THE FUNCTION OF VOCAL DUETS IN A NEW WORLD WARBLER

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ABSTRACT

In many species of birds, mated individuals sing duets. I reviewed avian duet research with a focus on adaptive functions. I also reviewed methods for territory estimation because I needed to calculate territories for my primary study, in which I used acoustic and spatial data to test the function of duetting. My study species, the Adelaide’s warbler (*Setophaga Adelaidae*), is a Neotropical wood-warbler in which females answer their mates’ songs to form duets. Females answered more of their mates’ songs around the time of aggressive encounters, and when they were close to the territory boundaries or their mate. Females tended to move toward their mate after he sang, but answering did not affect approach behaviour. My findings suggest that female answering functions to defend the female’s territory and partnership, but does not function in mate localization. This is the first evidence of duet function in a New World warbler.

CONTRIBUTIONS OF AUTHORS

I researched and wrote Chapters 1 and 2, and David M. Logue provided supervision and editing. A previous version chapter 2 was submitted to fulfill course requirements for GEOG 5999 taught by Stefan Kienzle and Marcos Dostie. Contributions for Chapter 3 are as follows: Samantha W. Krause: Conceptualization, project administration, funding acquisition, field work, data curation, analysis, visualization, library research, writing, and editing. Tyler R. Bonnell: Analysis assistance. Marcos J. Dostie: Spatial analysis assistance. Samantha I. Booth: Data curation. Peter C. Mower: Field work. D. M. Logue: Assistance with methodology, project administration, funding acquisition, resources, editing, and supervision.

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LIST OF ABBREVIATIONS

CI	Credible Interval
EPC	Extra-Pair Copulations
EPP	Extra-Pair Paternity
HR	Home Range
IID	Inter-Individual Distance
KDE	Kernal Density Estimator
LoCoH	Localized Convex Hull
MCMC	Markov Chain Monte Carlo
MCP	Minimum Convex Polygon
SD	Standard Deviation
SE	Standard Error
UD	Utilization Distribution

CHAPTER 1: INTRODUCTION

My thesis offers an opportunity to explore the early evolution of avian vocal duets. A vocal duet occurs when two individuals vocalize in temporal coordination (Hall, 2009; Logue & Krupp, 2016). One individual initiating a duet opportunity and another individual answering to produce a duet. Avian vocal duets appear in many songbird lineages. They are phylogenetically associated with non-migratory life histories (Benedict, 2008; Logue & Hall, 2014; Mitchell et al., 2019). My research on duet function is the first functional study of duetting in New World warbles, a clade of over 100 species in which ~ 20% duet (Mitchell et al., 2019). Unlike most studies of duet function that focus on species with evolutionarily ancient duets (e.g., wrens; Barker, 2017; Price et al., 2022), Adelaide’s warbler (*Setophaga adelaidae*) duets evolved recently (Mitchell et al., 2019). Studying the Adelaide’s warbler is an opportunity to witness a species in the early stages of duet evolution.

Adelaide’s warbler duets represent an uncommon duet structure that is seldom studied. All duets in this species follow the same pattern: the male sings and the female answers. There are termed female-controlled duets because there is no duet unless the female responds. There are several advantages to studying duets with this simple structure, including simplified analyses, straightforward interpretation, and the elimination of functional hypotheses that require the male to answer the female.

I took an observational approach to studying duet function. Most research on avian vocal duets has relied on playback experiments to assess duet function. These studies have provided insight into duet function in the context of aggressive intrusion. However, duet function often varies by context (Diniz et al., 2018; Hall, 2004, 2009; Koloff & Mennill, 2013; Mennill &

Vehrencamp, 2008; Odom et al., 2017). Observational methods offer an opportunity to observe duets in non-agnostic social contexts and to learn more about the species' ecology.

My primary study goal is to test two functional hypotheses of duet function in Adelaide's warblers. I used detailed observational data to test spatial and temporal predictions of the joint resource defence and mate localization hypotheses. With my study I also hope to provide the first functional study of a duetting New World warbler, offer insight into early duet evolution, and provide an example of rigorous observational methods for studying the broader ecological setting of duet behaviour. Historically, technological advances in recording methods and computational power have periodically sparked innovative experimental methods that have improved our understanding of duet structure, function and evolutionary origins. I hope my methods employing territory estimation techniques from spatial ecology and using the Bayesian statistical framework from broader ecological study, continue in this tradition.

My thesis is broken into five chapters. Chapter 1 introduces the reader to the broader context of my research, states my research goals, and outlines my thesis structure. Chapter 2 provides a review of vocal duetting research with a focus on adaptive functions. In this chapter I outline both the historical and theoretical context for my duet function study. I also navigate several sources of confusion and ambiguity in the duet literature by providing descriptions of the relevant theoretical foundations and clarifying definitions. Chapter 3 outlines the approach I took to selecting a territory estimation technique for my study. Recent methods for territory estimation along with small-scale radio-tracking technologies and new spatial software allowed me to estimate biologically-appropriate territory boundaries for my study species. Chapter 4, which is structured as a scientific paper, describes my research project. In this chapter I test two functional hypotheses of duet behaviour. I include an introduction to the theoretical background and specific predictions, a description of my observational methods and analysis, a summary of my findings, and a discussion interpreting my findings as they relate to my predictions and the existing literature. Finally, chapter 5 closes my thesis with conclusions drawn from my research.

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CHAPTER 2: REVIEW OF VOCAL DUETTING IN THE PERCHING BIRDS (*PASSERIFORMES*)

Introduction to Animal Communication and Vocal Duetting Behaviour

Coordinated vocal communication between two or more individuals has evolved in many lineages, including humans (Logue & Stivers, 2012), non-human primates (Clink & Lau, 2020), bats (Carter et al., 2009), cetaceans (Schulz et al., 2008), anurans (Etzel et al., 2020), insects (Bailey, 2003), and birds (Hall, 2004, 2009). The vocal duets of perching birds (*Passeriformes*) occur when two individuals, usually mates, vocalize in temporal coordination (Hall, 2009; Logue & Krupp, 2016). One individual initiates a duet opportunity and another individual answers to produce a duet. These duets are among the most complex forms of coordinated communication in non-human animals. By studying vocal duets in passerine birds, we can learn more about the general principles that influence the evolution of coordinated communication across taxa.

This chapter is a review of past and present avian duet research with a focus on the hypothesized adaptive functions of duets as discussed in current literature. I have focused primarily on the order Passeriformes because my study species, the Adelaide's warbler, is a small Oscine songbird. Oscines are a suborder within Passeriformes characterized by vocal learning, a distinct syringeal morphology, and complex neuromuscular control of song production relative to "suboscine" passerines (Garcia et al., 2017). However, I have chosen to include a few studies of non-Passeriformes species that have similar natural history to most Passeriformes species (e.g., territorial and socially monogamous). This chapter begins with a historical overview of avian duet research. A discussion of the history of duet research necessarily touches on various aspects of duetting biology, such as the functions and mechanisms. I will delve into the biology of duetting in detail later on in the chapter. The historical overview provides a contextual backdrop to my thesis by highlighting influential publications and theoretical milestones. Next, I describe the structure of passerine duets and proximate mechanisms of duet production. I then discuss our current understanding of the evolution of vocal duets in passerines. The following section, which comprises the bulk of this chapter, provides an overview of functional hypotheses of duet participation. The chapter closes with a summary of my thesis goals.

History of Avian Duet Research

The scientific study of avian duets began in the 1960s with William Thorpe's observation that certain African birds sing their antiphonal duets with exceptional temporal precision (Hall, 2004). In 1963, Thorpe described the auditory reaction times of the black-headed gonolek (*Laniarius erythrogaster*; Thorpe, 1963). He continued investigating duetting behaviour over the next 10 years, publishing several papers on the duets of the Ethiopian boubou (*Laniarius aethiopicus*; Thorpe & North, 1965; Thorpe & North, 1966). Other studies of auditory reaction times in duetting birds appeared soon after (Grimes, 1965; Payne & Skinner, 1970; Power, 1966). Diamond and Terborgh (1968) classified duets into three categories: (1) antiphonal, with partners alternating phrases, (2) simultaneous, with partners singing different phrases, and (3) simultaneous with partners singing identical phrases. Although modern researchers often characterize duet structure in greater detail by measuring the degree of overlap and the associated variation, the terms "antiphonal" and "simultaneous" still appear in the duetting literature.

A theoretical framework for duetting began to emerge in the 1970s. Todt (1970) and Payne (1971) discussed hypothetical duet functions including mate recognition, contact maintenance, pair-bond maintenance, reproductive synchronization, and territory defence. Both drew their hypotheses from an understanding of the local ecology referencing local vegetation, climate, and interactions with conspecifics. Payne (1971) also noted that duets appeared to serve multiple functions in nearly every species that had been studied. In 1972, nearly 10 years after his initial work sparked the field of duet research, Thorpe published a monograph summarizing the existing literature on duetting birds and a list of possible duet functions (Hall, 2004; Thorpe, 1972). Pair-bond maintenance was not acknowledged on his list; however, he added a new function: reassurance after disturbance.

Experimental playback methods appeared in duet research in the late 1960s, after their initial appearance in the broader bird song literature in the 1950s and 60s (Collias & Joos, 1953; Lemon, 1968; Marler, 1956; Stein, 1963; Weeden & Falls, 1959). Grimes (1966), Hooker & Hooker (1969), and Watson (1969), were among the first studies to use a loudspeaker to play a recorded duet to a mated pair. Acoustic playback quickly gained popularity in duetting research. Several labs used song playback as part of long-term studies of model duetting species.

Todt led an extensive study of duets in white-browed robin-chats (*Cossypha heuglini*), which demonstrated the value of studying a single species with a variety of methods (Hall, 2004). Field recordings revealed that white-browed robin-chats sing four categories of duets in different contexts, and that duetting partners approach each other before duetting (Todt et al., 1981). By manipulating the distance between males and females in an aviary, Todt (1975) demonstrated that sharing a territory is a requirement for duetting. Artificially muting the male or deafening the female did not cause pairs to divorce, which led to the conclusion that duets were not necessary for pair-bond maintenance (Todt & Hultsch, 1982). However, deafened females no longer engaged in reproductive activities, suggesting that duets were necessary for reproduction (Todt & Hultsch, 1982). Field experiments with model birds and song playback indicated that signal receivers perceive duets as more threatening when singers are in close proximity (Hultsch & Todt, 1984). In a summary of their research on white-browed robin-chats, Todt and Naguib

(2000) conclude duets function as an intra-pair greeting ceremony as well as in extra-pair territory defence.

Researchers began to reveal the behavioural mechanisms that drive duet structure by isolating individual-level singing behaviour of duetting pairs. Vencl and Souček (1976) were the first to record duetting partners in stereo to precisely define each bird's repertoire of duet phrases. They worked with crested laughing thrushes (*Garrulax leucolophus*) housed in a large greenhouse where they could control the birds' spatial arrangement in relation to their audio equipment. With one of the first applications of computer analysis in birdsong research, Vencl and Souček (1976) discovered that the sequence of male and female phrases that comprise duets were not random. Each male phrase type appeared to prompt the female to answer with a specific phrase of her own. This idea would re-emerge thirty years later (Logue, 2006).

Wickler (1974) also examined individual-level behaviours and the pair bond between duetting mates. He discovered that both male and female white-browed robin-chats could influence their mate's singing speed. This discovery led him to propose the "coy-ness" hypothesis, which states that difficult-to-learn duets function to prevent partners from deserting because they invested in learning the duet (Wickler, 1980). Shortly thereafter, Serpell (1981) argued the coy-ness hypothesis relies on the Concorde fallacy (a.k.a., sunk cost effect; Arkes & Ayton, 1999; Dawkins & Carlisle, 1976). Named after the supersonic passenger jet, the Concorde fallacy occurs when someone justifies continued investment in an endeavour on the basis of past investment. This justification is fallacious because past investment is irrelevant to the question of whether to invest further. According to Serpell (1981), Wickler incorrectly assumed that desertion following duet learning is more costly than desertion after time investment alone. Unless the energetic impact of duet learning impairs an individual's ability to obtain a new mate, the energetic investment in duet learning is a “sunk cost” that should not impact an individual’s decision to remain in the partnership or find a new pair mate. Further, coy-ness did not account for widespread observations that duet rates increased during aggressive contexts. Wickler (1980) also proposed that birds participate in duets to advertise mated status. Even though this idea had first been suggested by Tarboton in 1971, it is Wickler and Seibt (1980) who typically receive recognition for its conception (e.g., Hall, 2004; Marshall-Ball et al., 2006). Although advertising mated status was initially proposed within a cooperative behaviour framework, this idea inspired future conflict-based hypotheses. Rather than assuming duets were a cooperative behaviour, conflict-based hypotheses assume the interests of mated birds are not always aligned (Levin, 1996b).

An early entry in the conflict-based duetting literature was Brown and Lemon’s (1979) comparison of vocal behaviour in the duetting happy wren (*Thryothorus felix*) and the non-duetting Sinaloa wren (*Thryothorus sinaloa*). They concluded female duet contributions may be “discouraging [to] vagrant females”. Four years later, Sonnenschein and Reyer (1983) built on this and Wickler and Seibt’s (1980) idea of advertising mated status to define an explicitly conflict-based “acoustic mate-guarding” hypothesis. Citing Trivers’ (1972) work on parental investment and sexual conflict, Sonnenschein and Reyer (1983) suggest males attempt to prevent their mates from obtaining other sexual partners by answering the mate’s songs to advertise her mated status. Sonnenschein and Reyer’s publication cemented conflict between socially monogamous pair mates as a viable theory in duetting literature.

In 1982, Farabaugh published an influential review of avian duetting. Her review not only consolidated the duetting literature, but also provided a framework to quantify duet features. She suggested researchers describe four duet parameters: (1) Type of vocalization,

(2) percentage of vocalizations that occur in duets, (3) order of song elements, and (4) temporal precision between partners (Farabaugh, 1982; Hall, 2004). Four decades later, these parameters still form the basis of scientific duet descriptions. Farabaugh (1982) concluded that duetting species are typically tropical, non-migratory, year-round territorial, and tend to maintain long-term pair bonds. She did not find evidence that duetting was associated with sexual monomorphism. Although later studies based on phylogenetically explicit methods have called some of these conclusions into question (Logue & Hall, 2014; Tobias et al., 2016), Farabaugh's review marks an important early effort to understand traits that co-evolved with vocal duets. Farabaugh also summarized the existing evidence on duet function, concluding that the two most common duet functions were territory defence and pair-bond formation (Farabaugh, 1982).

The next major shift in the duetting literature came over a decade later, when two papers by Levin (Levin, 1996a, 1996b) concluded that conflict, not cooperation, drove the evolution of duetting in bay wrens (*Thryothorus nigricapillus*). Levin conducted mate-removal and playback experiments on colour-banded and surgically-sexed individuals. The mate-removal experiments revealed that bay wrens do not alter duet precision after re-pairing, failing to support the idea that duets function to maintain the pair bond. Further, unpaired birds do not lose their territories, failing to support the idea that two birds must work in concert to maintain a territory (Levin, 1996a). The playback experiments showed that females respond more strongly to female song than male song, unpaired males respond most strongly to female song (likely in an effort to attract a mate), and paired males respond most strongly to male song (Levin, 1996b). Based on sex-specific responses to playback, Levin concluded that female and male songs had different functions. Based on the strong response of paired males to male song combined with the seemingly attractive quality of female song, she also concluded that males participate in duets to acoustically guard their mates (Levin, 1996b). Although earlier researchers had suggested conflict could play a role in duet function, Levin was the first to directly test and find support for a conflict-based duet function.

Levin's work inspired a boom of experimental, field-based duetting research on duet function. Many new names appeared in the literature, and the volume of publications grew. Hall's work on Australian magpie-larks (*Grallina cyanoleuca*) tested the conflict/cooperation dichotomy and found clear support for cooperative duet function (Hall, 2000; Hall & Magrath, 2000). Mennill introduced new technologies and methodologies to the field with his work on rufous-and-white wrens (*Thryothorus rufalbus*) and established microphone arrays as a viable observational tool (Langmore, 2002; Mennill et al., 2006). Logue (2006, 2007b) tested predictions of functional hypotheses by observing individual-level behaviours in his experiments with black-bellied wrens (*Pheugopedius fasciatoventris),* and studied the individual-level behaviours that structure duets. Mann and Marshall-Ball found evidence that canebrake wren (*Cantorchilus zeledoni*) duets facilitate cooperation (Mann et al., 2003; Marshall-Ball et al., 2006). Gill et al. (2005) explored the natural history of the buff-breasted wren (*Cantorchilus leucotis*), and found evidence their duets were not used for mate-guarding. Benedict's work on the California towhee (*Melozone crissalis*), a temperate breeding sparrow, introduced a novel taxon to the duetting literature (Benedict, 2008b; Benedict & McEntee, 2009). These studies represent only a fraction of the duetting publications from the early 2000s.

The turn of the millennium saw numerous technological advances that enabled researchers to better measure duet structure and test predictions in new ways. Perhaps most importantly, the move from analog to digital recording and the availability of powerful personal computers revolutionized recording and playback techniques. More sophisticated interactive playback experiments became possible as new software was developed (Langmore, 2002; Mennill & Ratcliffe, 2000). Logue (2006) used Syrinx PC software (Burt et al., 2001) and interactive playback methods with individual female black-bellied wrens. Stereo duet playback experiments were introduced by Logue in the early 2000s. During a stereo duet playback, dual-channel duet recordings are played from two separate speakers. Stereo duet playback elicits stronger responses than monophonic playback, and permits the measurement of sex-specific territorial responses to duets (Logue, 2005; Logue & Gammon, 2004; Rogers et al., 2004).

Advances in spatial tracking systems led to advances in the spatial ecology of duetting. Logue (2007a) used radio tracking to monitor the locations of paired black-bellied wrens. Mennill and Vehrencamp (2008) used microphone arrays and triangulation to automate the process of recording and locating rufous-and-white wrens. Both studies concluded that pairs duet more when they are close together and that they use duets to maintain contact.

Hall contributed two influential review papers in the 2000s. The first provided an extensive overview of functional hypotheses for duetting behaviour (Hall, 2004). It also emphasized the importance of understanding the signaler’s intended receiver (intra- or inter-pair) when evaluating prospective functions. Her second review went beyond function to consider all aspects of avian duetting (Hall, 2009). There, Hall pointed out that little was known about the ontogenetic, neural, or hormonal causes of duetting behaviour. Her focus on the individual led her to critique the view that functional hypotheses could be classified as either conflict- or cooperation-based. A key question asked whether acoustic mate-guarding necessarily emerges from conflict between mates. Her argument asserted that if both partners stand to benefit from long-term pair-bonds, then mate-guarding could be mutually beneficial. Notably, her review also suggested that the individual-level behavioural mechanisms that influence duet structure, rather than pair-level metrics, should comprise the basis of functional and evolutionary studies of duet structure.

Hall (2009) summarized the support for five commonly studied functions for duet participation. (1) Joint resource defence seems to be the primary function of duetting behaviour. (2) Mate guarding for partnership defence is likely to be mutually beneficial and has reasonable support. (3) Mate guarding to guard paternity is difficult to test because its predictions overlap with those of other hypotheses. At the time of this review, there was little support for this hypothesis. (4) Recognition and contact functions were well-supported in a few species, but Hall recommended tests in more species. (5) Ensuring reproductive synchrony, had not been directly studied in a duetting species.

The early 2000's boom in duet research includes studies of phylogenetically diverse species. Wren species (*Troglodytidae* spp.) were pervasive in duet literature because mated pairs of many wren species produce intricate vocal duets (Logue, 2006). Bushshrikes (*Malaconotidae*) and antbirds (*Thamnophilidae*) also became more common in the literature (Hall, 2009). Other examples of novel duetting taxa in the literature include: purple-crowned fairy-wrens (*Malurus coronatus*), Eastern whipbirds (*Psophodes olivaceus*), and stripe-headed sparrows (*Aimophila r. ruficauda*; Hall, 2009).

Today, the field of duet research is robust and diverse. New research on ontogeny and neural mechanisms has begun to fill gaps in the literature (Coleman et al., 2021; Fortune et al., 2011; Rivera-Cáceres et al., 2018). Advances in computational power have facilitated new approaches to acoustic and statistical analyses. Recent phylogenetic studies have revealed meaningful patterns in the evolution of duetting behaviour (Mitchell et al., 2019; Odom et al., 2014). In particular, Odom et al. (2014) showed that females likely sang in the last common ancestor of extant songbirds (oscine passerines). This revelation, combined with recent efforts to highlight the significance of female song (Odom & Benedict, 2018; Riebel et al., 2005; Riebel et al., 2019), stimulated cultural (Webb et al., 2021), neurological (Coleman et al., 2021), and ontogenetic (Rivera-Cáceres & Templeton, 2019) research on female song and duetting. The field of duet research continues to benefit from advances in technology that open doors for innovative inquiry.

Duet Structure

Duets occur when two individuals vocalize with temporal coordination (Hall, 2009; Logue & Krupp, 2016) One bird "initiates" by singing spontaneously, and the other turns the solo into a duet by "answering." In some cases, it is difficult to determine whether two overlapping vocal signals constitute a duet. To be considered a duet, vocalizations should: (1) overlap more than expected by chance, (2) have a consistent temporal relationship, and (3) have a repeated, stereotyped structure (Taylor et al., 2019). If three or more individuals participate the resulting signal is referred to as a "chorus" (Logue & Krupp, 2016). Some species participate in both duets and choruses such as the rufous-naped wren (*Campylorhynchus rufinucha*; Bradley & Mennill, 2009), and the red-backed fairy-wren (*Malurus melanocephalus*; Dowling & Webster, 2013). The role of each sex in a duet varies by species. Male purple-crowned fairy-wrens initiate ~ 66% of duets (Hall & Peters, 2008), male tropical boubous (*Laniarius major*) initiate 89% of duets (Grafe et al., 2004), and female grey-breasted wood wrens (*Henicorhina leucophrys*) initiate ~ 65% of duets (Dingle & Slabbekoorn, 2018). In some species only one sex initiates duets. Only males initiate duets in Peruvian warbling-antbirds (*Hypocnemis peruviana*; Tobias & Seddon, 2009), white-bellied antbirds (*Myrmeciza longipes*; Fedy & Stutchbury, 2005), Eastern whipbirds (Rogers et al., 2007), Steere's liocichlas (*Liocichla steerii*; Weng et al., 2012), and

Adelaide's warblers (Staicer, 1991). There are no documented species with only female initiated duets.

Many duets are composed of non-random phrase type combinations. Non-random phrase type combinations are a pair-level phenomenon, which may result in discrete "duet types" (Logue, 2006). For some species, the same two phrases are repeated for the duration of the duet. It is also common for duets to be initiated with an introductory phrase (Mann et al., 2003). This creates a predictable A-B-A-B, or I-A-B-A-B pattern as seen in the canebrake wren (Logue, 2006; Mann et al., 2003). Plain-tailed wrens (*Pheugopedius euophrys*), riverside wrens (*Cantorchilus semibadius*), and black-bellied wrens also sing non-random phrase patterns, but use more phrase types to create longer patterns such as A-B-C-D-A-B-C-D (Coleman & Fortune, 2018; Logue, 2006; Quirós-Guerrero et al., 2017). Pairs with several distinct phrase combinations may sing with immediate variety, rapidly switching between different phrases, or with eventual variety, repeating one phrase type multiple times before switching to a new phrase (Hall, 2009). Repeat mode singing tends to be more common (Hall, 2009). Contrariwise, in white-browed sparrow weavers (*Plocepasser mahali*), duet bouts do not include any repeat phrase types, with males and females altering phrase order between every bout (Lemazina et al., 2021).

Scientists classify duets according to the relative timing of partners' vocalizations. Antiphonal duets occur when individuals alternate their vocalizations during the duet with little or no overlap. In some species there is virtually no pause (< 0.1 s) from the end of the first phrase to start of the second (Logue et al., 2008; Quirós-Guerrero et al., 2017; Templeton et al., 2013). Some of the most remarkable antiphonal singers include riverside wrens (Quirós-Guerrero et al., 2017) and plain-tailed wrens (Coleman & Fortune, 2018), whose duets sound like the song of a single bird to naïve human ears. Overlapping duets occur when the birds' songs overlap during the duet. Species that sing overlapping duets include purple-crowned fairy-wrens (Hall & Peters, 2008), white-eared ground sparrows (*Melozone leucotis*; Méndez & Sandoval, 2019), barred antshrikes (*Thamnophilus doliatus*; Koloff & Mennill, 2013b), and large-footed finches (*Pezopetes capitalis*; Trejos-Araya & Barrantes, 2017). Most often, duetting partners' phrases are structurally distinct and only overlap partially during a duet. However, a striking exception is the male-male duet of the lance-tailed manakin (*Chiroxiphia lanceolata*) in which the singers' phrases are identical and simultaneous (DuVal, 2007). Some species sing both alternating and overlapping duets. Grey-breasted wood wrens sing antiphonal duets 37-57% of the time and have low timing precision (Dingle & Slabbekoorn, 2018). In tropical boubous, ~ 60% of duet types are antiphonal (Grafe et al., 2004). Most white-browed coucal (*Centropus superciliosus*) pairs use a mixture of overlapping and antiphonal, but some pairs only sing antiphonal duets and others only overlapping (Brumm & Goymann, 2017). These three structural classes – antiphonal, overlapping, and mixed – are roughly equally represented among duetting species (Dahlin & Benedict, 2014).

Frequency is not often studied in duet research. In tropical boubous (Grafe et al., 2004), white-browed coucals (Brumm & Goymann, 2017), and black-bellied wrens (Logue et al., 2007), male and female duet phrases are sung at different frequencies. In the large-footed finch, the answering partner coordinates the frequency of their vocalization with the initiating partner, creating a gradual cascade of notes of descending frequency (Hz) as each partner alternates vocalizations within the duet (Trejos-Araya & Barrantes, 2017).

Duet amplitude remains poorly understood. Any mention of amplitude in the literature tends to be anecdotal (e.g., Mennill & Vehrencamp, 2005), such as Wickler's (1976) observation that duets are typically louder than necessary if the intended receiver is the duetting partner. Although low amplitude “soft song” is often discussed in broader songbird literature (R. C. Anderson et al., 2012; Logue, 2021), only one study has explored its aggressive function in a duetting species (Liu et al., 2023). Similarly, some species sing low-amplitude duets near the nest (Boucaud, Mariette, et al., 2016; Elie et al., 2010), but this is another area with scant current research. Limited quantitative research exists on the amplitude of duets because of the logistical challenges of measuring amplitude in the field. The accuracy of amplitude measurements in recorded sound depends on the distance between the observer and subject, recording equipment, microphone direction, and other environmental variables. However, new technologies may be able to overcome these challenges. Lemazina et al. (2021) and Hoffman et al. (2019) used microphones physically attached to individual birds during their studies of white-browed sparrow weavers, allowing exact temporal measurements of vocalization timing. This system may also offer opportunity for future researchers to measure amplitude.

Not all duets are composed of songs. In species like Nava’s wren (*Hylochilus navai*), Sumichrast’s wren (*Hylochilus sumichrasti*; de Silva et al., 2004), and Adelaide’s warbler (Staicer, 1991), duets occur when one pair member sings and the other produces call notes. In other species, like zebra finches (*Taeniopygia guttata*; D'Amelio et al., 2017), common redpolls (*Carduelis flammea*), and pygmy nuthatches (*Sitta pygmaea*; reviewed in Benedict, 2008a), both male and female use calls to duet.

Sex-specific phrases are common in duetting species. Examples of species in which males and females sing distinct duet phrases include crimson-breasted shrikes (*Laniarius atrococcineus*; van den Heuvel et al., 2012), grey-breasted wood-wrens (Dingle & Slabbekoorn, 2018), barred antshrikes (Koloff & Mennill, 2013b), tropical boubous (Grafe et al., 2004), Sclater's wrens (*Campylorhynchus rufinucha humilis*; Quiroz-Oliva & Sosa-López, 2021), common cuckoos (*Cuculus canorus*; Moskat & Hauber, 2021), Steere's liocichlas (Mays et al., 2005), and Adelaide's warblers (Staicer, 1991). In some species males occasionally sing "solo duets" or "pseudo duets" that seem to simulate true duets. Pseudo duets have been observed in tropical boubous (Grafe et al., 2004), white-browed sparrow weavers (Voigt et al., 2006), and Australian magpie-larks (P. Ręk & Magrath, 2017).

Duets are usually comprised of solo songs, calls, or a combination of the two, but some species have specific vocalizations reserved only for duets. Common cuckoo males sing a three-note variation of their two-note call when duetting (Moskat & Hauber, 2021). Whereas the *squeal* calls used by duetting California towhees are structurally distinct from solo vocalizations (Benedict & McEntee, 2009).

Some species pair duets with visual displays. In the manakin genus *Chiroxiphia*, pairs of males produce complex visual and acoustic displays to court a female (DuVal, 2007). The lance-tailed manakin's dance involves a "leapfrog" display in which the males jump over each other in rapid succession while duetting (DuVal, 2007). In blue-capped cordon-bleu (*Uraeginthus cyanocephalus*), both males and females sing and perform a rapid "tap dance" as part of their courtship display (Ota & Gahr, 2021; Ota et al., 2018). Australian magpie-larks' territorial displays often involve both wing movement and vocal duets; the more coordinated the movement, the more threatening the signal (Paweł Ręk & Magrath, 2022).

Phenology

Duetting is seldom studied outside of the breeding season. Consequently, there are relatively few published studies available of seasonal variation in duetting, and even fewer that report individual-level data. That said, the field of duet research continues to evolve, and more studies are slowly adding individual-level seasonal data to the literature (e.g., Diniz et al., 2018; Hall, 2006; Logue, 2004; Odom et al., 2017).

The limited studies available indicate that duetting behaviour varies by season. Male songbirds typically increase their singing activity just prior to and during the breeding season (Odom et al., 2016; Rundstrom & Creanza, 2021). However, the impact of breeding season on duetting behaviour is much less predictable, with individual initiation rates, answering proportions (answers / partner's initiations), and pair-level duet rates (duets / time) varying widely. In some species, males and females show similar seasonal trends in answering behaviour. In rufous horneros (*Furnarius rufus*), females initiate less, males initiate more, and both sexes answer more during the breeding season (Diniz et al., 2018). These changes in individual-level behaviours result in an increase in duet rates (Diniz et al., 2018). In Australian magpie-larks and Venezuelan troupials (*Icterus icterus*), females initiate less, males initiate more, and both sexes answer approximately the same proportion of their partner's songs during the breeding season (Hall, 2006; Odom et al., 2016). These changes in individual-level behaviours result in a decrease in duet rates in both species. Interestingly, despite the breeding season having a similar impact on all three species' initiation rates, the distinct effects on the proportion of answered songs in rufous horneros compared to Australian magpie-larks and Venezuelan troupials, is enough to produce opposing trends in duet rates (Diniz et al., 2018; Hall, 2006; Odom et al., 2016).

In some species, male and female answer proportions change in different ways over the course of the year. Black-bellied wrens and yellow-breasted boubous (*Laniarius atroflavus*) are two examples in which seasonal changes in individual-level vocalization rates produce complex seasonal trends in duet rates (Logue, 2004; Szymański et al., 2021). Male black-bellied wrens initiate more songs and females answer more often in the breeding season, resulting in more male-initiated duets, but a decrease in the proportion of male songs that are answered by the female (Logue, 2004). Female initiation rates were unaffected by season and males answer slightly less often in the breeding season, resulting in fewer female-initiated duets in the breeding season. During the breeding season, yellow-breasted boubou males initiate more, females initiate less, and male answer proportion is slightly less than during the post-breeding season (Szymański et al., 2021). Female answer proportions and pair-level duet rates are unaffected. These studies show how detailed individual-level measurements, especially in complex systems, are necessary to fully understand the seasonal changes in duetting behaviour.

From the above examples it is clear that individual-level behaviours can interact in various ways to produce similar pair-level duetting behaviours. Prior to recommendations of to report individual-level behaviours (Hall, 2009; Logue & Krupp, 2016), studies of duetting species often focused on pair-level behaviour and failed to report individual-level behaviour. One problem with that approach is that it is not always possible to work backwards from pair-level behaviours to calculate individual-level behaviours (Logue & Krupp, 2016). Failure to provide individual-level behaviour data limits the conclusions that can be drawn about the sex-specific functions of duetting behaviour.

To summarize trends in duetting species' vocal phenology: (1) Males tend to initiate song more throughout the year. (2) Females tend to initiate as much or less during the breeding season compared to the non-breeding season. (3) Both sexes tend to answer as much as or less during the breeding season, with few exceptions. (4) Duet rates vary widely among taxa, with reports of rates increasing, decreasing, and remaining the same during the breeding season. These trends should be viewed as provisional given the dearth of phenological data on vocal behaviour in duetting birds. Given that duets serve different functions in different species (Hall, 2004, 2009), it is not surprising to find so much phenological variety.

Proximate causes of duetting: Mechanisms and Ontogeny

Duetting is a pair-level behaviour, so it is useful to distinguish between the physiological and behavioural mechanisms that generate it. Physiological mechanisms are the processes that generate duetting behaviour in an individual. Examples include the way that testosterone affects song initiation rate, or how the brain chooses a song type to answer the mate. Behavioural mechanisms are patterns of behaviour at the level of the individual that generate group-level (e.g., pair-level) behaviours. Examples of behavioural mechanisms that generate duets include the tendency to answer the mate when s/he is close by, or the tendency to sing a particular song type in response to one of the mate's songs.

Physiological Mechanisms

Birds have specialized anatomy that allows them to produce complex vocalizations. The avian vocal organ called the syrinx, sits at the tracheobronchial junction (Goller, 2021). Each of the two bronchi contain a valve-like system of vibratory tissues (labia) that are individually controlled by the central nervous system and syringeal muscles (Goller, 2021). When a bird exhales, air flows through the vibratory tissue and causes it to oscillate, generating sound (Goller, 2021). Many songbirds divide the effort of song production between the two valves: typically higher fundamental frequencies are produced by the right valve and lower fundamental frequencies are produced by the left (Catchpole & Slater, 2008). The sound produced in the syrinx is modified as it travels up the vocal tract and out the bill (Catchpole & Slater, 2008; Goller, 2021).

Neurological control of song production occurs in the forebrain of songbirds in several connected areas known collectively as the “song system” (Coleman & Fortune, 2018). The principle motor pathway runs from the HVC (not an acronym; previously referred to as the “higher vocal center”) to the robust nucleus of the archistriatum (RA) and on to the tracheosyringeal portion of the hypoglossal nucleus (Catchpole & Slater, 2008). The connected hypoglossal nerve controls the syrinx and sound production. This song system is essential for producing learned songs, but not for producing innate calls (Catchpole & Slater, 2008). The HVC has neurons with both sensory and motor properties (Coleman & Fortune, 2018). These neurons activate when a bird sings or hears a playback of its own song. Feedback mediated by the HVC is essential for song learning and maintenance in songbirds (Coleman & Fortune, 2018).

In the duetting plain-tailed wren, the HVC neurons respond to both the bird’s own (autogenous) song and heterogenous song from the duet partner (Coleman & Fortune, 2018; Fortune et al., 2011). These neurons respond more strongly to playback of complete duets than they do to solo song (Fortune et al., 2011). This suggests HVC premotor circuits encode the whole duet, rather than just one individual’s contribution to the duet (Fortune et al., 2011). In some duetting species, the song control system is of similar size and contains similar steroid hormone receptors in both sexes, yet in others there are sex differences in size and structure (Rivera-Cáceres & Templeton, 2019). Although the song system tends to be larger in males than females, there is no evidence that this asymmetry explains sex differences in singing ability in duetting species (Gahr et al., 1998). It is now hypothesized that there may be a minimum size threshold in song nuclei required for song production (Lobato et al., 2015).

The HVC allows a bird to coordinate the timing of its songs relative to the partner's songs (Fortune et al., 2011). In white-browed sparrow weavers, the onset of the duetting partner's response triggers a change in the rhythm of the initiating bird's own neural activity and impacts its subsequent vocalizations (Hoffmann et al., 2019). Inhibition mechanisms may help mediate the exact timing of rapid turn taking in plain-tailed wrens (Coleman et al., 2021). Premotor activity during a bird's own vocalization alternates with the inhibitory effects of hearing the partner's vocalization (Coleman et al., 2021). The emergent sensory feedback loop is mirrored in both duetting individuals allowing exact temporal coordination (Coleman et al., 2021).

The auditory system of birds is similar to that of mammals and lizards. All three groups have tonotopic ears, meaning that the hair cells in the basilar membrane are organized along a frequency gradient with hair cells more sensitive to high frequency at one end and low frequency at the other (Bradbury & Vehrencamp, 2011). The smooth gradient of frequency-specific hair cells allows different hair cells to respond to different frequencies as sound propagates along the length of the cochlea (Bradbury & Vehrencamp, 2011). In general, mammals tend to be able to perceive a larger frequency range than birds, however, birds have greater temporal and amplitude resolution within their range due to a wider basilar membrane with higher numbers of hair cells (Bradbury & Vehrencamp, 2011). Unlike human hearing, bird auditory perception does not degenerate with age (Gall et al., 2011; Krumm et al., 2017; Langemann et al., 1999). In some species of birds, females are more sensitive to acoustic signals than males (Gall et al., 2011).

Birds have excellent vision. Most birds have tetrachromatic colour vision based on four types of cone cells that use opsin-based pigments and contain oil droplets (Kelber, 2019). Passeriform birds are able to perceive wavelengths that are visible to humans (400-700 nm), and most are also sensitive to ultra-violet light (< 400 nm; Ödeen et al., 2011). It is therefore unsurprising to find species with visual components to their duet displays (DuVal, 2007; Ota et al., 2018; Paweł Ręk & Magrath, 2016, 2022).

Hormones have the potential to influence duetting behaviour. I am not aware of any studies that address the influence of hormone levels on duetting behaviour. However, it is possible to draw comparisons to hormone studies in non-duetting songbirds. In male birds, testosterone influences multiple regions of the song system, altering song rates and stereotypy (Rundstrom & Creanza, 2021). These impacts of testosterone to singing behaviour are observed in males in both temperate and tropical songbird species (Voigt & Leitner, 2013). In Northern songbird species, annual changes in day-length trigger an increase in circulating testosterone levels and song rates during the breeding season (Gahr, 2020). In year-round resident species testosterone levels also increase during the breeding season, but may peak later in comparison to Northern species (Goymann & Landys, 2011). The elevated song rates during the breeding season seen in the males of many duetting species may be related to seasonal changes in testosterone. However, song rates outside of the breeding season are not explained by a testosterone-sensitive system (Gahr, 2020).

Hormones in female birds have not been studied as extensively as males, particularly in relation to singing behaviour. Female birds' auditory circuits are influenced by estrogen, and are likely to be more sensitive to auditory input when estrogen levels peak during the breeding season (Brenowitz & Remage-Healey, 2016; Maney et al., 2006). Females may be more interested in male singing behaviour during the breeding season, perhaps using male song as an indicator of male quality in selecting sexual partners (Ballentine et al., 2004; Drăgănoiu et al., 2002; Mountjoy & Lemon, 1996; Nowicki et al., 2002). Female song is common in many duetting species (Hall, 2004, 2009), and circulating testosterone has been found in singing female songbirds (Gahr, 2020). However, very little data exists on testosterone levels in female songbirds, especially during the female fertile periods (Gahr, 2020).

Other hormones may also play a role in duetting behaviour. Many duetting species adjust their duet structure as adults when re-mating (Logue & Krupp, 2016; Rivera-Cáceres & Templeton, 2019), indicating a type of open-ended vocal learning. Recent work on European starlings (*Sturnus vulgaris*), a temperate, open-ended learning species, revealed that the thyroid hormone may play an important role in seasonal neuroplasticity (Orije & Van der Linden, 2022). This area of research is in its infancy, and hopefully will grow to include duetting species in the future.

Behavioural Mechanisms

Duet participation requires adherence to consistent patterns of behaviour, or “rules”, by one or both duetting individuals. The minimum duet comprises an initiation followed by an answer. In some species, a simple initiation-answer exchange is the entire duet, but in others, both birds may continue to answer each other to form a longer duet (Hall, 2009). For a duet to occur, one bird must decide to sing spontaneously, and another must decide to answer. An individual bird will have internal rules to determine when to initiate a duet opportunity (i.e., spontaneously sing), and for many species these rules are related to external factors. Song rates can vary with breeding season, by time of day, by sex, by singing role within the duet, and by social context (Dingle & Slabbekoorn, 2018; Diniz et al., 2018; Koloff & Mennill, 2013b; Odom et al., 2017). Many species adhere to answering rules when selecting their phrase(s) for a duet. The rules that an individual follows to select the next phrase in a duet (i.e., its “duet code”) results in predictable phrase patterns within a duet (Logue, 2006). For example, if a female’s duet code causes her to answer male phrase A with female phrase X, and male phrase B with female phrase Y, then A will tend to precede X, and B will tend to precede Y. Duet codes have been found in black-bellied wrens (Logue, 2006), crimson-breasted shrikes (van den Heuvel et al., 2012), rufous-and-white wrens (Osmun, 2010), happy wrens (Templeton et al., 2013), canebrake wrens (Rivera-Cáceres et al., 2016), and other species (Hall, 2009). Even white-browed sparrow-weavers, a species with vast individual and duet repertoires, adhere to a kind of duet code (Lemazina et al., 2021).

Temporal answering rules govern the timing of individual phrases in temporally coordinated duets. In species with multiple antiphonal exchanges between duetting partners, one or both partners may alter their tempo to match their partner (Fortune et al., 2011; Logue et al., 2008; Rivera-Cáceres, 2015; Templeton et al., 2013; Trejos-Araya & Barrantes, 2017). In black-bellied wrens, both partners rapidly adjust the timing of their phrases to reduce overlap and silent gaps between phrases (Logue et al., 2008). However, in white-browed sparrow-weavers, only the initiating partner adjusts to the tempo of the answering partner (Hoffmann et al., 2019). During the simultaneous duets of large-footed finch, the answering partner synchronizes their notes with the initiating partner by adjusting the silent intervals (Trejos-Araya & Barrantes, 2017). Other species also adjust the silent intervals depending on their partner’s phrase. Canebrake wrens adjust the timing between each phrase depending on whether their previous phrase was answered, what phrase they last sang, and the position of the phrase within the duet (Rivera-Cáceres, 2015). Similarly, Female plain-tailed wrens increase their intersyllable intervals if their partner stops participating in a duet, suggesting they too alter their duet phrases depending on their partner’s phrases (Fortune et al., 2011). Sex-specific timing rules are not uncommon, with males adjusting their tempo more quickly (Koloff & Mennill, 2013b), more consistently (Hall, 2006), or more often than females (Rivera-Cáceres, 2015). Although the species-specific answering rules differ, they all result in temporally coordinated duets.

Some of the rules that govern duet structure are contingent on visual contact or distance between partners. Zebra finch pairs alter their vocal exchanges to incorporate more acoustic information (i.e., individual identity) when not in visual contact with their partner (Perez et al., 2015). Black-bellied wrens decease answer rates and duet duration when separated (Logue, 2007a). Other species adapt the timing of their duet contributions to compensate for the speed of sound including plain-tailed wrens (Coleman & Fortune, 2018), Australian magpie larks (Paweł Ręk & Magrath, 2016, 2020), and happy wrens (Templeton et al., 2013).

Ontogeny

Like parrots, hummingbirds, and possibly some suboscines, songbirds learn the structural details of certain vocal signals from other conspecifics (ten Cate, 2021). In songbirds (suborder Oscine), social learning during a critical sensitive period is essential for the development of fully functional species-specific song (Catchpole & Slater, 2008; Riebel, 2016; Thorpe, 1958). Both song learning and production use specific regions of the brain, and are influenced by the social environment (Rivera-Cáceres & Templeton, 2019). Not only do birds learn the song types they will go on to sing, but they also learn which song types to select for in their mate (Riebel, 2016). A female’s preference for male song is typically learned through exposure when young, and can influence which songs become popular within a population (Riebel, 2016).

In addition to learning song structures, duetting songbirds must also learn rules that govern the timing and phrase type choice of their duet contributions (Rivera-Cáceres & Templeton, 2019). There are two key differences between song learning and duet learning: (1) the location of song learning, and (2) the social context for learning at different stages of development (reviewed in Rivera-Cáceres & Templeton, 2019). Social context facilitates the development of species-specific duetting behaviour (Rivera-Cáceres & Templeton, 2019). For many species in which only males sing, song learning occurs after dispersal (Rivera-Cáceres & Templeton, 2019). That being said, young males in some species learn songs directly from their fathers, and there is evidence to suggest young males may learn social interaction rules for song while on natal territory (Rivera-Cáceres & Templeton, 2019). In contrast, delayed dispersal seems to be common in duetting species. Delayed dispersal offers the opportunity to learn species-specific duet composition and the answering rules that generate them. For example juvenile canebrake wrens learn and practice duet vocalizations with their parents and improve their adherence to duet codes over time (Rivera-Cáceres et al., 2018). In species with sex-specific phrases, physical tutors are required for juveniles to learn sex appropriate phrases (Rivera-Cáceres & Templeton, 2019). Not all species share the same ontogenetic timeline. Some, like rufous-and-white wrens, learn their songs after dispersal (Graham et al., 2018). Whereas others, like riverside wrens, learn songs and duet phrases before dispersal, and then settle on near-by vacancies when they appear (Quirós-Guerrero et al., 2020). Both learning strategies can result in geographic structure, such that sharing of duetting rules and duet structures declines with distance (Quirós-Guerrero et al., 2020).

In addition to learning species-specific duet contributions and duetting rules, some birds must also adapt their duetting behaviour to that of the partners', implying a second phase of learning after mating (Logue & Krupp, 2016; Rivera-Cáceres & Templeton, 2019). Different species have varying levels of plasticity in their duet structure. Canebrake and riverside wrens use a fixed phrase repertoire but adjust their duet codes when they mate with a new partner (Quirós-Guerrero et al., 2020; Rivera-Cáceres et al., 2016). The newly-formed pair then improves duet code adherence and temporal coordination over time. Plain-tailed wren duets and zebra finch "stack calls" also improve in temporal coordination with pairing duration (Coleman & Fortune, 2018; D'Amelio et al., 2017). Other species exhibit more limited or no flexibility after pairing (Benedict, 2010; Osmun, 2010; van den Heuvel et al., 2012).

Duet Evolution

Duetting species occur across avian taxa. Although most commonly studied and described in passerines, duets also occur in owls (Odom & Mennill, 2010; Odom et al., 2013; Yee et al., 2018), kiwi (Digby et al., 2013), cranes (Bragina & Beme, 2010; Klenova et al., 2020), geese (Gridley & Gardiner, 2021; Whitford, 1996), swans (Lumsden, 2018), parrots (Dahlin & Wright, 2012) and other taxa (Hall, 2009).

Estimates of the number of duetting species have been increasing in recent years. Hall (2009) estimated that 4.3% of all birds duet. In a study restricted to North American passerines, Benedict (2010) estimated that 7% of species duet. Two phylogenetically explicit analyses estimated that 15.6% of passerines (Logue & Hall, 2014), and ~16% of all birds (Tobias et al., 2016), duet. These estimates likely underrepresent the true number of duetting species, however, because many tropical species remain poorly studied.

Female song may be an evolutionary intermediary to duetting in some songbird lineages. Female song is widespread, ancestral, and functional in songbirds (Odom et al., 2014; Riebel et al., 2019). Females lost complex song but maintained song-answering behaviour in the lineage leading to Carolina wrens (*Thryothorus ludovicianus*; Price et al., 2022). In the blackbird family (Icteridae), the evolution of duetting was likely preceded by the evolution of female song (Odom et al., 2015). Although the evolution of duetting and female song is correlated in Icteridae (Odom et al., 2015), there is no evidence of such a correlation in Parulidae (Mitchell et al., 2019).

Duetting appears to have been gained and lost multiple times in Parulidae, with gains exceeding losses (Mitchell et al., 2019).

Duetting behaviour likely evolved via social selection pressure rather than sexual selection pressure. The term “social selection” encompasses all complex social factors that can result in differential reproductive success such as intra-sexual competition and social group dynamics (Rose et al., 2022; Tobias et al., 2012). Most duetting species sing duets year-round (Odom et al., 2017; Odom et al., 2016). The lack of association between duetting and the breeding season implies greater selection pressures from broader natural selection or social dynamics than from sexual selection (Odom et al., 2017; Tobias et al., 2012). In contrast, signals that are used exclusively in the breeding season are more likely to be shaped by sexual selection (Illes & Yunes-Jimenez, 2009; Odom et al., 2016; Price et al., 2008).

Avian duets are associated with specific natural histories. In 1972, duetting was suggested to be evolutionarily associated with tropical habitat and dense vegetation (Thorpe, 1972). However, more recent studies have failed to support this hypothesis (Hall, 2009; Keenan et al., 2020; Tobias et al., 2016). Phylogenetically explicit analysis of New World warblers show that duetting (Mitchell et al., 2019), but not female song (Najar & Benedict, 2015), is negatively associated with latitudinal migration. In Icteridae, when duetting is considered in conjunction with female song, both are phylogenetically associated with tropical breeding, social monogamy, territorial nesting, and sedentary behaviour (Odom et al., 2015). However, when limited only to taxa with female song, the life history associations disappeared, suggesting there may be additional selection pressures unique to duet evolution in Icteridae (Odom et al., 2015). More broadly, latitudinal migration and duetting are negatively correlated in North American passerines (Benedict, 2008a) and all songbirds (Logue & Hall, 2014). These phylogenetically explicit analyses suggest the evolution of duetting behaviour is likely linked to ecological conditions that promote a sedentary lifestyle and long-term social pairings (Logue & Hall, 2014). Individuals in long-term pairings largely share fitness outcomes with their partners, making it beneficial to work together to maintain their shared resources. Indeed, the best-supported functional hypotheses for duetting behaviour are based on the idea that mates cooperate (Hall, 2004, 2009). And finally, duetting behaviour is often associated with lower extra-pair copulations (EPC) and reduced extra-pair paternity (EPP; Cramer et al., 2011; Diniz, Macedo, et al., 2019; Douglas et al., 2012; Dowling & Webster, 2013; Gill et al., 2005; but see: Dowling & Webster, 2015; van den Heuvel et al., 2014a).

Until recently, it was unclear whether sexual monochromatism was associated with duetting behaviour (Hall, 2009). Benedict (2008a) did not find a correlation between duetting and sexual monochromatism in North American species, nor did Logue and Hall (2014) find a correlation in a stratified sample of all songbirds. Estrildid finch dance duets are not correlated with the evolution of dimorphic song or plumage colouration (Soma & Garamszegi, 2015). In barbets, a non-passerine, duets are correlated with group-living but not with sexual monochromatism (Soma & Brumm, 2020). Sexual monochromatism does not seem to be associated with duetting behaviour.

Although there are correlations between duetting and life history traits, it is important to recognize the challenge of differentiating evolutionary selection pressures for or against a particular trait (Price, 2015, 2019). For example, phylogenetic analysis of New World warblers suggests that selection pressures appear to be against female song, rather than for female song (Najar & Benedict, 2015). So rather than asking “why does female A sing?” we should be asking “why does females B not sing?”

Ultimate Causes of Duetting: Adaptive Functions

The pair-level behaviour of a vocal duet is the product of two coordinated individual-level behaviours, initiating and answering (Logue & Krupp, 2016). Selection pressures and fitness benefits of participating in a duet may be unique to each pair-member, so it is important to take an individual-level approach to duet function research. Initiating a duet may offer different fitness benefits, and therefore have a different function, than answering a duet (Diniz et al., 2018; Logue & Krupp, 2016). In fact, there may be selection pressures acting concurrently on duet initiation behaviour, duet answering behaviour, and the collective duetting behaviour (Logue & Krupp, 2016). Considering the investment required to produce coordinated vocal duets, it is reasonable to expect both pair-members to gain fitness benefits from duet participation under most circumstances. However, there are rare cases in which the answering partner may sabotage the initiator (discussed further below; Hall, 2009; Tobias & Seddon, 2009). Vocal duet research has not always parsed individual behaviours from the coordinated collective behaviour, making some older studies difficult or impossible to interpret in an individual-level framework (Logue & Krupp, 2016).

For most species, duet participation serves several adaptive functions (Dahlin & Benedict, 2014; Hall, 2009). These functions can vary with context and signal structure (Méndez & Sandoval, 2019; Mennill & Vehrencamp, 2008), and a single duet event can even serve multiple functions (Odom et al., 2017). This multifunctionally is evident in the coming sections, where a single study may be discussed in the context of multiple functional hypotheses.

Throughout this section, I use the term “duet participation” to be inclusive of species with duet-specific vocalizations, however, I focus primarily on the function of song answering. Although a few species initiate with duet-specific vocalizations, in most species duet initiation is indistinguishable from solo singing so answering transforms what would be a solo song into a duet.

Joint Resource Defence

The joint resource defence hypothesis states that duet participation helps pairs to cooperatively defend shared resources from conspecifics (Hall, 2004; Logue, 2005). For most species, the resources needed for survival and reproduction such as food, nesting sites, and shelter, are tied to a physical territory. Pair-members may benefit by defending shared resources as a coordinated pair rather than defending individually if two birds working in concert are more intimidating to potential territory usurpers (Logue, 2005). Joint resource defence is the best-supported functional hypothesis for duetting and chorusing in birds (reviewed in: Dahlin & Benedict, 2014; Hall, 2009; Logue, 2005). Only a few studies have tested for joint resource defence and failed to find support (Rogers et al., 2007; van den Heuvel et al., 2012). Indeed, the use of coordinated acoustic signals in cooperative resource defence occurs across animal taxa including shrimp (Toth & Duffy, 2005), wolves (Cassidy et al., 2020), and lions (McComb et al., 1994). It has even been suggested that early humans may have used group singing to defend territories (Hagen & Hammerstein, 2009).

The joint resource defence hypothesis offers many predictions pertaining to spatial patterns, duet structure, and social context. All predictions for this hypothesis are built on the assumption that near-by conspecifics are the signal receivers (Hall, 2004, 2009). Duets used in joint resource defence are predicted to be easily located and loud enough to transmit to potential intruders (Hall, 2004; Seibt & Wickler, 1977). This prediction is widely upheld. Red-backed fairy-wrens offer an extreme example in which duets are louder, longer, and easier to locate than solo songs (Dowling & Webster, 2013).

Several predictions of joint resource defence address spatial patterns of duet production. Duet participation is predicted to be spatially associated with territorial boundaries where most territorial intrusions occur (Hall, 2009; Mennill & Vehrencamp, 2008; Sandoval et al., 2015; Ward, 1986). This is a straightforward prediction, but few observational studies test it. The paucity of tests can largely be attributed to the logistical challenges of tracking birds in dense vegetation and defining physical territory boundaries. To date, Mennill and Vehrencamp (2008) have published the only quantitative test of whether duets are sung more near territory boundaries. Using a microphone-array system, they found duets were more often sung near the nest close to the territory center than near the territory boundaries (Mennill & Vehrencamp, 2008). A few publications have provided anecdotal evidence of duetting near territory boundaries (Cuthbert & Mennill, 2007; Sandoval et al., 2015; Ward, 1986). In Ward's (1986) publication on black-collared barbets (*Lybius torquatus*), he notes pairs will "patrol" their territory boundaries while audibly bill-wiping (a territorial behaviour) and duetting. Songbirds in general have been noted to alter their vocalizations near territory boundaries (Bolsinger, 2000; Kroodsma et al., 1989; Trillo & Vehrencamp, 2005), and participate in patrolling behaviour (Marshall, 1964). In 1964, Marshall describes the patrolling behaviour of both Albert's (*Melozone aberti*) and California towhees in which the male repeats "… piercing staccato notes while he dashes around the edges of his territory" (p. 353). Outside of direct inter-pair interactions, pairs of duetting species may sing duets near territory boundaries as part of patrolling efforts to acoustically delineate boundary lines.

A second spatial prediction addresses the distance between pair-mates: Pairs are predicted to be in physical proximity during duet vocalizations (Hall, 2009). If two birds working together to defend mutual territory are more effective than a single bird, duets at a distance might advertise weak resource defence (Logue, 2005). Indeed, two birds in close proximate elicit a more cautious reaction in white-browed robin-chats, suggesting two birds are perceived as more threating than one (Hultsch & Todt, 1984). There are several observational studies of natural duet rates that support this prediction by demonstrating that inter-individual distance (IID) is negatively correlated with duet production (Hall & Magrath, 2000; Logue, 2007a; Mennill & Vehrencamp, 2008). Additionally, Templeton et al. (2013) found experimental support for this prediction with an outdoor captivity experiment. Happy wren males answered playback of their mate's songs more when the speaker was placed closer to the cage than farther away. Some species that duet in close proximity to add a visual component to their vocal display. Australian magpie-larks use wing movement during vocal duets to increase the perceived threat of their duet; the more coordinated the movement, the more threatening the signal (Paweł Ręk & Magrath, 2022). Duetting in close proximity may benefit the pair by increasing their perceived threat-level to potential intruders.

Arguably, the most important prediction for the joint resource defence hypothesis addresses the context in which duets are delivered. If duets advertise a willingness to defend resources, we expect pairs to increase their duet output in conjunction with territorial intrusions by conspecifics. Pairs may be attempting to use duets as a warning to mitigate conflict. Both partners are predicted to increase their duet participation in conjunction with territorial defence activities (Diniz et al., 2018; Hall, 2004; Odom et al., 2017). As predicted, many duetting species increase their duet rates concurrent with other aggressive behaviours (e.g., song rates, approach behaviour, physical fights) during aggressive inter-pair interactions or playback of simulated intruders (Benedict, 2010; Brumm & Goymann, 2018; Diniz et al., 2018; Diniz, Rech, et al., 2019; Dowling & Webster, 2013; Fedy & Stutchbury, 2005; Odom et al., 2017; Odom & Omland, 2018; Sandoval et al., 2018; Templeton et al., 2011; Wheeldon et al., 2020).

Hall (2009) and Logue and Krupp (2016) promoted the importance of individual-level analysis, however this idea has not permeated predictions of increases in duet response. As written, the prediction above only addresses pair-level duet behaviour and leaves ambiguity around individual-level answering behaviour. Are pair-level duet rates (number of duets / time), or individual-level answering proportion (number of answers / partner total initiations, often called “answering rate”), expected to increase (Logue & Krupp, 2016)? From the signal receiver’s perspective, the number of duets per unit time seems likely to be the most meaningful metric. However, from the sender’s perspective, an increase in answering rate may be a stronger indicator that the focal bird is changing their answering strategy (Fedy & Stutchbury, 2005). Fedy and Stutchbury (2005) dismissed joint resource defence as a possible duet function in white-bellied antbirds because females did not increase their answering proportion during playback experiments. However, the female would have had to increase the number of male songs she answered in order to maintain a constant answering proportion while the male increased his song rate seven-fold. Although female white-bellied antbirds do not increase their answering proportion, their answering effort certainly increases. The ambiguity in predictions regarding duet rates versus answering proportion is persistent throughout the *Adaptive Function* section. I have used the general terms of “duet rate” or “answer more” where necessary to reflect the language of the original citations.

For duets to be an effective resource defence signal, they need to be perceived as threatening to the signal receivers. Indeed, signal receivers are often predicted to respond most strongly to duet vocalizations than to solo songs (Hall, 2000, 2004, 2009; Rogers et al., 2007).

Since two birds working together are expected to be more formidable than a single individual, a duet by two individuals should be more intimidating than a solo song by one individual (Logue, 2005). This prediction is one of the few that separates the joint resource defence hypothesis from the mate guarding hypothesis and is pivotal in many studies' interpretations of results from playback experiments (e.g., Diniz, Rech, et al., 2019; Koloff & Mennill, 2011; Sandoval et al., 2018; Templeton et al., 2011; van den Heuvel et al., 2014b). Many duetting species show support for this prediction by responding most strongly, or just as strongly, to playback of duetting birds than to solo song (Benedict, 2010; Brumm & Goymann, 2018; Odom & Omland, 2018; Sandoval et al., 2018; Templeton et al., 2011; but see Rogers et. al., 2007).

Song playback experiments are useful for testing predictions about receivers' response to duets. Birds' responses to these kinds of experiments require careful interpretation. A strong response to simulated playback may indicate the residents felt threatened, or alternatively, it may indicate they are confident they will win the encounter. Similarly, a weak response may indicate the residents felt too threatened to approach, or conversely, did not find the stimulus threatening enough to respond (Searcy & Beecher, 2009). Unpaired canebrake's wrens are less likely to engage in aggressive behaviours in response to duet playback than solo playback (Marshall-Ball et al., 2006). Marshall-Ball et al. (2006) interpret this behaviour, in conjunction with other conflict-avoidance behaviour, to mean that signal receivers perceive two birds to be more threating than one, and conclude that duets function in cooperative territory defence.

The joint resource defence hypothesis is compatible with observations of altered duet structure in aggressive contexts (Hall, 2009). In aggressive contexts pairs may increase their temporal coordination of their duet phrases (Hall, 2009; Hall & Magrath, 2007; but see Kovach et al., 2014), alter the frequency of their duet contributions (Méndez & Sandoval, 2019), or adjust their answering duration (Fishbein et al., 2018). Highly coordinated duets may be particularly strong signals of resource-holding potential if coordination indicates coalition quality (Diniz et al., 2021). Rufous hornero pairs increase their own duet coordination in response to coordinated duet playback, but physically respond more strongly to uncoordinated playback (Diniz et al., 2021). The author's interpretation is that coordinated duets convey coalition quality, and rufous hornero pairs are cautious about engaging physically with another coordained pair. Rather than adjusting duet coordination, white-eared ground-sparrows adjust the frequency characteristics of their duet in territorial defence contexts (Méndez & Sandoval, 2019). Pairs may also alter more than one aspect of their duet structure. Chestnut-backed antbirds (*Myrmeciza exsul*) adjust the frequency, duration, and timing of their duet vocalizations in response to frequency-manipulated playback (Fishbein et al., 2018). Whether and how these changes affect receivers' responses remains unknown.

Not all predictions of joint resource defence are equally informative. For example, some studies predict that pairs should approach territory defence with equal and coordinated responses to both intruding birds (Douglas & Mennill, 2010; Rogers et al., 2007). This prediction is supported in many duetting species in which pairs approach conspecific playback together while duetting (Brumm & Goymann, 2018; Dingle & Slabbekoorn, 2018; Koloff & Mennill, 2013a; Quirós-Guerrero et al., 2017). However, it is not always reasonable to expect equal effort by both pair members. Although mates may not demonstrate equal defence effort, any effort by a bird to help its partner defend against an opposite-sex intruder is cooperation (Logue, 2005). Stereo duet playbacks are an invaluable tool for differentiating sex-specific responses to duet playback, in which each sex-specific duet contribution is played through separate speakers (Logue, 2005; Logue & Gammon, 2004; Rogers et al., 2004). In species where the costs of defending differ between the sexes, we may expect unequal defence efforts. For example, in species with size dimorphism it may pose a greater risk for the smaller sex to confront the larger. In these cases, the smaller sex may defend primarily against same-sex intruders (Hall, 2004, 2009; Logue & Gammon, 2004; van den Heuvel et al., 2014b). This divide-and-conquer prediction is termed "division of labour" (Logue & Gammon, 2004). For example, happy wren and white-browed coucal pairs jointly defend territories, but females respond most strongly to playback with female vocals included (Brumm & Goymann, 2018; Templeton et al., 2011). This response asymmetry likely represents a division of labour, especially for white-browed coucals where males are 13% heavier than females (Brumm & Goymann, 2018).

Two final predictions of the joint resource defence hypothesis address seasonality in duetting behaviour. First, pairs should duet year-round if they also defend territories year-round (Diniz et al., 2018; Odom et al., 2017; Odom et al., 2016; van den Heuvel et al., 2014b; but see Dowling & Webster, 2013). Support for this prediction is found in many species in which joint resource defence is supported (Baptista, 1978; Benedict & McEntee, 2009; Bradley & Mennill, 2009; Fedy & Stutchbury, 2005; Hall, 2000; Hooker & Hooker, 1969; Odom et al., 2017; Szymański et al., 2021; Voigt et al., 2021). The second prediction states that duetting behaviour should peak during seasons of heightened territorial activity (Diniz et al., 2018; Hall, 2004). For some species this corresponds to the breeding season (Diniz et al., 2018), however, higher duet rates have also been observed during the dry season when resources are scarce (Fedy & Stutchbury, 2005; Odom et al., 2016). Most research on duetting species is conducted only in the breeding season, so evidence to address this hypothesis is lacking for many duetting species.

The joint resource defence hypothesis is well-supported by both theory and empirical evidence. Phylogenetic studies have found a negative correlation between migration and duetting, suggesting the ecological conditions that promote the evolution of duetting also promote the evolution of a sedentary lifestyle and long-term social pairings (Benedict, 2008a; Logue & Hall, 2014; Mitchell et al., 2019; Odom et al., 2015). Individuals in long-term partnerships with high mutual investment gain fitness benefit from coordinating their physical and vocal defence behaviours (Hall, 2004, 2009). However, the joint resource defence hypothesis and the mate guarding hypothesis have several predictions in common due to the shared assumption of an extra-pair audience (e.g., loud and easily locatable, used in inter-pair contexts). This can make parsing the two hypotheses difficult; studies often find support for both joint resource defence and mate guarding, concluding duets are multifunctional (e.g., Hall, 2009; Marshall-Ball et al., 2006), or may serve different functions for each pair member (e.g., Sandoval et al., 2018; van den Heuvel et al., 2014b).

Mate Guarding: Introduction

The mate guarding hypothesis is broad in scope. There are many different ways a bird can guard its mate, resulting in branching hypotheses nested within the broader class of “mate guarding” (Hall, 2004). The basic mate guarding hypothesis states that answering a partner’s song advertises the partner’s mated status to outsiders, thereby repelling would-be intruders attracted to the partner’s songs (Hall, 2004). This hypothesis can be subdivided into: (1) the partnership defence hypothesis and (2) the paternity guarding hypothesis. The partnership defence hypothesis is further broken down into two parts: It states that by advertising the partner’s mated status, a bird is either (a) defending its own position within the partnership, or (b) defending its partner’s position in the partnership (Hall, 2004). For example, a female bird acting aggressively toward an intruding female is defending her own position within the partnership by preventing the intruder from usurping her position. A female acting aggressively toward an intruding male is defending her mate's position within the partnership by preventing the intruder from usurping her mate. In either case, partnership defence is a cooperative function of song answering as long as both mates receive fitness benefits on average (Hall, 2004). If partnership defence activities by a bird result in fitness costs for the mate, then partnership defence could represent conflict between the pair. The paternity guarding hypothesis states that a male answers his mate's song to discourage extra-pair males from copulating with her (Hall, 2004; Sonnenschein & Reyer, 1983). Paternity guarding represents true conflict between the pair (Hall, 2009). Table 1 summarizes the different sub-hypotheses of mate guarding and offers a further breakdown of joint resource defence.

Table 1. Predictions for two key functional hypotheses to explain why a bird may decide to answer its mate to create a duet. Adapted with permission from van den Heuvel et al., 2014.

	Territory defence		**Mate guarding**		
Sub-hypotheses	**Joint** (Hall, 2000; Koloff & Mennill, 2013a; Quirós-Guerrero et al., 2017)	**Division-of-labour** (Logue & Gammon, 2004)	(1) **Partnership defence** (a) **Own position** (Rogers et al., 2007; Seddon & Tobias, 2006; Weng et al., 2012)	(b) **Partner's position** (Appleby et al., 1999)	(2) **Paternity guarding** (Kahn et al., 2018)
Timing	All year*	All year*	All year	All year	Fertile period
Strongest response to	Duet song	Duet song	Same-sex solo song	Opposite-sex solo song	Male solo song
Weakest response to	Solo song	Opposite-sex solo song	Opposite-sex solo song	Same-sex solo song	Female solo song
Response to duet song directed at	Both pair members	Biased toward same-sex stimulus	–	–	Male

*Stronger when territory pressure is high (Diniz et al., 2018; Hall, 2004).

Researchers often fail to differentiate which mate guarding hypothesis they are attempting to test. In most of these cases, they are actually testing hypothesis 1a: "partnership defence by defending the bird's own position" (e.g., Dingle & Slabbekoorn, 2018; Diniz et al., 2018; Douglas & Mennill, 2010; Dowling & Webster, 2013; Seddon et al., 2002). Failure to specify which hypothesis is being tested can lead to confusing interpretations of study results and unclear conclusions about duet function.

The second source of ambiguity comes from the misconception that mate guarding always represents conflict within the pair. This confusion is also associated with hypothesis 1a: "partnership defence by defending its own position." Many authors interpret evidence for this hypothesis as evidence of conflict between the pair mates because the guarding mate seems to be preventing the guarded mate from accessing other potential mates (e.g., Benedict & McEntee, 2009; Diniz, Rech, et al., 2019; Rogers et al., 2007; Seddon & Tobias, 2006; Weng et al., 2012). However, conflict is an unlikely explanation for duetting in most duetting species. In her 2009 review, Hall directly addresses the question of "Conflict or Cooperation?" with respect to mate guarding for partnership defence. She explains that experiments have failed to adequately support a conflict-based theory. Hall (2009) goes on to argue that mate guarding for partnership defence is evidence of intra-pair conflict when: (1) the guarded partner sings with the goal of attracting a new partner, (2) mates of low-quality partners benefit from re-pairing, and (3) there are opportunities to re-mate. So far, no research has found support for these predictions

There are also potential fitness consequences to consider for a conflict-based version of mate guarding for partnership defence. Switching mates can be reproductively costly (Black, 2001; Sánchez-Macouzet et al., 2014) and can increase rates of adult mortality (Jeschke & Kokko, 2008). For example, newly-formed pairs of Australian magpie-larks have lower reproductive success than long-term pairs (Hall, 1999). Finally, harassment by extra-pair males seeking copulation opportunities can negatively impact reproductive success in females (Low, 2008). In this case, having male partners defend their position in the partnership by chasing away intruding males could help mitigate the costs to females. The potential fitness costs associated with switching mates or receiving attention from extra-pair males can be high. Mate guarding for partnership defence is therefore more likely to be mutually beneficial in duetting species with long-term partnership and low divorce rates (Hall, 2009).

Recently, research on duet function has begun to move away from the conflict and cooperation dichotomy (Dahlin & Benedict, 2014). More researchers acknowledge that duets are multifunctional with function varying across contexts, and that there has been an over-emphasis on the importance of sexual conflict in socially monogamous avian species (Dahlin & Benedict, 2014; Griffith, 2019).

A final consideration is that joint resource defence and mate guarding are not mutually exclusive hypotheses (van den Heuvel et al., 2014b). Both hypotheses share behavioural and life history predictions, and many studies have found support for both within the same species (Dingle & Slabbekoorn, 2018; Diniz et al., 2018; van den Heuvel et al., 2014b; Weng et al., 2012). In most of these studies, the two functions are attributed to the different levels of behaviour, with individual answering providing a mate guarding function, and pair-level duetting providing a resource defence function (Dingle & Slabbekoorn, 2018; Diniz et al., 2018; van den Heuvel et al., 2014b).

Mate Guarding: Partnership Defence

The partnership defence hypothesis states that a bird answers song to defend its own position in the partnership, or to defend its partner's position in the partnership (Hall, 2004; van den Heuvel et al., 2014b). Most duetting species invest heavily in their partnership and losing a partner can have negative fitness consequences (Black, 2001; Hall, 2009). For these species, defending the partnership is likely to benefit both partners (Hall, 2009).

There are several shared predictions between partnership defence and joint resource defence that, although not helpful to distinguish between these two hypotheses, do differentiate them from other hypotheses. Both predict that the primary receivers of duets are extra-pair conspecifics, that duets are loud and conspicuous, and that duets will be associated with aggressive interactions with conspecifics (Hall, 2004, 2009; van den Heuvel et al., 2014b). These predictions are widely upheld in studies that find support for the partnership defence function of duetting. Both hypotheses also predict there should be little or no seasonal influence in guarding behaviour (Odom et al., 2017; van den Heuvel et al., 2014b). Duets have been observed year-round in several species that show additional support for partnership defence including crimson-breasted shrikes (van den Heuvel et al., 2014b), rufous horneros (Diniz et al., 2018), tawny owls (*Strix aluco*; Appleby et al., 1999), and grey-breasted wood wrens (Dingle & Slabbekoorn, 2018). Most research on duetting species is conducted only in the breeding season, so evidence to address this hypothesis is lacking for many duetting species.

The primary prediction of the partnership defence hypothesis is that solo intruders should be perceived as more threatening than paired intruders (Hall, 2004). Whether a same-sex or opposite-sex solo intruder is perceived as more threatening, depends on whether a bird is defending its own position in the partnership or its partner’s position (Table 1; Hall, 2004; van den Heuvel et al., 2014b). If a bird is defending its own position in the partnership, then solo same-sex intruders should be perceived as the most threating intrusion-type (Diniz et al., 2018; Odom et al., 2017; van den Heuvel et al., 2014b). If duet participation functions to defend a bird's own position in the partnership, then the defending bird should participate in duets more often in the presence of solo same-sex intruders.

Support for the partnership defence by defending its own position hypothesis is most often seen in species that demonstrate mutual mate guarding, wherein both pair members defend their own position within the partnership. However, each bird may use different vocal defence strategies (Dingle & Slabbekoorn, 2018; Diniz et al., 2018; Grafe & Bitz, 2004; van den Heuvel et al., 2014b). For example, grey-breasted wood wren and crimson-breasted shrike females both increase the proportion of male songs answered in response to simulated solo same-sex intruders, while males in both species respond to solo same-sex intruders by increasing solo song rates (Dingle & Slabbekoorn, 2018; van den Heuvel et al., 2014b). In canebrake wrens, a species with duet-specific vocalizations, both sexes sing their introductory duet elements more often, and the females increase their answering rates, in response to same-sex solo intruders (Marshall-Ball et al., 2006). Very few species have only one pair member that defends its own position (Rogers et al., 2007; Seddon & Tobias, 2006).

Conversely, if a bird is defending its partner's position, then solo opposite-sex intruders should be the most threating (van den Heuvel et al., 2014b), and the defender should participate in duets more often in the presence of solo opposite-sex intruders. There are many reasons a bird would want to defend its partner's position in the partnership: (1) the potential for reproductive success is greater the longer the pair bond; (2) an injured mate could compromise reproductive success in the current breeding season; and (3) combative ability may not be indicative of parenting ability, consequently, a mate with high reproductive potential may require assistance in combat (Logue, 2005).

For example, male white-browed coucals sing at slightly higher rates, although not significantly higher, in response to opposite-sex solo playback (Brumm & Goymann, 2018). This suggests males may be defending their partner's position. Similarly, male tawny owls respond equally to male and female solo playback, and are especially likely to respond to female playback if they successfully breed the season before (Appleby et al., 1999). These findings suggest males are defending their reproductive investment in their current mate by defending her place in the partnership. From the perspective of the male, the current partner offers reproductive security whereas other females are an unknown risk. To replace his mate, he would also have to invest time to attract a new female and allow time for her to acclimate to a new territory and mate. Therefore, the benefits of defending his mate likely outweigh the costs in many systems.

Notably, the predictions are nearly identical for the mate guarding by defending one's own position hypothesis and the joint resource defence with division of labour hypothesis (Table 1). Both predict birds will demonstrate sex-specific responses to duet playback and respond more strongly to opposite-sex solo song. Further, most studies that find evidence of sex-specific response to conspecific vocalizations also find other evidence that supports the joint resource defence hypotheses (e.g., Dingle & Slabbekoorn, 2018; Diniz et al., 2018; Marshall-Ball et al., 2006; van den Heuvel et al., 2014b). This overlap blurs the lines between the joint resource defence and partnership defence hypotheses and raises the question of whether attempting to distinguish between them is biologically relevant for many tropical duetting species.

As previously mentioned, maintaining long-term partnerships between mates offers fitness benefits for year-round territorial species (Hall, 2009; Logue & Hall, 2014) and mitigates the fitness consequences associated with switching mates (Black, 2001; Hall, 1999; Jeschke & Kokko, 2008; Sánchez-Macouzet et al., 2014). In species that live with year-round competition for physical resources (e.g., territory, food, nesting material, etc.) and high mutual fitness investment in partnerships (long-term pair bonds, low EPC rates, etc.), joint resource defence and partnership defence are intrinsically linked; mates and territories are both resources that require defence. In these systems, successful reproduction is only possible if pairs can maintain access to the resources for reproduction and maintain their partnership for reproductive opportunity. As a hypothetical example, whether a female is participating in territory defence with her mate to defend their partnership or the territory, the outcome of successful defence would be the same. If she successfully defends the partnership, she keeps her mate and access to his territory. If she successfully defends the territory, she keeps the territory and access to the male who claims it. In both cases, the female successfully maintains her access to both resources that are essential for successful reproduction: her mate and physical territory. Duetting species tend to have long-term partnerships and sedentary life history (Benedict, 2008a; Logue & Hall, 2014; Mitchell et al., 2019; Tobias et al., 2016), as well as low EPC rates (i.e., high fitness investment in mate; Cramer et al., 2011; Diniz, Macedo, et al., 2019; Douglas et al., 2012; Dowling & Webster, 2013; Gill et al., 2005). In these systems, joint resource defence and partnership defence may blend into a broader mutual investment defence effort.

Two rarely tested predictions address the intruder’s behaviour, and the possible role of sex-specificity in duet vocalizations. If unpaired birds are seeking new mates, then unpaired birds are predicted to be attracted to solo songs and deterred by duets (Hall, 2004; Seddon et al., 2002). The first half of this prediction is tentatively supported in Eastern whipbirds, in which unpaired females are attracted to opposite-sex, conspecific playback (Rogers et al., 2007). Unpaired birds may be deterred by duets in red-backed fairy wrens, potentially supporting the second half of the above prediction. During mate removal experiments, playback of the removed male’s duet contribution was more effective at deterring intruders than no playback, but not as effective as when the male was physically present (Dowling & Webster, 2018). The second uncommon prediction suggests individual duet contributions may be sex-specific to alert potential sexual partners to their pairing status (Benedict & McEntee, 2009; Hall, 2004). Sex-specific elements may allow potential rivals to more easily identify paired individuals in areas with high population density and many duetting pairs. There are a few species in which several predictions of partnership defence are supported including sex-specific duet elements (Diniz et al., 2018; Grafe & Bitz, 2004; Weng et al., 2012). However, this is not a strong prediction and is not often included in studies of partnership defence.

Mate Guarding: Paternity Guarding

The paternity guarding hypothesis states that a male answers his partner’s song to advertise her mated status to potential intruders for the purpose of preventing access to other sexual partners (Hall, 2004; Sonnenschein & Reyer, 1983). This type of guarding is only possible for males, and only in species in which the female initiates and the male answers. The paternity guarding hypothesis proposes true sexual conflict between mates; females are attempting to attract extra-pair partners and males are actively trying to prevent them from succeeding. Although a few studies have found evidence of paternity guarding, there is far more support for cooperative duet functions (Dahlin & Benedict, 2014; Hall, 2009). Theoretical mathematical models predict an association between low EPP rates and low levels of paternity guarding (Kokko & Morrell, 2005). Paternity guarding is therefore unlikely to be an important function of song answering because duetting species tend to have low EPP rates (Diniz, Macedo, et al., 2019; Douglas et al., 2012; Dowling & Webster, 2013; Gill et al., 2005). For example, purple-crowned fairy-wrens, a species with low EPP rates, show very low levels of paternity guarding (Hall & Peters, 2009).

The paternity guarding hypothesis shares several predictions with both the joint resource defence and partnership defence hypotheses: duet contributions are predicted to be directed at inter-pair individuals, loud, and easily located (Hall, 2004). These predictions are upheld in studies that find support for the paternity guarding function of duetting. As in partnership defence, individual duet contributions may be sex-specific (Hall, 2004). There is currently no evidence to support this prediction in a species that uses song answering in paternity guarding. Although the duets of the canebrake wren do have sex-specific phrases, when females are fertile, males increase their physical guarding effort rather than their acoustic guarding efforts (Marshall-Ball et al., 2006).

The paternity guarding hypothesis makes several sex-specific predictions. It predicts that the male will answer more of his mate's songs, or a higher proportion of her songs, during her fertile period (Hall, 2004; Hall & Peters, 2009). It is important to assess guarding behaviour during fertile and non-fertile periods to differentiate the paternity guarding hypothesis from the partnership defence hypothesis (Diniz et al., 2018; Odom et al., 2017). Elevated male answering rates should be particularly apparent in the real or simulated presence of a male intruder (Dingle & Slabbekoorn, 2018; Douglas & Mennill, 2010; Dowling & Webster, 2013). Support for this prediction is limited, but has been found in chirruping wedgebills (*Psophodes cristatus*) and canebrake wrens (Austin et al., 2019; Marshall-Ball et al., 2006). However, it seems to be more common for male birds to use a combination of physical and acoustic paternity guarding strategies rather than relying on acoustic mate-guarding alone (Dowling & Webster, 2018; Kahn et al., 2018; Odom et al., 2017).

There are also predictions of the paternity guarding hypothesis that address female behaviour. One states that a female sings to attract extra-pair sexual partners when she is fertile (Hall, 2004; Hall & Peters, 2009). Therefore, we would expect female song rates to increase during her fertile period. However, there is currently no evidence to support this prediction from a species that uses song answering in paternity guarding. In fact, many duetting species demonstrate the opposite trend, where female song rates decrease during the fertile period (Diniz et al., 2018; Hall & Peters, 2008; Logue, 2004; Topp & Mennill, 2008). If females are singing to attract an extra-pair sexual partner, we would also expect females to increase her singing effort in response to solo male song. However, the opposite is observed in female banded wrens (*Thryophilus pleurostictus)*; females respond less to male solo playback during their fertile period than outside of the fertile period (Hall et al., 2015).

Evidence that females sing to attract an extra-pair sexual partner is lacking, suggesting paternity guarding is not a common function of male answering in duetting species. The increased male answering observed during the breeding season in certain duetting species may represent a division of labour in joint resource defence or an effort to guard the partnership, especially when resources (including mates) are more limited during the breeding season. Females may be reducing their resource defence activities due to an increase in energetically costly breeding activities (Schwabl & Sonnenschein, 1992). It is also possible the increase in male answering may be a consequence of males’ tendency to increase song rates during the breeding season in general (Odom et al., 2016; Rundstrom & Creanza, 2021). Whatever the driving force behind increased male answering during the breeding season may be, paternity guarding is an unlikely explanation.

Pair-Bond Maintenance

The pair-bond maintenance hypothesis states that duet participation signals commitment to the partner (Hall, 2004, 2009). Following Hall (2004), I interpret “commitment” to mean a willingness to invest in activities essential for success of the partnership and reproduction, including resource defence, nest building, provisioning effort, etc. In the three hypotheses discussed so far, birds answer their mates to protect their resources and partnership from external pressures. In contrast, the pair-bond maintenance hypothesis states that answering encourages a mate to remain in the partnership. Although few studies have tested this hypothesis, there is some support for the pair-bond maintenance hypothesis in the duet literature.

Duetting requires high partner-directed attention and may function as an honest signal of commitment to the partner (Hall, 2004). Investing time to duet with a partner takes time away from other activities such as resource defence, foraging, or predator vigilance. A bird that is willing to invest in duetting with a partner may be honestly signalling that it is willing to remain in the partnership. During mate removal experiments, Levin (1996a) found resident bay wren males answered new partners less than their previous established partners. Reduced answering after a mate replacement is consistent with the idea that answering reflects a willingness to invest in the partnership (Hall, 2004). The resident male does not yet know the new female's quality (e.g., reproductive potential, parental care investment, territorial defense ability), or her willingness to invest in the partnership, so perhaps he is not (yet) willing to express his commitment to her.

The effort required to achieve improved duet coordination may also indicate commitment to the partnership (Hall, 2004; Wickler & Seibt, 1980). If duets function in pair-bond maintenance, duet coordination may improve with partnership duration (Hall, 2004). Support for this prediction has been found in several duetting species, however, not all studies suggest a connection to the pair-bond maintenance hypothesis (Coleman & Fortune, 2018; D'Amelio et al., 2017; Diniz et al., 2021; Hall & Magrath, 2007; Rivera-Cáceres et al., 2016; Rivera-Cáceres & Templeton, 2019). Increased duet coordination is also a prediction of the joint resource defence hypothesis which is more often the focus of duet function studies (Diniz et al., 2021; Hall & Magrath, 2007). Other studies have failed to find an effect of partnership duration on duet coordination (Benedict, 2010; van den Heuvel et al., 2012). Alternative aspects of duet production may also be predicted to improve over time such as repertoire consistency (Marshall-Ball et al., 2006). However, even if duet coordination (or another aspect of duet production) does not improve with the duration of the pair bond, duetting still requires on-the-spot adjustment indicating partner-directed attention and energetic investment (Hall, 2004).

Initiating a duet for the purpose of pair bond maintenance may not be a signal of commitment, but rather a test of the partner’s commitment to the pairing. In birds with long-term social pairings and low EPP rates, both partners invest in the partnership, and each bird’s reproductive success depends on the social mate (Black, 2001; Hall, 2004; Sánchez-Macouzet et al., 2014). In these species, individuals may benefit from assessing their mate’s willingness to continue investing in the partnership (Hall, 2004). By signalling their own commitment, a pair member may try to elicit a response to assess their mate’s commitment (Hall, 2004). Singing has a slight energetic cost for songbirds (Catchpole & Slater, 2008). From the initiating bird’s perspective, the energetic investment of initiating a duet opportunity, and any costs associated with sacrificing other activities (e.g., foraging, predator vigilance), may be a test to see if their partner is also invested (Smith, 1994; Zahavi, 1977). The initiator may be making a bid for attention, and asking: is this partnership worth the cost of answering? A committed pair member will be attentive to its partner, and answer quickly and accurately. Conversely, a pair member that does not value its partner will necessarily be less attentive, and answers will be less frequent and less coordinated. If duet initiation functions as a test of partner commitment, then consistent rates of song answering with high coordination may be an honest signal of commitment to the partnership. There may be an answering-effort threshold the initiating bird uses to assess the mate's commitment, such as a specific number of answers per hour or a certain proportion of the initiator's songs answered (Hall, 2004).

For species in which duets function as a test of commitment, if the answering partner is inattentive and signals a weak commitment by answering less, the initiating bird may also invest less in the pairing. In this case, both pair members may increase EPC rates, provision nestlings less, or cooperate less in territory defence and defend less against opposite-sex intruders. Thus, if duetting is an honest indicator of willingness to invest in a partnership, then duet participation may signal mate quality (Hall, 2004). A recent study found correlations between duet participation and reproductive success, suggesting a connection between an individual's energetic investment in duetting behaviour and mate quality (Diniz, Macedo, et al., 2019).

Pairs may need to reaffirm their pair bond after a period of separation. If duets function for pair bond maintenance, then duet rates should increase when pairs reunite after a period of separation (Perez et al., 2015). Support for this prediction has been found in zebra finches and Cuban grassquits (*Phonipara canora*), two species that seem to use duets for pair bond maintenance (Baptista, 1978; Perez et al., 2015). A special version of affirming the pair bond after a period of separation may occur during nest-relief activities. Both zebra finches and great tits (*Parus major*) sing low-amplitude duets during incubation (Boucaud et al., 2017; Boucaud, Valère, et al., 2016; Elie et al., 2010). These quiet duets have only been described for a few species, and likely serve additional function (see *Coordination of Breeding Activities*).

Localization

The localization hypothesis states that birds use duet contributions to acoustically locate their mates (Logue, 2007a). The premise is like a game of Marco Polo, in which the initiator calls “Marco!” to elicit the response “Polo!” from the answerer. A bird may localize its mate to maintain contact, or to physically approach the mate. The few studies that have tested the localization hypothesis have found strong supporting evidence.

The most important prediction of the mate localization hypothesis states that if an individual uses duet participation to localize and approach its mate, then one or both pair members should move toward each other more often after participating in a duet than after a solo song (Logue, 2007a). In black-bellied wrens, if pairs were over 10 m apart, male and female initiations were far more likely to be followed by approach behaviour if the mate answered (Logue, 2007a). In most cases, the initiator approached the answerer. Evidence of mate localization behaviour after answered songs compared to unanswered songs is also seen in California towhees (Benedict & McEntee, 2009) and Venezuelan troupials (Odom et al., 2017). Rufous-and-white wrens and banded wrens also show approach behaviour during bouts of answering (or, concurrent song, in banded wrens), however neither study design allows a comparison to unanswered songs (Hall et al., 2015; Mennill & Vehrencamp, 2008).

Duetting species that use duets as a localization tool may have individually-distinctive vocalizations (Hall 2004). If birds are relying on acoustic information alone, then it would be beneficial for the duet to reveal both the location and identity of the duetting individuals. In this way both partners ensure they are only cooperating with each other and not another conspecific.

The duets of California towhees (Benedict & McEntee, 2009) and black-bellied wrens (Logue & Gammon, 2004) both show evidence of individual-level identity and serve a localization function within these species.

Species in which duets function for mate localization are predicted to live in densely vegetated habitats (Hall, 2004; Logue, 2007a), and have easily locatable duet vocalizations (Hall, 2004). Although dense vegetation is not statistically associated with duetting behaviour in general (Keenan et al., 2020; Tobias et al., 2016), it is likely that species using duets for localization would tend to live in visually occluded habitats (Hall, 2004). These predictions are largely supported in species that show evidence of using duets for localization (Benedict & McEntee, 2009; Hall et al., 2015; Logue, 2007a; Mennill & Vehrencamp, 2008; Odom et al., 2017). Being able to reliably locate and coordinate activities with a partner would be beneficial in any season, and so if duet participation is used for localization, then duets should be observed year-round (Hall 2004). Limited studies are available that directly test this prediction, however both Venezuelan troupials (Odom et al., 2017) and black-bellied wrens (Logue, 2004) use duets for localization year round.

Mate Recognition

The mate recognition hypothesis states that duet participation facilitates mutual recognition (Hall, 2009). Pairs may use a unique pair-specific duet code or timing rule that allows for quick mutual identification. Having a reliable intra-pair identification signal may reduce or prevent misdirected aggression intended for an intruder (Dahlin & Benedict, 2014; Logue & Gammon, 2004; Rogers et al., 2007). By acting as an intra-pair “password”, pair members can quickly identify intruders by their lack of appropriate duet response (Feekes, 1977, 1982; Logue & Gammon, 2004). Unlike the other hypotheses discussed in this chapter, the mate recognition hypothesis is specifically about the function of answering rules, not about the function of song answering itself. Although a few studies have found preliminary support for the mate recognition hypothesis (e.g., Logue, 2006), it requires further testing.

Mate recognition could be important during territorial intrusions. If duet participation not only allows pairs to maintain contact, but also functions as a pair-specific “password”, then intruders should not be able to imitate the pair (Janik, 1998). Pairs should also be able to acoustically identify an intruder (Feekes, 1982). Further, incorrect answers (those that violate the duet code) should provoke non-cooperative behaviour (e.g., an attack) (Logue, 2006). There is currently no evidence to support these predictions in a species that uses song answering in mate recognition. However, a few studies have shown mated pairs of several duetting species are able to discriminate between neighbour and stranger duets, indicating an ability to, at the very least, identify pairs by their duets (Amorim et al., 2022; Hall, 2000).

Birds should benefit from avoiding misdirected aggression toward their partner. If duets facilitate identification (e.g., by acting like passwords), we can predict an increase in duet rates during an intrusion, and an increase in duet rates in the presence of same-sex intruders (Douglas & Mennill, 2010; Logue & Gammon, 2004). Many studies observing duetting behaviour in simulated and natural intrusions find support for this prediction. However, most do not include mate recognition as a possible explanation of duetting behaviour. Black-bellied wrens may use duets for mate recognition and as a “password” (Logue & Gammon, 2004). Black-bellied wrens live in visually occluded habitats, their duets are loud, easily locatable, duet codes are distinct to each pair, and males increase initiation rates during opposite-sex playback and both sexes increase answering during same-sex playback (Logue & Gammon, 2004).

Ensuring Reproductive Synchrony

The ensuring reproductive synchrony hypothesis states that duet participation helps to synchronize partners' reproductive biology (Hall, 2004, 2009). In areas with prolonged breeding seasons, it may be necessary for birds to synchronize the timing of reproduction with their mates. (Hall, 2009). Vocal signals have been shown to influence ovarian development and nest building activities in birds, supporting the notion that duet participation may facilitate reproductive synchrony (Bradbury & Vehrencamp, 2011; Catchpole & Slater, 2008; Hall, 2009). Ensuring reproductive synchrony is one of the less well-supported functional hypotheses, however few studies have tested this hypothesis (Dahlin & Benedict, 2014).

Predictions for ensuring reproductive synchrony focus on communication between pair members. In species where duets function for reproductive synchrony, duet participation rates should increase in the pre-breeding season compared to other breeding stages (Diniz et al., 2018). Both sexes of rufous hornero increase their answering rates during the pre-breeding and fertile stages, supporting this prediction (Diniz et al., 2018). Pairs are predicted to participate in duets outside of territorial aggressive contexts (Dowling & Webster, 2013). Evidence for this is seen in brown-headed cowbird (*Molothrus ater*) females who direct their "*chatter* calls" (duet responses) at their pair mate during the pre-breeding phrase (H. L. Anderson et al., 2020). If duet participation functions to ensure reproductive synchrony, then participating in a duet should influence the hormone profiles of either or both duetting partners (Hall, 2009). Pairs of duetting white-browed robin-chats that were experimentally prevented from vocalizing did not engage in reproductive activities, suggesting the importance of acoustic signals on hormone cascades and reproductive timing (Todt & Hultsch, 1982). One study demonstrated a correlation between female song answering and testosterone, but not estradiol or luteinizing hormone, suggesting the influence of song answering on breeding biology is either not straightforward or non-existent (Schwabl & Sonnenschein, 1992).

Coordination of Breeding Activities

The coordination of breeding activities hypothesis (a.k.a., coordination of parental care hypothesis) states that duet participation helps mated pairs coordinate their incubation and provisioning activities (Hall, 2004). In addition to being considered a function of duetting, coordination of breeding activities has been discussed as a broader function of female song (Langmore, 1998; Ritchison, 1983). Although not often included in duet function studies, several species show evidence that supports the coordination of breeding activity function (Boucaud, Valère, et al., 2016; Elie et al., 2010).

Duet participation that results in coordination of breeding activities should be directed at the pair mate, occur during incubation or nestling provisioning, and be associated with a change in incubation or provisioning behaviour. Examples include the duets of slate-coloured boubous (*Laniarius funebris*) which precede nest relief (Sonnenschein & Reyer, 1983) and those of tropical boubous which follow nest relief (Hooker & Hooker, 1969). In zebra finches and great tits, duets are also low amplitude, only sung at the nest, and comprised of several antiphonal phrases (Boucaud, Mariette, et al., 2016; Boucaud et al., 2017; Boucaud, Valère, et al., 2016; Elie et al., 2010). If duets function to coordinate breeding activities, changes to duet structure or rate should result in different nest-relief activities (Boucaud, Mariette, et al., 2016). In zebra finches, increased vocal rates and shorter duets result in partners hastening their return to the nest to change incubation shifts (Boucaud, Mariette, et al., 2016). In great tits, differences in duet vocalization frequency and temporal structure are consistently related to specific outcomes including the female leaving the nest, the male entering the nest box with food, or the males remaining in close proximity to the nest box (Boucaud, Valère, et al., 2016). In both great tits and zebra finches, there is strong evidence to suggest duets function in the coordination of breeding activities.

Similar coordination behaviours have been observed in Northern cardinals (*Cardinalis cardinalis*, Halkin, 1997), and white-throated dippers (*Cinclus cinclus*, Villain et al., 2017). Male northern cardinals are more likely to bring food to the nest when females sing a response to his song (Halkin, 1997). However, if females match the male's songtype, males are less likely to come to the nest (Halkin, 1997). Researchers recorded white-throated dippers vocal exchanges in and out of the breeding season (Villain et al., 2017). The acoustic and temporal structure of the duet vocalizations changed with the season and whether the female was actively incubating (Villain et al., 2017). Future research connecting these unique vocal exchanges to provisioning rates could potentially make white-throated dipper vocal exchanges a more compelling example of a duet that functions to coordinate breeding activities.

Summary

The joint resource defence hypothesis and mate guarding for partnership defence hypothesis are the two best-studied and best-supported hypotheses. Ambiguity about the definition of mate guarding has introduced opposing conclusions about whether mate guarding for partnership defence represents cooperation or conflict. However, when viewed through the lens of high mutual fitness investment and long-term social pairing, most studies of mate guarding for partnership defence suggest duetting species cooperatively defend both their territory and their mate. For many year-round territorial and socially monogamous duetting species, the lines between joint resource defence and mate guarding for partnership defence blur into a broader mutual resource defence effort.

Although there have been few tests of the localization hypothesis, those that are available provide strong evidence for this hypothesis. The localization hypothesis provides clear, testable predictions that make it attractive to include in studies of duet function. Conversely, there is little evidence to support for mate guarding for paternity guarding in duetting species. Studies have yet to demonstrate that females sing to attract extra-pair sexual partners during their fertile period. That fact, combined with the potential costs of mate switching, the high mutual fitness investment, and low EPP and EPC rates, makes the conflict-based paternity guarding hypothesis an unlikely explanation of duet participation.

Several functional hypotheses require further study. The pair-bond maintenance hypothesis offers an intriguing theoretical framework, and the coordination of breeding activities hypothesis has entered the literature with several compelling studies. Both are potentially challenging research areas that require careful observation of natural interactions between pairs. Moving forward, creative study design may provide further support and insight for these hypotheses. The ensuring reproductive synchrony hypothesis has a strong theoretical foundation, but requires additional studies of song answering and hormone profiles during different breeding phases to address the strongest predictions. Finally, the mate recognition hypothesis, which attempts to explain the function of answering rules, is currently untested. Further research may reveal more adaptive benefits from mutual investment in pair-specific answering rules.

As a final note, I focused this review on the best-studied functional hypotheses available in current duetting literature. However, the majority of these hypotheses were developed from birdsong research conducted primarily on temperate migratory species in which male song was studied in the context of the breeding season (Rose et al., 2022). More support for social- and natural selection-based functions may be documented as more tropical species are studied, and additional functions may yet be discovered (Rose et al., 2022).

Conclusions

Since the beginning of duet research in the early 1960s, researchers have strived to uncover the evolutionary drivers of duetting behaviour. There have been key milestones in duet research. Researchers now focus on individual-level theories and experiments, take an integrated approach to male and female vocalizations, and have access to new technologies opening doors to new observational and experimental possibilities. The field of duetting research is robust and diverse, and continues to reveal more about the evolution of duetting behaviour and cooperative behaviour in general.

Moving forward, the priority must be to fill the largest gaps in the literature. There are several broad areas that require additional work. We still know very little about the ontogeny and neural mechanisms that underpin duet behaviour (Coleman et al., 2021; Fortune et al., 2011; Rivera-Cáceres et al., 2018). Expanding our knowledge in this area could build more connections between the proximate mechanisms available for natural selection and the ultimate evolutionary purpose. Without life history information for duetting species, our ability to phylogenetically reconstruct the evolution of duetting and its associated traits is limited (Mitchell et al., 2019; Odom et al., 2014). The addition of species and duet diversity to the literature would expand theoretical and experimental opportunities. Although the diversity of species represented in the research continues to grow, many duetting taxa have yet to be studied (e.g., New World warblers, Mitchell et al., 2019). Most duetting research tends to focus on species with similar duet structure, whereas species with unique duet structure offer new opportunities for testing functional hypotheses in novel ways.

Other gaps in the literature occur from antiquated ideas, vague hypotheses, and trending methodologies. There has been confusion over the concepts of conflict and cooperation, and more studies with clearly defined hypotheses and predictions of individual-level behaviour will address this confusion. Most duetting research employs playback experiments to assess individual responses to conspecific duets, but for many species the broader behavioural context is missing. An effort to conduct rigorous observational studies of duetting behaviour may offer further insight into spatial and temporal context of duet vocalizations.

My thesis research addresses some of these gaps in the duetting literature. My primary study goal is to test two functional hypotheses of duet function in Adelaide's warblers. I used detailed observational data to test spatial and temporal predictions of the joint resource defence and mate localization hypotheses. With my project, I will add to the growing species diversity represented in the literature by being the first functional study of a duetting warbler. I will also add to the information available on female-controlled duet structure, and showcase the distinct advantage in results interpretation offered by a species where only one sex answers. And finally, I will add to the growing body of observational studies on duetting species with detailed tracking methods that capture the broader social context of duet behaviour. With these goals as the foundation, my thesis research continues to push the field towards more rigorous methods and clearly outlined theoretical frameworks.

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CHAPTER 3: AN EVALUATION OF THREE TERRITORY CALCULATION METHODS FOR A TERRITORIAL SONGBIRD

Territorial behaviour occurs when an animal actively defends an area from conspecifics through direct conflict, aggressive displays, or by leaving markings along territory boundaries (Bradbury & Vehrencamp, 2011). Any of these behaviours may result in spatial patterns of territory ownership. Examples occur throughout animal kingdom, including scent marking in African antelope (Brashares & Arcese, 1999) and Eurasian lynx (Allen et al., 2017), and acoustic displays in bullfrogs (Bee & Gerhardt, 2001), coyotes (Gese & Ruff, 1998), woodpeckers (Kilham, 1959), and loons (Walcott et al., 2006). In songbirds, song is the primary territorial display (Catchpole & Slater, 2008).

In many species of songbirds, males and females temporally combine their vocalizations to form duets (Hall, 2009). The joint resource defence hypothesis is the best-supported functional hypothesis for duetting (Hall, 2009). An important prediction of the joint resource defence hypothesis is that duets should be spatially associated with the physical boundaries of those resources (Hall, 2009; Mennill & Vehrencamp, 2008; Sandoval et al., 2015; Ward, 1986). Before I could test this prediction in Adelaide’s warblers, I needed to select a biologically appropriate method to define territorial boundaries. Although previous studies of duetting songbirds have calculated territory boundaries (e.g., Mennill & Vehrencamp, 2008), the past two decades have seen the release of new methods for territory estimation as well as new software for spatial calculations. In this chapter, I evaluate the advantages and disadvantages of three popular territory estimation methods.

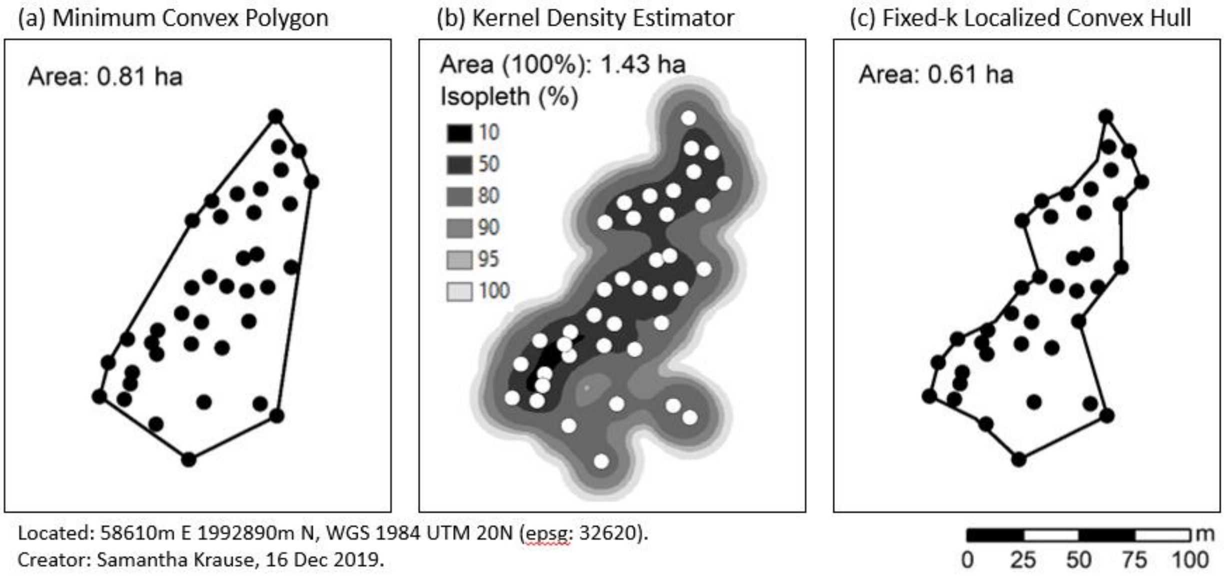
My goal is to estimate the mated pair’s territory, which is the area they actively defend (Noble, 1939). The territory is distinct from the home range (HR), which is the area that the pair uses during normal activity (Burt, 1943). If animals use space that they do not defend, the territory will be smaller than the home range. Misunderstandings regarding the difference between territory and HR in previous songbird literature have lead to poorly defined estimates of space use by various species (Anich et al., 2009). I isolate the territory by including only those locations where the focal male sang (Anich et al., 2009; Catchpole & Slater, 2008; Mennill & Vehrencamp, 2008).

Many studies of animal territories focus on habitat-selection or total territory area. To accommodate this kind of research, some territory estimation methods produce *utilization distributions* (UDs), which represent the relative frequency of space use through time (Barg et al., 2005; Van Winkle, 1975). UDs can be useful because they show how animals use some areas more than others. In the present study, however, I am not concerned with relative space use, but rather with the distance between birds and their territory boundaries. Calculating this distance requires an accurate delineation of territory boundaries

Three Common Territory Calculation Methods

I evaluated three common methods for calculating territories: Minimum Convex Polygons (MCP), Kernel Density Estimation (KDE), and Localized Convex Hulls (LoCoH). Examples of each method are shown in Fig. 1. Each of these methods has advantages and disadvantages (Fieberg & Börger, 2012; Malloy, 2010; Noonan et al., 2018; Signer et al., 2015; Steiniger et al., 2010). MCP is the simplest territory calculation method. It describes territory as a single polygon. KDE and LoCoH generate UDs resulting in both an outline of the territory and information about territory use. The latter is represented by lines called “percent isopleths,” which outline the areas where x % of locations were observed. The use of multiple isopleths on a single territory map can reveal “core” areas of the territory (Fig. 1b; Barg et al., 2005; Kernohan et al., 2001).

All three territory calculation methods have statistical requirements. All three methods are nonparametric (*MCP*: Barg et al., 2005; *KDE*: Kernohan et al., 2001; *LoCoH*: Getz et al., 2007), so no preparatory manipulations of the location data are required. A constraint common to all three methods is the assumption of statistical independence between consecutive locations (*MCP*: Barg et al., 2005; *KDE*: Kernohan et al., 2001; *LoCoH*: Getz et al., 2007). Statistical independence is possible when there are long time intervals between successive locations. However, achieving statistical independence is difficult in research that requires short time intervals between successive locations. Data collected in close temporal association are likely to be serially autocorrelated and therefore not statistically independent (Barg et al., 2005). Data are serially autocorrelated if the location at time $t + 1$ is influenced by the previous location at time t (Schoener, 1981; Swihart & Slade, 1985). Many techniques for determining songbird territories, including the techniques that I used, involve short bouts (on the scale of minutes to hours) of focal animal following that are expected to generate autocorrelated data (Barg et al., 2005).


(a) Minimum Convex Polygon

(b) Kernel Density Estimator

(c) Fixed-k Localized Convex Hull

Located: 58610m E 1992890m N, WGS 1984 UTM 20N (epsg: 32620).
Creator: Samantha Krause, 16 Dec 2019.

Figure 1. Comparison of three territory calculation methods for the same pair of Adelaide's warblers. (a) and (b) were calculated in ArcGIS, (c) was calculated using R.

A central debate in radiotracking data collection concerns the relative importance of statistical versus biological independence (Barg et al., 2005). For spatial data, biological independence requires “a sampling interval long enough to allow the animal to move from any point in its home range (or territory) to any other point” (Lair 1987, p. 1099). This sampling interval is based on the animal’s biology, and not an arbitrary unit of time determined by tests for statistical independence (i.e., serial autocorrelation). Researchers argue that if the location data can be considered biologically independent, then they need not also be statistically independent (Barg et al., 2005; de Solla et al., 1999; Kernohan et al., 2001). Barg et al. (2005) tested their songbird location dataset for serial autocorrelation (Schoener, 1981; Swihart & Slade, 1985). Even after increasing their sampling interval from 1 to 10 minutes, their data were still serially autocorrelated. Due to the reduced size of that dataset, it was no longer possible to outline a meaningful territory boundary. Further, eliminating autocorrelated data has been shown to reduce the accuracy of area estimations (de Solla et al., 1999; Kernohan et al., 2001). Other studies found adhering to biological independence rather than statistical independence had little impact on their area calculations (reviewed in Barg et al., 2005; but see Noonan et al., 2018). It seems for short time-scale measures of animal behaviour, statistical independence can be ignored as long as data are biologically independent (Kernohan et al., 2001). Logistical constraints that prevent the collection of statistically independent data (e.g., manpower, radio transmitter battery life, or difficult terrain) need not preclude spatial analysis.

Minimum Convex Polygon

Minimum convex polygons have been used to estimate territories for over 70 years (Mohr, 1947). The simplicity of this method is attractive. Minimal effort is required to calculate an animal’s territory and it is straightforward to compare territory properties between studies

(Barg et al., 2005). An MCP is calculated by connecting the outermost points of a location data set, resulting in a single polygon that outlines the entire area within which the animal was observed (Fig. 1a). Many ornithologists continue to rely on the MCP method (Getz & Wilmers, 2004; Mennill & Vehrencamp, 2008; Skorupski et al., 2017; Streby et al., 2012; Wagner et al., 2015).

The MCP method presents several disadvantages with respect to my study goals. The first disadvantage is that MCP calculations can only produce convex polygons. Real territories may not be convex polygons, especially in heterogeneous habitat (Anderson, 1982). Large areas that were never visited by the resident pair may be included within the territory polygon (Harris et al., 1990). These areas are unlikely to be defended by the resident pair and may in fact belong to a neighbouring pair or be ignored altogether. Another disadvantage is that the MCP method is highly sensitive to minor variation in the peripheral points, so even one inaccurate location can greatly alter the territory estimate (Harris et al., 1990). For these reasons, the nuances of territorial behaviour in my study species may be obscured by using the MCP method.

Kernel Density Estimation

KDE has become a mainstay for describing territories in ecology since it was recommended by Worton for territory calculations in 1987 (Getz & Wilmers, 2004). KDE describes a territory as a probabilistic cloud (Silverman, 1986). KDEs are calculated by applying a probability density function (i.e., the kernel function) to each location and summing the kernel outputs to create an overall kernel density function:

$$\hat{f}(x) = \frac{1}{nh^2} \sum_{i=1}^{n} K\left[\frac{x - X_i}{h}\right]$$

where $\hat{f}(x)$ is the estimated probability density function (or UD), n is the number of locations, h is the smoothing parameter (bandwidth), X contains the x and y coordinates for the n observed locations, x is the point at which the kernel estimate is calculated, and *K(.)* is the kernel function, a bivariate symmetric function (Kernohan et al., 2001; Worton, 1989). The kernel density function is evaluated over a grid to delineate a UD (Kernohan et al., 2001). KDE is common in ornithology literature (Carpenter & Wang, 2018; Diniz et al., 2019; Flockhart et al., 2016; Reitsma et al., 2017; Verheijen et al., 2019).

The most important component of the KDE calculation is the smoothing parameter, or bandwidth (Kernohan et al., 2001; Silverman, 1986). The bandwidth controls the size of the kernels which in turn control the smoothing of the data. Bandwidth can be calculated as an adaptive parameter where every point can have a different bandwidth value or as a fixed parameter where all points have the same fixed value. Lager bandwidths result in larger and smoother UDs. Various bandwidth selection techniques have been suggested. Examples include the Gussian reference function, autocorrelated-Gaussian reference function, Silverman's rule of thumb (used in Fig. 1b), and least squares cross-validation (Noonan et al., 2018). Bandwidth-selection techniques comprise most of the variation in the KDE family.

Despite the many advantages to KDEs there are also important disadvantages with respect to my study (Kernohan et al., 2001). Bandwidth selection strongly influence the size and shape of the territory estimate (Kernohan et al., 2001), and it is difficult to determine a biologically-grounded method for bandwidth selection. Further, KDE can produce discontinuous territories which are not biologically realistic for my study species (Barg et al., 2006; Kernohan et al., 2001; Osmun & Mennill, 2011). Finally, sample sizes strongly influences KDE-derived territory estimates, limiting comparability among territories (Getz & Wilmers, 2004).

Localized Convex Hulls

The ability of LoCoH to detect hard boundaries to movement or untenable habitat has made LoCoH a top competitor among territory/HR calculation techniques (Getz et al., 2007). The LoCoH method can be thought of as stacking many smaller MCPs on top of each other, and using the outer boundary of all the combined polygons as the final territory shape (Getz et al., 2007; Getz & Wilmers, 2004). This final polygon can contain both convex and concave angles (Fig. 1c).

The *k*-LoCoH algorithm calculates convex hulls (polygons) for each location by connecting it with its $k - 1$ nearest neighbours. It then orders and unites hulls, starting from the smallest and moving upward until x% of points are included (Getz et al., 2007; Getz & Wilmers, 2004). By specifying an x of points, it is possible to calculate a UD with a specific x% isopleth. The value *k* can be optimized by plotting *k* versus the area estimate and selecting the lowest *k* that approaches the asymptote (Getz et al., 2007). There are three types of LoCoH calculations: (1) *k*-LoCoH, as just described, uses a fixed number of points, (2) *r*-LoCoH uses all neighbouring points within a fixed radius (*r*) to calculate individual hulls, and (3) *a*-LoCoH calculates hulls by adapting the radius (*r*) of a variable sphere around a root point so that the sum of the distances between the neighbouring points and root point is $\leq a$ (Getz et al., 2007). *a*-LoCoH is useful for separating UD information in densely-used areas (Getz et al., 2007).

With respect to my study, there are only minor disadvantages to discuss for the LoCoH method. I have too few unique locations to optimize the *r*- and *a*-LoCoH methods, however, the basic *k*-LoCoH method is appropriate. A logistical disadvantage of LoCoH is that it is not currently available in ArcGIS software (as of version 10.6.1). Unlike KDE and MCP, LoCoH requires working knowledge of alternative software such as R (R Core Team, 2022).

Final Selection

MCP and LoCoH both offer a relatively simple approach to defining territory boundaries that allows for comparisons between territories. The greatest advantage of LoCoH compared to MCP is that LoCoH incorporates convex angles, allowing territory polygons to curve around each other and physical features. Adelaide’s warblers defend territories that curve around physical features as well as neighbouring conspecific territories, making LoCoH the superior choice for my study.

KDE and LoCoH share the ability to calculate territories without the constraint of convex angles, however, KDE presents other challenges that make it unsuitable for my study. A territory boundary calculated by the KDE method has ballooned edges that can encompass area far beyond the location itself (Fig. 1b) and can have discontinuous “islands” of territory (Osmun & Mennill, 2011). This ballooning, or smoothing, effect is controlled by manipulating the bandwidth parameter (Kernohan et al., 2001; Silverman, 1986). Although there are different bandwidth-selection tools available, it is difficult to make an ecologically appropriate decision about such an abstract parameter. The KDE method is also sensitive to sample size; increasing sample sizes can shrink the territory estimate. I do not have equal sample sizes across territories, so each territory polygon would be influenced differently, introducing inaccuracy in my spatial calculations.

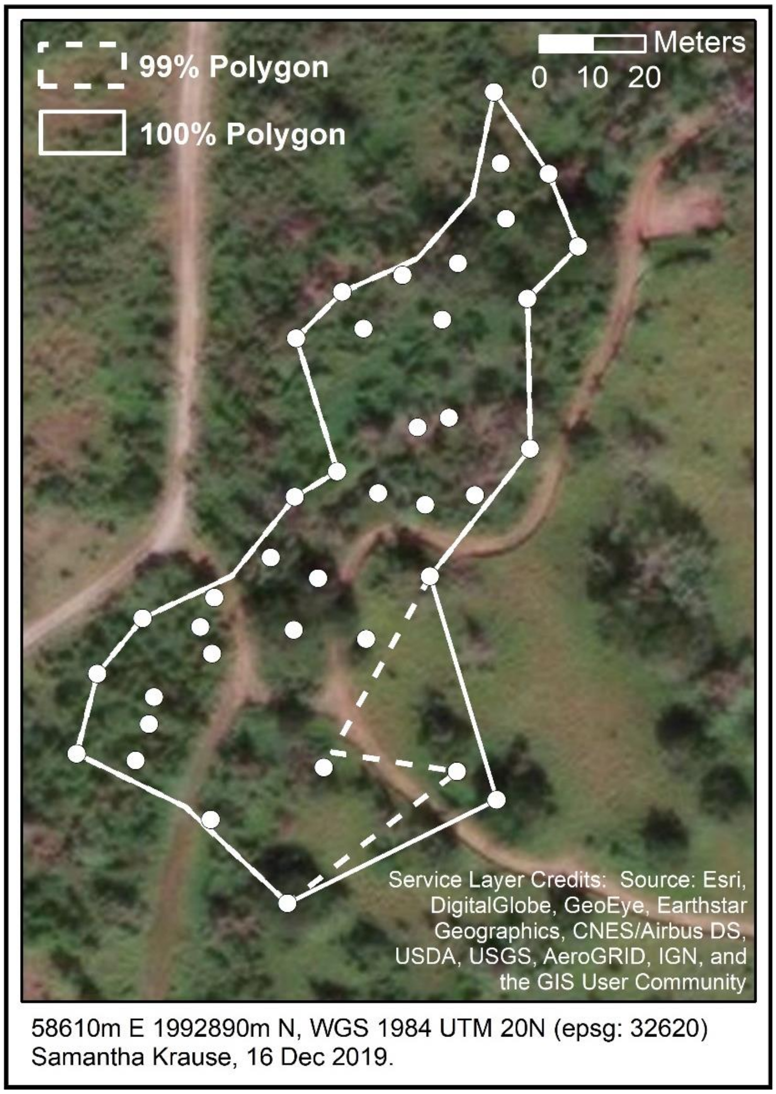
After careful consideration, I selected the LoCoH method to estimate territory boundaries in Adelaide’s warblers. LoCoH calculates territories that can have concave angles, do not contain “balloons” of space, are continuous, and can be compared between individual study animals. For my study, this method offers the greatest likelihood of accurately estimating biologically-relevant territory boundaries (Fieberg & Börger, 2012).

The fixed k-LoCoH Method: Isopleth Selection

LoCoH users need to choose the % isopleth. Typically, the 95th or 99th % isopleth is used in territory, HR, and UD calculations to control for the possibility of erroneous locations, especially in automated tracking studies. Outlying points can have a large influence on some territory calculation methods (e.g., MCP), and atypical or exploratory behaviour can result in locations that are not part of the animal's normal activity (Getz et al., 2007). In the case of my study, however, GPS coordinates were collected by researchers in the field with handheld units and later ground-truthed with satellite imagery. This reduced the likelihood that we included inaccurate points.

For additional accuracy, I calculated and visually assessed both the 99% and 100% isopleths superimposed onto satellite imagery (Fig. 2). In calculating the isopleths, I used unique *k* values for each pair to allow for variation within individual-use patterns (Carpenter & Wang, 2018; Wang et al., 2012). I wanted to determine if any song posts excluded by the 99% isopleth, but included within the 100% isopleth, were justifiably excluded. For example, if one song post was far away from the clustered territory, it could indicate a possible exploratory foray, or an intrusion into a neighbour's territory. In either of these cases, the 100% isopleth would include area not actively defended by the focal pair. However, I did not find any evidence of atypical locations for any song post included in the 100% isopleths.

As a final visual assessment, I also inspected the habitat in both the 99% and 100% isopleths. The area included in the 100% isopleths but excluded from the 99% isopleths typically contained no suitable vegetation for Adelaide's warblers to perch (e.g., parking lots, tall grass). An example can be seen in Fig. 2, where the majority of the habitat excluded from the 99% isopleth, but included in the 100% isopleth, is tall grass. Although the territory holders do not sing from the unsuitable areas, they are singing on the far side, suggesting that although there are no perches to sing from within the unsuitable habitat, the territory holders still consider the area theirs to defend. Based on my observations of their territorial behaviour in the field, I expect that if a neighbouring pair entered that open space, the residents would defend it. Given the habitat differences between the 99% and 100% isopleths, the in-person data collection methods, and the ground-truthed locations, I decided that 100% isopleth was the most biologically appropriate isopleth for this study system.



Service Layer Credits: Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

58610m E 1992890m N, WGS 1984 UTM 20N (epsg: 32620)
Samantha Krause, 16 Dec 2019.

Figure 2. Comparison of 100% and 99% isopleths of the fixed *k*-LoCoH method.

Conclusions

Recent advances in the field of spatial ecology offer an opportunity for innovative inquiry in the field of songbird research. Selecting a territory calculation technique that is biologically appropriate is challenging. Every territory calculation method has advantages and disadvantages that have to be assessed and balanced for each study. Given the parameters of my study system and research goals, LoCoH offered the most robust calculation method. More broadly, LoCoH is a good choice for studies of spatial proximity to territory boundaries. However, other territory calculation methods may be more appropriate for studies with different goals.

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CHAPTER 4: A SPATIAL APPROACH TO DUET FUNCTION IN THE ADELAIDE'S WARBLER (*SETOPHAGA ADELAIDAE*)

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Abstract

In many species of birds, mated individuals sing duets. In some duetting species, only females answer their mates' songs to form duets. Functional studies of these "female-controlled duets" offer a unique opportunity to focus on the female's decision to form a duet. In this observational study, we tested predictions of two functional hypotheses, joint resource defence and mate localization, to better understand the evolutionary pressures that act on species with female-controlled duets. Adelaide's warblers (*Setophaga adelaidae*) are a tropical, non-migratory wood-warbler (family: Parulidae). We used radio-telemetry to simultaneously record focal pairs over the course of several mornings. We found that females answered more when they were near territory boundaries or their mate, and around the time of aggressive encounters. Females tended to move towards the mate after he sang, but we did not find evidence that birds of either sex use duets *per se* to find the mate. Our results suggest female answering functions to defend shared resources including the partnership, but not to localize the mate. This is the first study of duet function in a warbler, and one of only a few observational studies based on simultaneous tracking of both pair members.

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[1] Contribution of authors. Samantha W. Krause: Conceptualization, project administration, funding acquisition, field work, data curation, analysis, visualization, library research, writing, and editing. Tyler R. Bonnell: Analysis assistance. Marcos J. Dostie: Spatial analysis assistance. Samantha I. Booth: Data curation assistance. Peter C. Mower: Field work assistance. D. M. Logue: Assistance with methodology, project administration, funding acquisition, resources, editing, and supervision.

Introduction

In about 16% of all songbird species, paired males and females produce vocal duets (Hall, 2009; Logue & Hall, 2014; Logue & Krupp, 2016). Duets serve many functions, including joint resource defence, partnership defence, and localization (Hall, 2009). Duet function can vary within a single species (Diniz et al., 2018; Hall, 2004, 2009; Koloff & Mennill, 2013b; Méndez & Sandoval, 2019; Mennill & Vehrencamp, 2008; Odom et al., 2017), and even a single duet can serve several adaptive functions (Odom et al., 2017). Duetting is a collective behaviour, that emerges from two individual-level behaviours: vocal initiation (spontaneous vocalization) and answering (an immediate vocal response to the duet partner's vocalization (Hall, 2009; Logue & Krupp, 2016). The fitness consequences, and thus the function, of duetting may be different for the initiator and the answerer (Diniz et al., 2018; Logue & Krupp, 2016).

Most hypothesized adaptive functions of duet participation assume duets are fundamentally cooperative (Hall, 2009). Duetting species tend to be non-migratory with long-term pair bonds. That life history favours cooperation because both mates benefit from working together to maintain their shared territory and raise their shared offspring (Logue & Hall, 2014). Two often-discussed cooperative functions of duetting are joint resource defence and mate localization (Hall, 2004, 2009). The joint resource defence hypothesis states that duet participation helps pairs cooperatively defend shared resource (e.g., the territory; Hall, 2004; Logue, 2005). Mated pairs should benefit by cooperatively defending their shared resources if two allied birds are more threatening to potential territory usurpers (Hultsch & Todt, 1984; Logue, 2005). The mate localization hypothesis states that birds use duets to acoustically locate their mates (Logue, 2007). The initiator may be trying to incite an answer to localize the mate, as in the game “Marco Polo,” or the answerer may be signal their approach. Both the joint resource defence and localization hypotheses are supported in the literature.

Duet structure is highly variable across duetting species. To be considered a vocal duet, phrases (the vocal units that comprise the duet) must have a consistent stereotyped structure and temporal relationship to each other (Farabaugh, 1982; Hall, 2004; Langmore, 2002; Taylor et al., 2019). The shortest possible duet comprises an initiation followed by a single answer (e.g., Male-Female; Mann et al., 2003; Rogers, 2005; van den Heuvel et al., 2012). Longer duets involve an initiation followed by alternating answers from the two partners (e.g., M-F-M-F-M-F; Lemazina et al., 2021; Logue, 2006). Duet partners may use sex-specific phrases, with each sex consistently contributing stereotyped phrases unique to that sex (Dingle & Slabbekoorn, 2018; Grafe et al., 2004; Koloff & Mennill, 2013b; Mennill & Vehrencamp, 2005; Moskat & Hauber, 2021; Quiroz-Oliva & Sosa-López, 2021). Birds can differ in the type of vocalizations they use, ranging from melodic exchanges of song (Coleman & Fortune, 2018; Logue, 2006; Quirós-Guerrero et al., 2017), to overlapping call notes (Benedict, 2008; D'Amelio et al., 2017), to a mixture in which one sex sings while the other calls (de Silva et al., 2004; Staicer, 1991). Finally, either sex can initiate a duet (Dingle & Slabbekoorn, 2018; Grafe & Bitz, 2004b; Hall & Peters, 2008) or one sex may initiate (Fedy & Stutchbury, 2005; Rogers et al., 2007; Tobias & Seddon, 2009; Weng et al., 2012).

For species in which only one sex initiates a duet, the answering sex determines whether their mate’s vocalization will be a solo or duet. In all such cases known to science, the male initiates the duet and the female answers, resulting in a simple M-F structure (Fedy & Stutchbury, 2005; Rogers et al., 2007; Tobias & Seddon, 2009; Weng et al., 2012). We refer to these duets as “female-controlled duets,” because the female determines whether a song will become a duet. Species with female-controlled duets offer a unique opportunity to elucidate the relationships between duet structure, function, and evolution. Studies with female-controlled duets can focus on the functions of male initiation and female answering, because males do not answer and females do not initiate.

The simple structure of female controlled duets narrows the set of possible functional hypotheses. For example, we do not need to consider the paternity guarding hypothesis in a study of female-controlled duets because that hypothesis requires males to answer their partners (Hall, 2004; Sonnenschein & Reyer, 1983). Similarly, the pair-bond maintenance hypothesis suggests that answering signals commitment to the partnership (Hall, 2004, 2009). If males do not answer, duets would not allow males to signal commitment. The simple female-controlled duet structure means that we do not have to address the complexities of multiple answers.

Female-controlled duets have been previously studied in only a few species, and with one exception, these studies are all based on playback experiments (Fedy & Stutchbury, 2005; Rogers, 2005; Rogers et al., 2007; Rogers et al., 2006; Tobias & Seddon, 2009; Weng et al., 2012). Playback experiments provide insights into duet function in the context of aggressive intrusion. However, given that duet function often varies by context (Diniz et al., 2018; Hall, 2004, 2009; Koloff & Mennill, 2013b; Mennill & Vehrencamp, 2008; Odom et al., 2017), it is important to observe duet production in the species' broader ecological setting. Observational studies can test for non-agnostic duet functions, like mate localization (Hall, 2004; Logue, 2007) and ensuring reproductive synchrony (Hall, 2004, 2009). The availability of small-scale, radio-tracking technology facilitates an observational approach to duet function (Lemazina et al., 2021; Logue, 2007).

For this study, two observers used radio tracking to continuously record the behaviour and locations of mated pairs of Adelaide's warblers (*Setophaga adelaidae*), a species with female-controlled duetting. At least 20% of New World warblers (family: Parulidae) produce vocal duets (Mitchell et al., 2019), but there are no peer-reviewed studies of duet function in this taxon. The Adelaide's warbler duet is always male-led and is composed of a single male song overlapped by a call from his mate (Fig. 1). Duetting behaviour appears to have evolved recently in this lineage (Mitchell et al., 2019). Many studies of duet function focus on lineages with ancient, complex duets, like wrens (Barker, 2017; Price et al., 2022). Functional studies on species from lineages with recently evolved duets, however, are lacking.

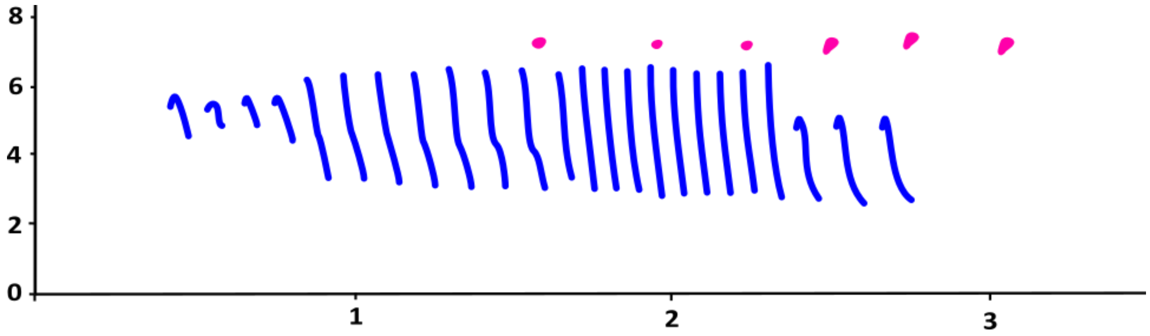

Figure 1. Spectrogram of a typical Adelaide's warbler duet. Male song (blue) is a rapid frequency-modulated trills. Female *pips* (pink) are high frequency notes.

We used our detailed observational data to test two cooperative functional hypotheses of duetting behaviour: joint resource defence and mate localization. If female answering functions in joint resource defence, we expect to find support for the following predictions: 1) Females will answer more around the time of an aggressive encounter (Diniz et al., 2018; Hall, 2004; Odom et al., 2017). If this prediction is upheld, the timing of female answers relative to aggressive encounters could offer insights into duet function. For example, if female answering increases only after an aggressive encounter, we would conclude that duets may function as "victory displays" (Grafe & Bitz, 2004a). 2) Females should answer more when they are near territory boundaries where most territorial intrusions occur (Hall, 2009; Mennill & Vehrencamp, 2008; Sandoval et al., 2015; D. Ward, 1986). 3) Females should answer more when the mate is close by (Hall, 2009; Hall & Magrath, 2007; Hultsch & Todt, 1984; Logue & Gammon, 2004). If two birds defending together are more effective than a single bird, then answering in close proximity should increase their perceived threat level, whereas answering when the mate is far away would reveal weakness (Hultsch & Todt, 1984; Logue, 2005).

If female answering functions in mate localization, we predict that: 1) Pairs should reduce their inter-individual distance (IID) more after an answered song than they do after an unanswered song (Benedict, 2010; Logue, 2007; Odom et al., 2017). This prediction can also be tested separately for each sex. The initiator may be trying to incite an answer to localize the mate, as in the game “Marco Polo,” or the answerer may signal their approach. 2) Females should answer their mate more when the pair are farther apart and out of visual line of sight. When mates are in proximity, their need to localize each other should be minimal. Our goals are to present the first functional study of duetting in a New World warbler, gain insight into the early stages of duet evolution, explore the broader ecological context of duetting, and demonstrate how modern geographical techniques can be integrated into the study of communication behaviour.

Methods

Study Site and Species

We collected data at the Cabo Rojo National Wildlife Refuge in South-Western Puerto Rico (17.9797, - 67.1661), in March and April of 2018. This area is mostly subtropical dry forest (Miller & Lugo, 2009). Adelaide’s warbler is a tropical, non-migratory wood-warbler endemic to Puerto Rico and Vieques (Staicer, 1991; Toms, 2010). Male repertoires comprise 29.0 ± 4.0 song types (mean ± SD), all of which are frequency-modulated trills (Kaluthota et al., 2019; Staicer, 1991). Males participate in the dawn chorus during the breeding season (March through June; Staicer, 1991). Early in the breeding season, the dawn chorus begins 20 min before sunrise (Staicer, 1991). As the breeding season continues, the dawn chorus begins earlier and earlier relative to sunrise, reaching a maximum of 45 minutes before sunrise (Staicer, 1991). During the dawn chorus, males sing at an elevated rate, switching song type with each song. After the dawn chorus, their song rate decreases, and they tend to deliver multiple renditions of a song type before switching types. Both pair members defend year-round territories that are 120 ± 25 m in diameter (present study). Females often overlap their mate's song with a train of high-frequency "pip" calls to form a duet (Fig. 1; Staicer, 1991). Pip calls are used by both sexes during normal daytime activity and are typically associated with movement (Staicer, 1991).

Ethics and Permits

During this study we adhered to the guidelines from the Institutional Animal Care and Use Committee at the University of Puerto Rico, Mayaguez (September 17, 2010), and the University of Lethbridge Animal Welfare Committee (protocol #1605). We obtained permission for our field work from the US Fish and Wildlife Service (permit #41521-2016) and the Puerto Rican Department of Natural Resource (Permit #2016-IC-068-1). All bird handling was conducted under David M. Logue's master banding license (#23969) from USGS Bird Banding Lab.

Field Methods

We captured eight mated pairs (eight males and eight females) of Adelaide's warblers in mist nets with acoustic lures. We took morphological measurements, drew blood, applied one USGS metal leg band and three coloured plastic bands for identification, and mounted an LB-2X radio transmitter (Holohil Systems Ltd., Ontario; hereafter, “radio tags”) on the bird’s back with an elastic leg-loop harness (Rappole & Tipton, 1991; Streby et al., 2015). The average body mass of an Adelaide’s warbler is 7.59 ± 0.75 g (*n* = 102; cumulative lab banding data), and the mass of the radio tags (without glue and harness) was 0.38 g, which represents 5.01% of the body mass of the average bird. After one of the antennas got caught in vegetation, we shortened the antennae to 8 cm to prevent further entanglements. All females captured during the study and definite brood patches, and one female was actively incubating. We captured and radio-tagged mated pairs two to three days prior to the first recording session.

We tracked birds with H-antennas and R1000 receivers (Communications Specialists). Each recording session started 0.5-1 hr before dawn and concluded 2.5 hrs after dawn. Initially, we began recording 33.6 ± 2.3 min (*n* = 8) before dawn, however, once we became aware of off-territory morning movements, and as the dawn chorus shifted earlier relative to sunrise, we began recording 53.9 ± 8.7 min (*n* = 14) before dawn. We followed one pair for four days, five pairs for three days each, one pair for two days, and one pair for one day, for a total of 22 recording days. Two pairs each had one recording session in which the female was radio-tagged but the male was not. On those days, we used visual and acoustic cues to track the male (similar to "spot-mapping"; Streby et al., 2012). After one recording of each pair, we recaptured the males and fitted them with radio tags as described above. We used the data from the two recording days that the males were not radio-tagged after excluding time that the recordist was uncertain of the male’s location during annotation (see below). We left at least 48 hours between sequential recording sessions of focal pair, with one exception. One morning when we were unable to record our scheduled pair due to a radio tag failure, and so opted to record our other radio-tagged pair to maximise our data collection efforts.

One recordist (Samantha W. Krause) tracked and recorded the female, while another (Peter C. Mower) simultaneously tracked and recorded the female, allowing each recordist to observe one focal bird (Altmann, 1974). Females were recorded with Olympus WS-852 digital voice recorders (.mp4 file format). Males were recorded with Marantz PMD 661 digital recorders and Sennheisser ME67 shotgun microphones (.wav file format; sampling rate = 44.1 kHz; bit depth = 16 bits). Recordists communicated with two-way radios. Recordists confirmed the identity of their focal bird after every vocalization, noted all locations the bird visited, and the time of flights, and described all aggressive encounters with neighbouring conspecifics. Recordists moved quietly and at a comfortable distance. If a focal bird seemed agitated or alarmed, the recordist backed away until the bird resumed normal activity. The refuge is frequented by staff, visitors, and educational tours, so the local birds are used to seeing and hearing humans. They quickly adapted to our presence.

Recordists used flagging tape attached to numbered clothespins to mark the birds' locations. Once a location was marked, it was referred to by name (e.g., "location 4") for the remainder of the recording session. If a bird returned to within 5 m of a previously marked location, we considered that bird to have revisited that location. We used handheld GPS units (GPSMAP 64s, GARMIN) to record the coordinates (WGS 84) of all marked locations after each recording session. The units were set to "waypoint averaging" to increase accuracy.

Audio Preparation and Annotation

We synchronized and combined the male and female recordings into a two-channel .wav audio file in Audacity v2.2.2 (Audacity Team, 2018) so annotators could listen to the recording they were annotating as well as the mate's recording. Annotators inspected spectrograms of recordings with Raven 1.5 Pro (Blackman window, size = 512 points; K. Lisa Yang Center for

Conservation Bioacoustics at the Cornell Lab of Ornithology, 2022). Three annotators inspected the female recording files. Each annotator scored at least one recording from each pair and did not score in chronological or recording order. The three annotators for the female recordings were all trained by the primary annotator (S.W.K.), who also reviewed all the female annotations prior to analysis. The primary annotator also annotated the recordings from all eight males. She assigned songs to song types based on their visual appearance on the spectrogram. When scoring, annotators annotated when and where the following events occurred: vocalizations and vocalization type (song, duet, chitburst, etc.), movements, aggressive behaviour, and any additional context noted by the field recordists. Annotators also annotated “OFF” when a recordist was out of contact with the focal bird.

Spatial Analysis

We conducted spatial analysis with R (R Core Team, 2022) in the RStudio environment (RStudio Team, 2018), running R markdown (Xie et al., 2018). We calculated territorial polygons and distances between focal birds and the nearest boundary using the following R packages: adehabitatHR (Calenge, 2006), rgdal (Bivand et al., 2013), sf (Pebesma, 2018), smoothr (Strimas-MacKey, 2007), and tidyverse (Wickham et al., 2019). We verified the location data with satellite imagery from Google Earth and ArcGIS 10.6.1 and visualized it with ArcGis 10.6.1. When locations from multiple recording days occurred within three meters of each other, we collated the locations and averaged the latitude and longitude. We assigned each unique location a code called (*TreeID*).

We used locations (*TreeID*s) where we observed the male singing (i.e., songposts) to estimate territory boundaries. Male song is a territorial signal, so we assumed that locations where male birds sing are in the territory (Anich et al., 2009; Catchpole & Slater, 2008). Female calls have a small active space, making them poor broadcast territorial signals compared to male song. Therefore, we did not use female calls to estimate territories.

We chose the Localized Convex Hulls (LoCoH) method to calculate territory boundaries for each pair (Getz et al., 2007; Getz & Wilmers, 2004). The LoCoH method offers several advantages for our study. Our field observations suggest Adelaide's warblers defend discrete, continuous territories with well-defined boundaries. These territories often curve around physical features or adjacent conspecific territories. Territories calculated with LoCoH are continuous and comparable, and unlike some popular methods, LoCoH permits concave angles (Getz et al., 2007; Getz & Wilmers, 2004). We rejected popular alternative methods (e.g., minimum convex polygons, kernel density estimators) because they are sensitive to sample size, require abstract parameters, do not allow concave angles, or produce discontinuous or bloated territory boundaries (Anderson, 1982; Fieberg & Börger, 2012; Harris et al., 1990; Kernohan et al., 2001; Noonan et al., 2018; Osmun & Mennill, 2011; Silverman, 1986).

We used the *k*-LoCoH option for construction using a fixed number of points (the *k* value; Getz et al., 2007; Getz & Wilmers, 2004). The *k*-LoCoH algorithm calculates convex hulls (polygons) for each location by connecting it with its *k*-1 nearest neighbours. These halls are then stacked and united, starting from the smallest and moving upward until x% of points are included (Getz et al., 2007; Getz & Wilmers, 2004). By specifying an x of points, it is possible to calculate a specific x% isopleth, or boundary. We calculated 100% isopleth *k*-LoCoH polygons for each focal pair as described by Getz et al. (2007). The 100% isopleth for song post locations is appropriate for our study because all locations were taken by trained observers on the ground, so there is no need to exclude potentially false outlying points. We chose *k* values separately for each pair to allow for variation in space-use patterns (J. P. Carpenter & Wang, 2018; Wang et al., 2012). We optimized the value of *k* for each focal pair by plotting area vs. *k* charts and selecting the lowest *k* that approaches the asymptote (Table 1; Getz et al., 2007; Getz & Wilmers, 2004).

Table 1. Parameters used to calculate 100% fixed k-LoCoH and territory area for each pair.

Pair	**Number of Song posts**	***k***	**Territory area (ha)**
● **1**	28	7	0.42
● **2**	31	10	1.19
● **3**	39	6	0.61
● **4**	34	7	1.05
● **5**	52	11	1.33
● **6**	41	11	1.05
● **7**	33	14	0.86
● **8***	8	-	-

*Excluded due to insufficient data.

Explanatory Variables

We analyzed two datasets. Both datasets were derived from the master dataset, which contained continuous observations of focal pairs. We built the binned dataset for modelling vocalization rates. It bins time into discrete blocks. We built the continuous dataset for modelling change in IID. It treats time as a continuous variable.

We calculated several variables for the master dataset. To control for the influence of the time of day on behaviour, we obtained the sunrise time from the website www.timeanddate.com and calculated the time relative to sunrise (*TimeRelSun*) for every observation from each recording day. We used the territory polygons to calculate the distance of the male and female to the territory boundary (*DistEdgeM* and *DistEdgeF*, respectively) for every Tree ID location. *IID* between focal birds was calculated by building a distance matrix between all *TreeID* locations.

We divided recording sessions into time before aggressive encounters and time after aggressive encounters to calculate time relative to aggressive encounters (*TimeRelAgg*). We considered an event to be an aggressive encounter if we saw physical chases between a focal bird(s) and nonfocal conspecific(s), or heard "chitburst" vocalizations directed at a nonfocal conspecific(s). Chitbursts are an aggressive signal in this species, and a typical aggressive encounter includes many repetitions of this vocalization (Staicer, 1991). We considered an aggressive encounter to have ended when no chases or chitbursts were observed for two minutes from the last observed chase or chitburst. We used two minutes because the distribution of time to next aggressive behaviour dropped to baseline levels at two minutes. When multiple aggressive encounters occurred within one recording session, we divided the time from the end of the last encounter to the onset of the next in half, and assigned all vocalizations and behaviours to the temporally closest encounter. For the time leading up to an aggressive encounter, we assigned negative values decreasing in absolute value to time 0, the encounter itself was assigned a time value of 0, and time moving away from an encounter was assigned positive values increasing in value the further from an encounter. Combining the "time to" and "time from" data produced the time relative to aggressive encounter variable (*TimeRelAgg*). We recorded only five songs (from four males) during five separate aggressive encounters (*TimeRelAgg* = 0), so vocal behaviour during the encounters not analysed further.

We built the binned dataset by dividing time into blocks of variable duration. Each block extends as long as both focal birds are stationary. Movement or aggressive encounters by either focal bird triggered the start of a new time block, so *IID*, *DistEdgeF*, and *DistEdgeM* remain constant within each time block. We labelled the duration of each time block (*blockDuration*). We calculated the temporal midpoint for *TimeRelFight* and *TimeRelSun* for each block by averaging the beginning and end times. We counted male initiations (*MaleInit*) and female answers (*FemaleAns*) by summing within each time block. We then removed time blocks that were shorter than three seconds to ensure each block was long enough for a male to sing a complete song and a female to answer (song duration = 2.0 ± 0.3 s; based on data from Kaluthota et al., 2019). We removed any time blocks when at least one pair member was off the territory (< -1.5 m *DistEdgeM* or *DistEdgeF*). We also removed time blocks during which one or both observers were OFF focal bird. Finally, we eliminated the dawn chorus from this dataset by removing time blocks prior to 700 s after sunrise (Kaluthota et al., 2019). We restricted our dataset to the time after the dawn because pairs do not duet while the male is singing the dawn chorus.[2] The explanatory variables in the binned dataset are summarized in Table 2.

Table 2. Summary of explanatory variables included in the binned datatset.

Variable	Description	Mean ± SD
TimeRelSun	Average time since sunrise for the time block; based on the temporal midpoints of each block	1.42 ± 0.70 hr
IID	Inter-individual distance	28.5 ± 25.3 m
MaleInit	Count of male initiations within a time block	0.7 ± 1.3
FemaleAns	Count of female answers within a time block	0.3 ± 0.6
TimeRelAgg	Average time relative to an aggressive encounter; based on the temporal midpoints of each block	0.07 ± 0.56 hr
blockDuration	Duration of a time block	93.3 ± 121.8 s
DistEdgeM	Male distance to the territory boundary	12.5 ± 11.0 m
DistEdgeF	Female distance to the territory boundary	13.5 ± 10.3 m
TreeID_M	Location of the male	NA
TreeID_FE	Location of the female	NA
PairID	Specific pair being observed	NA

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[2] It does seem, however, that females determine when their males stop participating in the dawn chorus. In 2018 and 2022, we observed that males stop dawn chorus singing almost immediately upon the arrival of their mates (which often prompts a duet). Females tend to be stationary during the dawn chorus, and often their first observable activities are to locate their mate and answer his song (S.W.K. *pers. obs.*).

The continuous dataset included times for each event, rather than binning time into blocks. We scored whether each vocalization was a solo male song or a duet (*Vocalization*). We calculated *DeltaIID* by subtracting the *IID* of the subsequent observation (typically vocalization or movement) from the *IID* of the current vocalization. We chose to categorize a vocalization as preceding movement only if the movement occurred within 60 s of a vocalization event. When we built the movement model, we compared the short time limit (60 s) to a longer time limit (open-ended) and determined they were qualitatively identical. We filtered out vocalizations in which pair members were within 10 m of each other (< 10 m *IID*) to remove any vocalizations where the pair were already together or likely within visual contact (Logue, 2007). We filtered out vocalization events without an associated change in *DeltaIID* (i.e., neither sex moved after the vocalization). Finally, we removed observations that occurred off-territory (< -1.5 m *DistEdgeM* or *DistEdgeF*) or during the dawn chorus (< 700 s *TimeRelSun*). The explanatory variables in the continuous dataset are summarized in Table 3.

Table 3. Summary of explanatory variables included in the continuous dataset.

Variable	**Description**	**Mean ± SD**
TimeRelSun	Time since sunrise for the observation	1.49 ± 0.73 hr
IID	Inter-individual distance	41.3 ± 25.6 m
DeltaIID	The change in IID after a song or duet.	-5.2 ± 20.4 m
Vocalization	Binary variable that describes whether the female answers a male’s song	NA
TreeID_M	Location of the male	NA
TreeID_FE	Location of the female	NA
PairID	Specific pair being observed	NA

On Rates and Proportions

When studying duetting, it is important to distinguish between individual-level and pair-level behaviour (Logue & Krupp, 2016). This distinction can be challenging, especially with respect to rates and proportions of behaviour. In this study we define three such metrics at the individual-level, and two at the pair-level (Table 4).

Table 4. Definition of vocalization rates and proportions used in this study.

Individual-level

Initiation Rate = Initiations / Minute

Answer Rate* = Answers / Minute

Answer Proportion** = Answers / Initiations

Pair-level

Solo Rate = Solos / Minute

Duet Rate* = Duets / Minute

* For species with exclusively female-controlled duets, these are mathematically equivalent.
** Called “answer rate” in some studies (e.g., Diniz et al., 2018; Logue & Krupp, 2016; Weng et al., 2012).

Statistical Analysis

We conducted all statistical analysis in R software (R Core Team, 2022) in the RStudio environment (RStudio Team, 2018), running R markdown (Xie et al., 2018). We cleaned, “tidied”, and visualized our data with tidyverse (Wickham et al., 2019), further visualized with ggpubr (Kassambara, 2023), and built and tested directed acyclic graphs (DAGs) with dagitty R (Textor et al., 2016). We fitted Bayesian models in Stan (B. Carpenter et al., 2017) with brms (Bürkner, 2017b) and ran residual diagnostics with DHARMa (Hartig, 2022) and model comparisons with loo (Vehtari et al., 2017).

We followed McElreath’s (2019) analytic approach by modelling causal relationships with DAGs and building Bayesian regression models. A DAG is a network diagram composed of nodes representing variables and arrows describing the direction of casual influence (McElreath, 2019). We used DAGs to identify statistical confounds in our study system (McElreath, 2019; Westreich & Greenland, 2013).

Bayesian inference is good for fitting models with many parameters including random terms and non-linear effects (splines). We used weakly informative priors centered on 0 with a Standard Deviation (SD) of 1 for all regression parameters associated with explanatory variables. For all models, we used the Markov Chain Monte Carlo (MCMC) conditioning engine with four chains and 1000 iterations to generate posterior distributions. We scaled the explanatory variables to facilitate model convergence and coefficient interpretation. We modeled temporal variables with splines to allow non-linear changes over time.

Male Initiation Rate Model

The first model based on the binned datatset predicts the individual-level behaviour, male initiation rate. We built a DAG based on our understanding of the causal relationships among the explanatory variables *IID*, *DistEdgeM, TimeRelAgg, TimeRelSun*, and the response variable *MaleInit* (Figure 2; Table 2). We assumed the time of day could influence the male’s distance to the territory boundary (Bolsinger, 2000; Liu & Kroodsma, 2007), willingness to engage in an aggressive encounter, the IID between the focal pair, and his likelihood of singing (Bolsinger, 2000; Bradley & Mennill, 2009; Koloff & Mennill, 2013b; Shy & Morton, 1986; Trillo & Vehrencamp, 2005), so we allowed *TimeRelSun* to affect *DistEdgeM, IID*, *TimeRelAgg*, and *MaleInit*. We assumed that the IID could influence the male’s distance from the edge, his willingness to engage in an aggressive encounter (Wheeldon, Szymański, & Osiejuk, 2020), and his singing behaviour (Leitão et al., 2022; Trillo & Vehrencamp, 2005), so we allowed *IID* to affect *TimeRelAgg*, *DistEdgeM*, and *MaleInit*. We assumed the temporal proximity to an aggressive encounter could influence the male's distance from the territory boundary (Vehrencamp et al., 2014) and his song rate (Mennill & Vehrencamp, 2008), so we allowed *TimeRelAgg* to affect *DistEdgeM* and *MaleInit*. It is possible the direction of the causal relationship between *TimeRelAgg* and *DistEdgeM* could be reversed if the male's proximity to the boundary precipitates an aggressive encounter (Vehrencamp et al., 2014). However, the direction of causal influence between these variables did not impact model construction (see below). Finally, we assumed the male's distance to the territory boundary could influence his song rate (Simpson, 1985), so we allowed *DistEdgeM* to affect *MaleInit*.

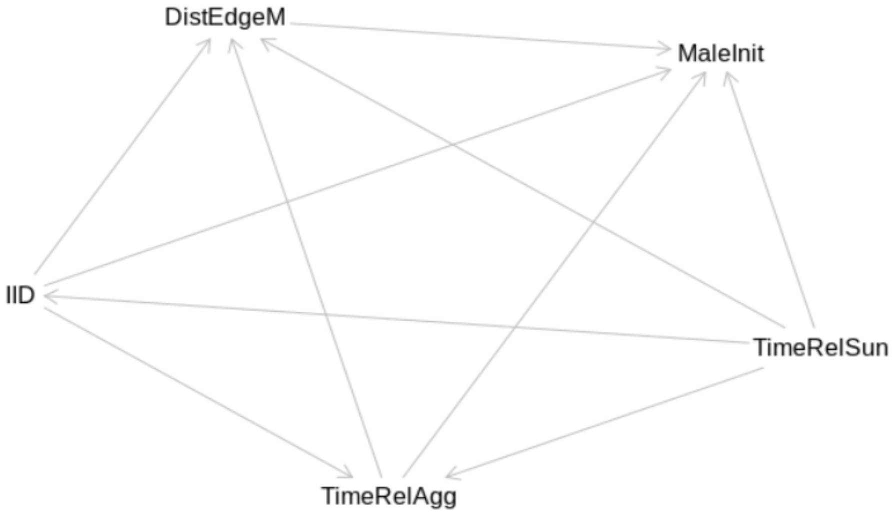


Figure 2. DAG representing variables (nodes) and the direction of causal influence (arrows) for variation in male initiation rates (*MaleInit*). Independent variables are inter-individual distance (*IID*), male distance to territory boundary (*DistEdgeM*), time relative to sunrise (*TimeRelSun*), and time relative to an aggressive encounter (*TimeRelAgg*).

We used the DAG to test conditional independencies with the impliedConditionalIndependencies function from the dagitty package. No conditional independencies were found. We then used the adjustmentSets function to identify which variables to include in our models to adjust for statistical confounds by testing each direct relationship between the response variable and our explanatory variables. The adjustmentSets output advised building a model with all four explanatory variables (*IID*, *DistEdgeM*, *TimeRelAgg*, and *TimeRelSun*) and our response variable, *MaleInit*.

We built a hurdle Poisson model with time bins as an offset term that also allowed variation in the probability of a time bin being zero. We chose to use the hurdle Poisson model because it addresses issues of zero deflation (Conceição et al., 2017). However, it also assumes all time bins have an equal probability of being zero. In reality, the longer a time bin, the more opportunity there is for a bird to sing and a female to answer. We overcame this constraint by using the *hu* term to model hurdle probability (Bürkner, 2023). Based on our analysis of the male initiation DAG, we included *IID* and *DistEdgeM* as linear fixed effects and included *TimeRelAgg* and *TimeRelSun* as non-linear fixed effects using splines. We included pair ID (*pairID*), male location (*TreeID_M*), and female location (*TreeID_F*) as random effects to control for the non-independence of male initiations within individual and at songposts.

We identified two plausible two-way interactions for the male initiation rate model. The first is between *IID* and *DistEdgeM*. We reasoned that the presence of the female may embolden the male to sing more often near the territory edge, or conversely, a male may compensate for the absence of the female by singing more and strengthening his “keep out” signal. The second interaction is between *IID* and *TimeRelAgg* because the presence of a female may influence the male to sing more and advertise readiness to defend in an aggressive encounter. To identify which interaction terms to keep in the model, we built and compared models containing all possible combinations of interaction terms. We used leave-one-out cross-validation (LOO) to choose which model best fit our data (Table 5). LOO scores are similar to Watanabe-Akaike information criterion (WAIC) but are more robust (Vehtari et al., 2017). The LOO scores indicated that including the interaction term *IID*TimeRelAgg* resulted in the best model fit (Table 5). The best fit model is represented by the following equation, where "t2" represents an interaction between explanatory variables with splines and "s" represents an explanatory variable with splines:

MaleInit ~ t2(IID, TimeRelAgg) + DistEdgeM + s(TimeRelSun) + offset(blockDuration) + (1 | PairID) + (1 | TreeID_M) + (1 | TreeID_F)

Table 5. LOO scores and standard error (SE) for the male interaction rate model containing different combinations of two-way interactions. Bold text indicates the best model (LOO = 0).

Fixed Effects	LOO / SE
IID, DistEdgeM, TimeRelAgg, TimeRelSun	-4.6 / 3.6
IID * DistEdgeM, TimeRelAgg, TimeRelSun	-4.8 / 3.6
IID * TimeRelAgg, DistEdgeM, TimeRelSun	**0.0 / 0.0**
IID * TimeRelAgg, IID * DistEdgeM, TimeRelSun	-1.3 / 1.1

Female Answer Proportion Model

The second model uses the binned dataset to predict the individual-level behaviour, female answer proportion. We built a DAG based on the causal relationships between the variables influencing the female's decision to answer her mate, given that the male has already sung. This DAG includes the explanatory variables *IID*, *DistEdgeF*, *TimeRelAgg*, *TimeRelSun*, and *FemaleAns* (Fig. 3; Table 2). We assumed the time of day could influence the female's distance to edge, willingness to engage in an aggressive encounter, the IID between the focal pair, and her likelihood of answering (Voigt et al., 2021), so we allowed *TimeRelSun* to affect *DistEdgeF*, *IID*, *TimeRelAgg*, and *FemaleAns*. We assumed that the IID could influence the female's distance from the edge, her willingness to engage in an aggressive encounter, and her answering behaviour (Hall & Magrath, 2000; Logue, 2007; Logue & Gammon, 2004; Mennill &

Vehrencamp, 2008; Templeton et al., 2013), so we allowed *IID* to affect *TimeRelAgg*, *DistEdgeF*, and *FemaleAns*. Given that females, like males, gain fitness benefits from maintaining and defending a territory, we assumed the temporal proximity to an aggressive encounter could influence the female's distance from the territory edge (Vehrencamp et al., 2014) and her likelihood of answering (Diniz et al., 2018; Hall, 2004; Mennill & Vehrencamp, 2008; Odom et al., 2017), so we allowed *TimeRelAgg* to affect *DistEdgeF* and *FemaleAns.* Just as in the male initiation model, it is possible the direction of the causal relationship between *TimeRelAgg* and *DistEdgeF* can be reversed if the female's proximity to the boundary precipitates an aggressive encounter (Vehrencamp et al., 2014). However, after testing both possibilities, we again determined the direction of causal influence did not impact model construction. Finally, we assumed the female's distance to the territory boundary could influence her likelihood of answering (Hall, 2009; Mennill & Vehrencamp, 2008; Sandoval et al., 2015; D. Ward, 1986), so we allowed *DistEdgeF* to affect the response variable *FemaleAns*.

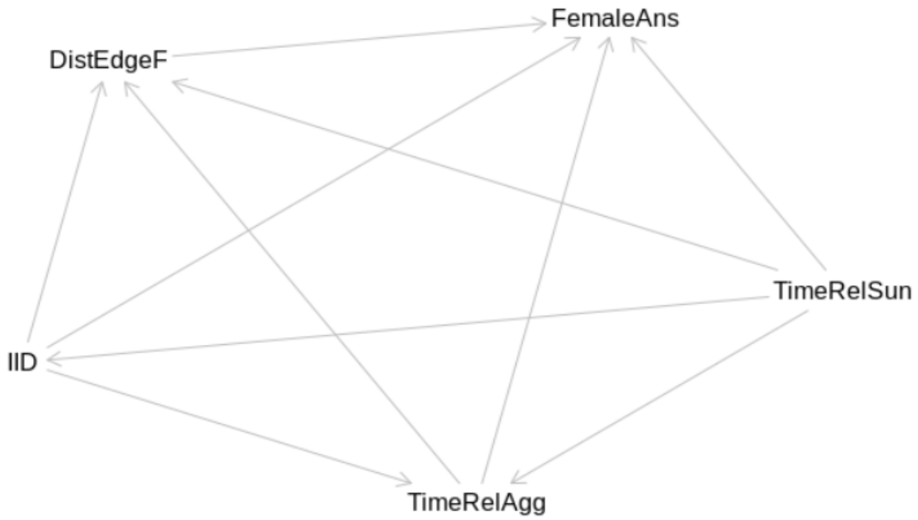


Figure 3. DAG representing variables (nodes) and the direction of causal influence (arrows) for variation in the female answer proportion (*FemaleAns*). Independent variables are inter-individual distance (*IID*), female distance to territory boundary (*DistEdgeM*), time relative to sunrise (*TimeRelSun*), time relative to an aggressive encounter (*TimeRelAgg*).

Following the same methods as described for the previous model, we used the DAG to test for conditional independences and identify statistical confounds. The adjustmentSets function advised we build a single model with all four explanatory variables (*IID*, *DistEdgeF*, *TimeRelAgg*, and *TimeRelSun*) and our response variable, *FemaleAns*.

We built a binomial model to predict the probability of a female answering her mate's song, given that he's already sung. Our male initiation data are in binomial format, such that every male song is labelled as answered (1) or unanswered (0). We included *IID* and *DistEdgeF* as linear fixed effects and included *TimeRelAgg* and *TimeRelSun* as non-linear fixed effects using splines. We included pair ID (*pairID*), male location (*TreeID_M*), and female location (*TreeID_F*) as random effects to control for the non-independence of female answering within individual and at songposts.

We identified two plausible two-way interactions for the female answer proportion model. The first is between *IID* and *DistEdgeF*. We reasoned that the presence of the male may embolden the female to answer more often near the territory edge. The second interaction is between *IID* and *TimeRelAgg* because the presence of a male may influence the female to answer more and advertise readiness to defend or engage in an aggressive encounter. To identify which interaction terms to include, we followed the same methods outlined previously. The LOO scores indicated the model with the interaction term *IID***DistEdgeF* best fit the data (Table 6):

FemaleAns ~ t2(IID, TimeRelAgg) + DistEdgeF + s(TimeRelSun) + (1 | PairID) +
(1 | TreeID_F) + (1 | TreeID_M)

Table 6. LOO scores and standard error (SE) for the female answer rate model containing different combinations of two-way interactions. Bold text indicates the best model (LOO = 0).

Fixed Effects	LOO / SE
IID, DistEdgeF, TimeRelAgg, TimeRelSun	-2.8 / 3.1
IID * DistEdgeF, TimeRelAgg, TimeRelSun	-19.4 / 8.6
IID * TimeRelAgg, DistEdgeF, TimeRelSun	**0.0 / 0.0**
IID * TimeRelAgg, IID * DistEdgeF, TimeRelSun	-0.3 / 1.9

Pair Duet Rate Model

The third model based on the binned dataset predicts the pair-level behaviour, pair duet rate, and uses the binned datatset. We built a DAG based on our understanding of the causal relationships among the explanatory variables *IID*, *DistEdgeM*, *DistEdgeF*, *TimeRelAgg*, *TimeRelSun*, and the response variable *PairDuet* (Fig. 4; Table 2). We assumed the time of day could influence the female's distance to edge, the male's distance to edge (Bolsinger, 2000; Liu & Kroodsma, 2007), the pair's willingness to engage in a fight, the IID between the focal pair, and the likelihood of a duet (Bradley & Mennill, 2009; Koloff & Mennill, 2013b; Voigt et al., 2021), so we allowed *TimeRelSun* to affect *DistEdgeF*, *DistEdgeM*, *IID*, *TimeRelAgg*, and *PairDuet*. We assumed that the IID could influence their respective distances from the boundary, their willingness to engage in an aggressive encounter (Wheeldon, Szymański, & Osiejuk, 2020), and the likelihood of a duet (Hall & Magrath, 2000; Logue, 2007; Logue & Gammon, 2004; Mennill & Vehrencamp, 2008; Templeton et al., 2013), so we allowed *IID* to affect *TimeRelAgg*, *DistEdgeF*, *DistEdgeM,* and the response variable, *PairDuet*. We assumed the distance of either bird to the territory boundary could influence the likelihood of a duet, so we made *DistEdgeM* and *DistEdgeF* affect the response variable *PairDuet* (Hall, 2009; Mennill & Vehrencamp, 2008; Sandoval et al., 2015; D. Ward, 1986). We assumed that temporal proximity to an aggressive encounter could influence the male and female's distances to the territory edge (Vehrencamp et al., 2014) and the likelihood of a duet (Diniz et al., 2018; Hall, 2004; Mennill & Vehrencamp, 2008; Odom et al., 2017), so we allowed *TimeRelAgg* to affect *DistEdgeF* and *DistEdgeM* and *PairDuet*. Just as in the previous two models, it is possible the direction of the causal relationship between *TimeRelAgg* and *DistEdgeF*, and *TimeRelAgg* and *DistEdgeM*, could be reversed if the female or male's proximity to the boundary precipitates an aggressive encounter (Vehrencamp et al., 2014). However, after testing the possible combinations, we again determined the direction of causal influence between these variables did not impact model construction. Finally, we assumed the female's distance to the territory boundary could influence the male's distance to the territory edge, so we made *DistEdgeF* affect *DistEdgeM*. This is another causal relationship that could possibly be reversed. However, the direction of this causal relationship also did not impact model construction.

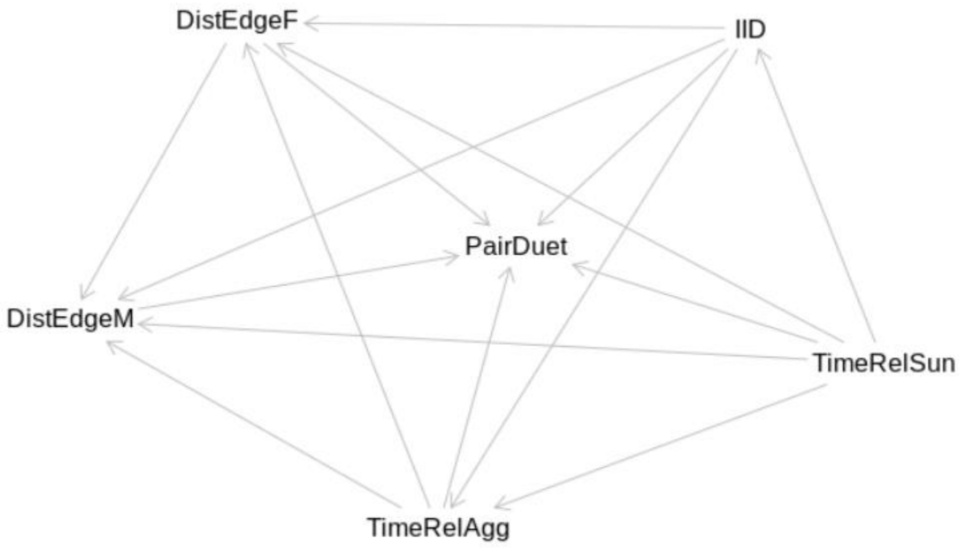


Figure 4. DAG representing variables (nodes) and the direction of causal influence (arrows) for variation in pair duet rates (*PairDuet*). Independent variables are inter-individual distance (*IID*), male distance to territory boundary (*DistEdgeM*), female distance to territory boundary (*DistEdgeF*), time relative to sunrise (*TimeRelSun*), time relative to an aggressive encounter (*TimeRelAgg*).

Following the same methods as above, we used the DAG to test for conditional independences and identify statistical confounds. The adjustmentSets function advised we build a single model with all five explanatory variables (*IID*, *DistEdgeF*, *DistEdgeM*, *TimeRelAgg*, and *TimeRelSun*) and our response variable, *PairDuet*.

Following the same methods as for the male initiation rate model, we built a hurdle Poisson model with time bins as an offset term that also allowed variation in the probability of a time bin being zero. We included *IID*, *DistEdgeF*, and *DistEdgeM* as linear fixed effects and included *TimeRelAgg* and *TimeRelSun* as non-linear fixed effects using splines. We included pair ID (*PairID*), male location (*TreeID_M*), and female location (*TreeID_F*) as random effects to control for the non-independence of male initiations within individual and at songposts.

We identified three plausible two-way interactions for the pair duet rate model. The first is between *IID* and *TimeRelAgg*. We reasoned that being in close proximity may embolden both birds to vocalize more and advertise readiness to defend or engage in an aggressive encounter. The second interaction is between *IID* and *DistEdgeM* because the presence of a female may embolden the male to sing more often near the territory boundary. Similarly, the third interaction is between *IID* and *DistEdgeF* because the presence of a male may embolden the female to answer more near the territory edge. We also identified a potential three-way interaction between *IID*, *DistEdgeM*, and *DistEdgeF* to account for the possibility that both the male and female are influenced by their proximity to each other as they approach the territory edge. We followed the same methods outlined above to identify which interaction terms to keep in the model. The LOO scores indicated that the model with *IID*TimeRelAgg* and *IID*DistEdgeF* fit the data best gave the best model fit (Table 7):

PairDuet ~ t2(IID, TimeRelAgg) + IID* DistEdgeF + DistEdgeM + s(TimeRelSun) + offset(blockDuration) + (1 | PairID) + (1 | TreeID_F) + (1 | TreeID_M)

Table 7. LOO scores and standard error (SE) for pair duet rate model containing different combinations of two-way and three-way interactions. Bold text indicates the best model (LOO = 0).

Fixed Effects	**LOO / SE**
IID, DistEdgeF, DistEdgeM, TimeRelAgg, TimeRelSun	-2.8 / 2.6
IID * DistEdgeF, DistEdgeM, TimeRelAgg, TimeRelSun	-0.3 / 1.2
IID * DistEdgeM, DistEdgeF, TimeRelAgg, TimeRelSun	-3.3 / 2.5
IID * TimeRelAgg, DistEdgeF, DistEdgeM, TimeRelSun	-2.1 / 2.1
IID * DistEdgeM, IID * DistEdgeF, TimeRelAgg, TimeRelSun	-0.7/ 1.4
IID * TimeRelAgg, IID * DistEdgeF, DistEdgeM, TimeRelSun	**0.0 / 0.0**
IID * TimeRelAgg, IID * DistEdgeM, DistEdgeF, TimeRelSun	-2.5 / 2.4
IID * TimeRelAgg, IID * DistEdgeM, IID * DistEdgeF, TimeRelSun	-0.8 / 0.7
IID * DistEdgeM * DistEdgeF, TimeRelAgg, TimeRelSun	-2.8 / 2.1
IID * DistEdgeM * DistEdgeF, IID * TimeRelAgg, TimeRelSun	-2.2 / 1.5

Movement Model

The final model uses the continuous dataset to predict the movement in both sexes after solos and duets, and uses the continuous dataset. This DAG includes the explanatory variables *IID*, *Vocalization*, *TimeRelSun*, *DeltaSex*, and the response variable *DeltaIID* (Fig. 5, Table 3). We assumed the time of day could influence the pair's IID during the vocalization, how likely they are to move after a vocalization, which sex is likely to move, and whether or the female answers the male, so we allowed *TimeRelSun* to affect *IID*, *Vocalization*, *DeltaSex*, and the response variable *DeltaIID*. The starting IID constrains how much the distance between pairs can change (e.g., if pairs start 10 m apart, they cannot reduce the distance between them more than 10 m), and we assumed their starting IID could influence their likelihood of moving, so we allowed *IID* to affect the response variable *DeltaIID*. We also assumed the starting IID could influence whether the female answers her mate or not (Hall & Magrath, 2000; Logue, 2007; Logue & Gammon, 2004; Mennill & Vehrencamp, 2008; Templeton et al., 2013), so we made *IID* affect *Vocalization.* Finally, we assumed whether a song was answered or unanswered could influence either bird's decision to reduce their IID (Logue, 2007; Odom et al., 2017), so we allowed *Vocalization* to influence *DeltaSex* and the response variable *DeltaIID*.

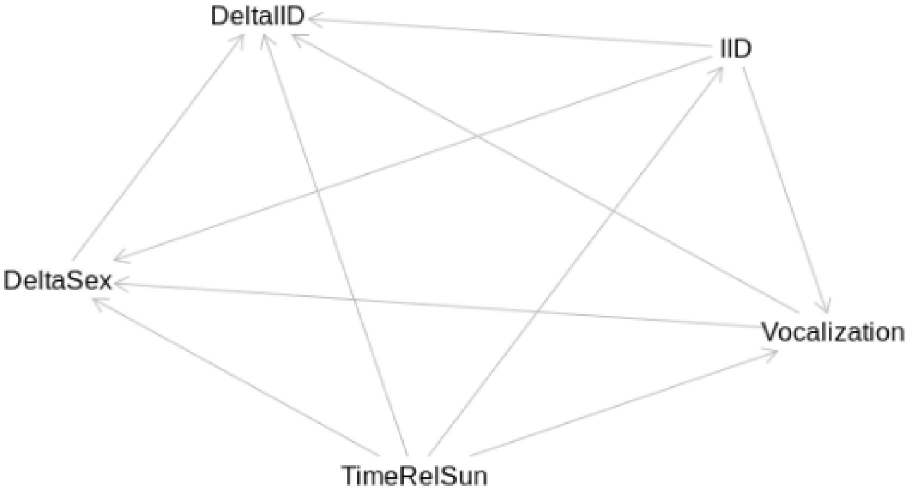


Figure 5. DAG representing variables (nodes) and the direction of causal influence (arrows) for variation in the change in inter-individual distance after a vocalization (*DeltaIID*). Independent variables are inter-individual distance at the time of the vocalization (*IID*), the type of vocalization (*Vocalization*), the sex that moves (*DeltaSex*), and time relative to sunrise (*TimeRelSun*).

We used the DAG to test for conditional independences and identify statistical confounds. The adjustmentSets function advised we build a single model with all four explanatory variables (*IID*, *DeltaSex*, *Vocalization*, and *TimeRelSun*) and our response variable, *DeltaIID*. We built a Gaussian model. Based on our analysis of the movement DAG, we included *DeltaSex* and *Vocalization* as linear fixed effects, and included *IID* and *TimeRelSun* as non-linear fixed effects using splines. We included pair ID (*PairID*), male location (*TreeID_M*), and female location (*TreeID_F*) as random effects to control for the potential non-independence of change in IID within individual and within preferred songposts.

We included the two-way interaction between *DeltaSex* and *Vocalization* because each sex may respond differently to unanswered versus answered male initiations. We made the *IID* a spline variable to allow for different approach behaviour at various IIDs. The model is represented by the following equation:

DeltaIID ~ DeltaSex + Vocalization + s(TimeRelSun) + s(IID) + (1 | PairID) + (1 | TreeID_F) + (1 | TreeID_M)

Model Validation

We evaluated model convergence by examining the R-hat statistic to determine if the MCMC chains converged. Generally, an R-hat value of 1.01 is acceptable with a value of 1 indicating complete convergence (Gelman et al., 2020). In all four of our final models, R-hat scores were < 1.01 for all explanatory variables and interactions.

We used the pp_check function in the brms R package (Bürkner, 2017a) to validate model fits. Posterior predictive checks produce a graphical comparison of simulated data using posterior predictive distributions (y_{rep}) to the observed data distribution (y). Comparing the two is a qualitative process (Gabry et al., 2019). The posterior predictive check indicated a good fit for all four models.

We also used the createDHARMa, testZeroInflation, and testDispersion functions from the DHARMa R package (Hartig, 2022) to assess model fit for the three vocalization models (male initiation rate, female answer proportion, and pair duet rate). These functions produce residuals plots, graphical and numerical tests of zero inflation or deflation, and graphical and numerical tests of data over- or under-dispersion, respectively. The zero inflation tests looked good for all three models. The male initiation rate and female answer proportion models were mildly under-dispersed, however the DHARMa residual plot visually indicated good model fit for both models.

Model Interpretation

To test our predictions of the cooperative resource defence hypothesis, and our vocalization-related prediction of the mate localization hypothesis, we interpreted the influence of each explanatory variable on the response variable for each of the three vocalization models. We did this by building simulations of our focal pairs and used them to generate predictions for the best-fit models. Using modeled predictions allowed us to elucidate the influence of our explanatory variables on our response variables. Simulations were easier to interpret than model parameters for the vocalization models because of their complex structure (Bürkner, 2017a),

For each simulation, we constructed a dataframe that varied only in the explanatory variable of interest, while the other variables were set to their average value. The only exception was *TimeRelAgg* which we set to 15 min prior to an aggressive encounter. We chose this time to avoid introducing additional variation from nuances in aggressive behaviour that we did not account for, such as whether the focal pair were invading or defending. For each simulated focal pair, we limited the variable of interest to the observed range. We selected locations for *TreeID_M* and *TreeID_F* that were closest to the average distance to the boundary and IID. We were then able to use the fitted function from the brms R package (Bürkner, 2017a) to generate predictions from the simulated dataframes. We visualized those predictions using ggplot2 from the tidyverse R package (Wickham et al., 2019) and the ggarange function from ggpubr package (Kassambara, 2023).

We used the model parameters to test the prediction of the mate localization hypothesis that pairs will tend to reduce IID more after a duet than after a solo song. It was not necessary to make predictions based on the simulated data for the movement model because the variables of interest ere either binary or linear values (Bürkner, 2017a).

To further interpret the results from all four models, we used conditional R^2 and marginal R^2 to evaluate the proportion of variance explained by all models and by their associated explanatory variables, respectively. We also assessed the proportion of variance attributed to each random effect by calculating the conditional R^2 with only one random effect included, then then subtracting the marginal R^2 value.

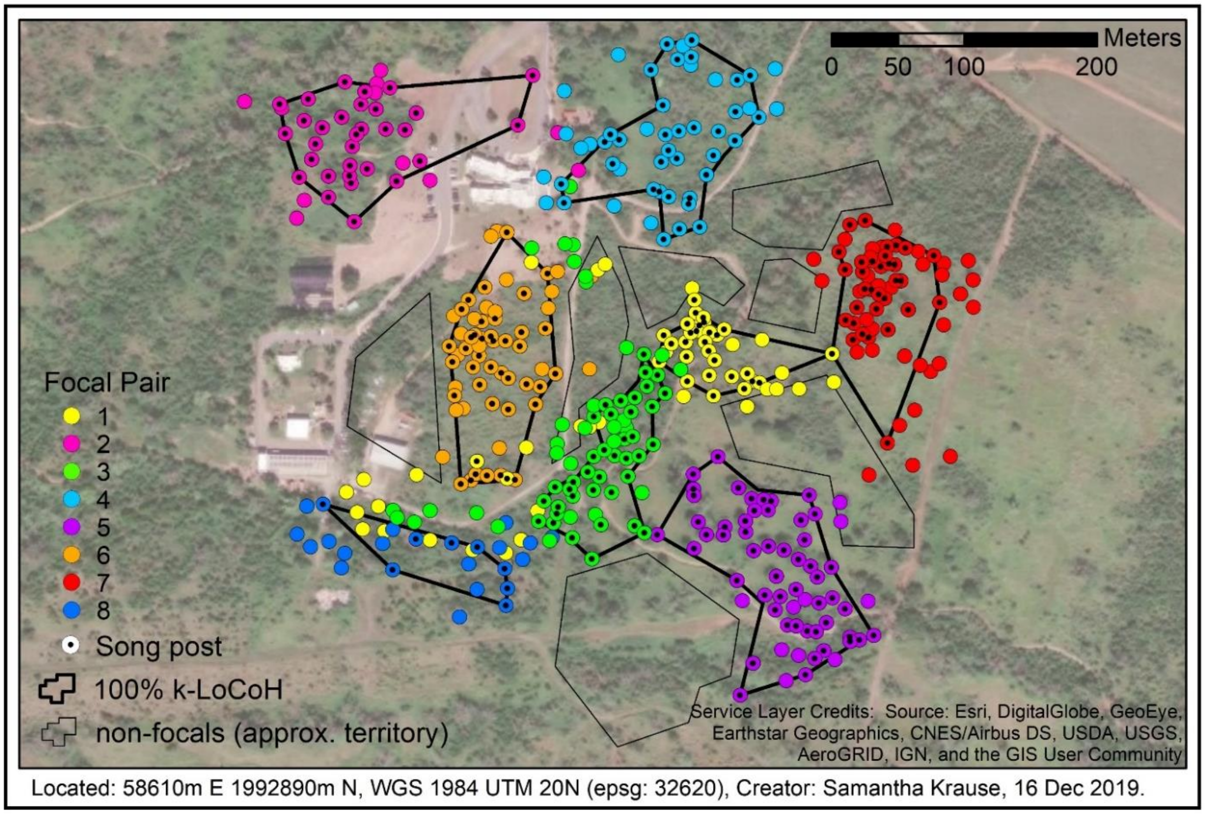
Results

We had to exclude two of our 22 recording sessions. Due to a radio tag failure, we were only able to conduct one recording session for Pair 8 and no duets or aggressive encounters were observed during this session. We therefore excluded Pair 8 from all analyses. We also excluded one recording session for Pair 1 because the focal female was off territory for the duration of the recording session. That left a total of 20 recording sessions (44.8 hours, not including the dawn chorus) from seven pairs.

Territories

The average territory size was 0.93 ± 0.32 ha (Table 1). Territories did not overlap, but the field crew observed all pairs outside of their defended territory (Fig. 6).

Pairs 1 and 3 were off-territory prior to the start of the dawn chorus on multiple occasions. We located Male 1, northwest of his territory, on Pair 6’s territory near their roost site, on April 9 and 14 (observed 56 ± 7 min before sunrise), referred to as the “North” location. The Male 1 then returned to his territory and participated in the dawn chorus (observed 29 ± 1 min before sunrise). We located Female 1 on Pair 8's territory and near the female's roost site, on April 5 and April 9 (observed 47 ± 6 min before sunrise), referred to as the "South" location. Female 1 slowly made her way back to her territory both mornings. On April 5 she had not returned to her territory by the end of the recording session (150+ minutes after sunrise), and on April 9 she returned 30 min after sunrise. Pair 3 showed similar behaviour. We located Male 3, also near the North location, on April 14, 16, 17, and 18 (observed 61 ± 1 min before sunrise, n = 4). Male 3 also returned to his territory and participated in the dawn chorus (observed 34 ± 3 min before sunrise, n = 3). We located Female 3, also near the South location, on April 16, 17, and 18 (observed 61 ± 0 min before sunrise, n = 3). Female 3 returned to the territory near the end of the dawn chorus (observed 12 ± 1 min before sunrise, n = 2).



Service Layer Credits: Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Located: 58610m E 1992890m N, WGS 1984 UTM 20N (epsg: 32620), Creator: Samantha Krause, 16 Dec 2019.

Figure 6. Territory boundaries of the mated pairs of Adelaide's warblers included in our study. Pair 8 are marked only for social context.

There is evidence to suggest these four birds roosted overnight at their morning starting locations. We were able to locate six birds (three pairs) one evening each at 20 ± 7 minutes after sunset. All six birds were in the same location the next morning at 59 ± 3 minutes before sunrise.

Description

The binned dataset omits 5.3 hours of recording because time blocks contained OFF time or focal birds were outside the territory boundary (Table 8). Of the omitted time, 57.8 minutes were due to off-territory activities, with a mean of 11.6 ± 8.0 min (*n* = 5) per pair. From the remaining recordings we observed each pair 3.1 ± 0.5 hours / day. Average daily totals were 77.8 ± 28 time blocks (at 93.4 ± 121.8 s / time block), 56.1 ± 33 song initiations, and 23.1 ± 10.1 answers. Four of the 59 aggressive encounters in the binned dataset occurred prior to 700 s after sunrise, so we only analyzed behaviour after those events, not before. See Appendix 1 for a breakdown of daily summaries.

Table 8. Summary of the time binned dataset we used for the vocalization models and vocalization simulations. Data are summarized by Pair ID and include totals by pair (Total), daily averages (Avg), and standard deviations (SD).

Pair ID	**Rec Day**	**Rec Times (hr)**			**Male Initiations**			**Female Answers**			**Aggressive Enc.**		
		Total	**Avg**	**SD**	**Total**	**Avg**	**SD**	**Total**	**Avg**	**SD**	**Total**	**Avg**	**SD**
1	2	3.8	1.9	0.6	248	124.0	28.3	42	21.0	11.3	4	2.0	1.4
2*	3	5.7	1.9	0.6	106	35.3	9.1	92	30.7	10.2	8	2.7	1.5
3	3	6.2	2.1	0.1	147	49.0	25.2	78	26.0	8.2	13	4.3	1.5
4*	2	2.5	1.2	1.0	61	30.5	23.3	37	18.5	13.4	9	4.5	2.1
5	4	8.9	2.2	0.0	319	79.8	16.0	110	27.5	12.2	11	2.8	0.5
6	3	6.6	2.2	0.2	158	52.7	3.5	65	21.7	6.1	4	1.3	1.5
7	3	5.7	1.9	0.2	78	26.0	8.5	36	12.0	4.6	10	3.3	0.6
Total	**20**	**39.5**	**2.0**	**0.5**	**1117**	**55.9**	**33.0**	**460**	**23.0**	**10.0**	**59**	**3.0**	**1.5**

*The males in these two pairs were not radio-tagged on the first observation day.

In the binned dataset, males spent 54% of their time and sang 51% of their total initiations within 10 m of the territory edge (Fig. 7a, c), while females spent 42% of their time and sang 40% of their answers within 10 m of the territory edge (Fig. 7b, d). The spike in female observations at 25 m from the boundary is attributable to the Pair 5 female, who spent most of her time on the nest.

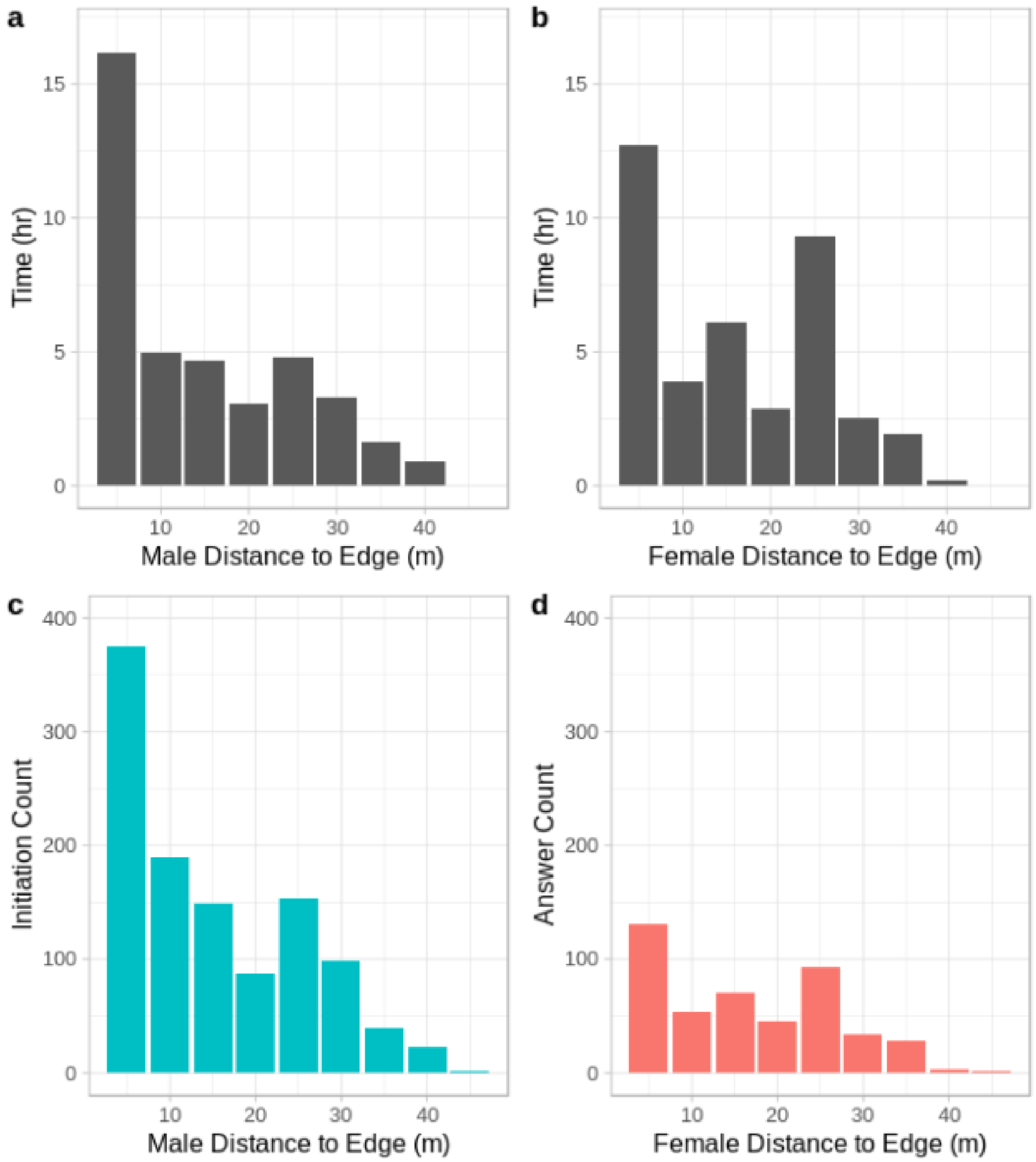


Figure 7. (a, b) Histograms of the time male and female Adelaide’s warblers spent at different distances to the territory boundary across all 7 pairs and 20 recording days. (c, d) Histograms of the number of male song initiations and female answers observed at different distances to the territory boundary.

Mates spent 45% of their time within 10 m of each other (Fig. 8a). Males sang 29% of their initiations and females sang 50% of their answers within 10 m of their partner (Fig. 8b). The highest answering proportion occurred when pairs were within 5 m of each other (Fig. 8b).

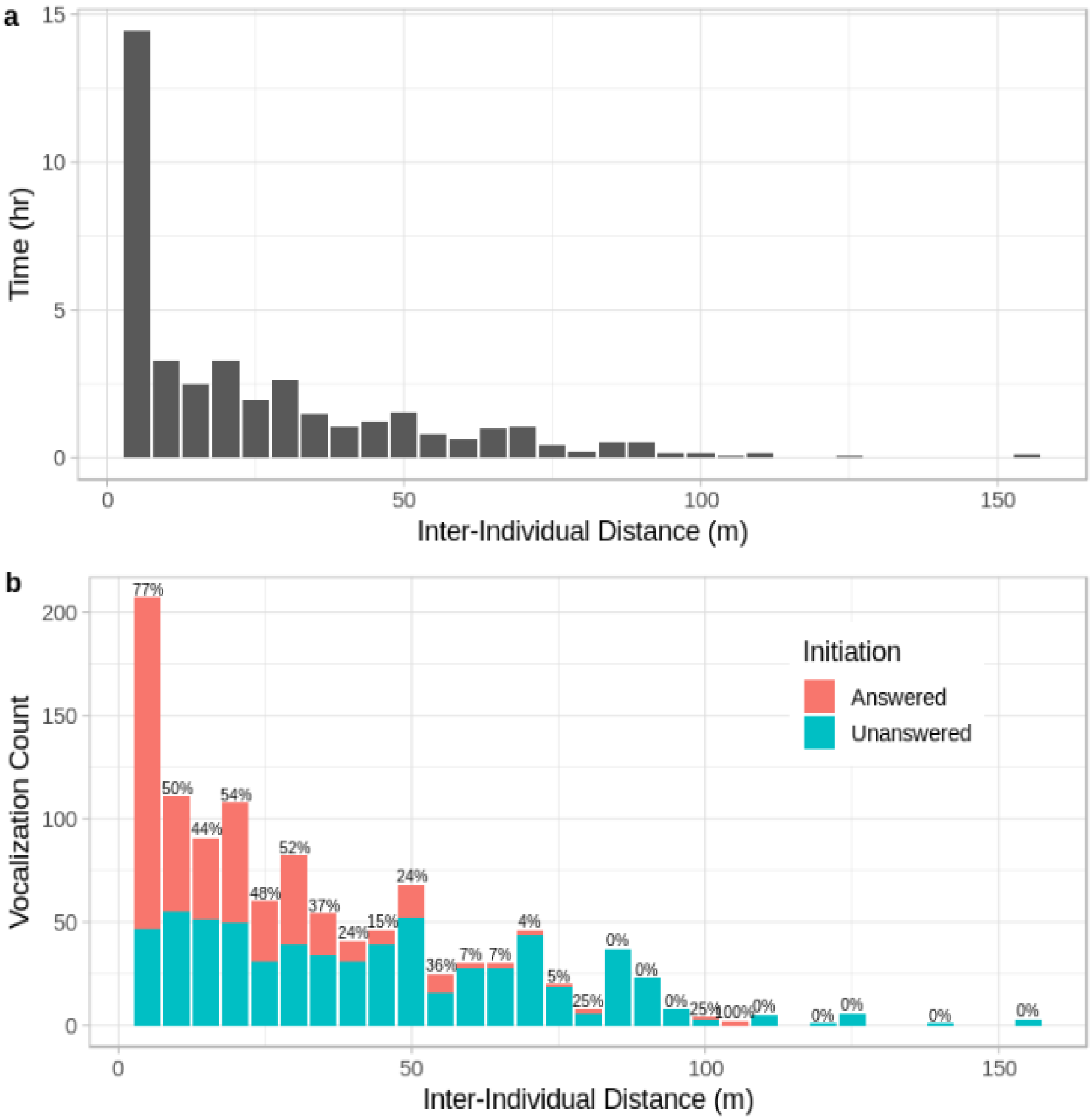


Figure 8. (a) Histogram of the time pairs of Adelaide's warblers spent at different inter-individual distances (IIDs). (b) Histogram of the number of vocalizations observed at different IIDs between focal pairs. Each stacked bar is the total male initiation count. The value listed above each stacked bar is the percentage of male songs that were answered within that IID bin.

We observed 55 aggressive encounters (1.5 ± 0.8 aggressive encounters / hour), with individual pairs representing a wide range (0.6 to 3.2 fights / hour). Male initiation rates and duet rates increased shortly before aggressive encounters, and remained elevated for approximately 30 min, but rates varied substantially from bin-to-bin (Fig. 9). We observed 47 aggressive encounters that occurred after the dawn chorus and not during active nesting. Of these, pairs engaged in aggressive encounters together (0 = *IID* at the beginning of an aggressive encounter) 62% of the time.

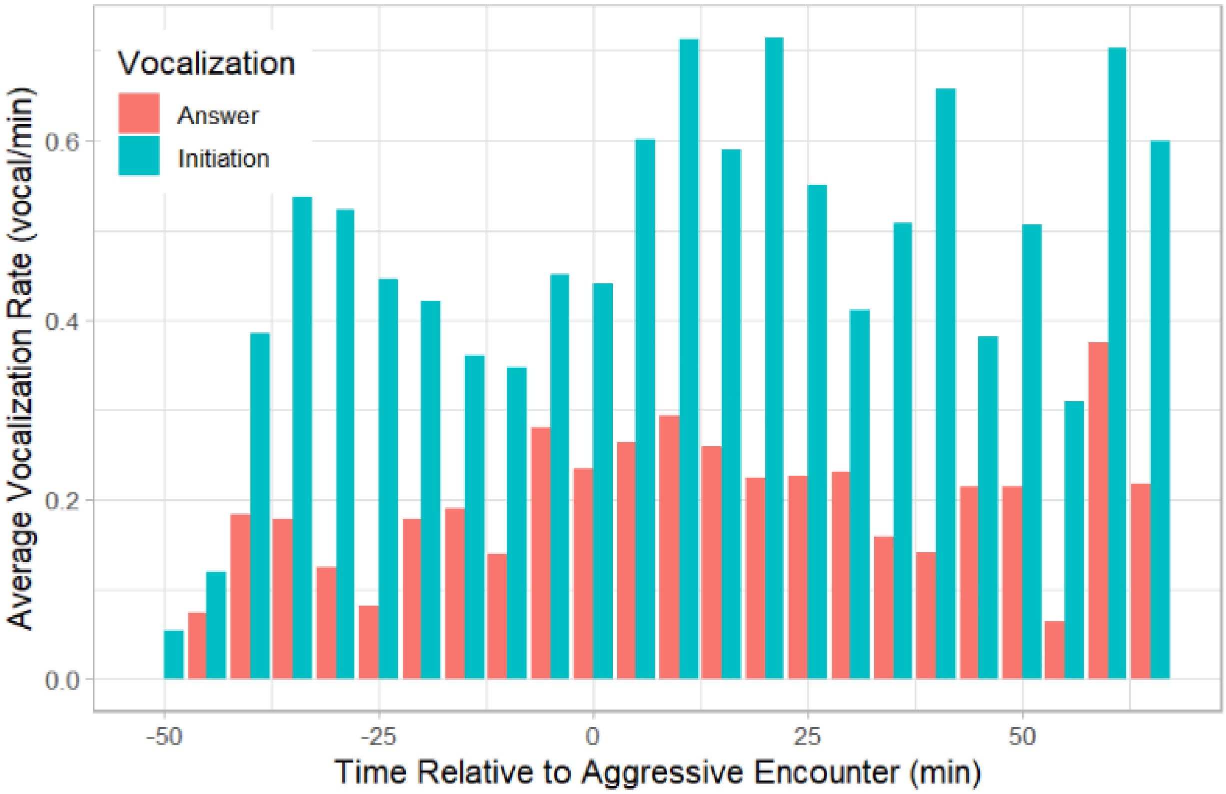


Figure 9. The average vocalization rate (vocal/min) observed at different times relative to an aggressive encounter (5-minute time bins) averaged across all pairs and recording days. The x-axis is truncated to ensure at least three pairs contribute data to each time bin.

We recorded 945 male initiations when pairs were ≥ 10 m apart. The pair changed IID within one minute after 365 (39%) of these; 217 changes in IID followed unanswered initiations (male = 106, female = 111), and 148 followed duets (male = 44, female = 104). Of the 580 male initiations that were not followed by a change in IID within one minute, 422 were after unanswered initiations, and 158 were after duets. The mean change in IID attributable to female movement was similar after answered (-11.4 ± 14.9 m) and unanswered (-10.0 ± 18.2 m) songs. The mean change in IID attributable to male movement was also similar after answered (6.1 ± 23.3 m) and unanswered (1.4 ± 22.4 m) songs (Fig. 10). Both males and females showed a wide range of change in IID both towards and away from their partners. We did not detect any relationship between the IID before a vocalization and the change in IID after a vocalization (Fig. 11).

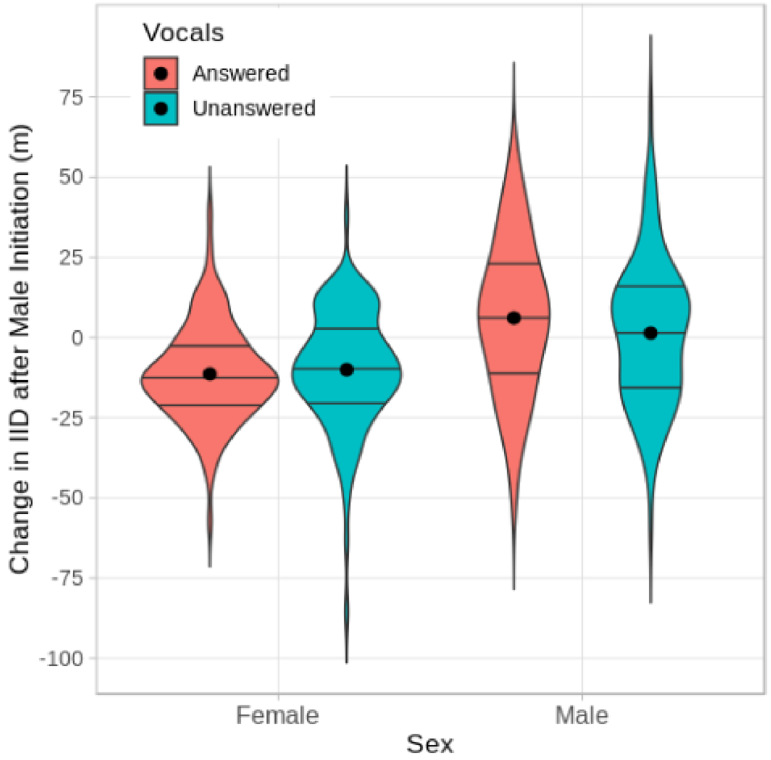


Figure 10. The change in inter-individual distance (IID) observed after a male solo song or duet when pair-members were at least 10 m apart when the male sang. Black points represent the mean change in IID, and the black bars represent the 75, 50, and 25 quantiles.

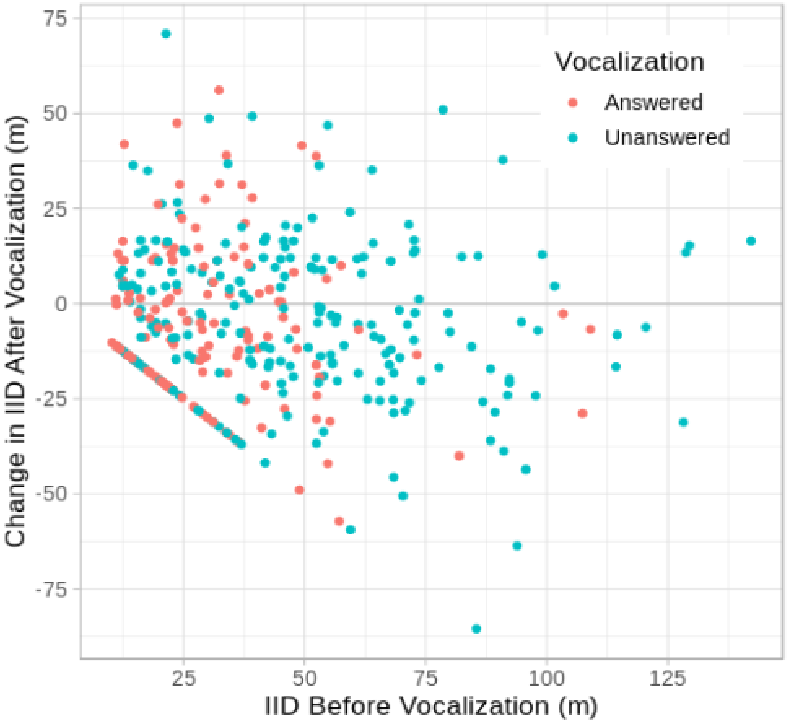


Figure 11. The change in inter-individual distance (IID) after a vocalization event versus the initial IID during the vocalization event.

Vocalization Models

Simulations based on the male song rate model indicate that males sing at higher rates when they are farther from their territory boundary and farther from their mate (Fig. 12a, b). The simulations indicate that male initiation rates began increasing 50 min prior to an aggressive encounter and continued to increase for 50 min after the encounter (Fig. 12c). The raw data, however, suggest this increase begins 5 min prior to the encounter and ends 25 min after the encounter (Fig. 9). Our model detected no effect of time since sunrise on song rate (Fig. 12d).

Simulations based on the female answer proportion indicate that female answer proportions were negatively associated with both distance to the territory boundary and distance to the mate (Fig. 13a, b). The latter effect was particularly strong. Answer proportions were not affected by aggressive encounters, but tended to decrease gradually over time, beginning about an hour after sunrise (Fig. 13c, d).

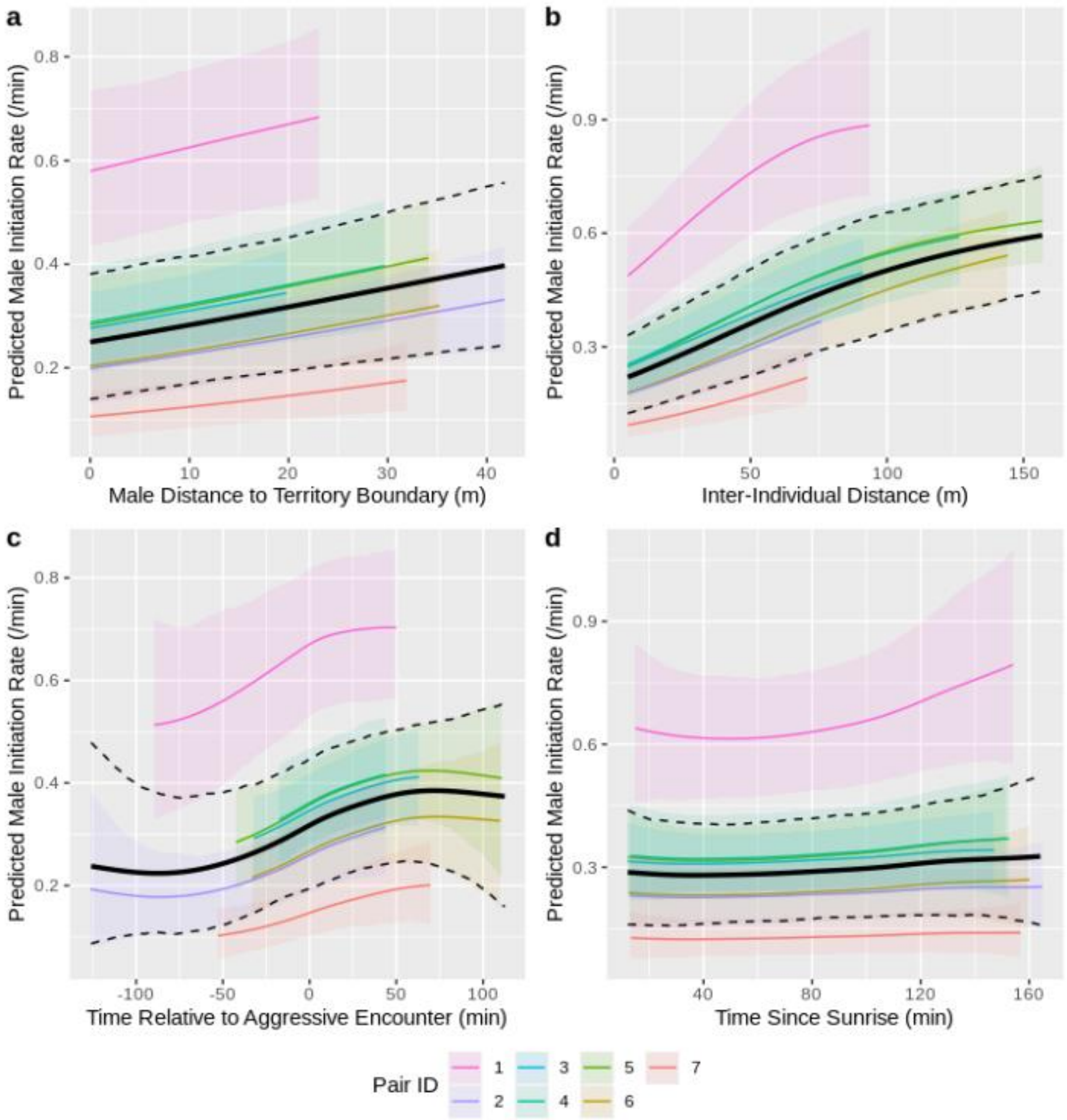


Figure 12. Predictions based on Bayesian models of male song rate in Adelaide's warblers. Lines indicate how male initiation rates covary with (a) distance to the territory boundary, (b) distance to the mate, (c) time relative to the temporally closest aggressive encounter, and (d) time relative to sunrise. The coloured lines represent estimates for each individual, and the semi-transparent coloured shading represents the 95% credible intervals for those estimates. The black solid lines and the dashed lines represent the average effect and its 95% credible interval, respectively.

Simulations showed that pair-level duet rates were weakly and positively associated with females' distance from the territory boundary, but were unaffected by the males' distance from the territory boundary (Fig. 14a, b). Duet rates were much higher when pair mates were close to one another than when they were far apart (Fig. 14c). The estimates show pair duet rates began to increase approximately 50 min prior to the aggressive encounter and remained elevated until 50 min after the encounter (Fig. 14d). However, the raw data suggests the effect was limited to 5 min prior and 25 min after the encounter (Fig. 9). Duet rates decreased gradually over the course of the morning observation period (Fig. 14e).

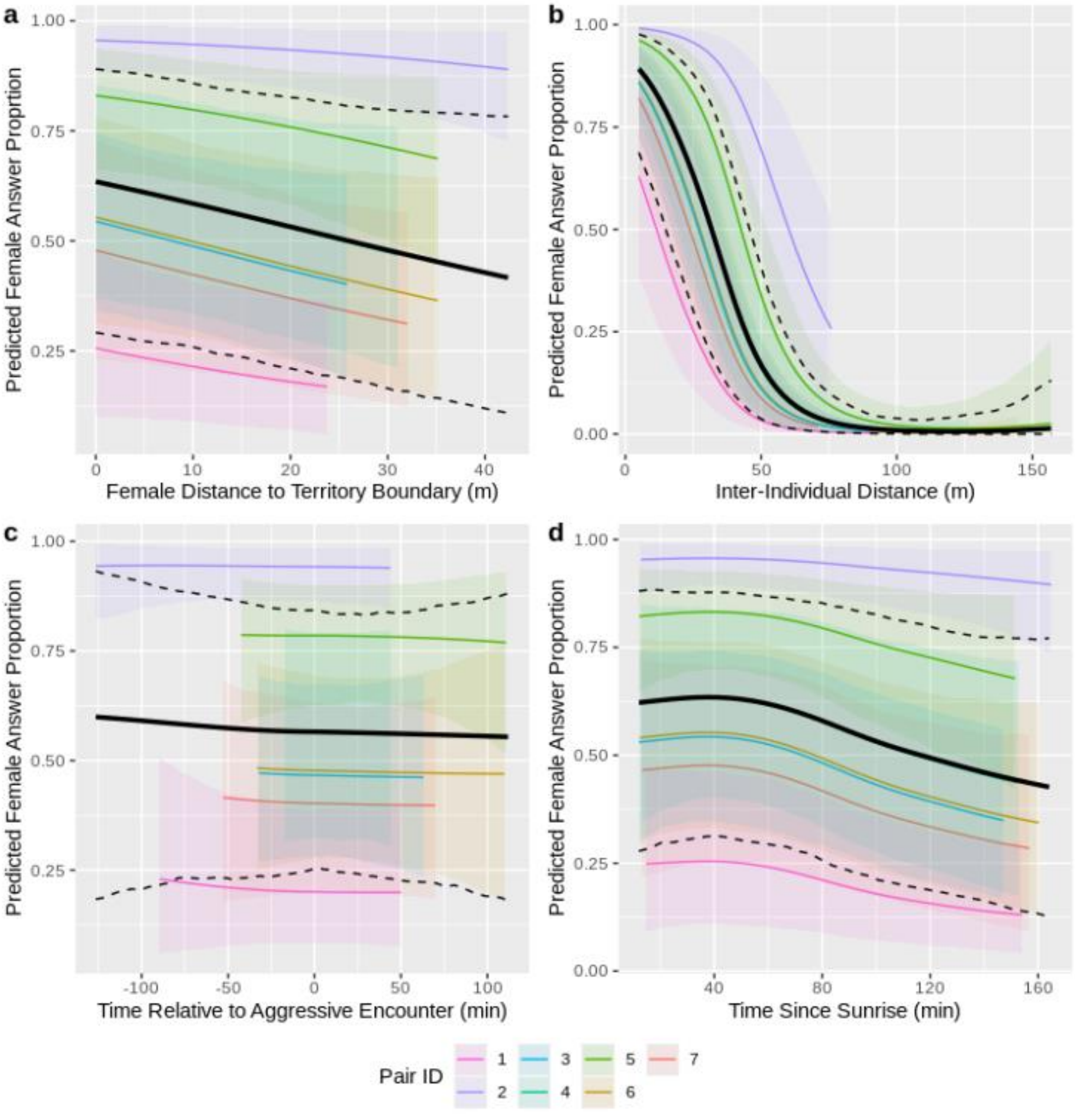


Figure 13. Predictions based on Bayesian models of female answer proportions in Adelaide's warblers. Lines indicate how female answer proportions covary with (a) distance to the territory boundary, (b) distance to the mate, (c) time relative to the temporally closest aggressive encounter, and (d) time relative to sunrise. The coloured lines represent estimates for each individual, and the semi-transparent coloured shading represents the 95% credible intervals for those estimates. The black solid lines and the dashed lines represent the average effect and its 95% credible interval, respectively.

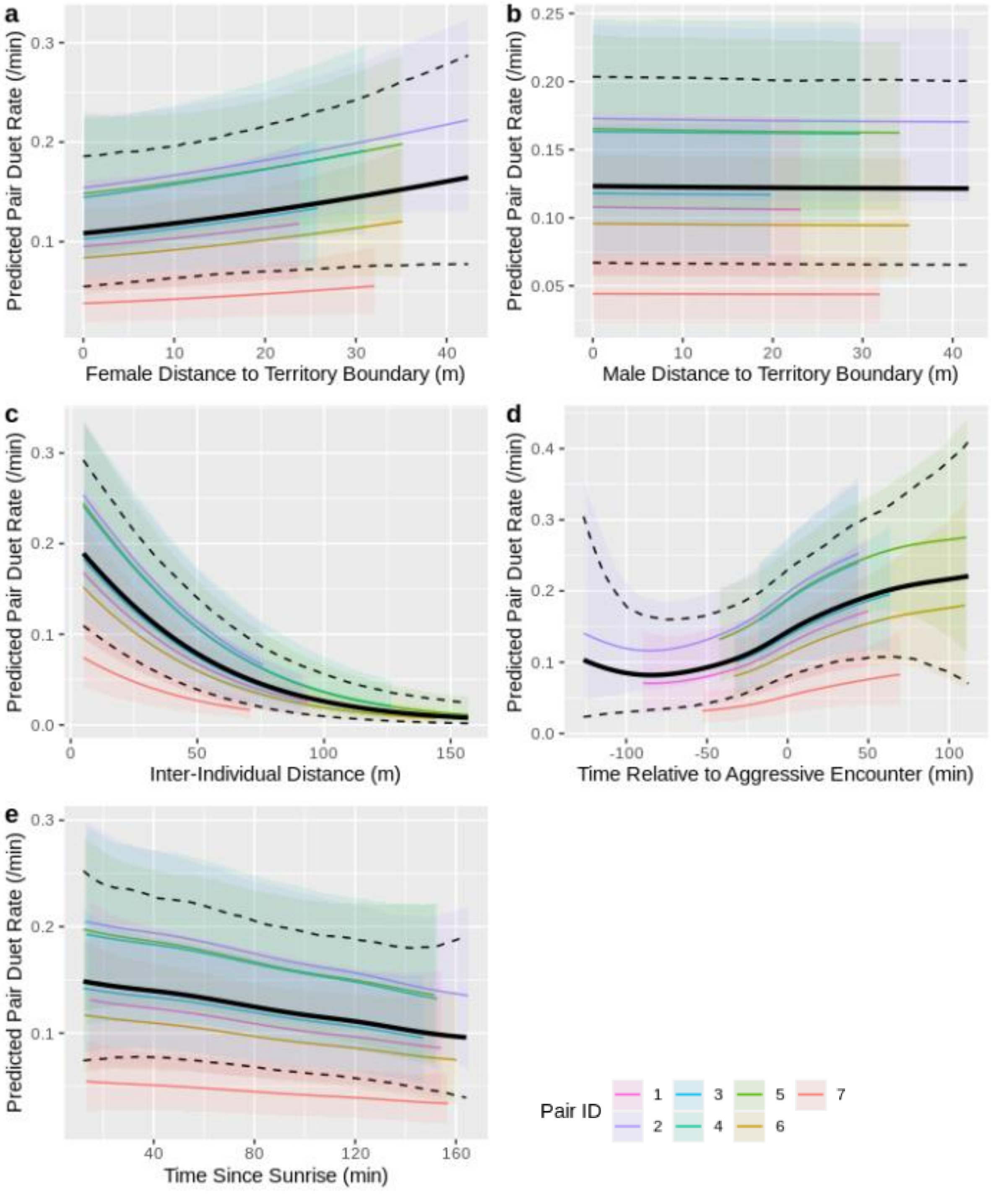


Figure 14. Predictions based on Bayesian models of pair duet rates in Adelaide's warblers. Lines indicate how pair duet rates covary with (a) female distance to the territory boundary, (b) male distance to the territory boundary), (c) distance to the mate(d) time relative to the temporally closest aggressive encounter, and (e) time relative to sunrise. The coloured lines represent estimates for each individual, and the semi-transparent coloured shading represents the 95% credible intervals for those estimates. The black solid lines and the dashed lines represent the average effect and its 95% credible interval, respectively.

For all vocalization models, the conditional R^2 and marginal R^2 showed that the percent of variance explained by the whole model was higher than the percent explained by the explanatory variables alone (Table 9). These results indicate the random variables helped explain the variance in all our vocalization models. Among the random variables, *PairID* explained the most variance for the male vocalization rate and female answer proportion models, but all three random variables explained comparable variation in the duet rate model (Table 10).

Table 9. Conditional R^2 and marginal R^2 for each of vocalization rate model.

Model	Conditional R^2	Marginal R^2
Male Initiation Rate	0.594	0.227
Female Answering Rate	0.775	0.585
Pair Duet Rate	0.301	0.153

Table 10. Conditional R^2 limited to the variance attributed to each random effect in the vocalization rate models.

Model	Random Effect	Limited Conditional R^2
Male Initiation Rate	PairID	0.215
	TreeID_M	0.090
	TreeID_F	0.004
Female Answering Proportion	PairID	0.116
	TreeID_M	0.022
	TreeID_F	0.018
Pair Duet Rate	PairID	0.041
	TreeID_M	0.036
	TreeID_F	0.056

Movement Model

Simulations showed that females reduced IID more than males after a song or duet (Fig. 15). Females reduced IID slightly more after answered songs (duets) than unanswered songs (male solos; Fig. 15). Males, however, increased IID slightly after both duets and solos (Fig. 15). The 95% CI estimate for *DeltaSex* does not contain 0, so sex has a statistically significant effect on how much IID changes after a song or duet (Table 11). The effects of *Vocalization* and the interaction between *Vocalization* and *DeltaSex* were not statistically significant (Table 11).

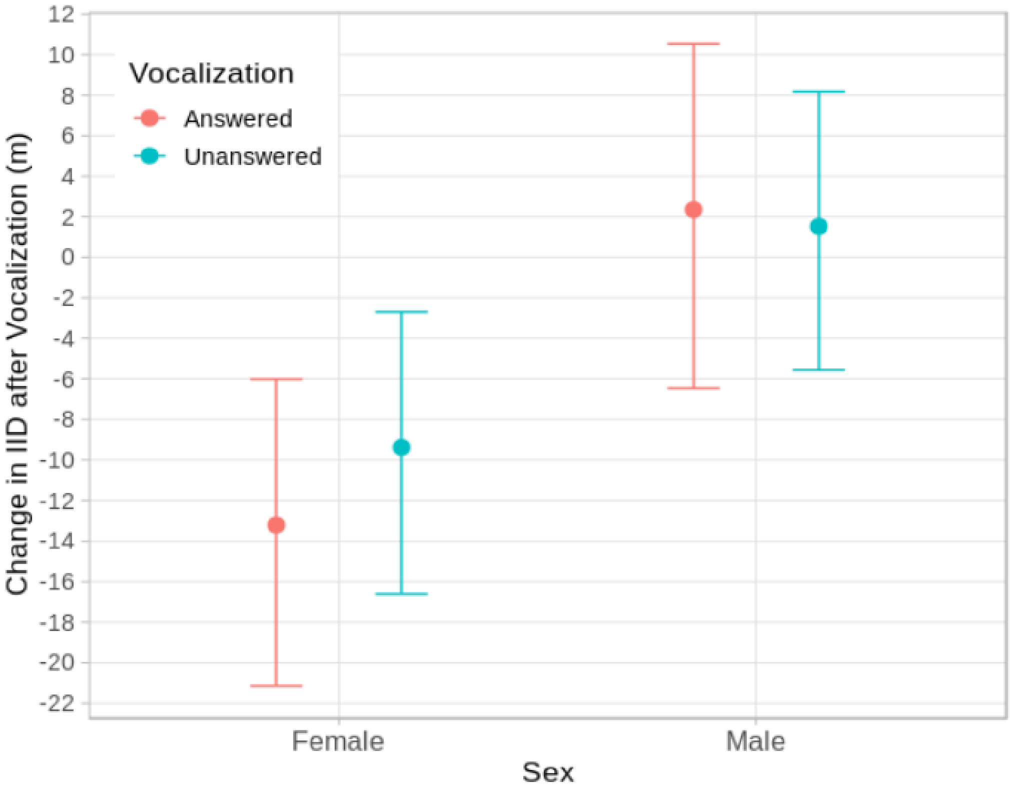


Figure 15. Dot and whiskers plot of the effect of the sex of the moving bird and vocalization type on delta IID after a vocalization in Adelaide's warblers. Whiskers indicate the 95% confidence interval.

The conditional R^2 and marginal R^2 showed that the percent of variance explained by the whole model was higher than the percent explained by the explanatory variables alone (conditional R^2 = 0.254; marginal R^2 = 0.159). The proportion of variance explained by the random effect *PairID* was lower than that explained by locations (Table 12).

Table 11. Population-level effects from the movement model estimates. Bold indicates explanatory variables with 95% credible intervals (CI) that do not include 0.

Parameter	Estimate	Estimated Error	Lower 95% CI	Upper 95% CI
Intercept	-0.39	0.15	-0.71	-0.12
DeltaSex	**0.73**	**0.17**	**0.40**	**1.07**
Vocalization	0.18	0.14	-0.10	0.45
DeltaSex*Vocalization	-0.23	0.21	-0.62	0.17
s(TimeRelSun)	0.22	0.66	-1.21	1.47
s(IID)	-0.00	0.96	-1.82	1.89

Table 12. Conditional R^2 limited to the variance attributed to each random effect in the movement model.

Model	Random Effect	Limited Conditional R^2
Delta IID model	PairID	0.012
	TreeID_M	0.032
	TreeID_F	0.043

Discussion

We used radiotelemetry to simultaneously observe free-living pairs Adelaide's warblers. Our goals were to describe the spatial, temporal, and social context of male initiation and female answering, and statistically test predictions of the joint resource defence and the mate localization hypotheses of duet function. We found strong evidence that duets function in joint resource defence: duets were associated with aggressive encounters, the territory boundary, and pair proximity. However, our findings do not support a localization function. Neither males nor females reduced their IID more after duets than after solos.

Description

The defended territories of our study pairs did not overlap, but all pairs spent time outside their territories (Fig. 6). These results suggest that Adelaide's warblers demonstrate typical home range and territory behaviour. A home range includes the area used during normal activity (Burt, 1943), while a territory is typically smaller and defended from conspecifics (Noble, 1939). Territories averaged 0.93 ± 0.32 ha (Table 1) which is similar to territory sizes reported for other New World warbler species (Anich et al., 2009; Flockhart et al., 2016; Lankau et al., 2013; Streby et al., 2012; Wagner et al., 2015). However, it is important to note that each study calculates territory area differently which limits comparison (Anich et al., 2009; Barg et al., 2005).

We observed two pairs roosting off territory. Both males roosted on the edge of another pair's territory near the resident pair's roost site, and both females roosted on the edge of a different pair's territory also near the resident pair's roost site. These locations are separated by 250 m and a full territory (Fig. 6). Both males and returned to their territories in time to participate in the dawn chorus. On April 16, both males roosted within 20 m of each other. This behaviour has not been reported before in this species. Overnight, off-territory, roost locations have been described in other songbirds species, including several warblers species (J. P. Carpenter & Wang, 2018). Possible explanations range from thermoregulation, predator avoidance, habitat composition, to EPC opportunity (J. P. Carpenter & Wang, 2018; M. P. Ward et al., 2014). Our findings are similar to the nocturnal forays observed in yellow-breasted chats (*Icteria virens*; M. P. Ward et al., 2014). In this species, males and females visit the same off-territory areas ("night clubs") during nocturnal forays, which likely offers EPC opportunities. Pairs of Adelaide's warblers may be exhibiting similar nocturnal behaviour, with pairs roosting at separate “night club” locations for EPC opportunities. Future investigation with nocturnal radio-tracking and audio recording would provide further insight into this overnight roosting behaviour.

Both males and females spent a lot of time near their territory boundary where they vocalized frequently (Fig 7). Males in several species of songbird countersing at territory boundaries during the dawn chorus, but few include a description of singing behaviour later in the morning (Lein, 2007; Liu & Kroodsma, 2007; Trillo & Vehrencamp, 2005). During the breeding season, chipping sparrows (*Spizella passerine*) countersing from territory boundaries during the dawn chorus, and sing from the territory center after the dawn chorus (Liu & Kroodsma, 2007). Adelaide’s warbler males appear to have the opposite trend. Males typically participate in the dawn chorus from one or two central locations (unpublished data), and then spend time near territory boundaries during the morning. Few duetting studies include detailed spatial data, but a few mention that duets are common near territory boundaries (Cuthbert & Mennill, 2007; Sandoval et al., 2015; D. Ward, 1986). The only published test that relies on systematically collected data did not reveal any association between duets and territory boundaries in rufous-and-white wrens (*Thryophilus rufalbus*; Mennill & Vehrencamp, 2008). Field observers noted pairs of Adelaide’s warblers appeared to patrol their territory boundaries while duetting, a behaviour noted in several other duetting species (D. Ward, 1986).

The mated birds in our study were often in close proximity (≤ 5 m, 37% of the time). It is not uncommon for duetting species to spend a lot of time together during the breeding season (Fedy & Stutchbury, 2005; Gill et al., 2005; Hall & Magrath, 2000; Hall & Peters, 2008). In a histogram of vocal behaviour over IID, male initiations, female answers, and female answering proportion all peaked in the first bin (0 - 5 m; Fig. 8). Although this appears contradictory to our male initiation rate model in which male initiation rates increase with IID (Fig. 12), this apparent paradox is driven by the amount of time pairs spend in close proximity. Even though the male initiation rates are low when pairs are close, the total number of initiations over time is still high.

We observed an average of 1.5 ± 0.8 aggressive encounters / hr. This is double the average aggressive encounters per hour in rufous horneros (*Furnarius rufus*; 0.73 ± 0.05; mean ± SE), another duetting, Neotropical species (Diniz et al., 2018). Male initiation rates and pair duet rates increased with temporal proximity to an aggressive encounter, and female answer proportion remained fairly constant (Fig. 9). Increases in male initiation rates and pair duet rates around the time of aggressive encounters occurs in many duetting species (Diniz et al., 2018; Odom et al., 2017). These increases are routinely observed in response to conspecific playback (Benedict, 2010; Brumm & Goymann, 2018; Diniz, Rech, et al., 2019; Fedy & Stutchbury, 2005; Mennill & Vehrencamp, 2008; Rogers et al., 2007; Templeton et al., 2011; van den Heuvel et al., 2014; Weng et al., 2012; Wheeldon, Szymański, & Osiejuk, 2020). It is not uncommon for duetting species to maintain answer proportion across aggressive contexts (Diniz et al., 2018; Fedy & Stutchbury, 2005; Hall, 2006). Rufous horneros maintain a constant answer proportion across naturally occurring aggressive encounters (Diniz et al., 2018). Similarly, happy wrens (*Pheugopedius felix*) and white-browed coucals (*Centropus superciliosus*) respond to all playback stimuli with a consistent answer proportion (Brumm & Goymann, 2018; Templeton et al., 2011).

Pairs did not reduce their IID more after solo songs than duets (Fig. 10). In many duetting species in which both sexes initiate and answer, pairs tend to reduce IID after duets (Benedict, 2010; Hall et al., 2015; Logue, 2007; Mennill & Vehrencamp, 2008; Odom et al., 2017). Female Adelaide’s warblers tended to move toward their mates after both solos and duets, but males did not. We did not detect any relationship between starting IID and the change in IID after a vocalization (Fig. 11). In contrast, Logue (2007) found that pairs of black-bellied wrens (*Pheugopedius fasciatoventris*) are more likely to reduce IID after a duet when >10 m apart to begin with.

After the dawn chorus, male initiation rates held steady for the duration of the recording session, while both female answer proportion and duet rates declined (Figs. 12d, 13d, 14e). After an initial bout of "wake up" song, white-browed sparrow weavers (*Plocepasser mahali*) also decrease rates of duetting and chorusing over the course of the morning (Voigt et al., 2021). Conversely, yellow-breasted boubous (*Laniarius atroflavus*) maintain fairly constant duet rates throughout the day (Wheeldon, Szymański, Budka, et al., 2020).

Joint Resource Defence

Our results support the hypothesis that female Adelaide's warblers use song answering to cooperatively defend their territories from conspecifics. This conclusion is consistent with many studies in other species (Benedict, 2010; Brumm & Goymann, 2018; Diniz et al., 2018; Diniz, Rech, et al., 2019; Dowling & Webster, 2013; Logue & Gammon, 2004; Mennill & Vehrencamp, 2008; Odom et al., 2017; Sandoval et al., 2018; Templeton et al., 2011; Wheeldon, Szymański, & Osiejuk, 2020).

If birds use duets to defend their territories, then answering should be associated with aggressive encounters (Diniz et al., 2018; Hall, 2004; Odom et al., 2017). In support of this prediction, we found that both male initiation rates and duet rates tended to increase shortly before aggressive encounters and remained elevated for about 30 min after the encounter (Figs. 9, 12, 14). Both behaviours increased by ~100% relative to baseline, suggesting these are biologically relevant effects (Figs. 12, 14). Notably, however, our model of female answer proportion showed that it was independent of aggressive encounters (Fig. 13).

These findings highlight a source of ambiguity in the duet literature. Many studies of duet function predict changes in answering behaviour, but few specify whether the duet rate or answer proportion should change. Failing to specify between duet rate or answer proportion can lead to confusing or contradictory conclusions. In their observational study of rufous horneros, Diniz et al. (2018) found an increase in duet rate, but not answering proportion in aggressive contexts. They conclude that duets likely serve a joint resource defence function, but that song-answering likely does not. After finding similar trends in the white-bellied antbird (*Myrmeciza longipes*), Fedy and Stutchbury (2005) concluded that duets are unlikely to function in joint resource defence because answer proportion did not increase in response to playbacks. In both studies, the answer proportion was unchanged, but the answering effort increased to keep pace with the partner's increased initiation rate.

From the perspective of a potential intruder who receives the signal, there are three combinations of individual behaviours that necessarily result in a higher duet rate: an increase in initiation rate and a constant answer proportion, a constant initiation rate and an increase in answer proportion, or an increase in both initiation rate and answer proportion (Logue & Krupp, 2016). We consider any of these trends as support for the joint resource defence hypothesis because all three result in an increased signal rate from the receiver's perspective. In our study, we observed an increase in initiation rate and a constant answer proportion. Thus, the female's effort and the number of duets salient to potential intruders increased, but the proportion of songs answered did not. So, if we are asking about effort or signal density, there was an increase. If instead we are focused on proportion, there was no change. We conclude that the observed increase in female answering effort (duet rate), supports our prediction that female answering is associated with aggressive encounters.

Three field observations provide additional evidence that pairs use duets to defend the territory cooperatively: 1) Pairs often approach aggressive encounters simultaneously (Diniz, Rech, et al., 2019; Hall & Peters, 2008; Koloff & Mennill, 2013a; Sandoval et al., 2018; Templeton et al., 2011). 2) Although we did not measure signal amplitude, it was our impression that female duet vocalizations were often louder near the time of aggressive encounters than during normal activity. If females cooperatively defend against conspecifics, increasing signal amplitude would help the signal reach the intended receivers and could signal motivation. 3) Females sometimes included aggressive chitburst calls in duets around the time of aggressive encounters, either by replacing the pip train with a chitburst or by transitioning from pips to chits (also observed by Staicer in 1991).

Female answers and male initiations may be effective in cooperative territory defence by functioning as signals of aggressive (or defensive) intent. Searcy and Beecher (2009) suggested three criteria to determine if a signal should be classified as aggressive: (1) the signal should increase in aggressive contexts, (2) the signal should predict aggressive escalation, and (3) receivers should differentially respond to the signal. Our results show strong support criterion (1), and the increase in song and duet rate prior to an aggressive encounter is consistent with criterion (2). We are unable to address criterion (3) with our current study, and there are no published data on Adelaide warbler response to duet playback. Future playback studies will be able to confirm if Adelaide's warbler songs and duets function as a signal of aggressive intent.

Female answers and male initiations may also function as a post-conflict display. Although both pair members increased their vocal efforts prior to an aggressive encounter in both the raw data and our simulations, the initiation and duet rates continue to climb after the conflict and remain elevated for about 30 minutes. We could not identify the winners and losers for each aggressive encounter in order to test the predictions of either the victory display hypothesis (Grafe & Bitz, 2004a; Mouterde et al., 2012), or the loser-display hypothesis (Lippold et al., 2008). However, it is likely the increased initiation and duet rates act to re-establish territory boundaries between the dueling neighbours, but also may act as a signal to eavesdroppers that the pair is still present and still ready to defend their territory. Our results are similar to Trillo and Vehrencamp's (2005) observation that banded wrens (*Thryophilus pleurostictus)* sung at increased rates on days with boundary disputes.

Our second prediction based on the joint resource defence hypothesis was that females would answer more when they were near the territory boundary. Indeed, we found that females answered a higher proportion of their mates' songs when the females were near the boundary (Figs. 7, 13). However, duet rates were slightly higher when the female was farther from the territory boundary (Fig. 14). Of course, that trend was driven by the positive association between male initiation rates and male distance from the boundary (Fig. 12). The negative association between female answer proportion and distance from the boundary, combined with the positive association between male initiation rates and distance from the boundary, results in a slight positive relationship between duet rate and distance from the boundary (Figs. 12, 13, 14). The divergent trends in duet rate and female answer proportion create an intriguing scenario for interpretation and exemplifies the importance of considering both individual-level and pair-level behaviours in duet research (Hall, 2009; Logue & Krupp, 2016).

From the female's perspective, she is choosing to answer the male more often when near the territory boundary (Fig. 13). Additionally, pairs spend the majority of their time near the boundary, resulting in the highest number of initiations and answers observed within 5 m of the boundary (Fig. 7). These results support our prediction that females would answer more near territory boundaries. However, as previously discussed, if pair-level duets indicate the pair's motivation to jointly defend the territory, then duet rate may be more salient to receivers than answer proportion. In that case, the increase in duet rate towards the territory center would contradict our prediction. Although several studies have predicted a spatial association between duets and the territory boundary (Hall, 2009; Mennill & Vehrencamp, 2008; Sandoval et al., 2015; D. Ward, 1986), only a few have tested this prediction, and most provide only anecdotal support (Cuthbert & Mennill, 2007; Sandoval et al., 2015; D. Ward, 1986). The only published test with systematically collected data failed to show an association between duets and boundaries in rufous-and-white wrens (Mennill & Vehrencamp, 2008). However, it is important to note, these studies fail to specify if they used duet rates, answer proportion, or counted individual duets near territory boundaries. As our results demonstrate, the specific metric could change the conclusions drawn. The vague reporting in the literature limits our ability to draw meaningful comparisons.

The observed increase in male initiation rates towards the center of the territory may reflect males' effort to simultaneously advertise territory ownership to as many neighbours as possible from the territory center. Alternatively, males may increase their acoustic defence to compensate for their physical distance when they are farther from the territory boundary. Adelaide's warbler territories are typically 50 - 150 m in diameter, and male song can often be heard by human observers 1 - 2 territories away. Singing from the territory center would likely ensure a male's song is heard by all immediate neighbours. A third possible reason why male song rates increase with distance to the boundary is that singing near a shared territory boundary may be an inflammatory signal to immediate neighbours and result in aggressive encounters (Vehrencamp et al., 2014). Nearly all of the aggressive encounters we observed were adjacent to territory boundaries. Thus, males may sing at lower rates near territory boundaries to reduce the risk of inciting aggressive encounters with their neighbours. Other male songbirds change their vocalization behaviour at the territory boundary, or near conspecifics. Some species increase song output near the boundary (Lein, 2007), but others decrease song output (Simpson, 1985), and some alter other aspects of song production such as song type (Bolsinger, 2000; Kroodsma et al., 1989; Trillo & Vehrencamp, 2005). Further study is needed to discriminate among these possibilities.

If males sing at lower rates near territory boundaries to reduce the likelihood of inciting an aggressive encounter, then our results may reveal a trade-off when duetting near territory boundaries. Pairs of Adelaide’s warblers may benefit by advertising a strong defence unit to other conspecifics, but may also incite aggressive encounters if they signal too often. Pairs of other duetting species respond most strongly, or just as strongly, to playback of duetting birds than to solo song (Benedict, 2010; Brumm & Goymann, 2018; Odom & Omland, 2018; Sandoval et al., 2018; Templeton et al., 2011), suggesting duets are perceived as a threatening signal. Female Adelaide’s warblers may answer their mates more often near territory boundaries to ensure that when the male does sing to advertise his presence and territory ownership, the signal is the most efficient threatening signal. We conclude that the increase in female answer proportion and the high number of male initiations and female answers observed along territory boundaries supports out second prediction. However, we also acknowledge there may be constraints limiting the value of signalling near territory boundaries.

Our third prediction based on the joint resource defence hypothesis was that females would answer more when they were close to their mate. Indeed, we found that female answer proportion was strongly and negatively correlated with IID (Figs. 8, 13). Previous studies have also shown that birds answer their mates more when they are in close proximity (Hall & Magrath, 2000; Logue, 2007; Logue & Gammon, 2004; Mennill & Vehrencamp, 2008; Templeton et al., 2013). Mates spent over 50% of their time within 15 m of each other, which is comparable to other duetting species during the breeding season (Fedy & Stutchbury, 2005; Gill et al., 2005; Hall & Magrath, 2000; Hall & Peters, 2008). If pairs defend the territory jointly, potential intruders should perceive two birds as more threatening than one, so answering at a distance may advertise a weakened territory defence (Logue, 2005). In addition, females may answer less at large IIDs to reduce their likelihood of engaging in an aggressive encounter without their mate present. Although a female may benefit from entreating the mate to join her, female Adelaide warbler vocalizations are not acoustically structured for transmission, and are unlikely to be an effectively signal at large IIDs. It seems likely the risk of advertising a compromised defence may be too great to attempt to signal her mate to join her. A third explanation for the negative relationship between IID and answer proportion is that the acoustic degradation of male song at large IIDs may limit the female's ability to identify her mate. Song types are shared among neighbouring males, which may mate individual recognition at a distance difficult. This seems an unlikely explanation, as male song is able to be heard by human observers 1 - 2 territories away. A final possibility is that males are unable to hear the female when mates are far apart, and therefore unable to respond in a coordinated manner. This is likely an additional contributing factor given the limited transmission of female answers.

Males showed the opposite pattern as females by increasing their vocalization rates at greater IIDs (Fig. 12). Trillo and Vehrencamp (2005) also noted male banded wrens (*Thryophilus pleurostictus*) sing at lower rates when their females were present, although did not offer speculation as to why. Male Adelaide warblers may be attempting to increase their acoustic territory defence while their mate is absent. Alternatively, a male may sing more when IID is large as a way of calling for his mate. If two birds are perceived as more threating than one (Hultsch & Todt, 1984; Logue, 2005), then a solitary male may be more vulnerable to attack from neighbouring mated pairs, and he may want to increase his defence by entreating his mate to join him. Unlike female vocalizations, male song is able to transmit over distance. The likelihood of successfully signalling the mate may outweigh the risk of advertising a compromised defence. Our finding that on average, females tended to reduce IID after male song (Fig. 15), supports this idea. A final possibility is that males sing more at large IIDs to attract extra-pair copulation (EPC) opportunities. However, we never observed any EPCs for either pair member.

Mate Localization

We did not find strong support for predictions based on the mate localization hypothesis. The first prediction we tested was that pairs should answer each other more at greater IIDs. If a bird uses duets to find its mate, we would expect more answers when pairs are separated. However, we found the opposite pattern: female answer proportion was strongly and negatively correlated with IID (Fig. 13).

Our second prediction states that pairs should reduce their IID more after an answered initiation than after an unanswered initiation (Benedict, 2010; Logue, 2007; Odom et al., 2017). If males approach females, then males may be trying to incite an answer to localize the mate, if females approach males, the females may be signalling their approach. Our results do not show strong support for this prediction. Females reduce the IID slightly more after duets compared to male solos, but the effect was small and did not reach statistical significance (Figs. 10, 15). Both the descriptive and simulated mean *DeltaIID* values for the male were positive. Given female duet contributions are too quiet to transmit over long distances, males may be unable to hear and locate the female answers at large IIDs.

Our model did show that females reduce the distance to their mate more than males after a vocalization event. This suggests females may use male initiations to locate and approach the mate, regardless of the female's own answering behaviour. Similarly, in Venezuelan troupials (*Icterus icterus*), the answering individual moves towards the initiator more often than the initiator moves towards the answerer (Odom et al., 2017). However, the opposite pattern was observed in black-bellied wrens and rufous-and-white wrens (Logue, 2007; Mennill & Vehrencamp, 2008). In all three species, duets were concluded to have a mate localization function. Taken together, our findings suggest that males do not use female answers to localize their mates (and thus, duets do not function in mate localization), but females do attend to their mate's vocalizations and may use them to localize the male.

Adelaide's warbler duets may be in the early stages of evolving a mate localization function. Females appear to already use male song to localize their mate. Although female pips are low amplitude and difficult to detect at long distances, they are currently used over a range of IIDs (Fig. 11). If the amplitude or structure of female pips changes over evolutionary time to allow males to better detect them, males may begin to attend to their use and begin singing to intentionally illicit a response to localize the female. In this way, pips that signal movement in this species, may be co-opted for localization following the "sender-precursor model" of signal evolution (Bradbury & Vehrencamp, 2011). Further, males could evolve to answer female vocalizations and females could, in turn, evolve to attend to and illicit male answers for mutual mate localization.

Blurred Lines: Mate Guarding and Joint Resource Defence

The mate guarding hypothesis is broad in scope, resulting in branching hypotheses (partnership defence and paternity guarding) that are often confounded in the duet literature. The partnership defence hypothesis states that answering a partner's song advertises the partner's mated status to potential intruders in order to protect one or the other partner's position in the partnership (Hall, 2004). The paternity guarding hypothesis states that a male answers his mate's song to discourage extra-pair males from copulating with her (Hall, 2004; Sonnenschein & Reyer, 1983). Researchers often fail to differentiate which mate guarding hypothesis they're testing, leading to confusing interpretations of study results (e.g., Dingle & Slabbekoorn, 2018; Diniz et al., 2018; Douglas & Mennill, 2010; Dowling & Webster, 2013; Seddon et al., 2002). Additionally, many studies interpret evidence of a bird defending its own position in the partnership as evidence of conflict between the pair, because the guarded mate appears to be prevented from accessing other potential mates (e.g., Benedict & McEntee, 2009; Diniz, Rech, et al., 2019; Rogers et al., 2007; Seddon & Tobias, 2006; Weng et al., 2012). However, there is no published evidence to support conflict as an explanation for duetting (reviewed in Hall, 2009). Throughout the discussion, we use the term partnership defence (as defined above) to clearly indicate we are describing cooperative mate-guarding activities.

Our evidence in support of the joint resource defence hypothesis is also evidence for the partnership defence hypothesis (Hall, 2009). All three of our tested predictions are shared between the two hypotheses. The nearly complete overlap of our predictions for the joint resource defence and partnership defence hypotheses raises the question of whether these are truly distinct hypotheses with respect to our study system. Adelaide’s warblers live with year-round competition for physical resources (e.g., territory, food, nesting material) and high mutual fitness investment in partnerships including long-term pair bonds and low EPC rates (Staicer, 1991). These life history traits are common in duetting species (Benedict, 2008; Cramer et al., 2011; Diniz, Macedo, et al., 2019; Douglas et al., 2012; Dowling & Webster, 2013; Gill et al., 2005; Logue & Hall, 2014; Mitchell et al., 2019; Tobias et al., 2016). Additionally, unpaired Adelaide’s warbler females do not hold territories, and unpaired males typically do not hold territories larger than a few adjacent trees (unpublished data), suggesting social pairing may be essential for maintaining access to physical resources. Whether a female Adelaide’s warbler is defending her mate or their territory may be a distinction without a difference. Either way, she excludes potential usurpers to maintain the status quo.

Many duet function studies have found support for both joint resource defence and partnership defence in a single species (Dingle & Slabbekoorn, 2018; Diniz et al., 2018; van den Heuvel et al., 2014; Weng et al., 2012). Some researchers have suggested that joint resource defence and partnership defence are not mutually exclusive theories (van den Heuvel et al., 2014; Weng et al., 2012). Likewise, studies have assigned the two functions to different levels of analysis, suggesting individual answering functions in mate guarding, while pair-level duetting functions in territory defence (Diniz et al., 2018; van den Heuvel et al., 2014). Applying this principle to species with female-controlled duets (including the Adelaide’s warbler), in which individual female answers generate every pair duet event, implies female answers have both joint resource defence and partnership defence functions. Perhaps for the Adelaide’s warbler, and other duetting species with similar life histories (long-term pair bonds, sedentary life history, and low EPC rates), joint resource defence and partnership defence blend into a broader mutual investment defence effort.

Tell Me You Love Me: The Pair-bond Maintenance Hypothesis

According to the pair-bond maintenance hypothesis, duet participation signals commitment to the partner (Hall, 2004, 2009). Although we did not intend to test this hypothesis, some of our results are consistent with its predictions. Following Hall (2004), we interpret “commitment” to mean a willingness to invest in activities essential for success of the partnership and reproduction, including resource defence, nest building, and provisioning. In species with high mutual fitness investment, individuals may benefit from assessing their partner’s willingness to continue investing in the partnership (Hall, 2004). The initiator may make a bid for attention and ask the mate: is this partnership worth the cost of answering (Smith, 1994; Zahavi, 1977)? A committed pair member will be attentive to its partner, and answer quickly and accurately. The initiating bird may use an answering-effort threshold to assess the mate’s commitment, such as a specific number of answers per hour or a certain proportion of the initiator’s songs answered (Hall, 2004). The initiator may also make more bids for attention when there are potential threats to the partnership, such as aggressive encounters with conspecifics. In species where both individuals initiate and answer, both pair members are able to test and affirm commitment. Although this hypothesis does not require duets to be low amplitude, it is consistent with a low amplitude duet structure because it sees song answering as directed at the partner and not neighbouring conspecifics.

In the case of our study species, male Adelaide’s warblers may make bids for attention, and female Adelaide’s warblers may answer to signal commitment to their mates. Females appear to maintain a relatively stable answer proportion relative to aggressive encounters, and to a lesser extent, over the course of a morning. By maintaining an answer proportion across social context and time, females may provide a consistent signal of their commitment. In aggressive contexts, it may be important to not only increase pair-level duets as a signal of joint resource defence, but to also maintain a certain individual-level answer proportion to reassure the partner of the answerer's commitment to defence. For female Adelaide's warblers, maintaining a constant answer proportion while the male initiation rate increases accomplishes both goals. In this scenario, signalling commitment and signalling an intention to jointly defend mutual resources are not mutually exclusive functions of song answering.

The pair-bond maintenance hypothesis is difficult to separate from other hypotheses. If answering functions as an honest signal of commitment, we would expect committed partners to answer more than uncommitted partners. We could measure proxies of commitment by assessing the relationship between answering rates and provisioning rates, EPC and EPP rates, and cooperation during territory defence (e.g., response to opposite vs same-sex playback). In this case, answering behaviour may also indicate mate quality (Hall, 2004). In support of this idea, a recent study found correlations between duet duration and offspring survival in rufous horneros (Diniz, Macedo, et al., 2019).

We speculate that a pair-bond maintenance function may have driven the evolution of duetting in Adelaide's warblers. Female answering may have initially evolved as a way for females to confirm their commitment to the partnership (e.g., by showing males they were close by and attentive), and so encourage males to defend the female's position in the pair-bond. Eavesdropping conspecifics that attended to this signal would have benefitted by avoiding aggressive encounters with pairs with frequent female answers, which in turn would have benefitted the focal pair. These fitness benefits would have added selective pressure for females to answer louder and more often in aggressive contexts. Perhaps the fact that we observed females increasing the amplitude of their answers in aggressive contexts suggests the duets are still under selective pressure to be effective signals in joint resource defence.

Our study also suggests that resource and mate defence may be the main functions of duetting in the early stages of duet evolution. Support for these functional hypotheses is extensive and widespread in birds (Benedict, 2010; Brumm & Goymann, 2018; Dahlin & Benedict, 2014; Dingle & Slabbekoorn, 2018; Diniz et al., 2018; Diniz, Rech, et al., 2019; Dowling & Webster, 2013; Grafe & Bitz, 2004b; Logue & Gammon, 2004; Marshall-Ball et al., 2006; Mennill & Vehrencamp, 2008; Odom et al., 2017; Sandoval et al., 2018; Templeton et al., 2011; van den Heuvel et al., 2014; Weng et al., 2012; Wheeldon, Szymański, & Osiejuk, 2020). Over time, duets may evolve more elaborate structures that permit a broader variety of functions.

Future Directions

There are additional factors that may influence female answering behaviour. Male Adelaide’s warblers, like many New World warblers, sing many song types that can be divided into two song categories (Kaluthota et al., 2019; Staicer, 1991). It has been suggested that one category functions in male-male territory negotiations, while the other is attractive to females (Kaluthota et al., 2019; Kroodsma et al., 1989; Spector, 1992; Staicer, 1996). It would be interesting to determine whether male song categories and male song types influence female answering. This comparison would clarify the function of the two song categories. It may also clarify the influence of female answering on the dawn chorus. We observed males ending their dawn chorus singing upon the arrival of their female (which often prompted a duet). Although observed in other species, this phenomenon is not well understood (Trillo & Vehrencamp, 2005).

Further investigation into territory and home range use by our study species may offer further insight into the spatial ecology of duets. Although we assessed the relationship between the proximity to territory boundary and vocalization behaviour, our histogram of vocalizations at different distances to the territory boundary does not account for the increase in area with increased distance from the territory center. For example, the area contained within a 5 m radius from the territory boundary is greater than the area contained in the ring spanning 5 – 10 m. Accounting for area would permit more accurate estimates of the spatial aspects of duetting

Further data collection, both observational and experimental, could help to strengthen our support for the resource and partnership defence hypotheses. Observational studies of year-round female answering behaviour could reveal nuances of female answering rates and social context as well as address seasonal predictions of several functional hypotheses (Diniz et al., 2018; Odom et al., 2017). Playback studies would elucidate how duet participation functions in aggressive encounters, and what role each sex plays in resource defence (Diniz, Rech, et al., 2019; Rogers et al., 2007; van den Heuvel et al., 2014; Wheeldon, Szymański, & Osiejuk, 2020). These additional data may also offer further insight into duet evolution in species with simple, female-controlled duet structure.

The New World warblers represent an opportunity to examine the relationship between evolutionary time and duet structure. The New World warbler clade shows both ancient and recent gains of duetting (Mitchell et al., 2019). This clade therefore offers the opportunity for comparing duet structure over evolutionary time. A key question is whether clades that recently evolved duetting sing simpler duets than clades that evolved duets farther back in their evolutionary history.

Conclusions

We conclude that female answering in Adelaide's warblers is cooperative. Females increased their answering efforts in aggressive contexts, near territory boundaries, and when mates are nearby, supporting both the joint resource defence and the partnership defence hypotheses. For duetting species with high mutual fitness investment, year-round territoriality, and low EPC rates, the mate is a valuable resource, blurring the lines between these two hypotheses. We hypothesize that females may answer their mates at consistent rates across aggressive contexts and throughout the morning to affirm their commitment to their mates. Although female answering does not function in mate localization, females may use male initiations to localize their mate. Adelaide's warbler duets may be in the early stages of evolving a mate localization function.

Studying a species with female-controlled duets allows for a relatively simple analysis of female answering behaviour. We were able to focus on fitness benefits for the female, while acknowledging the males may also benefit from female answering. Additionally, studying a species with a recently evolved, simple duet offers unique clues about early duet evolution. Our study contributes to the growing body of work that demonstrates that carefully designed observational methods combined with careful statistical analysis are able to reveal diverse and unique findings that further our understanding of duet function and evolution (Odom & Omland, 2018). This study also emphasizes the value of integrating modern geographical techniques in the study of animal communication, and furthers our understanding of duets as a model of cooperative behaviour and conversation-like communication.

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CHAPTER 5: CONCLUSIONS

My research offers insight into the selective pressures on early duet evolution. The recently evolved duets of Adelaide's warblers have a simple structure. The male is always the initiator, and the female is always the answerer, resulting in a female-controlled duet structure. Through detailed observational methods, I was able to test several predictions of two functional hypotheses: cooperative resource defence and mate localization. I found that females increased their answering efforts around the time of aggressive encounters, near territory boundaries, and when near their mates. These results are supportive of both the joint resource defence and partnership defence hypotheses, suggesting female Adelaide's warblers answer to cooperatively defend both their mate and territory. For tropical species with high mutual fitness investment (e.g., low EPC rates, year-round territoriality, and long-term social pairings), my study suggests that the mate is another resource to defend, blurring the line between joint resource defence and partnership defence. Perhaps in the early stages of duet evolution, selection favours duets that function to keep a mate and a territory as part of broader mutual defence effort.

Although we did not find support for the mate localization function in Adelaide's warblers, females may use male initiations to localize their mate. Additionally, if the amplitude or structure of the female's answering vocalizations changes over evolutionary time to be more easily detected, males may evolve to use female answers to localize the female. Adelaide's warbler duets may thus be in the early stages of evolving a mate localization function.

My study results are also compatible with the pair-bond maintenance hypothesis, where partners use duets to signal commitment (Hall, 2004, 2009). Female answering effort is consistent across aggressive encounters and over the course of the recorded mornings, and is highest when the pair mates are close to one another. These results offer an opportunity to speculate about early selective pressures on tropical species with high mutual fitness investment. Maintaining a mate and territory for reproduction is paramount, and having a way to assess the mate's commitment would allow the males to invest only in social pairings with a committed female. By signalling commitment, females strengthen the bond with their mate, and maintain access to his territory. Eavesdropping conspecifics would benefit from attending to the female's signal and using that information to inform whether they challenge the territory residents or not. The focal pair would also benefit, increasing the selective pressure for the female to be loud and to answer the mate more often in contexts where conspecifics are listening. Perhaps initial duet evolution is driven by the need to confirm commitment to your mate, but then the additional fitness benefits derived from broadcasting that commitment in extra-pair contexts allows evolution to shape the duet to serve additional mutual resource defence functions.

As the first study of duet function in a New World warbler, my research contributes to the growing taxonomic diversity represented in the duet literature. This diversity is necessary for phylogenetically explicit analyses exploring cladistic trends in the evolution of duets (e.g., Benedict, 2008; Logue & Hall, 2014; Mitchell et al., 2019) and for a more generalized understanding of duets including their function, ontogeny, evolution, etc. Additionally, the New World warbler lineage contains examples of both recent and ancient duets (Mitchell et al., 2019) which offers a unique opportunity to explore the relationship between evolutionary time, duet structure and duet function. My study is a starting point for this research.

New technologies continue to offer innovative opportunity. The field of spatial ecology has grown to include a wide array of technologies that allow detailed data collection, and computational technologies have advanced to allow powerful spatial and statistical calculations. My study explored the application of several spatial ecology tools and statistical methods, and combined them in a novel approach to duet function. The lightweight radiotags I used as part of my study open doors for studying smaller songbird species. The need for smaller and more energy efficient tracking technologies continues to push manufacturers to find creative solutions. The LoCoH territory estimation technique fills a niche in songbird research, allowing biologically-relevant territories to be estimated without the drawbacks of other common methods. The availability and flexibility of R software makes spatial calculations more accessible, especially when industry-standard software does not necessarily include novel spatial calculation methods. Lastly, the availability of computers with the computational power required for running complex Bayesian statistical models allows for statistical approaches that have been previously unattainable. I hope my methods incorporating these technologies help advise future observational studies of duetting species.

The field of duet research is robust and diverse. Since the 1960s, the field has grown exponentially and seen immense innovation both in experimental methods and in the theoretical framework. However, gaps in the literature remain. We still know very little about the neural and hormonal mechanisms that underpin duet vocalizations. There is limited information about the life histories and ecological context for most duetting species, and there are still duetting taxa that have yet to be studied. Most studies feature species with complicated multi-phrase duets, but there are other duet structures that may offer additional insight to duet function and evolution. There are weaknesses in the literature owing to antiquated ideas and vague hypotheses. Researchers need to clarify their theoretical framework and clearly define which individual-level behaviours they intend to measure and analyze.

Duet research has also suffered from several confusing theoretical misconceptions as well as ambiguity in behavioural descriptions. First, there is confusion over whether or not the broad functional hypothesis called “mate guarding” necessarily represents conflict between the pair. Second, inconsistent use of terminology for various functional hypotheses has led to confusing conclusions about duet function and exacerbated the previous issue. Finally, many studies have failed to differentiate between individual- or pair-level behaviours, leading to confusing or contradictory conclusions. Moving forward, I hope my literature review provides a cohesive theoretical framework with clear definitions to address these issues.

Studying duets through the inherited lens of a Northern-latitude bias can be a hindrance. The existing theoretical framework for studying the function of avian vocalizations comes from research conducted on temperate migratory species in which male song was studied in the context of the breeding season (Rose et al., 2022). The existing canonized functions for songbird vocalizations may not be well-suited to the unique ecology of non-migratory, tropical species. In fact, more support for social- and natural selection-based functions may be documented as more tropical species are studied, and additional functions may yet be discovered (Rose et al., 2022). Duet research continues to challenge what we know about song learning, social selection, and evolutionary origins of female song.

My thesis contributes to the growing body of work that demonstrates that carefully designed observational studies combined with powerful statistical analysis can reveal nuances of duet behaviour that further our understanding of duet function and evolution (Odom & Omland, 2018). By studying duet behaviour at both the individual- and pair-level, we were able to learn about the selection pressures driving the evolution of cooperative communication in the Adelaide’s warbler.

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APPENDICES

Appendix 1. Daily summary of time blocked data.

ID	Rec. Dates 2018	Rec. Time (hr)	Sum	Avg	SD	# Init.	Sum	Avg	SD	# Ans.	Sum	Avg	SD	# Agg.	Sum	Avg	SD
1	04-02	2.31				144				13				1			
	04-05	Excluded due to atypical female behaviour															
	04-09	1.47	**3.78**	**1.89**	**0.59**	104	**248**	**124.0**	**28.3**	29	**42**	**21.0**	**11.3**	3	**4**	**2.0**	**1.4**
2*	03-16	1.17				25				19				3			
	03-21	2.29				39				35				4			
	03-27	2.29	**5.75**	**1.92**	**0.65**	42	**106**	**35.3**	**9.1**	38	**92**	**30.7**	**10.2**	1	**8**	**2.7**	**1.5**
3	04-14	1.96				32				17				4			
	04-16	2.07				78				28				6			
	04-18	2.21	**6.24**	**2.08**	**0.13**	37	**147**	**49.0**	**25.2**	33	**78**	**26.0**	**8.19**	3**	**13**	**4.3**	**1.5**
4*	03-15	0.57				14				9				3			
	03-22	1.92	**2.49**	**1.25**	**0.95**	47	**61**	**30.5**	**23.3**	28	**37**	**18.5**	**13.4**	6**	**9**	**4.5**	**2.1**
5	04-17	2.20				98				14				3			
	04-20	2.19				82				30				2			
	04-21	2.28				59				23				3			

	04-23	2.25	**8.92**	**2.23**	**0.04**	80	**319**	**79.8**	**16.0**	43	**110**	**27.5**	**12.2**	3	**11**	**2.8**	**0.5**
6	03-29	2.40				49				15				0			
	04-03	2.02				53				23				1			
	04-06	2.18	**6.60**	**2.20**	**0.19**	56	**158**	**52.7**	**3.5**	27	**65**	**21.7**	**6.1**	3	**4**	**1.3**	**1.5**
7	03-31	2.01				18				11				4**			
	04-04	1.65				35				17				3			
	04-07	2.06	5.72	1.91	0.22	25	**78**	**26.0**	**8.5**	8	**36**	**12.0**	**4.6**	3**	**10**	**3.3**	**0.9**
8	04-13	Excluded due to insufficient data															
Totals	**20**		**39.49**	**1.97**	**0.45**		**1117**	**55.9**	**33.0**		**460**	**23.0**	**10.1**		**59**	**3.0**	**1.5**

*First recording: radio-tagged female and spot-mapping male.

**Only post-aggressive encounter data are available for the first aggressive encounter included in the dataset because the aggressive encounter itself occurred prior to 700 s after sunrise.