have certain repertoires of song types, this may result in the use of different answering rules across regions (e.g. between nearby or adjacent populations). Additionally, song matching would be more likely with individuals who share the same song types. In this case it may be beneficial to live in the same area where songs were acquired (Beecher et al. 2000, Nordby et al. 1999). Studies on song type matching and song learning in duetting birds are rare, and are critical for understanding duetting behaviour and the use of duet codes. Performing acoustic playback studies using duet types shared in the population is an excellent way to

experimentally determine if Rufous-and-white Wrens and other duetting birds use their duet songs in countersinging interactions similar to solo-singing temperate birds.

Specific duet types in the Tropical Boubou serve different intra and inter-pair functions. One duet type is used as a post conflict display (Grafe and Bitz 2004a) while others are used for territorial defence and mate guarding (Grafe and Bitz 2004b). The closely related Slate-coloured Boubous also use their duet types for specific purposes including two duet types for territorial interactions and one duet type to coordinate breeding (Sonnenschein and Reyer 1983). Rufous-and-white Wrens may use their population-wide duet code for similar purposes. Certain duet types may be used in specific contexts or to communicate motivations. Close monitoring of duets seasonally could determine if duet types indicate breeding stage. As well, simulating territorial interactions may determine whether birds use certain duets to communicate aggression.

Rufous-and-white Wrens as a population have certain song types that they combine into duets more often (Figure 2.5). This is in contrast to what Mennill and Vehrencamp (2005) discovered where Rufous-and-white Wrens avoided song type matching in duets. In our analysis, song type matching was not avoided and occurred just as often as combining different song classes. Mennill and Vehrencamp (2005) may have had too small of a sample size to detect common duet types in the population.

Rufous-and-white Wrens follow a population-wide duet code, which is a different strategy than their closest relatives that have been studied to date. Plain Wrens (Marshall-Ball et al. 2008), Black-bellied Wrens (Logue 2007b, Logue 2006), and Bay Wrens (Levin 1996a) all have pair-specific or individual-specific duet codes. According to Mann

et al. (2009), most of the wrens in the group of birds formerly united within the *Thryothorus* genus follow pair-specific duet codes. Rufous-and-white Wrens are the first wren of the species from the former *Thryothorus* genus to show a population-wide duet code, a different strategy for using a duet code than its close wren relatives. The *Thryophilus*, *Pheugopedius* and *Cantorchilus* lineages may have evolved different types of duet codes depending on life history or duet and song form. Comparing life history traits and form and function of songs and duets in these species may explain differences in the evolution of duet codes (Mann et al. 2009).

Duet codes may be influenced by the complexity of duetting. Plain Wrens and Bay Wrens have very fast and intricately coordinated duets (Cuthbert and Mennill 2007, Mann et al. 2003, Levin 1996a). Black-bellied Wrens have less complex duets and Rufous-and-white Wrens have the simplest duets of the four species (Mann et al. 2009, Mennill and Vehrencamp 2005, Logue and Gammon 2004). Duet complexity may influence whether pair-specific or population-level duet codes occur. Levels of song sharing or the learning strategy employed by juveniles may also influence which type of duet code species employ. If song and duet sharing are high in a species (or population) then population-level duet codes may be favoured. If birds disperse far from their natal site then song sharing may be low and may favour pair-specific duet codes. Very little research has been done on tropical bird dispersal behaviour and song learning, which may be important in duetting species (Marshall-Ball and Slater 2008). Deciphering whether duet codes are population-level or pair-specific and relating it to life history may help to understand why duet codes have evolved in a number of species (Mann et al. 2009).

Logue (2007b) argues that an experimental approach is helpful for studying duet codes in order to conclude that outside cues, pair-directed signals or repertoire cycling aren't affecting duet codes. For example, if both males and females choose songs based on external cues or if males and females cycle through their repertoire at the same rate, this could create the impression of answering rules and duet codes. In Rufous-and-white Wrens it can be argued that answering rules drive the duet code even without experimental justification. Both in terms of external outside cues and pair-directed signals affecting song choice, Rufous-and-white Wrens spend much time performing duets when visually separated and they use duets in order to find each other in dense vegetation (Mennill and Vehrencamp 2008). Birds in different areas cannot see each other to base song type choice on visual cues. In addition previous research has firmly established that males and females have different repertoire sizes and males sing more often than females (Mennill and Vehrencamp 2005). Even if pairs did cycle through their repertoires, the sexes would not move through their repertoires in synchrony because of this variation in repertoire size. Moreover, in our analyses, pairs were recorded over many days, and it is unlikely that repertoires would sync up consistently from day to day purely by chance. Experimental studies of the duet code of Rufous-and-white Wrens, however, are the logical next step in uncovering more about answering rules in this species and will add more credence to this observational analysis.

This research highlights the lack of understanding of duet codes and how duet codes relate to the life histories of duetting birds. Determining the purpose of pair-specific or population-level duet codes may elucidate the functions of duetting and duet evolution. Differential adherence to duet codes within pairs and between pairs may communicate

levels of commitment, the strength of a pair bond or represent a sex-biased benefit to duetting. How and where duetting birds learn their song may influence duet codes and therefore communication strategies. Using a comparative approach to study closely related birds with different types and variations of duet codes may reveal the evolution of duet codes and their function in duetting birds. As well, more studies on duet code and answering rules will increase our understanding of the use of repertoires by duetting birds.

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Species	Population-wide or pair-specific duet code	Which sex creates most duets	Which sex controls the duet code	Which sex follows the code more strictly	Duet functions	Citations
African Drongo (<i>Dicrurus macrocercus</i>)	Pair-specific	Unknown	Unknown	Unknown	Unknown	Wickler 1976
Australian Magpie (<i>Cracticus tibicen</i>)	Pair-specific	Unknown	Unknown	Unknown	Territorial defence, group bond maintenance	Brown & Farabaugh 1991
Australian Magpie-larks (<i>Grallina cyanoleuca</i>)	Pair-specific	Equal	Unknown	Unknown	Territorial defence, pair bond maintenance	Hall 2006, Hall 2000
Bay Wren (<i>Cantorchilus nigricapillus</i>)	Pair-specific	Males	Males	Unknown	Territorial defence, mate guarding (males only)	Levin 1996a, Levin 1996b
Black-bellied Wren (<i>Phlegopedius fuscioventris</i>)	Pair-specific	Males	Females	Females	Territorial defence, contact maintenance	Logue 2007a, Logue 2007b, Logue 2006, Logue and Gammon 2004
Buff-breasted Wren (<i>Cantorchilus leucotis</i>)	Pair-specific	Females	Unknown	Unknown	Unknown	Gill et al. 2005, Farabaugh 1982
Eastern Whipbird (<i>Phosphodes olivaceus</i>)	Population	Females	Females	Females	Territorial defence, mate guarding	Rogers 2005
Plain Wren (<i>Cantorchilus modestus</i>)	Pair-specific	Females	Unknown	Unknown	Territorial defence, mate guarding, pair bond formation and maintenance	Marshall-Ball and Slater 2008, Marshall-Ball et al 2006, Mann et al 2003
Rufous-and-white Wren (<i>Thryophilus rufalbus</i>)	Population	Females	Unknown	Females	Territorial defence, mate guarding, maintaining contact, breeding synchrony	Mennull and Velrencamp 2008, Topp and Mennull 2008, Mennull and Velrencamp 2005
Slate-coloured boubous (<i>Laniarius funebris</i>)	Pair-specific	Females	Unknown	Males	Territorial defence, mate guarding, coordinate breeding activities	Serbt & Wickler 2000, Sonnenschein and Reyer 1983
Tropical Boubous (<i>Laniarius aethiopicus</i>)	Population	Males	Neither	Neither	Territorial defence, mate guarding	Grafé et al. 2004b, Grafé and Britz 2004
White-browed Sparrow Weaver (<i>Plocepasser mahali</i>)	Pair-specific	Equal	Unknown	Unknown	Territorial defence, pair bond maintenance	Vogt et al. 2006
White-crested laughing Thrush (<i>Garrulax leucotophus</i>)	Unknown	Unknown	Unknown	Unknown	Unknown	Soucek & Vencel 1976

Table 2.1. Summary and comparison of the 13 species of bird where duet codes have been reported to date.

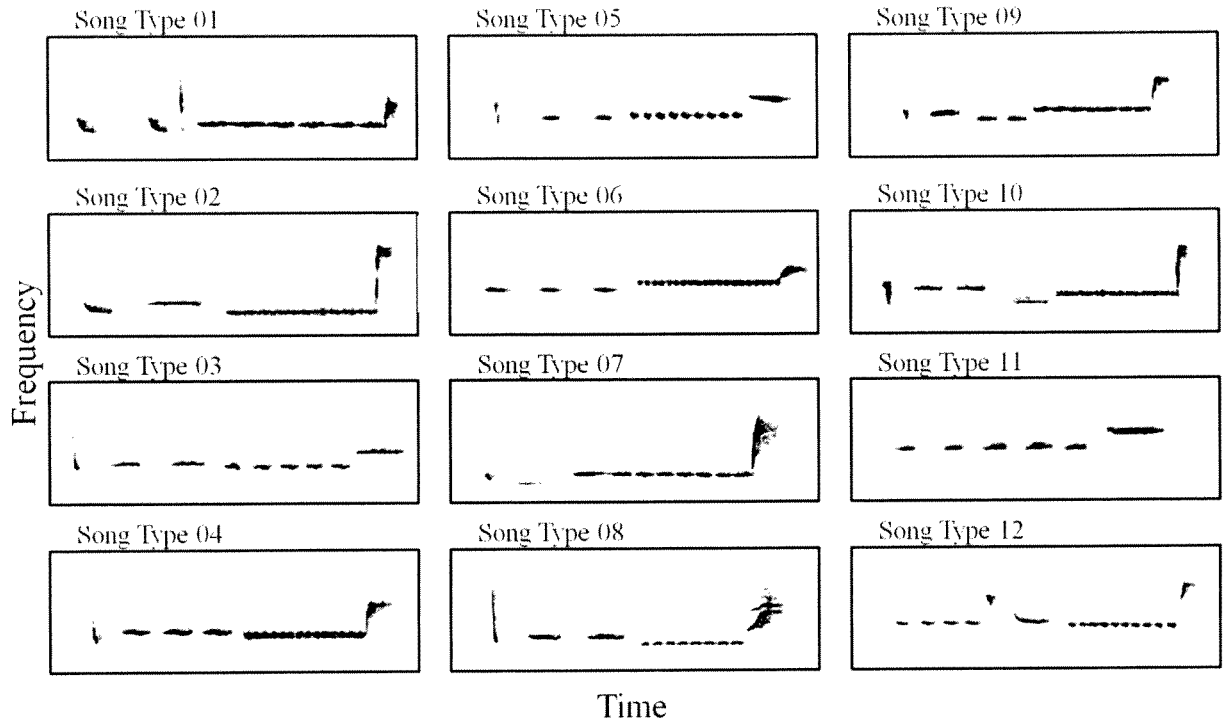


Figure 2.1. Sound spectrograms showing examples of each of the twelve song type categories common in my study population. Most Rufous-and-white Wrens song types were easily classified into one of these twelve population level song types based on the number of notes, the relative pitch of the notes, and the rate of syllable repetition in the middle trill section. These twelve classes were found in both male repertoires and female repertoires.

		Female Song Types							
		02	03	04	05	06	07	08	11
Male Song Types	01	1	0	0	0	0	9	0	0
	02	22	0	0	0	0	8	1	0
	04	0	0	16	0	0	3	0	6
	05	0	0	1	7	0	0	0	0
	06	1	0	0	0	0	1	2	0
	07	0	1	1	0	0	40	0	0
	08	2	0	0	0	1	16	0	0
	09	2	0	0	0	0	7	0	0

Figure 2.2. An example of a matrix used to calculate duet code, based on 148 duets collected from pair SYMY (male) and SMBM (female). The duet composed of the male song type 7 and the female song type 7 is an example of a common duet type and is probably an answering rule as well as the other highlighted duet combinations.

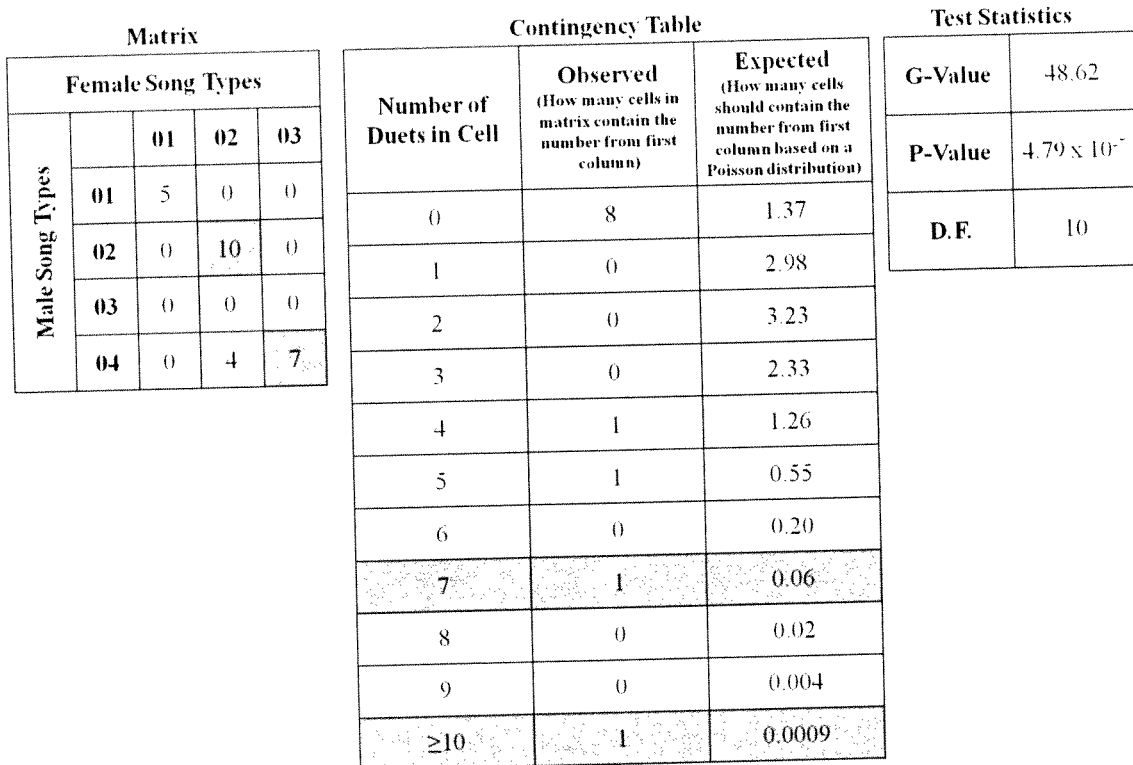


Figure 2.3. A hypothetical example of how a matrix would be used to calculate a G-value. The matrix is converted into a contingency table which is then used to calculate a G-value based on observed and expected values. Highlighted cells in the matrix correspond to highlighted rows in the contingency table.

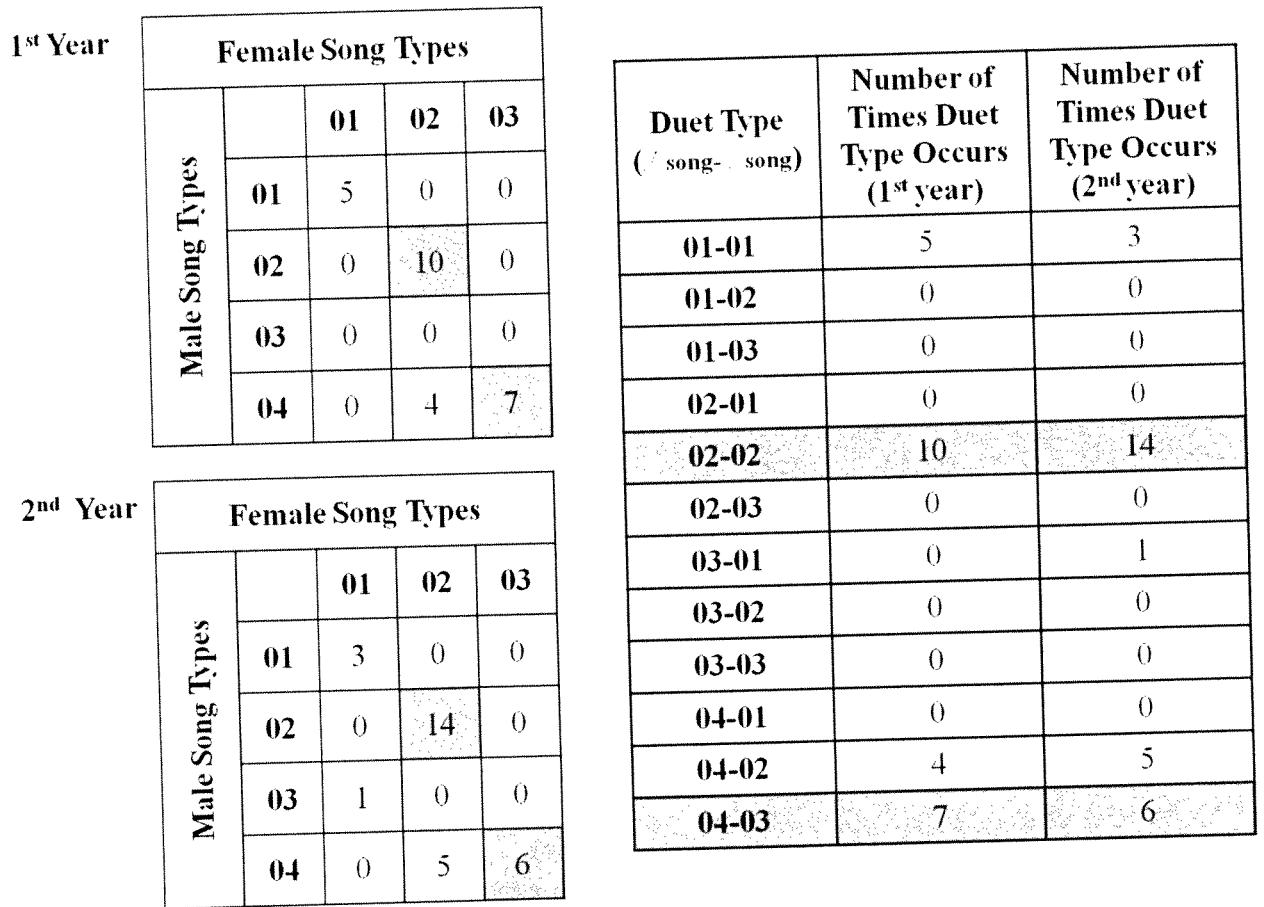


Figure 2.4. A hypothetical example of how duet types would be rearranged from duet matrices into a table for Spearman's rank correlation Analysis. The two matrices represent the two years a pair of birds were social partners and the duets they sang. The table on the right contains all the individual duet types in the left column and how many times these duet types occurred in the columns to the right of it. These numbers would then be ranked by Spearman's rank correlation analysis to test for similarity between years (in this example) or between different breeding partners.

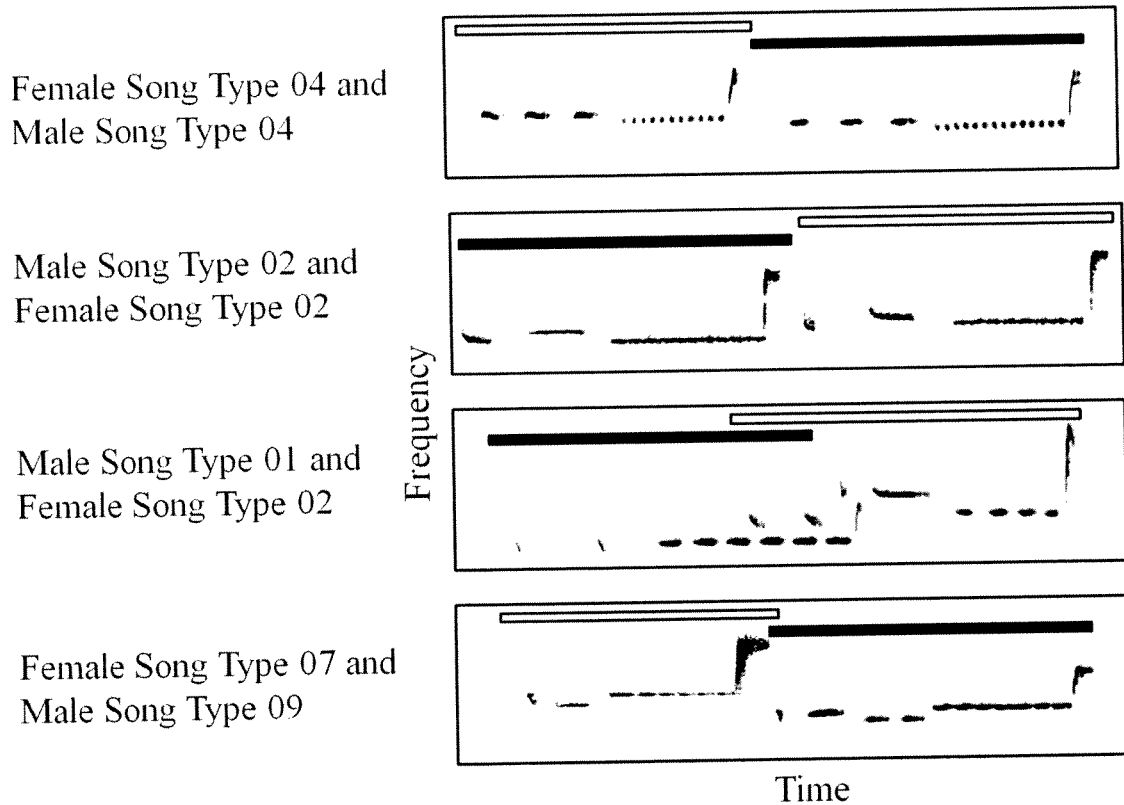


Figure 2.5. The four most common duet types in the population, ranked in order of the most common to the least-common. The representative combinations are presented as spectrograms with male contributions indicated by black bars and female contributions indicated by white bars. These duet types can be either male or female initiated. Rufous-and-white Wrens do not avoid song matching when creating duets but also use different song types to create duets.

Thesis Summary

Although research on duets has increased in recent years, there are still many aspects of duetting that are not well understood. One of these aspects is the use of duet codes, a behaviour where birds combine songs in their repertoires non-randomly into duets. Duet codes are found in a wide variety of bird taxa. My thesis explores duet codes in detail through an investigation of Rufous-and-white Wrens (*Thryophilus rufalbus*). I performed Randomization Tests to evaluate thousands of duets recorded from more than a hundred pairs of Rufous-and-white Wrens and found that certain male-female song combinations occur more often than expected by chance, indicating that pairs follow a duet code. Half the pairs in the population were found to follow a duet code, while the other half most likely had too small of sample sizes to detect a duet code statistically. I found that duet code adherence was stronger in females than in males, indicating that females follow answering rules more strictly. Duet codes do not change between years of partnership; answering rules remain consistent for the length of a partnership. Similarly, answering rules do not change with partner changes, revealing that duet codes are consistent between individuals in the population. Indeed, the population-level matrices, containing all duets I recorded over seven years, tested significant for a duet code. Rufous-and-white Wrens follow a population-level duet code; all birds in the population have the same set of answering rules.

Changes in duet code adherence may provide clues to how birds learn answering rules. Since Rufous-and-white Wrens show no changes in duet code adherence with length of partnership and adhere to a population-level duet codes, it is unlikely that they require time to learn answering rules when forming new pairs. Determining where birds

learn songs, whom they learn to sing from, and the importance of learning in establishing duet codes is an important, although challenging, area for future research.

The form of a duet code can offer some insight into the possible functions of answering rules, duet codes, and the evolutionary significance of duetting behaviour. Duet codes may have intra and inter-pair communication functions. Duet code adherence may function in intra-pair communication such as signalling commitment. Since Rufous-and-white Wrens do not appear to vary in their duet code adherence through time, it is unlikely that duet code is used for pair bond maintenance. However, they may use the different duet types in their duet repertoire to signal different states of motivation. Duet types may be used to coordinate breeding activities or communicate intentions to a partner. Duet codes may also function in inter-pair communication. The strength of duet code adherence may signal pair bond and coalition strength of a pair. This may function in mate guarding and to deter other birds from attempting extra-pair copulations or mate usurpation. If a pair appears to be highly coordinated it may also deter rivals from aggressive interactions. The shared duet types observed in my population of Rufous-and-white Wrens may be used in countersinging interactions with rival pairs. As well, certain duet types may signal greater aggression or higher motivation to fight.

Comparing Rufous-and-white Wrens to their close relatives is crucial for understanding the evolution of duet codes. Plain Wrens (*Cantorchilus modestus*), Bay Wrens (*Cantorchilus nigricapillus*), and Black-bellied Wrens (*Pheugopedius fasciatoventris*) all follow pair or individual-specific duet codes. The Rufous-and-white Wren is the only wren studied so far with a population-wide duet code. Comparing duet

structure, function and life history traits of these species may provide clues to the evolution of these different forms of duet codes.

The study of duet codes requires large data sets, taken over large time scales and is a challenging new area of research. However, it is crucial to understand duet code in order to understand the form and functions of duetting, as well as its evolution. More research into duet codes will increase our understanding of duetting bird behaviour and tropical birds.

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