

# **Song and duet function of the Chirruping Wedgebill** *(Psophodes cristatus)*



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## Contents

General Abstract .....	4
Declaration.....	5
Additional declaration page for the Masters of Research thesis .....	6
Acknowledgements.....	7
Preface.....	9
Chapter One .....	11
A longitudinal study of song and duetting in breeding Chirruping Wedgebills ( <i>Psophodes cristatus</i> ). .....	11
Abstract.....	12
Introduction.....	13
Materials and methods .....	16
Species .....	16
Study site.....	16
Observation .....	17
Establishing stage of reproduction .....	17
Behavioural observations.....	18
Song analysis .....	20
Defining duets .....	20
Statistical analysis.....	21
Results.....	22
Temporal precision of joint song .....	22
Occurrence of female solo song.....	22
Spectrograms.....	22
Diel song rate .....	23
Song rate across the breeding cycle .....	24
Discussion.....	27
Male song longevity.....	27
Male and female song rates and the reproductive cycle .....	27
Duets and the reproductive cycle .....	29
Conclusion .....	31
Acknowledgements.....	32
References.....	33
Chapter Two.....	37
Duetting in an arid zone endemic, the chirruping wedgebill ( <i>Psophodes cristatus</i> ). .....	37
1. Introduction.....	38

2. Materials and methods .....	42
2.1 Study site and species .....	42
2.2 Defining duets .....	43
2.3 Song files .....	43
2.4 Playback methodology .....	44
2.5 Statistical analysis .....	47
3. Results .....	48
3.1 Temporal precision of duets .....	48
3.2 Response to playback .....	48
4. Discussion .....	53
4.1 Reactions to solo intruders: Evidence of sexual conflict or cooperation? .....	53
4.2 Response to pair invasion: Evidence of cooperation? .....	56
5. Conclusion .....	58
Acknowledgements .....	59
References .....	60
Concluding remarks .....	67
ANIMAL RESEARCH AUTHORITY (ARA) .....	68

## General Abstract

The Chirruping Wedgebill (*Psophodes cristatus*) is medium sized, monomorphic passerine that is endemic to the arid regions of Central Australia. Despite highly conspicuous singing behaviours, particularly by males, this species has yet to be formally studied. This lack of study represents broader trends in behavioural ecology research in Australia where despite 70% of the continent is classified as arid zone, the majority of species in this area have not been the subject of research. Male Chirruping Wedgebills possess a trill syntax song type, a simple repetitive form of song that is physically very difficult to produce. In addition, females of this species sing and both males and females are known to form antiphonal duets, a temporally precise form of joint song. These interesting singing behaviours present us with an opportunity to further develop our understanding of song function and also provide us with a foundation for understanding this species behavioural ecology. By examining duet function in this habitat type and by including females in our examination of song rates, we are able to address current biases that exist in the study of song. In addition, by studying the Chirruping Wedgebill, we are able to contribute valuable information to a small amount of research being conducted on the behavioural ecology of arid zone species in Australia.

## Declaration

I certify that the work in this thesis entitled “Song and duet function of the Chirruping Wedgebill (*Psophodes cristatus*)” has not previously been submitted for a degree nor has it been submitted as part of the requirements for a degree to any university institution other than Macquarie University.

I certify that this thesis is an original piece of research and that it has been primarily written by me. Where co-authored, my contributions and those of all other authors have been clearly indicated. Any help and assistance that I have received has been appropriately acknowledged. I certify that all information sources and literature are indicated in this thesis.

The research indicated in this thesis was approved by the Macquarie University Animal Ethics Committee (No. 2013/030 – 3).

Victoria I. Bywater

April, 2015

## **Additional declaration page for the Masters of Research thesis**

This thesis is written in the form of a journal articles from:

1. *Emu*
2. *Behavioural Processes*

### **Declaration**

I wish to acknowledge the following assistance in the research detailed in this report:

Dr Simon Griffith (Principal supervisor)

Dr Andrew Russell (Supervisor)

Lalage Grundy (Field Assistant)

Caitlin Higgott (Field Assistant)

Antonin Viguier (Field Assistant)

All other research described in this report is my own original work.

Victoria Bywater

23/04/2015

## **Acknowledgements**

Firstly I would like to thank my principal academic supervisor, Dr Simon Griffith for his guidance throughout this project. The detailed feedback I was provided with and our frequent discussions have improved my critical thinking greatly. In addition, while challenging at times, allowing me to take charge of this project has developed my leadership skills and built confidence. As such, the skills I gained from this project have extended well beyond the field of scientific investigation. Thank you.

I would also like to thank my associate supervisor Dr Andrew Russell from the University of Exeter. Andy provided me with guidance on my observational methodologies and assistance in the field which I was extremely grateful for. He also laughed at my first attempt at setting up a mist net. Despite his laughter, Andy encouraged me to practise a lot throughout the field season. As such, I have now developed this valuable fieldwork skill. Thanks Andy.

Next, I would like to extend sincere gratitude and thanks to Lalage Grundy, Caitlin Higgott, and Antonin Viguiet, my field assistants. All three of these people worked extremely hard and it is because of their help that we had such a successful season. They put up with early mornings (4am type early), long walks, every kind of prickle and spike imaginable, long days, longer weeks and late nights doing everything they could to help me with data collection and management. I sincerely appreciate the effort you all put into this project.

Antonin Viguiet is listed as second author on the first paper in this thesis. Not only did he assist in the field for this study, but he assisted me in sampling thousands of hours of sound recordings; a tedious job which added greatly to the content of the paper. Caitlin Higgott is listed as second author on the second paper in this thesis. She was my primary assistant during the experiment and I could not have completed it without her. Caitlin also assisted in finding and preparing songs used in the experiment

A special thank you to Matthew Austin for his assistance in the field, on all things computer related and for his unwavering support. Your encouragement to keep going when I was absolutely exhausted and your endless patience in listening to everything Wedgebill related has kept me going. As I am certifiably computer illiterate, your patience in explaining all things Excel has prevented many a tear of frustration. Thank you.

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Finally, thank you to everyone at Fowlers Gap Research Station, in particular Professor Keith Leggett and Gary and Vicki Dowling. You are all extremely helpful and approachable people and contributed to making my time at Fowlers so enjoyable. Thank you Gary and Vicki for inviting all of us researchers into your home on a regular basis and for cooking a mean BBQ. I feel I can speak for everyone in saying that these breaks from work prevented us all from going a little insane.



## Preface

Admitted into the second year of the new Macquarie University Masters by Research Program in July 2014, I began four months of field research in August 2014 at Fowlers Gap Arid Research Station. During this period I managed a small group of volunteers and we conducted field observations seven days a week during this time. Behavioural observations were conducted from before sunrise until late morning. Afternoons were spent locating nests, banding chicks, measuring nest site characteristics and moving remote recording equipment around to different parts of the research site. In the final month I also designed and conducted a playback experiment. Researching a previously unstudied species, we were unsure of what we would find, and we targeted lots of information to develop a preliminary understanding of the species' behaviour and ecology as we worked. Data collection was largely successful and we were pleased with what was achieved during this first field season.

In this thesis I present two manuscripts based on the data collected during that relatively short field season. I finished my fieldwork on the 24<sup>th</sup> of November 2014, and have had less than five months to process acoustic recordings, transcribe field notes, analyse data and write these manuscripts, by the deadline of the 24<sup>th</sup> of April 2015. Whilst we were instructed to present our thesis as a manuscript prepared for submission to a journal, I felt that the more substantive paper resulting from my experimental work needed to be contextualised by a first, more descriptive and lower impact manuscript, given the absence of any previous work on this species. As a result, I have completed two manuscripts. The first describes acoustic activity in both male and female wedgebills across a period of breeding activity. This paper attempts to address biases in previous research in this research area by including female song rates and the occurrence of duets. It provides a basis for understanding when these birds sing and duet, and possible functions for their song. This observational study will prove valuable as a foundation for future research on the Chirruping Wedgebill and will be submitted to the journal *Emu*. The second paper presented is an experimental study focusing on the function of duets in this species. This paper will be submitted to the journal *Animal Processes*.

My academic supervisor Dr Simon Griffith assisted me broadly in these projects in conception, discussion and writing and is listed as co-author on both chapters. My co-supervisor Dr Andy Russell assisted with conception and methodology of chapter one and is also listed as co-author. I received help in the field and in examining many hours of recordings and as such, Antonin Viguier is also listed as co-author of chapter one. Concerning chapter two, Caitlin Higgott assisted me in the field with data collection and experiment preparation and as such is listed as co-author.

My estimated contribution to these joint papers:

Chapter One: Conception 80%, data collection 70%, analysis 100%, writing 95%

Chapter Two: Conception 90%, data collection 70%, analysis 100%, writing 95%

Front Cover photo: Victoria Bywater

Chapter Two photo: Antonin Viguier

Chapter Three photo: Camille Duval

# Chapter One

**A longitudinal study of song and duetting in breeding  
Chirruping Wedgebills (*Psophodes cristatus*).**



Prepared for submission to journal *Emu*

# **A longitudinal study of song and duetting in breeding Chirruping Wedgebills (*Psophodes cristatus*).**

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**Abstract.** The variation in the expression of song at different stages of the avian reproductive cycle can provide useful insight into the underlying function of song. However, much of our understanding of song originates from studies of species in the northern hemisphere where breeding seasons are short and highly synchronised at the population level. By comparison, acoustic behaviour in southern hemisphere species, where breeding cycles are less predictable, and less synchronised are poorly studied. Both female song, and duets - a temporally precise form of joint song largely between males and females - are prevalent in species in the southern hemisphere and have been the focus of relatively little work. We examined song rates of male and female Chirruping Wedgebills (*Psophodes cristatus*), a species of passerine endemic to the arid regions of Central Australia, across a four-month period of breeding activity. Unlike many species who sing largely at dawn, male Wedgebills and can be heard singing throughout the day. We demonstrate this by using recordings to examine male song rate from sunrise to sunset. In addition using field observations, we examined male and female song rates and duets throughout the reproductive cycle by timing how long males sang for per hour and by counting the number of female songs per hour. The occurrence of duets was also noted. We show that stage of reproduction effects the singing rate in both males and females as well as the number of duets they produce. In so doing we provide the first account of duet use in this species and suggest it may serve multiple functions such as assisting in breeding synchrony and mate guarding.

**Additional keywords:** song rate, southern hemisphere, breeding cycle, female song, duets

## Introduction

The variation in the expression of song at different stages of the avian reproductive cycle can provide useful insight into the underlying function of song with respect to mate selection, territorial defence or maintenance of the pair bond (Catchpole and Slater 2003; van Dongen 2006). Even simple observational studies that take a longitudinal approach to the collection of song can therefore provide an important platform for developing an understanding of the function in a species (Kroodsma and Byers 1991; Morton 1996; van Dongen 2006). In turn, understanding song function can greatly inform our understanding of behavioural ecology (Catchpole and Slater 2003) and communication across species and taxa (Hall 2009).

However despite evidence that song originated in passerines of the Australasian region (Barker, Barrowclough *et al.* 2002), much research in this area has focused on species in the northern hemisphere, where most researchers are based. Typically, classic northern hemisphere study species have very short and highly synchronised breeding seasons at both a species and population level (Morton 1996; van Dongen 2006). As different hemispheres possess diverse representations of the avian families, a problem here is that the life-history and reproductive biology of seasonal and migratory species are quite different from many sedentary southern species (Russell, Yom-Tov *et al.* 2004).

By contrast, song rates of southern hemisphere species, where breeding cycles are much less predictable have been relatively poorly studied. Indeed, the breeding cycles of many Australian birds reflect similar patterns to tropical species, where breeding activity may be spread throughout the year opportunistically and is dependent on rain or food availability that can be very unpredictable (Catchpole and Slater 2003; Martin 1996). Many species will have more than one breeding attempt in a relatively long breeding season that may stretch for more than half of the months of the year (Russell, Yom-Tov *et al.* 2004). In northern temperate species, there is often an intense bout of singing connected with the population-wide establishment of territories and laying of eggs (Catchpole and Slater 2003). Given the typically long breeding seasons of Australian birds, we might expect a different pattern of longitudinal variation over a breeding period than these northern species. However, few studies have examined song rates of Australian species across a period of breeding activity from the individual and population perspective.

Accompanying these geographical biases, many studies have focused exclusively on male song even though female song, and duets between males and females, are widespread among species (Odom, Hall *et al.* 2014). These biases are likely to impact the broader understanding of the evolution of acoustic communication in birds. Female song is phylogenetically widespread (Odom *et al.* 2014), and has been greatly neglected by researchers, leaving us with a poor understanding of its function both independently and in relation to males (Hall, Rittenbach *et al.* 2015). However, it is likely to serve similar purposes to male song (Langmore 1998). Examples include the use of song in female Song Sparrows (*Melospiza melodia*) immediately before nest building due to high female competition (Arcese, Stoddard *et al.* 1988), in female Northern Cardinals (*Cardinalis cardinalis*) to communicate with males at the nest, coordinating bi-parental care (Halkin 1997) and in female Eastern Whip birds (*Psophodes olivaceus*) who use song to mate guard (Rogers, Mulder *et al.* 2006).

Duets are a temporally precise form of joint song (Hall 2009; Langmore 2002) that were commonly thought to be particularly prevalent in the tropics (Slater and Mann 2004). However, Benedict (2008) conducted an extensive review on the occurrence of duets in North American passerines and found that 7% of these species formed duets. This is a very high proportion given that only 3-4.3% of avian species worldwide had been thought to duet (Farabaugh 1982; Hall 2009). There exist numerous hypotheses that attempt to explain the function of these joint songs (reviewed in Hall 2004) that may be used in both sexual conflict and cooperation (Hall 2009). For example, many studies show an increase in duet use around the time of nest building (Catchpole and Slater 2003; Hall 2009). As this is the female's most fertile period it is thought that duets likely play a role in breeding synchrony, by assisting pairs in coordinating their reproductive efforts (Hall 2009; Méndez-Cárdenas and Zimmermann 2009). In addition, duets may also be used in mate guarding. By duetting with a partner members of a pair may know their whereabouts at all times and thus may prevent attempts at extrapair copulations. Thus if duets were used in mate guarding we might expect an increase in duet rate accompanied by a decreased distance between pairs (Hall 2004). As joint song shows coordination and thus likely displays a more aggressive signal than solo song, duets have also been shown to be used cooperatively in territorial defence. Examining duet use as different stages of the reproductive cycle may provide insight as to duet function within a species. However, complicating our understanding of duet function, these hypotheses are not mutually exclusive with duets being shown to be used for different

purposes within a single species (Hall 2004; Sonnenschein and Reyer 1983) in both sexual conflict and cooperation (Hall 2004; Koloff and Mennill 2011; Mennill and Vehrencamp 2008). In addition, there exists great diversity in duet form and structure with even closely related species displaying variation in complexity and temporal precision (Mann, Dingess *et al.* 2009). These reviews and comparative studies (Benedict 2008, Hall 2009, Mann *et al.* 2009) have all called for further intensive studies of duetting species in a greater diversity of habitat types and regions. In so doing, researchers may provide greater breadth of understanding into the function, evolution and ecology of this important element of bird song.

From the context of these known gaps in our understanding of female song and duets, as well as the need to understand the ecology of bird song in a greater diversity of habitats, we examined the song and duet rates of male and female Chirruping Wedgebills (*Psophodes cristatus*) across a period of breeding activity. Locally endemic to the arid regions of Central Australia (Marchant and Higgins 2002), males are highly conspicuous, and can be heard singing loudly and for extended periods of time from the tops of bushes and trees. The song of male Wedgebills can be classed as a trill syntax song type; a simplistic, repetitive song structure that is likely to be physically challenging to produce over long periods (Ballentine, Hyman *et al.* 2004; Podos 1997). The repetitive structure of trill syntaxes requires coordination of the vocal tract and is constrained by how far apart a bird can move its beak (Podos 1997). To produce trills at a fast pace and consistently, a bird's beak must open and close at a short distance in rapid succession, a movement which is energetically taxing (Ballentine, Hyman *et al.* 2004; Podos 1997). As such, in birds that trill, selection acts not on the complexity of song repertoires, but on song performance and endurance (Ballentine, Hyman *et al.* 2004; Cardoso and Hu 2011). Accordingly, male Wedgebills can be heard singing loudly and for extended periods of time. Females also sing, however they are less conspicuous and their song is less complex than males, consisting of one note that can be used individually or repeated temporally. Males and female Wedgebills are also known to form antiphonal duets (Marchant and Higgins 2002). Despite the conspicuous nature of these birds in their arid zone habitat, research has yet to be conducted on the behavioural ecology of this species.

In this study we conducted daily observations over four months of breeding activity. Seeking to provide context and gain a more detailed understanding of singing behaviour of both males and females across the breeding cycle, we used in field observations as opposed to recording for this component of our study. Unlike many studies, we also specifically monitored female song rates and the occurrence of duets. Given the incessant singing of males, we also wished to examine diel singing rates and endurance. To do this we used remote recording equipment, allowing us to monitor individual acoustic activity of males over a longer period.

## **Materials and methods**

### *Species*

The Chirruping Wedgebill is a small, monomorphic grey passerine (Marchant and Higgins 2002). Of the genus *Psophodes*, it is closely related to both the Chiming Wedgebill (*Psophodes occidentalis*) and Eastern Whipbird (*Psophodes olivaceus*) (Toon, Joseph *et al.* 2013). Occupying the arid regions of Australia, the environment these birds inhabit is harsh, typified by infrequent and unpredictable rainfall (Mabbutt, Burrell *et al.* 1973), a distinct absence of tall trees and a dominance of shrubs such as saltbush. Previous observations suggest that Wedgebills breed between July and January (Marchant and Higgins 2002), and they had begun breeding prior to commencement of this study in August 2014 and were continuing to breed on the completion of fieldwork in late November.

### *Study site*

We studied pairs of Chirruping Wedgebills from August to November 2014 at the University of New South Wales Arid Zone Research Station at Fowlers Gap, 112 km north of Broken Hill in far western New South Wales, Australia (31°05'S, 142°42'E). The climate of this area is arid, typified by cool winters, hot summers and low rainfall (below 200mm per annum) (Mabbutt, Burrell *et al.* 1973). The habitat at Fowlers Gap can predominantly be described as low open chenopod shrubland and gibber (Mabbutt, Burrell *et al.* 1973).



This study was conducted under authority of the Animal Ethics Committees at Macquarie University, a Scientific Research Permit from the New South Wales Parks and Wildlife Service and a banding Authority of the Australian Bird and Bat Banding Scheme.

### *Observation*

43 pairs of Wedgebills were observed over the course of this study. Using a stratified random sample design (Brewer 1999; Hansen, Hurwitz *et al.* 1953) we endeavoured to observe pairs at least once in a random order before observations were repeated. Male Wedgebills begin singing at sunrise and in such an open landscape, were relatively easy to locate as they sing from prominent perches on vegetation. Of the observed birds, 11 adults were banded. While the majority of birds were un-banded, the presence of nests in territories allowed researchers to observe singing rates of un-banded pairs with reasonable confidence. Bird attendance at nests was frequent and singing occurred from the nest or near to it. Given the strong territoriality of the species and the known location of nests, we can be confident that all repeated observations conducted during nest building (1-2 days), incubation (14 days), nestlings (10 - 12 days) were from the territory holders (Marchant and Higgins 2002). At fledging, young remained on the ground for approximately two weeks where adults would continue to provision them. Furthermore, most nestlings were banded prior to fledging and we could therefore ascertain that tracked fledglings being provisioned belonged to a particular pair.

### *Establishing stage of reproduction*

Nests were located by monitoring singing locations of males and females, and observing their movements and activities around the territory. Two-hour observation sessions allowed researchers to examine singing rates and behaviours such as nest building, incubation swaps and provisioning which indicated stage of reproductive cycle. Both males and females provision and incubate, and while incubating, females will call frequently from the nest (*pers obs*). Nests with eggs were found by monitoring where song was coming from during the observation period and then searching the respective bushes at the end of the watch. After nests searches were conducted researchers left the territory immediately to reduce disturbance. Once a nest had been located nests were monitored by inspection every second day to determine the outcome. Laying dates, clutch size, hatch dates and brood size were

recorded. Offspring were monitored every second day until they were banded when they were eight or nine days old and thereafter left undisturbed to reduce the risk of force fledging. Once fledged, young remained on the ground hidden by bushes where they were provisioned by adults. Adults and fledglings could be heard making soft contact calls. Monitoring provisioning and listening for these calls allowed us to establish if fledglings were present. Young were classed as juveniles when they had full tail feathers and could fly. While we did witness juveniles being provisioned by adults, it was less frequent than in the first few weeks after fledging. Juveniles were readily discernible from adults by the colour of their beak. Previous records of Wedgebills state that juveniles possess an orange beak (Marchant and Higgins 2002), however, fledglings and young juveniles initially possessed a grey beak and adults, a black beak. As juveniles became older their beak turned orange making them quite recognisable from mature birds. Wedgebills were classified as 'not breeding' when there was no evidence of a nest on the territory and when the provisioning of juveniles became infrequent or ceased.

#### *Behavioural observations*

Given the small size, scarcity of foliage and often large distances between trees, singing males were easily located. As such it was unlikely that neighbouring bird song rates would be counted by mistake as it was rare that a singing bird could not be located visually. Females were more difficult to locate due to an apparent preference for sitting in shrubs or on lower branches. However females were usually in close proximity to their mate. As nests were well camouflaged, there existed potential for researchers to unknowingly take up observation near nests. This had the potential to prevent birds from incubating or provisioning and also risked biasing singing and call rates. As such, we were sensitive to distress calls and signs of stress such as aggressive postures (Duncan 1974) and excessive preening (Delius 1988), and moved to more appropriate positions as needed. If observer presence was thought to impact on bird behaviour, observations were ceased and any data collected during this time was removed from the analysis. To ensure that distances estimated between birds were as accurate and as consistent as possible, we estimated distances between fixed points in territories that were later measured with tape and GPS.

We examined song rates of pairs of Wedgebills over the course of three months during the breeding season resulting in a total of 217 individual two hour long observations on 43 pairs of Wedgebills. Due to the number of birds being monitored, song rates of individual pairs were monitored in detail approximately every 7-10 days. Observations were conducted in two sessions each morning; the first early in the morning (sunrise approximately 5am) and the second at mid-morning (approximately 8am). Unlike some species that only sing during the dawn chorus, pilot studies revealed that Wedgebills continue singing at a relatively high rate throughout the morning. However, observations were ceased after 10am to minimise the effect of different times of day on singing rates, as it is well established that rates of song become more variant after the early part of the day (Amrhein, Kunc *et al.* 2004; Catchpole 1973; Staicer, Spector *et al.* 1996). Each researcher conducted two, two-hour observations per morning. Once Wedgebills were visually located researchers approached to the boundaries of territories and sat in one location for the duration of the observation period. To minimise the effects of human presence on the birds, researchers remained as concealed as possible and did not move once the observation period began. For the first hour of the observation period song rates were recorded for both sexes. Using stop-watches and timing to the nearest second, researchers timed and noted the incidence of male singing for one hour. This was easily achievable as the songs are repetitive and continuous with few gaps and often take place for long periods of time. Due to the simple structure of the female song consisting of one note, it was not possible to time the length of female song. As such, individual 'songs' or notes were counted per minute for one hour.

The occurrence of duets was also monitored across the whole first hour. The sex that initiated the duet was established by noting whether males sang and then females began singing (a male led duet), or whether females began singing and then males began singing (a female led duet). The distances between the members of a pair was also noted while they were duetting.

After one hour of observation, researchers ceased recording song rates but remained in place and continued to observe behaviour for a further hour, noting behaviours such as feeding, provisioning and territorial displays. This second hour was also important for establishing the stage of the breeding cycle and finding nests, although we only approached potential sites and

searched at the end of this second hour of observations. If a nest was not located within 15 minutes, we left the area to limit undue stress to the birds and attempted again at a later date.

### *Song analysis*

While we did not record songs during the observation periods we recorded acoustic behaviour from 33 different males by recording a continuous 12 hour sample on three separate occasions (for each one), from sunrise to sunset, using Song Metre SM3 (Wildlife Acoustics) remote recording equipment. In each case, the equipment was placed in the centre of the males' territory and in close proximity to the song perches that a male had been observed as using consistently in the behavioural observation sessions.

Raven Pro 1.5 (Bioacoustics Research Program, The Cornell Lab of Ornithology, Ithaca, NY, <http://www.birds.cornell.edu/raven>) was used to examine song spectrograms. Using a random number generator we selected a six minute period from every hour and manually scored that period, resulting in the examination of  $N = 1147$  samples or  $N = 147$  hours in total. For simplicity we counted the number of male syllables present in each of these examined six-minute sections.

### *Defining duets*

Two of the main characteristics that define a duet have been described as; 1) 'a constant time lag between the contributions of the two individuals' and 2) 'a stereotyped structure that occurs repeatedly and predictably in time' (Langmore 2002). A common method for determining the existence of temporal precision in joint song is an examination of the 'coefficient of variation' ( $CV = 100 \times SD/mean$ ) (Elie, Mariette *et al.* 2010; Farabaugh 1982; Hall 2009). This method requires the measurement of the start time of the initiating vocalisation to the start time of the responding vocalisation using spectrograms. We selected samples of duets from 5 pairs and examined their coefficient of variation using Raven Pro 1.5. (Bioacoustics Research Program, The Cornell Lab of Ornithology, Ithaca, NY, <http://www.birds.cornell.edu/raven>).

As males in this species sing much more often than females it is possible that the duets heard occur simply because there is not the opportunity for females to sing independently of their mate. As such by choosing a random sample of observations from 19 different pairs (n=19) we also examined how many female songs were sung independently of males and how many formed joint songs.

For the field observations, a joint song was only considered to be a duet if females contributed two or more notes to a male song. This was done in an attempt to account for random solo female song that was not intended to form a duet. Most often, duets continued for extended periods and thus, rather than count each individual female contribution as an individual duet, we counted 'bouts' of joint singing. For example, if males and females sang together for 30 seconds and then stopped, this was one duet. The start time was determined when a second bird contributed to a song that was being sung and the end time was determined when two birds ceased to sing together.

### *Statistical analysis*

All data was analysed using IBM SPSS 22. (IBM Corporation). Song rate data was transformed and normalised using a log10 plus one transformation and analysed using ANOVA followed by Bonferroni post hoc tests to examine pairwise comparisons. Independent samples T-tests were used to examine differences in song rate between the two observation periods. Duetting data could not be normalised and was analysed using Kruskal-Wallis tests. Dunn-Bonferroni post hoc tests were then used to examine differences between groups in this nonparametric data. Pearson Chi square tests were used to examine sex to initiate duets. Correlations were examined using Pearson correlation tests.

## Results

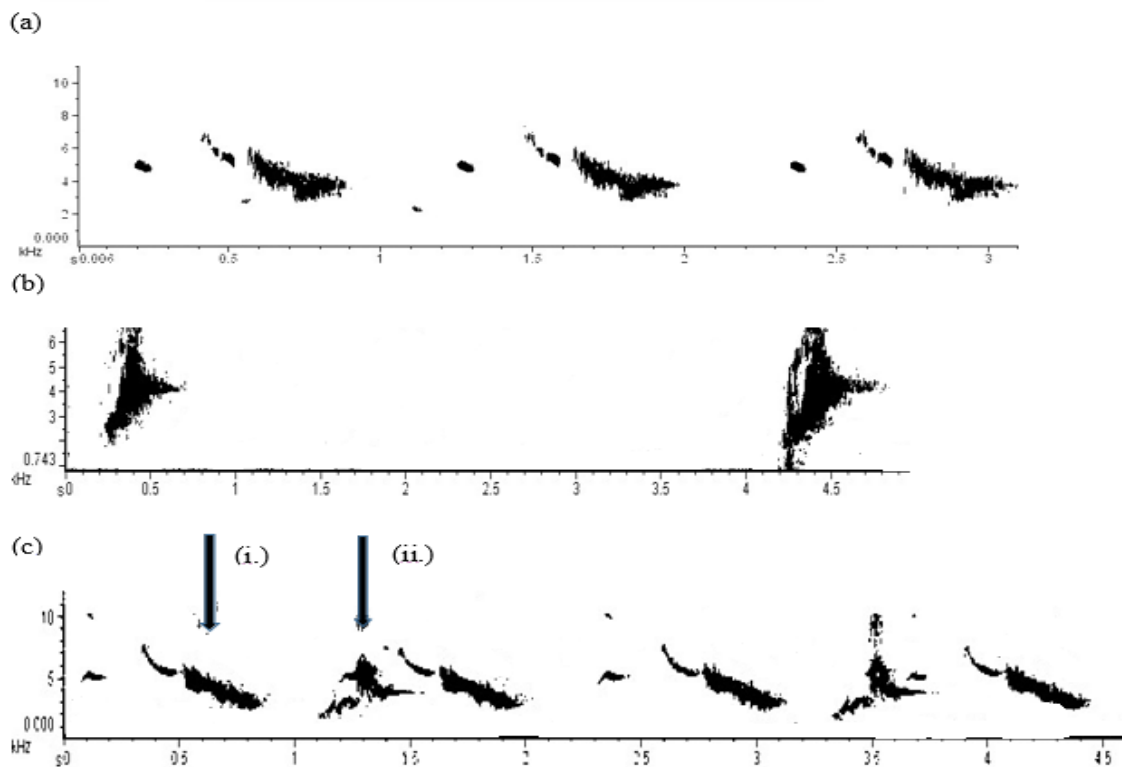
### *Temporal precision of joint song*

We randomly sampled the temporal precision of  $N = 77$  ( $X+SE = 0.805 + 0.029$ ) duets by measuring the start time of initiating vocalisations to the start time of responding vocalisations from  $n = 5$  different pairs of Wedgebills. This resulted in a total coefficient of variation of 32.47 ( $CV=32.47$ ).

### *Occurrence of female solo song*

We randomly sampled morning song rates from  $N = 19$  different females resulting in  $N = 803$  individual female songs. Of these 803 female songs, 335 were sung in conjunction with a male song meaning that 41.7% of female songs were sung as part of a duet while 58.3% were sung independently of males. There was great variation among females however with the lowest occurrence female song being sung in conjunction with a male being 8.6% and the highest occurrence of joint song being 100%.

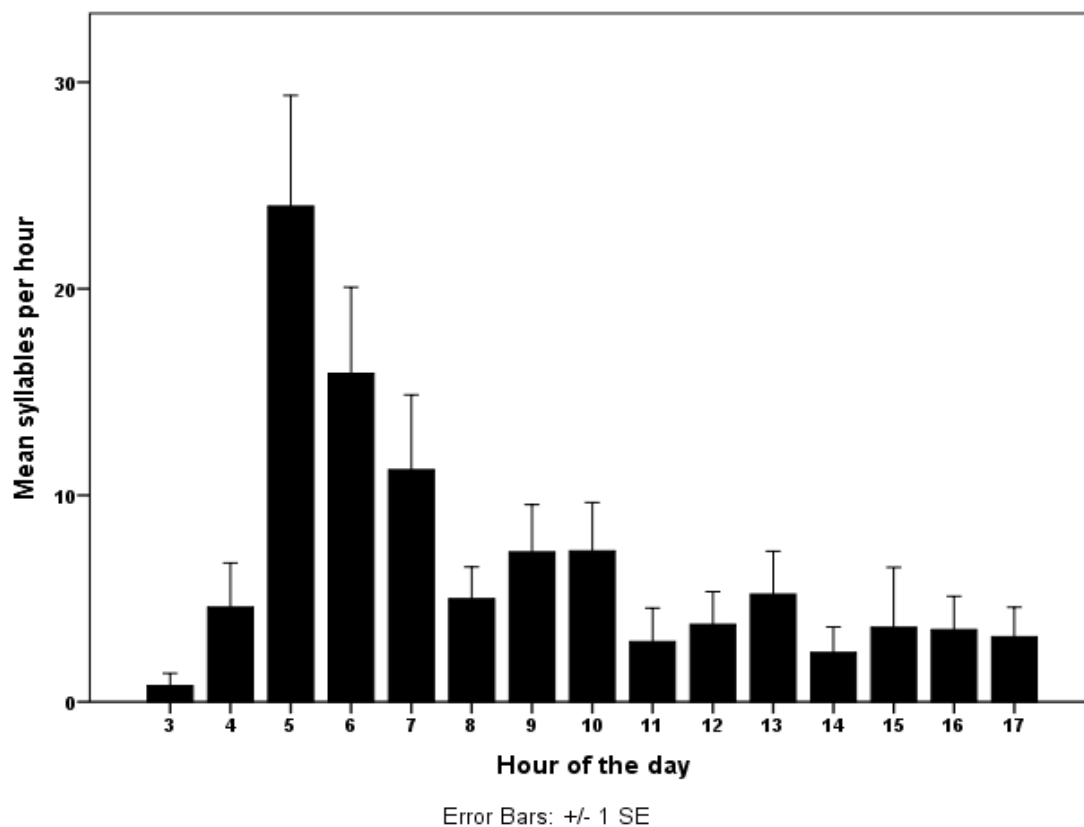
### *Spectrograms*



**Fig. 1.** Image (a) depicts the trill of male Chirruping Wedgebill (Raven Pro 1.5). Each repeated phrase consists of three notes. Image (b) shows a repeated female song. Structurally the simplicity of this song might lend it to be classified as a call. However, given its apparent function or association with breeding, we define the female note as a song. Image (c) shows a portion of a duet between male (i.) and female (ii.)

### *Diel song rate*

There was a significant effect of time of day on male song rates (ANOVA:  $F_{14,667} = 4.760$ ,  $N = 1147$ ,  $P = 0.001$ ) with a peak in singing at sunrise that declined thereafter (Fig. 2). However, singing continued throughout the day with reasonably consistent effort. In accordance with this, males sang significantly less during the second observation period (8.30 am onward) than during the first observation period (Sunrise- 8am) (Independent samples T-Test;  $t_{3.910}$ , d.f. 165.321,  $P < 0.000$ ). A similar pattern was witnessed for females who also sang more during the early morning observations compared to mid-morning observations (Independent samples T-Test:  $t_{3.144}$ , d.f. 175.497,  $P < 0.002$ ).



**Fig. 2.** The song rate of male Wedgebills throughout the day measured from a random sample of  $N=114$  hours of recording compiled from  $N=33$  different males. Song rate measured as the number of syllables sung in each recording sample. The peak in singing activity in the early morning is consistent with singing undertaken during the dawn chorus. Rate of singing decreases dramatically across the morning but remains fairly stable throughout the day.

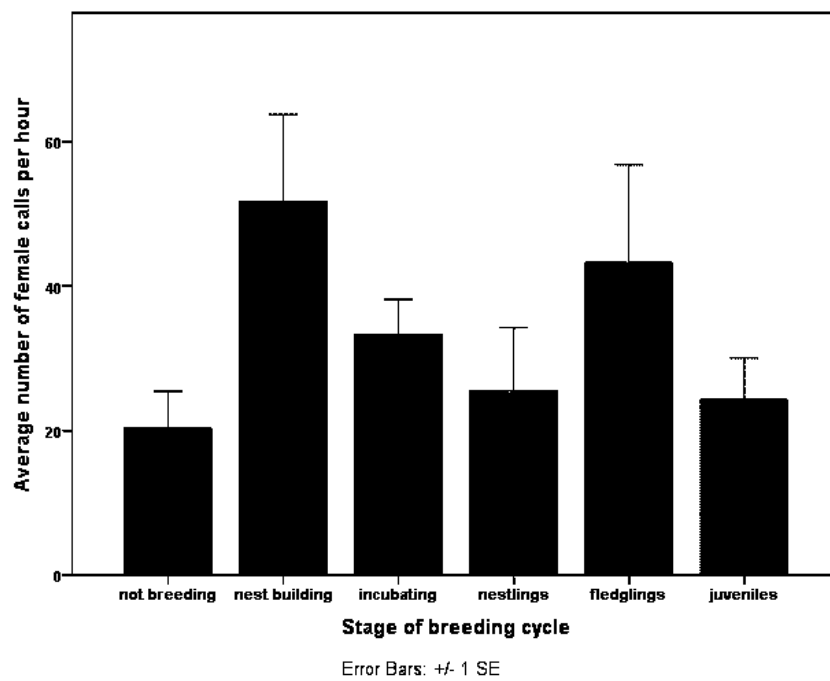
### *Song rate across the breeding cycle*

There was a significant effect of breeding stage on male song rate (ANOVA:  $F_{6,198} = 5.355$ ,  $P = 0.001$  Fig. 3a) and female song rates (ANOVA:  $F_{6,198} = 3.123$ ,  $P = 0.001$ : Fig. 3b) with a peak in singing during nest building. There were also significant correlations between male and female song rates during incubation (Pearsons Correlation;  $r_s 0.288$ ,  $n = 51$ ,  $P = 0.041$ ) and when not breeding (Pearson Correlation;  $r_s 0.306$ ,  $n = 59$ ,  $P = 0.018$ ). For both males and females, rates of singing were highest during nest building and when fledglings were present and were at their lowest when not breeding and when juveniles were present.

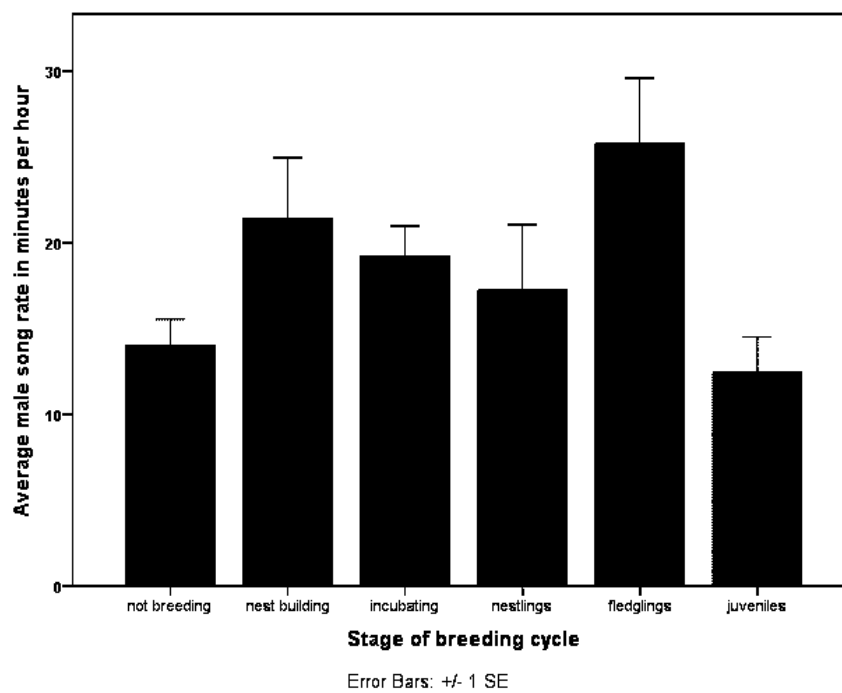
There was a significant effect of breeding stage on the number of duets sung (Kruskal-Wallis:  $H_6 = 66.664$ ,  $N 245$ ,  $P = 0.001$ : Fig. 4a) with the highest number of duets occurring during nest building (Dunn-Bonferroni:  $P = 0.001$ ). While pairs appeared to be closer together during nest building, there was no significant effect of stage of breeding cycle on the distance between pairs while performing duets (ANOVA:  $F_{5,240} = 2.200$ ,  $P = 0.091$ : Fig. 4b). However, there was large variation across pairs in the distance maintained during duets over different stage of the breeding cycle (ANOVA:  $F_{5,184} = 9.495$ ,  $P = 0.001$ ). Males initiated more duets than females (Chi Squared test:  $\chi^2 73.62$ ,  $N = 246$ ,  $P = 0.001$ ) and here was no significant effect of breeding stage on which sex was more likely to initiate duets (Chi Squared test:  $\chi^2 7.491$ ,  $N = 246$ ,  $P = 0.006$ ).



(a)

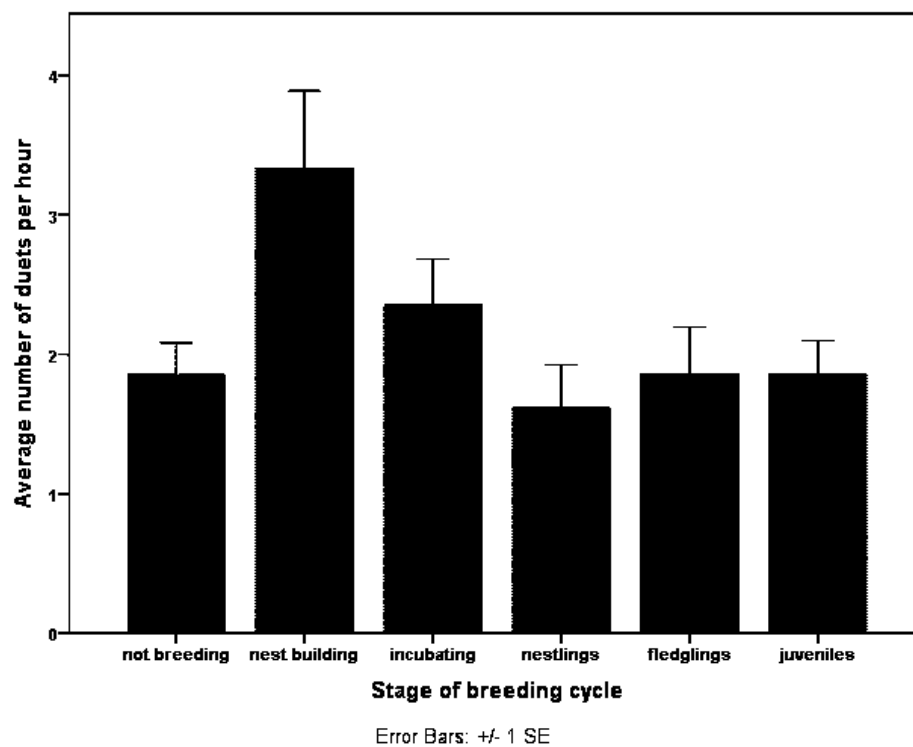


(b)

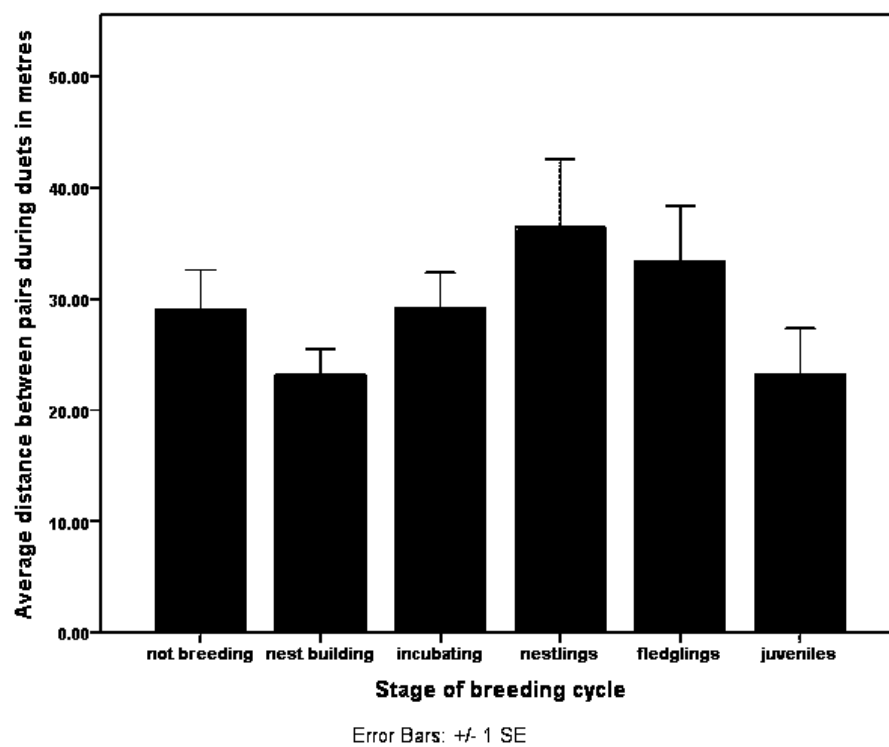


**Fig. 3.** Part (a) depicts female song across stages of the breeding cycle. Part (b) depicts male song across the same stages. We see peaks of singing activity in both males and females during nest building and when fledglings are present. There were also correlations in male and female song rates when incubating (Pearsons Correlation; 117.173,  $n = 51$ ,  $P = 0.041$ ) and not breeding (Pearsons Correlation; 140.616,  $n = 59$ ,  $P = 0.018$ ).

(a)



(b)



**Fig. 4.** Part (a) shows the number of duets performed across the breeding cycle. There are significantly more duets during nest building than at any other stage. Part (b) depicts the distances between pairs at different stages of the reproductive cycle while duetting. There appears to be a shorter distance maintained between pairs while nest building, however results were not significant.

## Discussion

Analysis of recording data shows that male Wedgebills sing consistently throughout the day. Our observations showed that stage of reproduction affected both male and female singing rates and the occurrence of duets in the Chirruping Wedgebill, with duets sung most frequently during nest building. Furthermore, song rates of both males and females reflected similar patterns to each other, with pooled data showing correlations between male and female song rates when they were not breeding and when juveniles were present. For both males and females we witnessed peaks in singing activity around the time of nest building and when fledglings were present.

### *Male song longevity*

Our study confirmed that male Wedgebills continue singing throughout the day, with a reasonable constant rate of singing from mid-morning until the early evening. The dawn chorus is a well-documented occurrence among many avian species (Catchpole and Slater 2003; Mace 1987b; Staicer, Spector *et al.* 1996), and unsurprisingly male Wedgebill song rate is highest at this time. It is thought that this morning song may help in establishing territorial boundaries (Kacelnik and Krebs 1983) and in mate attraction (McNamara, Mace *et al.* 1987). However, continued song throughout the day may serve different functions from morning song and these functions are not necessarily mutually exclusive (Liu 2004). Males who can sing for longer are also thought to be more attractive to females because they are of better physical quality (Hutchinson, McNamara *et al.* 1993) and occupy better territories (Yasukawa 1981). Individual males in this study showed significant differences in song rate and as such, it would be interesting to consider the implications of this on physiology and reproductive success in future research.

### *Male and female song rates and the reproductive cycle*

Nest building can be presumed to be the females most fertile period (Catchpole and Slater 2003) and increased singing rates by male Wedgebills at this time may be an attempt to guard against the potential of extra-pair males (van Dongen 2006). Elevated male song rates during the female's fertile period are common signs of paternity guarding (Moller 1991). By increasing song rate male Wedgebills may seek to show commitment to their partner,

reaffirm their territory and guard paternity of their offspring. Furthermore, singing for extended periods of time may advertise male quality to females and other potential mates (Gil and Gahr 2002; Kroodsma and Byers 1991) and has been witnessed in other species that trill such as Swamp Sparrows (*Melospiza georgiana*) (Ballentine, Hyman *et al.* 2004) and Sedge Warblers, (*Acrocephalus schoenobaenus*) (Catchpole 1986). This may account for the continued singing by male Wedgebills throughout the day. This is particularly relevant with the trill syntax song type given selection for longevity and performance of song over complexity of song (Cardoso and Hu 2011). As such, increased rates of singing during the female fertile period likely serve a dual function; to advertise fitness while ensuring paternity (Gil and Gahr 2002; Kroodsma and Byers 1991). Given the significant differences in song rate of different males in our study it would be interesting to examine whether or not these rates of song could be related to male quality where quality is measured by morphology; weight, wing length, tarsus length or reproductive success; rate of paternity. Given what we know of the trill syntax song type and its relation to fitness (Podos 1997) we would predict that males who sing for longer may be of higher quality and thus would likely farther more offspring. However in turn, if these males spend more time singing, there may be a trade off with how much time they invest in parental care that would have consequences for reproductive success (Catchpole and Slater 2003). The observational methodologies utilised in this study accompanied with a small sample size for analysis of rates of extra pair paternity mean we could not examine this. Future research would benefit by recording rates of song for individual males throughout the reproductive cycle and by monitoring investment in parental care.

While increased song rates around the time of nest building have been witnessed in females of many species such as, Song Sparrows (*Melospiza melodia*) (Arcese, Stoddard *et al.* 1988) and Yellow Warblers (*Setophaga petechial* formerly *Dendroica petechial*) (Hobson and Sealy 1990), these song rates decline quickly hereafter. In contrast in this study, female Chirruping Wedgebill song rates showed a similar pattern to males, being used continually throughout the breeding cycle and showing peaks at nest building and when fledglings were present. Little is known about the effects of female solo song on males (Hall, Rittenbach *et al.* 2015), but given its consistent use throughout the breeding cycle in this species it is possible that it serves similar function to male song (Langmore 1998). For example as a sign of their own individual quality, singing females may advertise their nest site selection and

nest building capabilities. Alternatively, increased song rates at this time may serve as a signal of fertility, not only to partners but to potential extra pair mates (Gill, Vonhof *et al.* 2005; Mace 1987a). Just as males may be motivated to seek extrapair copulations, females may also benefit, particularly if their mate is of lesser quality than a neighbour (Griffith, Owens *et al.* 2002). The examination of rates of extrapair paternity should be a high priority of future studies of this species.

It could be argued that the increase in singing rate in both sexes when fledglings were present is evidence of preparation for another breeding attempt. However, if this were the case, given the likely function of duets in maintaining the pair bond and in breeding synchrony (Catchpole and Slater 2003; Hall 2009) we would predict an increase in duets rates at this time as well. However our results did not support this, with duet rates when fledglings were present showing little change from other parts of the breeding cycle (not breeding, incubating, and nestlings present). Instead, we propose that increased song rates at this time serve the same function for males and females and likely arise due to life history traits of biparental care and presence of altricial offspring. As fledglings leave the nest at a very young age (11/12 days *pers obs*) (Marchant and Higgins 2002) they spend a good portion of their time on the ground. During this stage of development they are highly mobile and can be seen moving between bushes for cover (*pers obs*). Given their mobility, song rates of males and females may rise during this period out of a need to maintain contact with their offspring and to keep them within territorial boundaries (Ritchison 1983). Indeed, Ritchison (1983) made similar findings in Black-Headed Grosbeaks (*Pheucticus melanocephalus*) with rates of female singing rising around the time fledgling were present. In this study it was concluded that peaks in singing at this stage enabled females to maintain contact with their offspring.

#### *Duets and the reproductive cycle*

Our study confirmed the existence of temporal precision of joint song and thus the existence of duets in this species which has previously been stated by Toon *et al.* (2012). This in itself is interesting given that the closely related Chiming Wedgebill (*Psophodes occidentalis*) which is of the same genus, is not known to duet (Toon *et al.* 2012; Marchant and Higgins 2002). As such, the Chirruping Wedgebill and the Chiming Wedgebill may present a rare opportunity to examine life history and ecological traits that may lead to the existence of

duets in one species but not in the other. Such research may provide us with valuable insight into the evolutionary origin of duets.

Elevated duet rates around the time of nest building may serve as a cooperative display with a possible function in breeding synchrony (Catchpole and Slater 2003; Hall 2009). Correlations between male and female song rate at incubation add further evidence to support a coordination of efforts. Higher levels of coordination between pairs in activities such as incubation have been shown to lead to increased success rates in the hatching of eggs (Spoon, Millam *et al.* 2006). As such, increased occurrence of duets at the time of nest building might also play a part in breeding synchrony as joint signals may increase pair bonds (Hall 2009; Méndez-Cárdenas and Zimmermann 2009) and coordination in preparation for incubation and provisioning of young (Hall 2009). As Wedgebills display bi-parental care, the ability for partners to coordinate their efforts and provisioning behaviours may greatly affect their reproductive success (Mariette and Griffith 2012). However, examining the effects of duets on reproductive synchrony is difficult to quantify, and would require manipulative experiments of reproductive investment. The observational nature of our data and the relatively small sample of duets that we have so far assayed for each pair makes it difficult for us to draw meaningful conclusions. Future studies would benefit from continuous sampling of duets and song rates of individual pairs throughout the breeding cycle and comparing these rates with reproductive success, particularly if coupled with experimental manipulations of reproductive effort.

In addition to cooperation, duets have also been shown to be used in sexual conflict in a variety of species such as Barred Antshrikes (*Thamnophilus doliatus*) and Bay Wrens (*Thryothorus nigricapillus*) (Koloff and Mennill 2011; Levin 1996b). As such, it is possible that duets are also used by Wedgebills in sexual conflict. For example, increased rates of duets around the female fertile period may be an attempt by male Wedgebills to guard paternity. By maintaining constant vocal contact with females, males are informed of their whereabouts and have a greater chance of reducing the occurrence of extra pair copulations (Hall 2004). In addition, the need for males to mate guard during incubation is no longer present and may explain why singing rates drop during this period compared with nesting (van Dongen 2006). While the result was not significant, there was a tendency for pairs to be

closer together during nest building, which was consistent with mate guarding. Females may also seek to use these joint songs in sexual conflict. By contributing to male songs to form duets, females may display their commitment and quality to their mate (Hall 2004; Hall 2009). In addition however, females may also seek to acoustically mate guard their partner by blocking male signals and preventing rival females from joining in (Hall 2004; Sonnenschein and Reyer 1983b). This would be of particular important in the presence of high levels of same-sex competition. For example in the closely related Eastern Whipbird there exists high same-sex competition among females resulting in acoustic mate guarding (Rogers, Langmore *et al.* 2007). Our observational study provides a sound overview of when duets occur naturally and provides insight into the potential function of these joint songs. However, it is difficult to distinguish between cooperative and conflict behaviours using observational methodology alone and we should hesitate in drawing firm conclusions. Furthermore, as conflict and cooperation are not mutually exclusive (Hall 2004; Koloff and Mennill 2011; Mennill and Vehrencamp 2008), it is also possible that they occur at the same time. Experimental methodology in the form of playback experiments (Douglas and Mennill 2010) would provide greater insight into duet function and allow us to distinguish between conflict and cooperation in greater detail.

## **Conclusion**

Our study provides the first account of song and duet use in the Chirruping Wedgebill (*Psophodes cistatus*) and contributes towards our understanding of the behavioural ecology of arid zone species within Australia. By including females in this study we have shown that despite their simple song and less conspicuous nature, female song use reflects similar patterns to males across the breeding cycle. As such, it is highly likely that female song in the Chirruping Wedgebill is functional and serves similar purpose to that of males. This finding supports recent work by Odom *et al* 2014 and Hall *et al.* 2015 highlighting that function of female song warrants investigation in and of itself. As such, given the pattern of singing in females of this species and its similarity to male song rates, the Chirruping Wedgebill may present an ideal species for the exploration of song function in females. In addition, this study provides the first account of duet use in this species. Future studies that incorporate an experimental approach would provide valuable insight into the function of these joint songs.

Future research on Wedgebill song and behavioural ecology would also benefit from a comparative approach, comparing singing behaviour in breeding and non-breeding seasons. Such comparative cross-seasonal studies have been conducted on relatively few other species (Hall 2000; Fedy & Stutchbury 2005; Topp and Mennil 2008) and provided important insight into the evolution of song and duets in these species. In addition, the high level of singing throughout the day in the Chirruping Wedgebill makes them a notable acoustic feature of the arid zone. The function of this conspicuous signal remains elusive and demands further study.

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## References

- Amrhein, V., Kunc, H.P., Naguib, M., and Nelson, D.A. (2004) Seasonal patterns of singing activity vary with time of day in the Nightingale (*Luscinia megarhychos*). *The Auk* **121**(1), 110-117.
- Arcese, P., Stoddard, P.K., and Hiebert, S.M. (1988) The Form and Function of Song in Female Song Sparrows. *The Condor* **90**(1), 44-50.
- Ballentine, B., Hyman, J., and Nowicki, S. (2004) Vocal performance influences female response to male bird song: an experimental test. *Behavioral Ecology* **15**(1), 163-168.
- Barker, F.K., Barrowclough, G.F., and Groth, J.G. (2002) A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proceedings of the Royal Society of London B: Biological Sciences* **269**(1488), 295-308.
- Brewer, K.R.W. (1999) Design-Based or Prediction-Based Inference? Stratified Random vs Stratified Balanced Sampling. *International Statistical Review / Revue Internationale de Statistique* **67**(1), 35-47.
- Cardoso, G.C., and Hu, Y. (2011) Birdsong performance and the evolution of simple (rather than elaborate) sexual signals. *The American Naturalist* **178**(5), 679-686.
- Catchpole, C. (1986) Song repertoires and reproductive success in the great reed warbler *Acrocephalus arundinaceus*. *Behavioral Ecology and Sociobiology* **19**(6), 439-445. [In English]
- Catchpole, C.K. (1973) The Functions of Advertising Song in the Sedge Warbler (*Acrocephalus Schoenobaenus*) and the Reed Warbler (a. *Scirpaceus*). *Behaviour* **46**(3), 300-319.
- Catchpole, C.K., and Slater, P.J. (2003) 'Bird song: biological themes and variations.' (Cambridge University Press)
- Delius, J.D. (1988) Preening and Associated Comfort Behavior in Birds. *Annals of the New York Academy of Sciences* **525**(1), 40-55.
- Douglas, S.B., and Mennill, D.J. (2010) A review of acoustic playback techniques for studying avian vocal duets
- Una revisión de las técnicas de la reproducción de sonidos grabados para el estudio de las duetas vocales de las aves. *Journal of Field Ornithology* **81**(2), 115-129.
- Duncan, I.J.H. (1974) A scientific assessment of welfare. *Proceedings of the British Society of Animal Production (1972) (New Series)* **3**, 9-19.
- Elie, J.E., Mariette, M.M., Soula, H.A., Griffith, S.C., Mathevon, N., and Vignal, C. (2010) Vocal communication at the nest between mates in wild zebra finches: a private vocal duet? *Animal Behaviour* **80**(4), 597-605.
- Farabaugh, S.M. (1982) The ecological and social significance of duetting. *Acoustic communication in birds* **2**, 85-124.
- Gil, D., and Gahr, M. (2002) The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution* **17**(3), 133-141.

- Gill, S., Vonhof, M., Stutchbury, B.M., Morton, E., and Quinn, J. (2005) No evidence for acoustic mate-guarding in duetting buff-breasted wrens (*Thryothorus leucotis*). *Behavioral Ecology and Sociobiology* **57**(6), 557-565. [In English]
- Griffith, S.C., Owens, I.P., and Thuman, K.A. (2002) Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* **11**(11), 2195-2212.
- Halkin, S.L. (1997) Nest-vicinity song exchanges may coordinate biparental care of northern cardinals. *Animal behaviour* **54**(1), 189-198.
- Hall, M.L. (2004) A Review of Hypotheses for the Functions of Avian Duetting. *Behavioral Ecology and Sociobiology* **55**(5), 415-430.
- Hall, M.L. (2009) Chapter 3 A Review of Vocal Duetting in Birds. In 'Advances in the Study of Behavior. Vol. Volume 40.' (Eds. N Marc, Z Klaus, SC Nicola and MJ Vincent) pp. 67-121. (Academic Press)
- Hall, M.L., Rittenbach, M.R., and Vehrencamp, S.L. (2015) Female song and vocal interactions with males in a Neotropical wren. *Frontiers in Ecology and Evolution* **3**, 12.
- Hansen, M.H., Hurwitz, W.N., and Madow, W.G. (1953) Sample Survey Methods and Theor.
- Hobson, K.A., and Sealy, S.G. (1990) Female song in the yellow warbler. *Condor*, 259-261.
- Hutchinson, J.M., McNamara, J.M., and Cuthill, I.C. (1993) Song, sexual selection, starvation and strategic handicaps. *Animal Behaviour* **45**(6), 1153-1177.
- Kacelnik, A., and Krebs, J.R. (1983) The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. *Behaviour* **83**(3), 287-308.
- Koloff, J., and Mennill, D. (2011) Aggressive responses to playback of solos and duets in a Neotropical antbird. *Animal Behaviour* **82**(3), 587-593.
- Kroodsma, D.E., and Byers, B.E. (1991) The Function(s) of Bird Song. *American Zoologist* **31**(2), 318-328.
- Langmore, N.E. (1998) Functions of duet and solo songs of female birds. *Trends in Ecology & Evolution* **13**(4), 136-140.
- Langmore, N.E. (2002) Vocal duetting: definitions, discoveries and directions. *Trends in Ecology & Evolution* **17**(10), 451-452.
- Levin, R.N. (1996) Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: II. Playback experiments. *Animal Behaviour* **52**(6), 1107-1117.
- Liu, W.-C. (2004) The effect of neighbours and females on dawn and daytime singing behaviours by male chipping sparrows. *Animal Behaviour* **68**(1), 39-44.
- Mabbutt, J.A., Burrell, J.P., Corbett, J.R., and Sullivan, M.E. (1973) Land systems of Fowlers Gap station. *Lands of Fowlers Gap Station, New South Wales*, 25-43.
- Mace, R. (1987a) The dawn chorus in the great tit *Parus major* is directly related to female fertility.
- Mace, R. (1987b) Why do birds sing at dawn. *Ardea* **75**(1), 123-132.

- Mann, N., Dingess, K., Barker, K., Graves, J., and Slater, P. (2009) A comparative study of song form and duetting in neotropical *Thryothorus* wrens. *Behaviour* **146**(1), 1-43.
- Marchant, S., and Higgins, P.J. (2002) Handbook of Australian, New Zealand and Antarctic birds; volume 6.
- Mariette, M.M., and Griffith, S.C. (2012) Nest visit synchrony is high and correlates with reproductive success in the wild Zebra finch *Taeniopygia guttata*. *Journal of Avian Biology* **43**(2), 131-140.
- Martin, T.E. (1996) Life History Evolution in Tropical and South Temperate Birds: What Do We Really Know? *Journal of Avian Biology* **27**(4), 263-272.
- McNamara, J.M., Mace, R.H., and Houston, A.I. (1987) Optimal daily routines of singing and foraging in a bird singing to attract a mate. *Behavioral Ecology and Sociobiology* **20**(6), 399-405. [In English]
- Méndez-Cárdenas, M.G., and Zimmermann, E. (2009) Duetting—A mechanism to strengthen pair bonds in a dispersed pair-living primate (*Lepilemur edwardsi*)? *American Journal of Physical Anthropology* **139**(4), 523-532.
- Mennill, D.J., and Vehrencamp, S.L. (2008) Context-Dependent Functions of Avian Duets Revealed by Microphone-Array Recordings and Multispeaker Playback. *Current Biology* **18**(17), 1314-1319.
- Moller, A.P. (1991) Why mated songbirds sing so much: mate guarding and male announcement of mate fertility status. *American Naturalist*, 994-1014.
- Morton, E. (1996) A comparison of vocal behavior among tropical and temperate passerine birds. *Ecology and evolution of acoustic communication in birds*, 258-268.
- Odom, K.J., Hall, M.L., Riebel, K., Omland, K.E., and Langmore, N.E. (2014) Female song is widespread and ancestral in songbirds. *Nat Commun* **5**.
- Podos, J. (1997) A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution*, 537-551.
- Ritchison, G. (1983) The function of singing in female black-headed grosbeaks (*Pheucticus melanocephalus*): family-group maintenance. *The Auk*, 105-116.
- Rogers, A.C., Langmore, N.E., and Mulder, R.A. (2007) Function of pair duets in the eastern whipbird: cooperative defense or sexual conflict? *Behavioral Ecology* **18**(1), 182-188.
- Rogers, A.C., Mulder, R.A., and Langmore, N.E. (2006) Duet duels: sex differences in song matching in duetting eastern whipbirds. *Animal Behaviour* **72**(1), 53-61.
- Russell, E.M., Yom-Tov, Y., and Geffen, E. (2004) Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behavioral Ecology* **15**(5), 831-838.
- Slater, P.J.B., and Mann, N.I. (2004) Why Do the Females of Many Bird Species Sing in the Tropics? *Journal of Avian Biology* **35**(4), 289-294.
- Sonnenschein, E., and Reyer, H.U. (1983) Mate-Guarding and other Functions of Antiphonal Duets in the Slate-coloured Boubou (*Laniarius funebris*) 1. *Zeitschrift für Tierpsychologie* **63**(2-3), 112-140.

- Spoon, T.R., Millam, J.R., and Owings, D.H. (2006) The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, *Nymphicus hollandicus*. *Animal Behaviour* **71**(2), 315-326.
- Staicer, C., Spector, D., and Horn, A. (1996) The dawn chorus and other diel patterns in acoustic signaling. *Ecology and evolution of acoustic communication in birds*, 426-453.
- Toon, A., Joseph, L., and Burbidge, A.H. (2013) Genetic analysis of the Australian whipbirds and wedgebills illuminates the evolution of their plumage and vocal diversity. *Emu* **113**(4), 359-366.
- van Dongen, W.F. (2006) Variation in singing behaviour reveals possible functions of song in male golden whistlers. *Behaviour* **143**(1), 57-82.
- Yasukawa, K. (1981) Male quality and female choice of mate in the red-winged blackbird (*Agelaius phoeniceus*). *Ecology*, 922-929.

# Chapter Two

**Duetting in an arid zone endemic, the chirruping wedgebill  
(*Psophodes cristatus*).**



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# Duetting in an arid zone endemic, the chirruping wedgebill (*Psophodes cristatus*)

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## ABSTRACT

The function of duets, a temporally precise form of joint song, has been the focus of many recent studies of bird song. It has been recognised that this form of joint signal may serve multiple functions within and between species. While spatial information is extremely important in determining duet function, examining movements of birds in response to playback experiments within a natural setting can present difficulties for researchers due to habitat structure. Using unknown wedgebill song in playback experiments we examine the use of duets in arid zone species of Australasian passerine the chirruping wedgebill (*Psophodes cristatus*). We visually tracked both males and females for the duration of our experimental trials, ascertaining how males and females responded to each other and the presentation of experimental calls. Our results indicated duet use in territorial defence against two intruders. However duet function in the context of solo intruders was less clear. We suggest that examining movements and non-vocal signals in response to playback, such as postures, may provide greater insight into duet function.

**Keywords:** duet function, sexual conflict, cooperation, spatial data, signals

## 1. Introduction

A duet is a temporally precise form of joint song (Hall 2004; Wickler and Seibt 1982) that can occur between same sex individuals but is most common between members of the opposite sex (Hall 2004). Duets can occur synchronously in which two birds will sing jointly at the same time, or antiphonally, in which two birds will alternate notes with high temporal precision (Hall 2004; Hall 2009). Despite the fact that only 3-4.3% of known avian species form duets, the occurrence of this rare form of joint song is spread widely across the taxa being found in approximately 40% of avian families (Farabaugh 1982; Hall 2009). Given that

duets are widespread they likely experience strong selective pressure (Von Helversen 1980) and thus their function is of great interest. Understanding the function of avian duets and their roles in sexual conflict and cooperation is important as it may facilitate understanding of joint signalling and communication in other taxa (Hall 2004). However, our understanding of duet function may be impacted by a bias toward studying species from one part of the globe (Benedict 2008a). In addition, distinguishing between hypotheses of duet function and their role in sexual conflict and cooperation through experiments can be difficult (Grafe and Bitz 2004), particularly if information on the movement of individuals cannot be reliably gathered (Mennill and Vehrencamp 2008).

Although there are numerous hypotheses that attempt to explain the function of duets in avian species (reviewed in Hall 2004 and 2009), two key hypotheses are territorial defence and mate guarding. The territorial defence hypothesis predicts that duets will be used cooperatively in the defence of territories and that this defence will occur in one of two forms; (1) joint defence in which a pair work together, using duets to confront and repel intruders (Grafe and Bitz 2004; Sonnenschein and Reyer 1983a) and; (2) a division of labour where members of a pair will use duets but will focus their efforts on same sex rivals (Levin 1996b; Marshall-Ball, Mann *et al.* 2006; van den Heuvel, Cherry *et al.* 2014). In contrast, the mate guarding hypothesis predicts that duets are a result of sexual conflict, deterring partners from being usurped or from seeking extra pair copulations (Hall 2009; Levin 1996b). Despite these independent hypotheses, it has been increasingly accepted that the function of duets are not mutually exclusive and can be context dependent (Hall 2004; Mennill and Vehrencamp 2008), serving multiple purposes between and within species (Dahlin 2014; Hall 2009). The multi-functionality of duets was first recognised by Sonnenschein and Reyer (1983) when they showed that the duets of the slate-coloured boubou (*Laniarius funebris*) were used for mate guarding, territorial defence and breeding synchrony (Sonnenschein and Reyer 1983a). Since then, multiple functions have been shown in a variety of species including tropical boubou (*Laniarius aethiopicus*) (Grafe and Bitz 2004), plain wrens (*Thryothorus modestus zeledoni*) (Marshall-Ball, Mann *et al.* 2006) and rufous and white wrens (*Thryothorus rufalbus*) (Mennill and Vehrencamp 2008). We can start to distinguish between these functions if we can examine interactions between pairs.

Determining duet function can be difficult as many behaviours exhibited are commonly shared among theories (Grafe and Bitz 2004). For example, many hypotheses predict that birds should respond loudly and aggressively to intrusion accompanied by an increased

incidence of duets (Grafe and Bitz 2004). The resulting difficulty is that distinguishing between hypotheses can be complicated, particularly during the breeding season when instances of territoriality and mate guarding may be heightened (Hall 2004). However, the use of playback experiments that examine a variety of responses of focal birds to simulated intrusions have allowed for functions of duets to be determined (Douglas and Mennill 2010; Hall 2009). Examining vocal responses to intruders provide researchers with an easily measureable response variable. However, of particular importance in these experiments are methodologies that also incorporate spatial data (Hall 2009; Mennill and Vehrencamp 2008) particularly when referring to aggressive behaviours.

Increased song rates alone are thought to be lacking as a measure of aggression (Searcy and Beecher 2009). Instead, movements towards speakers should also be considered as these movements are thought to indicate an intent to escalate aggression (Searcy and Beecher 2009). For this reason, gathering spatial data when performing playback experiments should be considered as important as vocal responses. In saying this, we should acknowledge that measuring intent to escalate aggression to attack is difficult to quantify as most playback experiments use song only which means there is no 'intruder' to attack (Laidre and Vehrencamp 2008). However it can also be argued that a bird's willingness to approach a speaker involves a calculation of risk, especially in a scenario where the intruder cannot be seen. Applying the concept of the 'vulnerability handicap' model in signalling, to approach an unseen bird indicates a heightened response and one that would only be undertaken by a motivated individual toward a strong threat (Vehrencamp 2001). Signals are often multimodal, and song may be used in coordination with postures and movement that reveal more information about an intruder's intent than just song itself (Laidre and Vehrencamp 2008; Partan and Marler 2005). Consequently, being unable to see these signals and their intent may increase levels of risk (Enquist 1985) and thus, likely reveal strong motivation and aggression in individuals who choose to approach an unseen rival. By recording movements toward speakers and monitoring the distance between pairs in response to different playbacks, researchers can deduce more information than from studying song rates alone (Hall and Peters 2008; Searcy and Beecher 2009). By examining where pairs are in relation to each other, we can infer levels of aggression and the individuals that instigate the duet (Hall and Peters 2008). We may even be able to understand in greater detail how a territory or habitat is used or defended. This visual data accompanied with song rates allow us to understand behaviour in greater detail and increases accuracy in interpretation of results.



Recording movement and spatial data in playback experiments can be difficult in the natural setting because of habitat structure and density. Many species inhabit forests or areas of dense vegetation that can make visual monitoring difficult (Mennill and Vehrencamp 2008). The eastern whipbird, also of the genus *Psophodes* provides an example of this. As a species that forms duets, has a distinct song type and is of a medium size (approximately 60gm) we would expect these birds to be relatively easy to monitor (Rogers and Mulder 2004). However occupying coastal forests, these birds are notoriously difficult to observe due to the often dense understory of the habitat they reside in and general behavioural ecology (Watson 1969). As such, while comprehensive studies have been conducted on their behavioural ecology and duet function (Rogers, Langmore *et al.* 2007; Rogers and Mulder 2004; Watson 1969), spatial data during studies of duets was difficult to reliably gather (Rogers, Langmore *et al.* 2007). Similar problems have been encountered in studies of purple crowned fairy wrens which live in very dense stands of cane grass (Hall and Peters 2008). There are of course duetting species that have been studied in detail that are easy to monitor visually such as the magpie lark (*Grallina cyanoleuca*) (Hall 2000; Mulder, Bishop *et al.* 2003; Rogers, Ferguson *et al.* 2004) and these studies have contributed greatly to our understanding of duet function.

In light of these issues we examined duets in the previously unstudied Chirruping Wedgebill (*Psophodes cristatus*), a species of passerine endemic to the Australian arid zone. Despite 70% of the Australian continent being classified as arid zone, and 90% as arid/semi-arid (Byrne, Steane *et al.* 2011) the majority of species in this area have not been formally studied, with most research focused on species that live in the open Eucalyptus woodland along the coastal fringe, around the major cities. In addition to the value of studying duetting in the Australian Arid zone, Wedgebills live in a very open landscape that facilitates their behavioural study and should provide greater insight into the interaction between partners. Males are highly conspicuous and sing loudly for extended periods of time at the tops of trees and bushes, making them easy to locate (Marchant and Higgins 2002). With trees in very low density (Mabbutt, Burrell *et al.* 1973), the arid habitat they occupy is relatively open which presents opportunities to reliably gather spatial information that could enhance our understanding of duet function. The isolated location of their habitat also provides an opportunity to study behaviour in a less constructed and human impacted environment than many species and contributes to our understanding of duets use across habitats. Importantly, studying song and occurrence of duets in this species also presents an opportunity to

encourage the exploration of the behavioural ecology of arid zone species in general, challenging the perception that studies of arid zone species are difficult due to terrain and accessibility. In order to examine the purpose of song and duet function in the chirruping wedgebill, we performed a series of playback experiments over the course of four weeks in October/November 2014. We presented pairs of wedgebills with three trials, each with a different type of wedgebill song; unknown male song, unknown female song and unknown duet and recorded (1) male and female song rates (2) reaction times (3) occurrence of duets, (4) distance between partners while duetting and (5) distance to the speaker.

## 2. Materials and methods

### 2.1 Study site and species

The chirruping wedgebill (*Psophodes cristatus*), is a medium sized (approximately 44g) sexually monomorphic grey passerine (Marchant and Higgins 2002). These birds occupy arid regions of Australia, where the vegetation is dominated by shrubs such as saltbush (Mabbutt, Burrell *et al.* 1973). Other than one study examining the phylogeny of the genus *Psophodes* (Toon, Joseph *et al.* 2013) and brief records of behaviour (Marchant and Higgins 2002) the behavioural ecology of this species has not yet been examined.

We studied pairs of chirruping wedgebills from August to November 2014 at the University of New South Wales Arid Zone Research Station at Fowlers Gap, 110 km north of Broken Hill in far western New South Wales, Australia (31° 05' S, 142° 42' E). The climate of this area is arid, typified by cool winters, hot summers and low rainfall (below 200mm per annum) (Mabbutt, Burrell *et al.* 1973). The habitat in which we studied the wedgebills at Fowlers Gap Arid Zone Research Station was low open chenopod shrubland. Trees are sparse and occur primarily along dry creek beds that run throughout the area, with the main species being *belah* (*Casuarina pauper*), Mulga and Rosewood (*Heterodendrum oleifolium*) with tall shrubs such as prickly wattle (*Acacia victoriae*) and dead finish (*A. tetragonophylla*) also abundant. The ground vegetation is dominated by shrubs which largely consist of low bluebush (*M. astrotricha*); black bush (*Maireana pyramidata*), pearl bush (*M. sedifolia*), thorny saltbush (*Rhagodia spinescens*), copperburrs (*Sclerolaena spp.*) and small shrubs such as popping saltbush (*Atriplex holocarpa* and *A. spongiosa*) (Mabbutt, Burrell *et al.* 1973; Portelli, Barclay *et al.* 2009).

This study was conducted under an approval from the Animal Ethics Committee at Macquarie University, a Scientific Research Permit from the New South Wales Parks and Wildlife Service and a banding Authority of the Australian Bird and Bat Banding Scheme.

## 2.2 *Defining duets*

Two main characteristics that define a duet have been described as; 1) ‘a constant time lag between the contributions of the two individuals’ and 2) ‘a stereotyped structure that occurs repeatedly and predictably in time’ (Langmore 2002). A common method for determining the existence of temporal precision in joint song is the examination of the ‘coefficient of variation’ ( $CV = 100 \times SD/mean$ ), which examines the variation of temporal precision between an initiator of a duet and a responder (Elie, Mariette *et al.* 2010; Farabaugh 1982; Hall 2009). This method requires measurement of the start time of the initiating vocalisation to the start time of the responding vocalisation and was achieved by examining spectrograms in Raven Pro 5.1 (Bioacoustics Research Program, The Cornell Lab of Ornithology, Ithaca, NY, <http://www.birds.cornell.edu/raven>). In the field, joint song was only considered to be a duet if females contributed two or more notes to a male song. We used this definition to account for random singing by females that may occur in sync with or overlap with male song by chance and without intent. As males sing for extended periods of time, rather than count each individual female note as a separate duet, duets were counted in bouts of singing. For example, if a male sang for the length of one minute and a female contributed one note every two seconds for that minute, the one minute of combined singing was counted as a single duet.

## 2.3 *Song files*

Songs selected for playbacks were recorded from birds at least 2km away from focal animals (following (Rogers, Langmore *et al.* 2007)). Two male songs, two female songs and two duets were selected. We ensured that the recordings each contained a similar amount of syllables so as to ensure consistency of call type (Hall and Peters 2008). To avoid pseudo-replication (Catchpole 1989) and habituation (Dong and Clayton 2009), a pair were not presented with a particular song more than once. Duet recordings were taken from different birds to the ones used for solo male and female songs.

All songs used were normalised to 5 decibels (dB) using program ‘Audacity’ (audacity.sourceforge.net) (Templeton, Ríos-Chelén *et al.* 2012). Duets played utilised a dual speaker design as this design is thought to more accurately mimic spatial dimensions and sound of a real duet (Douglas and Mennill 2010; Rogers, Ferguson *et al.* 2004). Files were split using program ‘Audacity’ so that male calls were played through one speaker and female calls played through another. The speakers used were Logitech Pure-Fi Anywhere 2 (Model number: S-00001) and were adjoined, separated by approximately 200 mm of plastic. The structural design of these speakers saw both speakers fused together, leaving them unable to be separated.

#### 2.4 Playback methodology

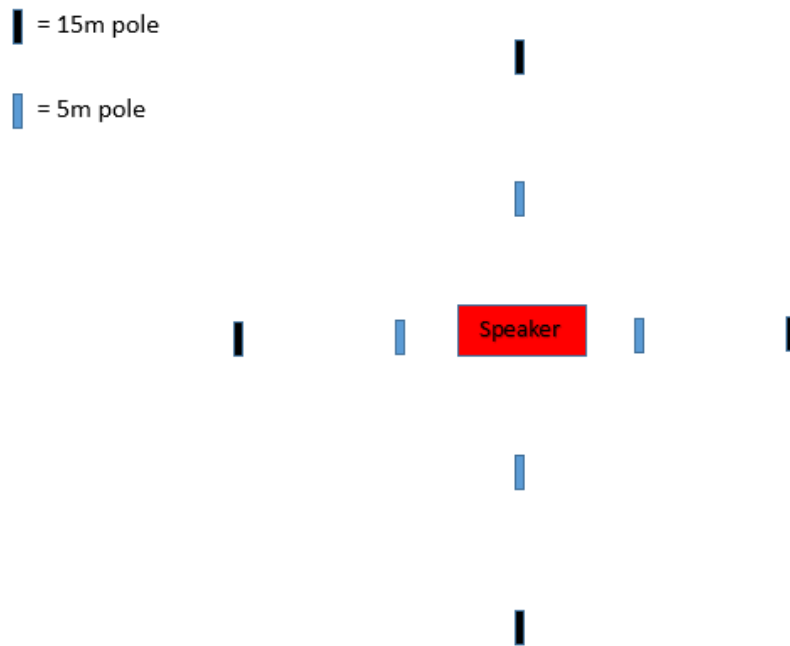
Our methodology was an adaptation of that used by Hall (2000) and Rogers *et al.* (2007). Song files were 16 minutes long, 11 minutes of silence and five minutes of song. The first minute of silence enabled researchers’ time to move away from the speaker and assume a position for observation. The remaining ten minutes of silence was played to allow birds to resume normal behaviour and to provide a base line for the comparison of behaviour. During this silence, behavioural observations were recorded. After the playback had finished, observations continued for another ten minutes. Results analysed examined behaviour five minutes before, five minutes during and five minutes after playback to ensure that length of time was comparable.

Twenty pairs ( $n = 20$ ) of wild wedgebills were used in this experiment. Territories were located, marked using GPS and areas mapped frequently in order to monitor territorial boundaries. Of the 40 adults that made up these pairs, 11 were banded. Most territories contained banded juveniles that were observed being provisioned by adults. In addition, we were also monitoring nests during this period as part of other work. As such, we were confident that birds used for each trial were the same individuals i.e. they were in the same location and tending offspring of the same age, or a nest in the same location as on previous regular visits to the territory. Each pair was presented (in a random order) with three different treatments over the course of one month; an unknown male song, unknown female song and unknown duet.

To limit differences in behavioural responses due to time of day (Catchpole and Slater 2003), playback experiments were conducted between 6 and 10.30 in the morning. In order to

avoid influencing behaviour and results through pseudo-replication (Catchpole 1989), habituation (Dong and Clayton 2009) and eavesdropping (McGregor 1993; Naguib, Amrhein *et al.* 2004), neighbouring birds were not trialled on the same day and each pair had at least four days in between trials before being presented with another playback type. Previous studies have presented birds with different trials on the same day (Koloff and Mennill 2011; Mennill and Vehrencamp 2008), but this was not possible because wedgebills had strong and extended reactions to playbacks. Given that song rate and movement data needed to be recorded simultaneously two researchers were present during each playback. One focused entirely on recording song rates and the other focused on spatial data.

Speakers were placed in the centre of territories inside a bush. Eight bamboo poles were placed around the speaker, with markings to distinguish distance (de Kort *et al* 2009). Four poles were placed concentrically five metres from the speaker; and four were 15m from the speaker and marked with two black stripes to distinguish them (Figure 1). Bamboo poles provided researchers with an inconspicuous means of estimating distance of birds from the speaker during the experiment.



**Figure 1.** Speakers were placed in the centre of the territory inside a bush so as to remain inconspicuous. Eight bamboo poles were used to mark distances surrounding the speaker. Four were paced at five metres from the speaker and four at eight metres from the speaker. The 15 m poles were marked with two black stripes to enable researchers to easily distinguish them at a distance. After activating recordings, researchers retreated to a distance of at least 25m away and remained hidden so as not to distract the focal birds.

Song rates provided an easily identifiable behavioural response to playback. As such researchers noted song rates of males and females for the ten minutes of silence, for the five minutes during the playback and for ten minutes after playback using stop watches. Male song was recorded to the nearest second every minute. Due to the simplistic and short structure of female song, they were not timed and instead were counted per minute. As wind can affect the ability of song to be heard, and therefore had the potential to impact upon reaction times of birds, trials were not conducted during windy conditions.

Time taken to respond spatially to the playback were noted for males and females. Distance of birds from the speaker and the time spent at those distances was noted before during and after the playback as were the distances of each movement. The times taken to initiate these movements from the start of playback were also noted. Distances of partners from each other during duets were also recorded. Previous playback experiments have utilised a taxidermy model to examine intent to escalate aggression (Searcy and Beecher 2009). This study hypothesised that if a response to an intruder was truly aggressive than

focal birds would likely attack the model. However, as postures can also convey information about an intruders intent (Laidre and Vehrencamp 2008) a model risked sending mixed signals that may have impacted results.

## *2.5 Statistical analysis*

SPSS version 22. (IBM Corporation) was used for statistical analysis. Data pertaining to male song and female call rate represented a Poisson distribution and were unable to be normalised. As such, we used methods similar to those used by Grafe and Bitz (2004), whereby Kruskal-Wallis non-parametric tests were used and were followed by Dunn-Bonferroni post hoc tests to test for pairwise comparisons. Distance and reaction time data also had an uneven distribution, however these data was able to be transformed using log10 transformation. Distance and reaction time data was subsequently analysed using ANOVA. Bonferroni post hoc tests were used to allow for pairwise comparisons. Kruskal-Wallis tests were again used to examine time of first movement and number of movements toward the speaker accompanied with Dunn-Bonferroni pairwise comparisons. A Mann-Whitney U test was used to examine the amount of time spent within 5 and 15 metres of the speaker. Data on sex and duet initiation rates was categorical and were analysed using Pearson Chi Square Test.

### 3. Results

#### 3.1 Temporal precision of duets

We randomly sampled the temporal precision of  $N = 77$  duets ( $X + SE = 0.805 + 0.029$ ) from  $n = 5$  different pairs of Wedgebills resulting in a total coefficient of variation of 32.47% ( $CV = 32.47$ ), confirming the existence of temporal precision in joint song

#### 3.2 Response to playback

There was no significant effect of playback type (either duet, male solo or female solo) on the song rates of male (Kruskal-Wallis test:  $H_2 = 0.466$ ,  $N = 150$ ,  $P = 0.792$ ) or female wedgebills (Kruskal-Wallis test:  $H_2 = 1.265$ ,  $N = 150$ ,  $P = 0.531$ ) (figure. 2). There was a significant effect of experimental stage (before, during and after) on male song rates (Kruskal-Wallis test:  $H_2 = 25.071$ ,  $N = 165$ ,  $P = 0.001$ ) and female song rates (Kruskal-Wallis test:  $H_2 = 38.174$ ,  $N = 165$ ,  $P < 0.001$ ), with males and females singing more during (Dunn-Bonferroni:  $P = 0.001$ ) and after (Dunn-Bonferroni:  $P = 0.001$ ) playbacks than during the silent pre-playback period (figure. 2).

There was no significant difference between males and females in the time it took for birds to respond to the recordings (ANOVA:  $F_{2,79} = 0.717$ ,  $P = 0.491$ ). However, there was a significant effect of the song type played (either duet, male solo or female solo) on singing reaction times (ANOVA:  $F_{1,76} = 3.507$ ,  $P = 0.035$ ) with females taking more time to respond vocally to unknown duets compared to the other song types (ANOVA:  $F_{2,38} = 3.538$ ,  $P = 0.040$ ). The song type played also affected the number of duets pairs performed, where pairs performed significantly more duets during playbacks of unknown duets than during the two solo song trials (Kruskal-Wallis test:  $H_2 = 16.740$ ,  $N = 125$ ,  $P = 0.001$ ). Females also led significantly more duets than males during trials of unknown female song (Chi-Square test:  $X^2_2 = 10.358$ ,  $P = 0.006$ ).

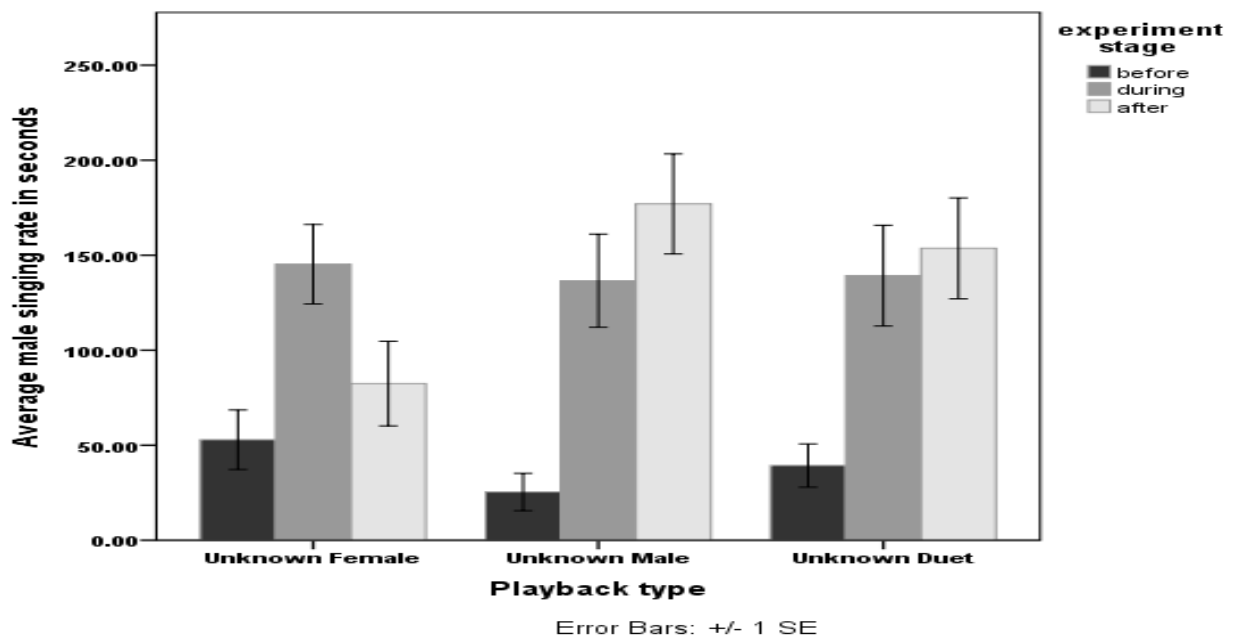
Overall, there was no significant effect of playback type on the distance between individuals whilst duetting (ANOVA:  $F_{2,203} = 0.095$ ,  $P = 0.909$ ). However, there was a significant effect of the stage of the experiment (ANOVA:  $F_{2,203} = 7.985$ ,  $P = 0.001$ ). In all three trials, pairs moved closer together during playback than they were before during the silent period prior to playback. After playbacks had finished, pairs moved apart again in trials of duets and male solo songs. However, after exposure to female solo songs, pairs remained



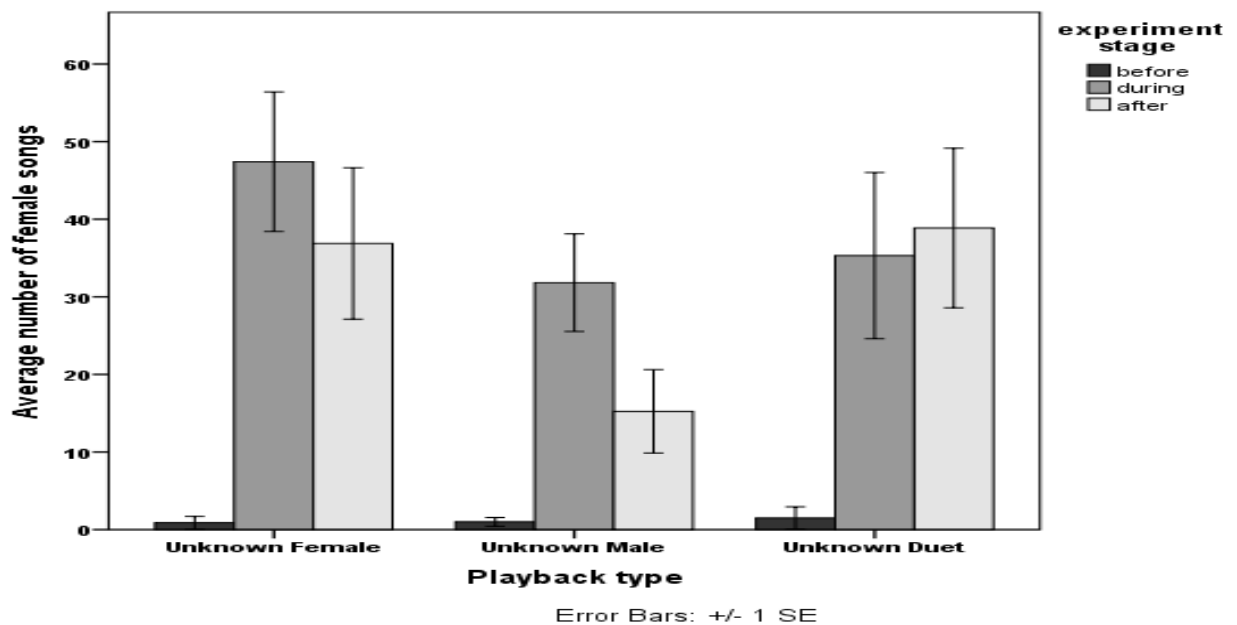
close together even after the song had finished playing. The distance between the pair was not influenced by the sex that initiated the duet (ANOVA:  $F_{2,205} = 279$ ,  $P = 0.757$ ).

Both males and females moved towards the speaker during playbacks, but there was no significant difference between males and females in the number of movements made (Mann-Whitney  $U$  test:  $U = 1765.5$ ,  $P = 0.092$ ). Males and females were equally likely to approach a speaker across the different song-type trials. However, the playback type did affect the number of movements pairs made toward the speaker (Kruskal-Wallis test:  $H_2 = 14.706$ ,  $N = 110$ ,  $P = 0.001$ ), making significantly less movements during trials of duet song (Dunn-Bonferroni:  $P = 0.044$ ). Yet there was no significant effect of song type on time taken to initiate first movement (Kruskal-Wallis test:  $H_2 = 0.029$ ,  $N = 110$ ,  $P = 0.986$ ) and no significant difference between male and females in the time it took to initiate first movement (Kruskal-Wallis test:  $H_1 = 0.296$ ,  $N = 110$ ,  $P = 0.587$ ). Males and females were equally likely as each other to be positioned at 5m or 15m from the speaker (Mann-Whitney  $U$  test:  $U = 6110.5$ ,  $P = 0.837$ ). Both males and females spent more time at 15 metres from the speaker than at 5 metres (Mann-Whitney  $U$  test:  $U = 5370.0$ ,  $P = 0.020$ ).

a)

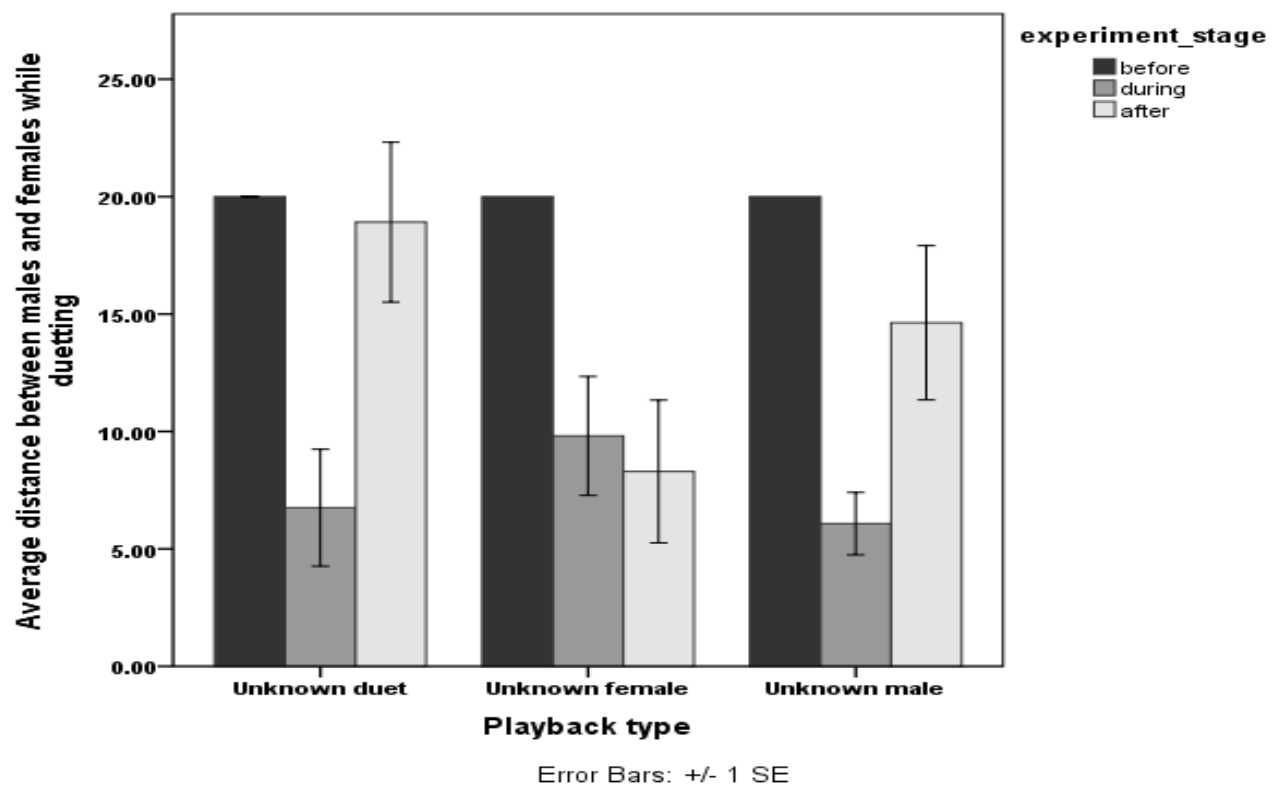


b)

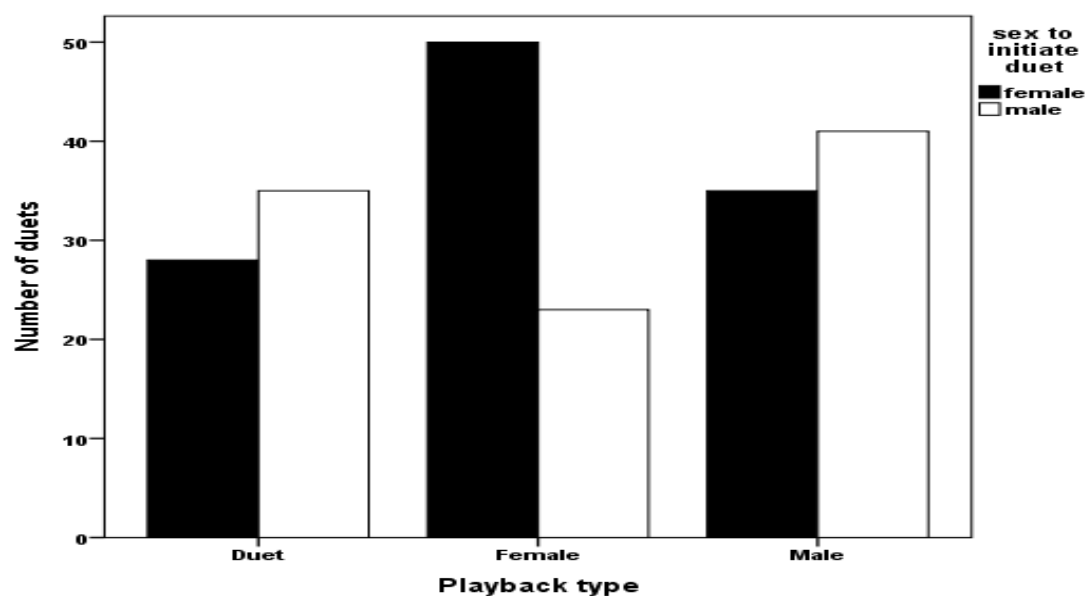


**Figure 2.** Part (a) shows male and part (b) female song rates during the three different playback types. Song rates during the different stages of the experiment (before, during and after) are shown in sequential order. There was no significant effect of playback type on song rates for males ( $P = 0.792$ ) or females ( $P = 0.531$ ). However, there was a significant effect of experiment stage on male ( $P = 0.001$ ) and female ( $P = 0.001$ ) song rates. There were strong sustained same sex responses from both males and females. However, song rate declined quickly after playback ceased when exposed to trials of opposite sex song.

a)

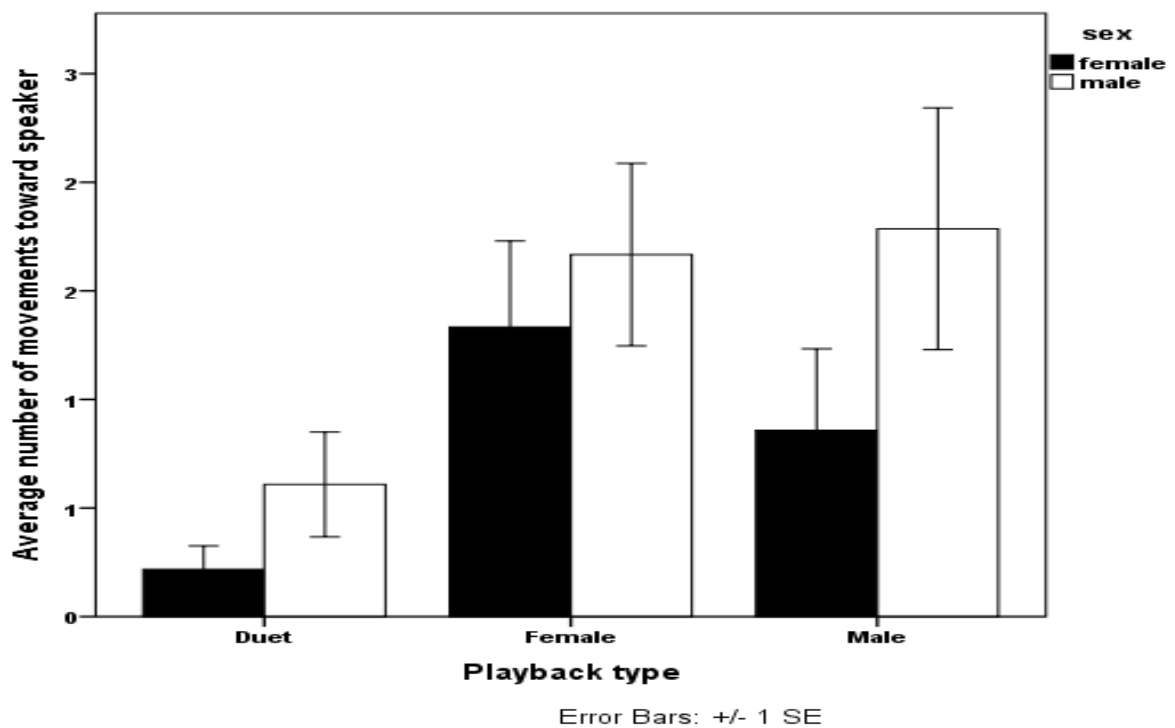


b)

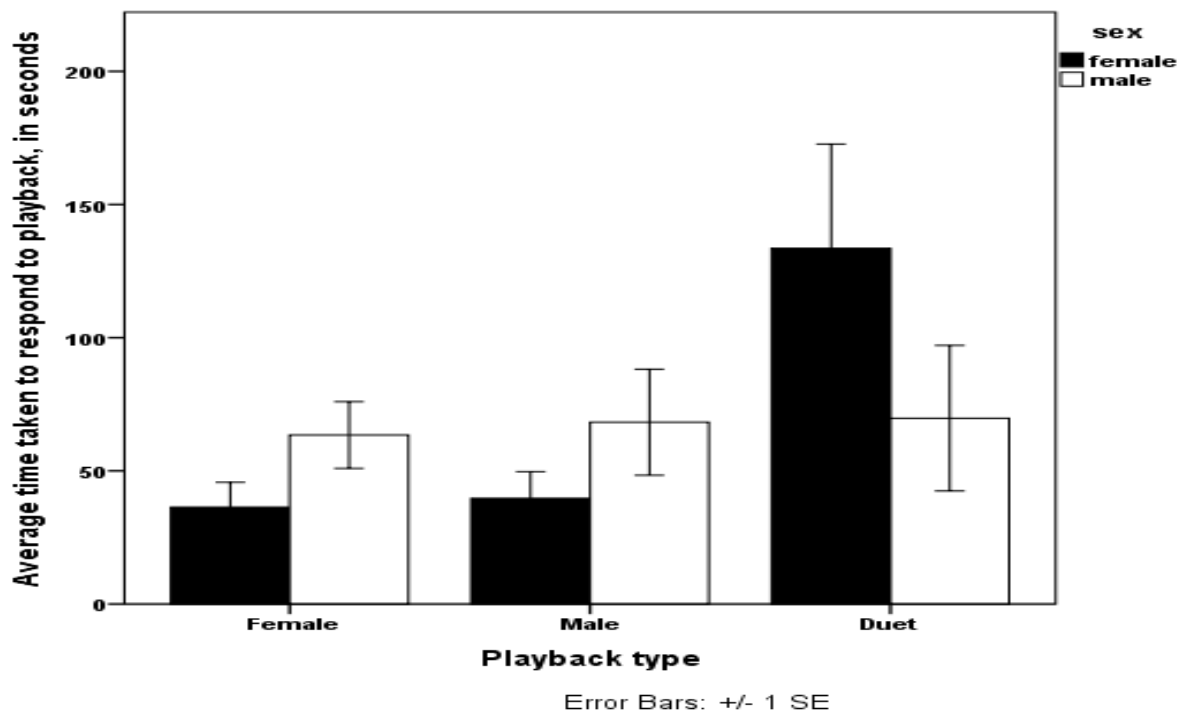


**Figure 3.** Image (a) shows the distance between pairs while duetting during the different playback trials (unknown male, unknown female and unknown duet) and during the three stages of each trial (before, during and after). There was a significant effect of playback stage on distance between pairs ( $P = 0.001$ ). Image (b) shows the number of duets initiated by each sex. Females initiate significantly more duets than males during trials of unknown female song ( $P = 0.006$ ).

a)



b)



**Figure 4.** Part (a) depicts the average number of movements taken by males and females during the different playback types. There was a significant effect of playback type on the number of movement made ( $P = 0.001$ ) with less movements toward the speakers during trials of duets. Part (b) depicts the average time of both males and females to respond to playback. There was no significant difference between the sexes. However females took significantly longer to respond to unknown duets than the other playback types ( $P = 0.035$ ).

## 4. Discussion

Both male and female wedgebills showed strong sex specific vocal aggression, yet the playback type did not affect their latency to approach the speaker. In addition, pairs performed more duets when confronted with an unknown duet, indicating a cooperative aggressive signal. However, their willingness to approach the speaker decreased compared to solo intruder trials. Examining these complex responses, we suggest that in the event of territorial invasion by two birds, duets are likely used in cooperative territorial defence. However, in context of invasion by a single bird, duet function is harder to determine, with evidence to support both conflict and/or cooperation.

### *4.1 Reactions to solo intruders: Evidence of sexual conflict or cooperation?*

When confronted by a same sex solo playback, vocal responses continued after the playback period had ceased. In contrast, song rates of the opposite sex partner dropped markedly in the period after playback of these trials (Figure 2a and b). This result may represent different motivations between the sexes and introduces the idea of inter-sexual conflict (Chapman, Arnqvist *et al.* 2003; Hall 2009). Individuals may risk being usurped by an intruder of the same sex and as such, continued sustained responses by males and females once the stimulus was stopped may be reflective of the level of threat that birds were faced with (Vehrencamp 2001). The motivation to continue signalling and reaffirm ones position would be high in this case (Vehrencamp 2001), and likely explains the continued singing by birds even after the same sex song had ceased. From this perspective of motivation, it is also not surprising that song rates of opposite sex partners dropped quickly after playback of opposite sex songs had ceased. Opposite sex partners may benefit from the invasion of a solo bird by achieving access to a better quality mate (Griffith, Owens *et al.* 2002; Hall 2009). Alternatively, there may simply be little threat to an individual's position in a pair and as such, the motivation to continue signalling is less pressing.

Given the strong sex specific responses witnessed in males and females it is likely that high levels of same sex conflict occurs within this species. Recently Dahlin (2014) showed that 96% of duetting species were socially monogamous. However, it is well established generally that significant levels of genetic polyandry can occur in most socially monogamous birds (Griffith *et al.* 2002), even in duetting species (Benedict 2008b). The drive to ensure

paternity provides an obvious explanation as to why male wedgebills would respond more to male song than to female song. However, same sex responses by females appeared to be stronger than male same sex aggression.

Females should have no reason to mate guard, unless they risk reduced male investment or direct competition from rival females (van den Heuvel, Cherry *et al.* 2014). Consequently sex specific aggression by females is thought to be indicative of high female competition (Langmore 1998). Preliminary field observations suggest high female competition may exist in wedgebill populations. Three females in our study appeared to raise broods on their own (*pers obs*), suggesting social polygyny may be present. Evidence suggests that the nestlings of secondary females in polygynous mating systems receive less provisioning from their father than those in socially monogamous nests, and experience decreased fitness as a result (Korpimäki, Salo *et al.* 2011). As such, if social polygyny is present, then it can lead to high levels of intra-sexual conflict in females (Veiga 1990). Consequently, by singing more and initiating more duets during invasion by solo females, female wedgebills may be able to acoustically mate guard their mate, preventing potential rivals from duetting with their partner and preventing their partner from singing with the intruder (Levin 1996a; Sonnenschein and Reyer 1983b). In addition, by remaining close to her male even after the threat as passed, females can be assured of their mates whereabouts and thus prevent extra pair copulations from occurring (Hall 2004; Hall 2009). Sex specific responses have been witnessed in other species such as barred antshrikes, (*Thamnophilus doliatus*) (Koloff and Mennill 2011), and the close wedgebill relative, the eastern whip bird (*Psophodes olivaceus*) (Rogers, Langmore *et al.* 2007) and are also thought to be indicative of same sex aggression and mate guarding (Hall 2004).

While mate guarding and sexual conflict provide a highly plausible explanation of duet function given the behaviours we witnessed, from a different perspective, there remains the possibility that duets function cooperatively in this context. Firstly, it is possible that the sex specific vocal responses witnessed in this study are indicative of a division of labour by the two sexes towards the defence of the territory (Marshall-Ball, Mann *et al.* 2006). This idea proposes that birds of the same sex will be of similar size and weight. As such, by attacking the same sex, efficiency of defence may be increased and cooperation achieved (Marshall-Ball, Mann *et al.* 2006). Secondly, maintaining close distances with a partner is thought to represent a united more threatening signal (Hall 2009). This may explain why birds came close together while duetting during the playback period. It may also explain why pairs

remained close together even after playback of female songs had ceased. If female solo intruders are particularly threatening, duetting and remaining close together represents a particularly strong retaliation. In addition, the distance between partners can affect the tempo of a duet. As sound has to travel, birds that are further apart likely have slower reaction times and thus slower tempos (Hall 2006; Hall 2009). This may have implications for temporal precision and thus perceived quality of the signal to receivers (Hall and Magrath 2007); potentially influencing the outcome of an invasion. As such it benefits pairs to be closer together in the presence of a threat in order to produce as precisely timed duets as possible. From these perspectives, it can be argued that duet use against solo intruders is a cooperative action used to display commitment and defend the territory. In support of this, a study on duet use in happy wrens (*Pheugopedius felix*, formerly *Thryothorus*) showed that while females responded aggressively to same sex intruders, they showed commitment to their mate by only responding to his song instead of type matching intruding females (Templeton, Rivera-Cáceres *et al.* 2011). While we did not examine response rates of singing, this example in happy wrens displays that the occurrence of same sex aggression and cooperative functions of duets are not necessarily mutually exclusive. As such, we must remain open to the possibility that duet use in the presence of solo intruders may serve cooperative functions.

Given the strong sex specific vocal reactions of males and females and the apparent aggression witnessed in the field, we would expect to see same sex aggression reflected in movements toward the speaker as well. If the solo signals presented are as threatening as the vocal response imply than we would expect that the receiver would be more motivated to approach or attack the speaker (Vehrencamp 2001). However this was not the case with males and females equally likely to approach the speaker regardless of the song type played (Figure. 4a). Furthermore, the physical reaction times (the amount of time it took for birds to respond to the playback by moving toward it) did not differ for males and females in response to solo songs from either sex. This result may again be explained in the context of inter-sexual conflict (Chapman, Arnqvist *et al.* 2003; Hall 2009). It may benefit a bird to approach a same sex intruder as quickly as possible to establish dominance and prevent oneself from being usurped. Conversely, the opportunity for extra-pair copulations or a more suitable mate provide motivation for the opposite sex partner to also approach. Alternatively, pairs may actually approach in tandem, showing cooperation and increasing the chance of successful outcome in face of threat.

As movements may provide more information about intent than song alone (Mennill and Vehrencamp 2008), future studies may more confidently confirm mate guarding behaviour and sexual conflict by examining movements of a pair toward and away from each other (Gill, Vonhof *et al.* 2005) and tandem movements toward the speaker. Furthermore, animals can make signals using their entire bodies (Partan and Marler 2005). As such, in addition to these movements, we may learn much more about the context of duet function and be more readily able to decipher between functions in general by examining multimodal signalling. Increased song rates alone may be seen as an ambiguous signal (Partan and Marler 2005), and even movements toward and away from a speaker may require us to infer information about intent. However, examining postures and behaviours may reveal more about context. For example, female red wing black birds (*Agelaius phoeniceus*) use the same visual displays for aggression and courtship, yet it is the different vocalisations they use in conjunction with these that establish context and intent (Beletsky 1983). This displays how two signals used in conjunction can result in different meanings. As such, the lack of difference in reaction times between male and female wedgebills in this study may be better understood by examining postures and movement in detail (Laidre and Vehrencamp 2008). It is possible that members of a pair respond to cues from each other before reacting to an intruder. By examining movements and postures we may greater understand whether members of a pair are initially responding to an intruder or in fact to each other. This would provide heightened insight as to whether cooperation or conflict was occurring. Such monitoring may be achieved with the use of video monitoring and the subsequent detailed examination of aggressive postures (Duncan 1974) and comfort behaviours that may indicate stress (Delius 1988).

#### *4.2 Response to pair invasion: Evidence of cooperation?*

Male and female wedgebills made less movements toward the speaker during duet trials suggesting a less aggressive response (Hall 2009; Searcy and Beecher 2009). This reaction is not unusual and has been witnessed in other studies of other species such as the eastern whipbird (Rogers, Langmore *et al.* 2007) and warbling antbird (*Hypocnemis cantator*) (Seddon and Tobias 2006). Hesitancy to physically approach duetting rivals could be indicative of increased risk associated with approaching two birds. By approaching two unknown birds that cannot be seen, the risk of losing one's territory may be high due to uncertainty about the signallers (Enquist 1985). Given duets are thought to be a more



aggressive signal due to coordination and joint effort (Farabaugh 1982; Hall 2000; Molles and Waas 2006; Wickler 1976), duetters are likely perceived as a higher threat than a single bird (Fedy and Stutchbury 2005). Thus, pairs should retaliate with a similar signal, rather than approach and risk physical altercation. By working together pairs may have a better chance at warding off rivals and defending a territory (Hall 2009). It is interesting to note that females took longer to respond vocally during playback of unknown duets than the other song types. Signal game models predict that a receiver will pause when receiving a signal from a weaker individual, giving the weaker rival an opportunity to escape (Enquist 1985; Vehrencamp 2001). As such, the delayed response from female wedgebills may indicate that the duet chosen for use in playback was from a pair where one or both individuals were of lesser quality. Alternatively, females may simply be assessing the level of threat before deciding on how to respond.

Replicating the results of previous studies (Marshall-Ball, Mann *et al.* 2006; van den Heuvel, Cherry *et al.* 2014) and supporting the territorial defence hypothesis, duet rates increased when presented with unknown duet playback compared with the other two trials. Males and females were also equally likely to initiate duets at this time. Two birds are thought to be more threatening than one and more likely to gain access to new territories. Furthermore, there is also a mutual risk for males and females of being usurped (Hall 2009). By duetting more in the presence of a rival pair, wedgebills may reveal their quality as individuals and as a pair, displaying their coordination and endurance as well as their commitment to each other (Hall 2004; Hall 2009; Wickler and Seibt 1982). In addition, wedgebills can display their quality, strength and coordination without having to engage in physical altercation. The point here is twofold; (1) that duets themselves are more threatening than solo songs and are used in situations of increased risk such as territorial invasion by two birds; (2) and that as a result of the threatening nature of the signal, birds are less likely to engage in physical altercation. The movement of pairs away from each other after playback could also be argued to provide further evidence of duet use in territorial defence. Compared to the other two trials, male and female wedgebills moved significantly further apart after playback of unknown duets (Figure. 3a). This behaviour may represent guarding of territorial boundaries; continuing to duet after the threat has ceased maintains a display of strength and ongoing commitment to each other, while the increased distance between birds may enable them to assess the point of intrusion and maintain and reassert territory boundaries.

It has been recognised that conflict and cooperation are not mutually exclusive in duet function (Koloff and Mennill 2011) and that not all duets are considered to be cooperative displays (Levin 1996b). Unlike previous studies that have concluded duet use as cooperative territorial defence (van den Heuvel, Cherry *et al.* 2014), our results do not provide enough evidence to conclude that this behavioural response in wedgebills is entirely cooperative. The speakers used in our experiment were close together (less than 1m). This means we could not determine if males and females showed sex specific aggression while duetting. It is possible that if speakers had been positioned further apart that males and females may have shown a sex specific response even while duetting. This would be indicative of same sex rivalry and a division of labour within territorial defence (van den Heuvel, Cherry *et al.* 2014). As such, we are unable to comment on whether this joint display to defend territories is entirely cooperative.

## 5. Conclusion

This study is the first to examine the function of duets in arid zone species the chirruping wedgebill (*Psophodes cristatus*). We suggests that duets likely serve multiple functions that are context dependent. Similar responses to duets by both males and females suggest duet use in territorial defence and thus cooperation when confronted by two intruders. However, duet use in the context of solo intrusion is less clear as there is evidence to support sexual conflict and cooperation. The difficulty in deciphering between behaviours highlight the problems associated with determining duet function (Grafe and Bitz 2004). It also highlights the need to examine as many movements and behaviours as possible when attempting to determine duet function.

In line with work previously conducted by Mennill and Vehrencamp (2008), we highlight the importance of spatial and movement data in interpreting results of playback experiments, and the additional insight that the spatial movements of birds towards threats and the interaction with each other, provides. In addition and in light of difficulty in confidently deciphering between conflict and cooperation, we suggest that examining multimodal signals such as postures and initial reactions may add greatly to our understanding of duet function. Given the difficulty in examining duet function in a natural setting due to visual impairments (Mennill and Vehrencamp 2008) we present the chirruping wedgebill as a species for which to study duets. We acknowledge that the idea of a visually

impaired environment is contingent upon perspective, and to the wedgebills who spend much time on the ground or in bushes, their habitat is visually complex and they may often be out of visual contact with their partner. However, their conspicuous behaviours and arid environment they inhabit present them as an interesting and ideal study species for researchers.

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## References

- Amrhein, V., Kunc, H.P., Naguib, M., and Nelson, D.A. (2004) Seasonal patterns of singing activity vary with time of day in the Nightingale (*Luscinia megarhychos*). *The Auk* **121**(1), 110-117.
- Arcese, P., Stoddard, P.K., and Hiebert, S.M. (1988) The Form and Function of Song in Female Song Sparrows. *The Condor* **90**(1), 44-50.
- Ballentine, B., Hyman, J., and Nowicki, S. (2004) Vocal performance influences female response to male bird song: an experimental test. *Behavioral Ecology* **15**(1), 163-168.
- Barker, F.K., Barrowclough, G.F., and Groth, J.G. (2002) A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proceedings of the Royal Society of London B: Biological Sciences* **269**(1488), 295-308.
- Beletsky, L.D. (1983) Aggressive and Pair-bond Maintenance Songs of Female Red-winged Blackbirds (*Agelaius phoeniceus*). *Zeitschrift für Tierpsychologie* **62**(1), 47-54.
- Benedict, L. (2008a) Occurrence and life history correlates of vocal duetting in North American passerines. *Journal of Avian Biology* **39**(1), 57-65.
- Benedict, L. (2008b) Unusually high levels of extrapair paternity in a duetting songbird with long-term pair bonds. *Behavioral Ecology and Sociobiology* **62**(6), 983-988. [In English]
- Brewer, K.R.W. (1999) Design-Based or Prediction-Based Inference? Stratified Random vs Stratified Balanced Sampling. *International Statistical Review / Revue Internationale de Statistique* **67**(1), 35-47.
- Byrne, M., Steane, D.A., Joseph, L., Yeates, D.K., Jordan, G.J., Crayn, D., Aplin, K., Cantrill, D.J., Cook, L.G., Crisp, M.D., Keogh, J.S., Melville, J., Moritz, C., Porch, N., Sniderman, J.M.K., Sunnucks, P., and Weston, P.H. (2011) Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *Journal of Biogeography* **38**(9), 1635-1656.
- Cardoso, G.C., and Hu, Y. (2011) Birdsong performance and the evolution of simple (rather than elaborate) sexual signals. *The American Naturalist* **178**(5), 679-686.
- Catchpole, C. (1986) Song repertoires and reproductive success in the great reed warbler *Acrocephalus arundinaceus*. *Behavioral Ecology and Sociobiology* **19**(6), 439-445. [In English]
- Catchpole, C.K. (1973) The Functions of Advertising Song in the Sedge Warbler (*Acrocephalus Schoenobaenus*) and the Reed Warbler (*a. Scirpaceus*). *Behaviour* **46**(3), 300-319.
- Catchpole, C.K. (1989) Pseudoreplication and external validity: Playback experiments in avian bioacoustics. *Trends in Ecology & Evolution* **4**(10), 286-287.

Catchpole, C.K., and Slater, P.J. (2003) 'Bird song: biological themes and variations.' (Cambridge University Press)

Chapman, T., Arnqvist, G., Bangham, J., and Rowe, L. (2003) Sexual conflict. *Trends in Ecology & Evolution* **18**(1), 41-47.

Dahlin, C.R. (2014) Angry Birds Need Not Apply: A Perspective on the Flexible form and Multifunctionality of Avian Vocal Duets. *Ethology* **120**(1), 1-10.

Delius, J.D. (1988) Preening and Associated Comfort Behavior in Birds. *Annals of the New York Academy of Sciences* **525**(1), 40-55.

Dong, S., and Clayton, D.F. (2009) Habituation in songbirds. *Neurobiology of Learning and Memory* **92**(2), 183-188.

Douglas, S.B., and Mennill, D.J. (2010) A review of acoustic playback techniques for studying avian vocal duets

Una revisión de las técnicas de la reproducción de sonidos grabados para el estudio de las duetas vocales de las aves. *Journal of Field Ornithology* **81**(2), 115-129.

Duncan, I.J.H. (1974) A scientific assessment of welfare. *Proceedings of the British Society of Animal Production (1972) (New Series)* **3**, 9-19.

Elie, J.E., Mariette, M.M., Soula, H.A., Griffith, S.C., Mathevon, N., and Vignal, C. (2010) Vocal communication at the nest between mates in wild zebra finches: a private vocal duet? *Animal Behaviour* **80**(4), 597-605.

Enquist, M. (1985) Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour* **33**(4), 1152-1161.

Farabaugh, S.M. (1982) The ecological and social significance of duetting. *Acoustic communication in birds* **2**, 85-124.

Fedy, B.C., and Stutchbury, B.J. (2005) Territory defence in tropical birds: are females as aggressive as males? *Behavioral Ecology and Sociobiology* **58**(4), 414-422.

Gil, D., and Gahr, M. (2002) The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution* **17**(3), 133-141.

Gill, S., Vonhof, M., Stutchbury, B.M., Morton, E., and Quinn, J. (2005) No evidence for acoustic mate-guarding in duetting buff-breasted wrens (*Thryothorus leucotis*). *Behavioral Ecology and Sociobiology* **57**(6), 557-565. [In English]

Grafe, T.U., and Bitz, J.H. (2004) Functions of duetting in the tropical boubou, *Laniarius aethiopicus*: territorial defence and mutual mate guarding. *Animal Behaviour* **68**(1), 193-201.

Griffith, S.C., Owens, I.P., and Thuman, K.A. (2002) Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* **11**(11), 2195-2212.

Halkin, S.L. (1997) Nest-vicinity song exchanges may coordinate biparental care of northern cardinals. *Animal behaviour* **54**(1), 189-198.

Hall, M.L. (2000) The function of duetting in magpie-larks: conflict, cooperation, or commitment? *Animal Behaviour* **60**(5), 667-677.

Hall, M.L. (2004) A Review of Hypotheses for the Functions of Avian Duetting. *Behavioral Ecology and Sociobiology* **55**(5), 415-430.

Hall, M.L. (2006) Convergent vocal strategies of males and females are consistent with a cooperative function of duetting in Australian magpie-larks. *Behaviour* **143**(4), 425-449.

Hall, M.L. (2009) Chapter 3 A Review of Vocal Duetting in Birds. In 'Advances in the Study of Behavior. Vol. Volume 40.' (Eds. N Marc, Z Klaus, SC Nicola and MJ Vincent) pp. 67-121. (Academic Press)

Hall, M.L., and Magrath, R.D. (2007) Temporal coordination signals coalition quality. *Current Biology* **17**(11), R406-R407.

Hall, M.L., and Peters, A. (2008) Coordination between the sexes for territorial defence in a duetting fairy-wren. *Animal Behaviour* **76**(1), 65-73.

Hall, M.L., Rittenbach, M.R., and Vehrencamp, S.L. (2015) Female song and vocal interactions with males in a Neotropical wren. *Frontiers in Ecology and Evolution* **3**, 12.

Hansen, M.H., Hurwitz, W.N., and Madow, W.G. (1953) Sample Survey Methods and Theor.

Hobson, K.A., and Sealy, S.G. (1990) Female song in the yellow warbler. *Condor*, 259-261.

Hutchinson, J.M., McNamara, J.M., and Cuthill, I.C. (1993) Song, sexual selection, starvation and strategic handicaps. *Animal Behaviour* **45**(6), 1153-1177.

Kacelnik, A., and Krebs, J.R. (1983) The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. *Behaviour* **83**(3), 287-308.

- Koloff, J., and Mennill, D. (2011) Aggressive responses to playback of solos and duets in a Neotropical antbird. *Animal Behaviour* **82**(3), 587-593.
- Korpimäki, E., Salo, P., and Valkama, J. (2011) Sequential polyandry by brood desertion increases female fitness in a bird with obligatory bi-parental care. *Behavioral Ecology and Sociobiology* **65**(5), 1093-1102. [In English]
- Kroodsma, D.E., and Byers, B.E. (1991) The Function(s) of Bird Song. *American Zoologist* **31**(2), 318-328.
- Laidre, M.E., and Vehrencamp, S.L. (2008) Is Bird Song a Reliable Signal of Aggressive Intent? *Behavioral Ecology and Sociobiology* **62**(7), 1207-1211.
- Langmore, N.E. (1998) Functions of duet and solo songs of female birds. *Trends in Ecology & Evolution* **13**(4), 136-140.
- Langmore, N.E. (2002) Vocal duetting: definitions, discoveries and directions. *Trends in Ecology & Evolution* **17**(10), 451-452.
- Levin, R.N. (1996a) Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: I. Removal experiments. *Animal Behaviour* **52**(6), 1093-1106.
- Levin, R.N. (1996b) Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: II. Playback experiments. *Animal Behaviour* **52**(6), 1107-1117.
- Liu, W.-C. (2004) The effect of neighbours and females on dawn and daytime singing behaviours by male chipping sparrows. *Animal Behaviour* **68**(1), 39-44.
- Mabbutt, J.A., Burrell, J.P., Corbett, J.R., and Sullivan, M.E. (1973) Land systems of Fowlers Gap station. *Lands of Fowlers Gap Station, New South Wales*, 25-43.
- Mace, R. (1987a) The dawn chorus in the great tit *Parus major* is directly related to female fertility.
- Mace, R. (1987b) Why do birds sing at dawn. *Ardea* **75**(1), 123-132.
- Marchant, S., and Higgins, P.J. (2002) Handbook of Australian, New Zealand and Antarctic birds; volume 6.
- Mariette, M.M., and Griffith, S.C. (2012) Nest visit synchrony is high and correlates with reproductive success in the wild Zebra finch *Taeniopygia guttata*. *Journal of Avian Biology* **43**(2), 131-140.
- Marshall-Ball, L., Mann, N., and Slater, P.J.B. (2006) Multiple functions to duet singing: hidden conflicts and apparent cooperation. *Animal Behaviour* **71**(4), 823-831.

Martin, T.E. (1996) Life History Evolution in Tropical and South Temperate Birds: What Do We Really Know? *Journal of Avian Biology* **27**(4), 263-272.

McGregor, P.K. (1993) Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **340**(1292), 237-244.

McNamara, J.M., Mace, R.H., and Houston, A.I. (1987) Optimal daily routines of singing and foraging in a bird singing to attract a mate. *Behavioral Ecology and Sociobiology* **20**(6), 399-405. [In English]

Méndez-Cárdenas, M.G., and Zimmermann, E. (2009) Duetting—A mechanism to strengthen pair bonds in a dispersed pair-living primate (*Lepilemur edwardsi*)? *American Journal of Physical Anthropology* **139**(4), 523-532.

Mennill, D.J., and Vehrencamp, S.L. (2008) Context-Dependent Functions of Avian Duets Revealed by Microphone-Array Recordings and Multispeaker Playback. *Current Biology* **18**(17), 1314-1319.

Moller, A.P. (1991) Why mated songbirds sing so much: mate guarding and male announcement of mate fertility status. *American Naturalist*, 994-1014.

Molles, L.E., and Waas, J.R. (2006) Are two heads better than one? Responses of the duetting kokako to one- and two-speaker playback. *Animal Behaviour* **72**(1), 131-138.

Morton, E. (1996) A comparison of vocal behavior among tropical and temperate passerine birds. *Ecology and evolution of acoustic communication in birds*, 258-268.

Mulder, R.A., Bishop, H., Cooper, M., Dennis, S., Koetsveld, M., Marshall, J., Saunders, B.L., and Langmore, N.E. (2003) Alternate functions for duet and solo songs in magpie-larks, *Grallina cyanoleuca*. *Australian Journal of Zoology* **51**(1), 25-30.

Naguib, M., Amrhein, V., and Kunc, H.P. (2004) Effects of territorial intrusions on eavesdropping neighbors: communication networks in nightingales. *Behavioral Ecology* **15**(6), 1011-1015.

Odom, K.J., Hall, M.L., Riebel, K., Omland, K.E., and Langmore, N.E. (2014) Female song is widespread and ancestral in songbirds. *Nat Commun* **5**.

Partan, S.R., and Marler, P. (2005) Issues in the Classification of Multimodal Communication Signals. *The American Naturalist* **166**(2), 231-245.

Podos, J. (1997) A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution*, 537-551.



Portelli, D.J., Barclay, H., Russell, D.J.F., Griffith, S.C., and Russell, A.F. (2009) Social organisation and foraging ecology of the cooperatively breeding Chestnut-crowned Babbler (*Pomatostomus ruficeps*). *Emu* **109**(2), 153.

Ritchison, G. (1983) The function of singing in female black-headed grosbeaks (*Pheucticus melanocephalus*): family-group maintenance. *The Auk*, 105-116.

Rogers, A., Ferguson, J., Harrington, H., McDowell, S., Miller, A., and Panagos, J. (2004) Use of Stereo Duet Playback to Investigate Traditional Duet Playback Methods and Mechanisms of Cooperative Territorial Defence in Magpie-Larks. *Behaviour* **141**(6), 741-753.

Rogers, A.C., Langmore, N.E., and Mulder, R.A. (2007) Function of pair duets in the eastern whipbird: cooperative defense or sexual conflict? *Behavioral Ecology* **18**(1), 182-188.

Rogers, A.C., and Mulder, R.A. (2004) Breeding ecology and social behaviour of an antiphonal duetter, the eastern whipbird (*Psophodes olivaceus*). *Australian Journal of Zoology* **52**(4), 417-435.

Rogers, A.C., Mulder, R.A., and Langmore, N.E. (2006) Duet duels: sex differences in song matching in duetting eastern whipbirds. *Animal Behaviour* **72**(1), 53-61.

Russell, E.M., Yom-Tov, Y., and Geffen, E. (2004) Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behavioral Ecology* **15**(5), 831-838.

Searcy, W.A., and Beecher, M.D. (2009) Song as an aggressive signal in songbirds. *Animal Behaviour* **78**(6), 1281-1292.

Seddon, N., and Tobias, J.A. (2006) Duets defend mates in a suboscine passerine, the warbling antbird (*Hypocnemis cantator*). *Behavioral Ecology* **17**(1), 73-83.

Slater, P.J.B., and Mann, N.I. (2004) Why Do the Females of Many Bird Species Sing in the Tropics? *Journal of Avian Biology* **35**(4), 289-294.

Sonnenschein, E., and Reyer, H.-U. (1983a) Mate-Guarding and other Functions of Antiphonal Duets in the Slate-coloured Boubou (*Laniarius funebris*)1. *Zeitschrift für Tierpsychologie* **63**(2-3), 112-140.

Sonnenschein, E., and Reyer, H.U. (1983b) Mate-Guarding and other Functions of Antiphonal Duets in the Slate-coloured Boubou (*Laniarius funebris*) 1. *Zeitschrift für Tierpsychologie* **63**(2-3), 112-140.

Spoon, T.R., Millam, J.R., and Owings, D.H. (2006) The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, *Nymphicus hollandicus*. *Animal Behaviour* **71**(2), 315-326.

- Staicer, C., Spector, D., and Horn, A. (1996) The dawn chorus and other diel patterns in acoustic signaling. *Ecology and evolution of acoustic communication in birds*, 426-453.
- Templeton, C.N., Ríos-Chelén, A.A., Quirós-Guerrero, E., Mann, N.I., and Slater, P.J.B. (2012) Female happy wrens select songs to cooperate with their mates rather than confront intruders. *Biology Letters*.
- Templeton, C.N., Rivera-Cáceres, K.D., Mann, N.I., and Slater, P.J.B. (2011) Song duets function primarily as cooperative displays in pairs of happy wrens. *Animal Behaviour* **82**(6), 1399-1407.
- Toon, A., Joseph, L., and Burbidge, A.H. (2013) Genetic analysis of the Australian whipbirds and wedgebills illuminates the evolution of their plumage and vocal diversity. *Emu* **113**(4), 359-366.
- van den Heuvel, I., Cherry, M., and Klump, G. (2014) Land or lover? Territorial defence and mutual mate guarding in the crimson-breasted shrike. *Behavioral Ecology and Sociobiology* **68**(3), 373-381. [In English]
- van Dongen, W.F. (2006) Variation in singing behaviour reveals possible functions of song in male golden whistlers. *Behaviour* **143**(1), 57-82.
- Vehrencamp, S.L. (2001) Is song-type matching a conventional signal of aggressive intentions? *Proceedings of the Royal Society of London B: Biological Sciences* **268**(1476), 1637-1642.
- Veiga, J. (1990) Sexual conflict in the house sparrow: interference between polygynously mated females versus asymmetric male investment. *Behavioral Ecology and Sociobiology* **27**(5), 345-350. [In English]
- Von Helversen, D. (1980) Structure and function of antiphonal duets. *Acta XVIII Int. Orn. Congr.*
- Watson, M. (1969) Significance of Antiphonal Song in the Eastern Whipbird, *Psophodes olivaceus*. *Behaviour* **35**(1/2), 157-178.
- Wickler, W. (1976) Duetting songs in birds: biological significance of stationary and non-stationary processes. *Journal of Theoretical Biology* **60**(2), 493-497.
- Wickler, W., and Seibt, U. (1982) Duetting and the pair bond. *Animal Behaviour* **30**(3), 943-944.
- Yasukawa, K. (1981) Male quality and female choice of mate in the red-winged blackbird (*Agelaius phoeniceus*). *Ecology*, 922-929.

### **Concluding remarks**

These two papers present the first research conducted on the behavioural ecology of the Chirruping Wedgebill (*Psophodes cristatus*). The function of highly conspicuous singing behaviours of males leave many questions relating to signalling and fitness that warrant further research. In addition, despite being less conspicuous, females of this species have proven very interesting. Similar patterns in song rates to males across the breeding season likely indicate similar functionality of female song. As such, female Chirruping Wedgebills may present an ideal study species for future research in this highly understudied area of song. Wedgebills have proven an interesting and ideal species to work with in the field. Further studies of these birds may not only enhance our understanding of song, but have the potential to contribute greatly to our understanding of the behavioural ecology of arid zone species in general.

Pages 68-69 of this thesis have been removed as they may contain sensitive/confidential content