AGONISTIC SINGING BEHAVIOUR IN ADELAIDE'S WARBLER (*SETOPHAGA ADELAIDAE*)

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Bachelor of Science, University of Lethbridge, 2018

A Thesis Submitted
in Partial Fulfilment of the Requirements for the Degree of

MASTER OF SCIENCE

In

PSYCHOLOGY

Department of Psychology
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

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Date of Defence: November 7, 2023

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DEDICATION

I dedicate this thesis to the Adelaide’s warblers of the Cabo Rojo Wildlife Refuge, to each individual that I knew by name and song. Their complex lives are the heart of this work.

> *“Zumbando entre los árboles, orquestal y divino,*
> *como una lengua llena de guerras y de cantos.”*
> -
> “Resounding among the trees, orchestral and divine,
> like a language full of war and song.”
>
> Pablo Neruda

ABSTRACT

Animals use agonistic signals to mitigate the cost of conflict over resources. Bird song has long been thought to function as an agonistic signal in songbirds. Many songbird species vary aspects of their singing behaviour in and around agonistic encounters. For example, low amplitude “soft song” often precedes attack, and song rate can increase with aggressive motivation. In agonistic encounters, singing behaviour may be used to fill a number of agonistic signalling functions like communicating aggressive intent, social dominance or submission, and victory. Most of the studies on singing behaviour as a signal in agonistic contexts, however, rely on song playback to simulate an agonistic context. Remarkably few studies link singing behaviour to agonism in unmanipulated, natural systems. Adelaide’s warblers (*Setophaga adelaidae*) are an ideal study species in which to study natural agonistic signalling because neighbours frequently engage in conspicuous territorial skirmishes. I analyzed focal recordings of 23 individually marked males and characterized three singing behaviours around the time of natural agonistic encounters (n = 4,531 songs, 254 encounters): song type switch rate, within-repertoire song type frequency, and song rate.

As predicted, results from Bayesian mixed-effects models indicate that all three singing behaviours vary with time to the nearest agonistic encounter. Song type switch rate dropped substantially before and after agonistic encounters, reaching a low point several minutes after the encounter, which may indicate its use as a post-conflict agonistic signal like a victory signal. Song type frequency increased slightly before an encounter, and returned to baseline well after the encounter was over. Though the effect is small, it could indicate that frequently-used song types are used as a signal of aggressive motivation. Finally, song rate decreased moderately immediately before encounters and returned to normal levels shortly after the encounter. This drop in song rate may be a signal of aggressive intent. In all three behaviours, the magnitude of this behavioural variation exceeds that produced by randomized data. However, effect sizes varied from small (in the case of song type frequency) to moderate (song rate) to large (song type switch rate) and alternative hypotheses may better explain some of these patterns, such as interactions between the singing behaviour and other agonistic behaviour.

ACKNOWLEDGEMENTS

To my mentor, David Logue, I cannot begin to express my gratitude. There are countless Logue-isms that I can only hope have rubbed off on me: the idea that good science is simple yet elegant, that a delicious dish is never an accident, and that deliberate empathy is a kind of strength. Thank you for sharing the world you see with your students. We are the lucky ones.

I owe much to my long-suffering committee members: Serge Pellis and Stefan Kienzle, who trusted and challenged me through countless delays and changes to my project. Your encouragement to pursue my own happiness is well beyond the scope of what one can expect from a committee. Without your frank advice and kindness this not have been possible. To J.B. Leca, for your example of principled science and measured grace. I'm glad for your involvement.

Thank you to my family, who has supported me in so many ways. Mom and Dad, you taught me to be a scientist a long time ago. Thank you for only ever telling me one thing my entire life: "You can."

Thank you to my friends. To everyone who relaxed with me by the fires, argued over beers, commiserated over coffee or walks across campus, or patiently listened as I recounted the latest disaster in my life: thank you.

To *mi pana*, Francisco: you deserve absolutely no thanks, yet your friendship is absolutely central to this story. Our nights of jazz, video games, arguments, and patio beers were my rock for these years. I'm proud to call you my friend — if only I could be so grossly incandescent!

Jules Vazquez Cardona, this accomplishment is yours, too. Thank you for sharing these beautiful birds and so much more with me. Thank you for laughing at me, for your unwarranted confidence in me, and for finding joy with me no matter the circumstance. I couldn't ask for a better lab-mate and partner. To more blessings!

There are many others who deserve my thanks Alexandra Elbakyan, for your dedication to open knowledge on Sci-Hub. Tanya Martinez, for your unwavering kindness and exemplary badassery - you will always be family. Jennifer Mather, your kindness was a highlight of my years at the U of L. Mary Kavanaugh, thank you for the use of her "palace of meditation" while I was writing. Moonir: I'm just a happy boy, too. My thanks to all who passed through the Birdsong Lab (whether migratory or resident). Liam, Bert, and Nolan - you guys helped me in far more ways than coding and brainstorming. Also to Sydney, A.J., Mostafa, all the Sams, the Leca lab, and the many, many others who lent me their invaluable camaraderie: my deepest thanks to all of you.

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1.1 Agonistic signals

Intraspecific competition arises when conspecifics compete for access to finite resources, such as mates, food, or territories. Physical fights are one way to settle these conflicts, but escalated conflicts can incur the risk of injury or death for both winners and losers (Reddon et al., 2021). It is therefore in both competitors' interest to resolve conflicts without fighting. Agonistic signals are signals that animals use in the context of contests over resource ownership (Briffa, 2015). They include signals of aggressive intent (willingness to fight), submission, resource holding potential (fighting ability), social dominance rank, and others.

Asymmetries between participants can predict the victor in an escalated fight. Particularly important are asymmetries between the individuals in level of motivation to obtain the resource, in fighting skill, or in physical condition. Revealing such asymmetries helps both competitors estimate the likelihood of winning, and encourages one of them to de-escalate if the asymmetry is not in their favour (Bradbury & Vehrencamp, 2011). Agonistic signals reduce the risk of an escalated fight by revealing asymmetries between competitors.

Animal signals are adaptations that influence the behaviour of other individuals. Individuals that produce signals are called "senders" and those that perceive signals are "receivers." Selection favours signalling if signals' influence on receivers provides a net benefit to the sender. Selection favours receivers responding to signals if doing so benefits the receiver. According to honest signalling theory, these opposing evolutionary pressures maintain signals that reliably ("honestly") reflect the condition of the sender or the environment, and eliminate those that do not.

The male field cricket's (*Teleogryllus oceanicus*) "rivalry song" is an example of a signal that reveals asymmetries in an agonistic context (Phillips & Konishi, 1973). Silenced or deafened males engage in more fights compared to males with intact signalling systems (Logue et al., 2010; Phillips & Konishi, 1973). Without the ability to use agonistic signals, animals must engage in riskier behaviour to settle disputes over limited resources. The field cricket's rivalry song reveals an asymmetry in aggressive intent (i.e., the signaller is willing to attack), allowing contestants who are not willing to escalate to withdraw before the encounter escalates to a physical contest. Agonistic signals are as varied in form as the attributes that predict the outcome of a fight. Here, I detail some functional categories of agonistic signals. This is not an exhaustive list, and it is important to note that a single signalling behaviour can fulfil more than one agonistic signalling function.

The topic of this thesis is how songbirds use their song in agonistic contexts. In this chapter, I discuss a general taxonomy of agonistic signals by function, to place my research in the broader context of agonistic signalling. I go on to review how songbirds use their songs in agonistic contexts and conclude that there is a dearth of studies of song use during natural agonistic encounters. In Chapter 2, I address this knowledge gap by testing whether three singing behaviours are associated with natural agonistic events in a tropical warbler. I discuss my results and integrate my findings with the agonistic signalling literature in Chapter 3.

1.1.2 Signals of Fighting Ability

An individual's resource-holding potential (RHP) describes its ability to win an escalated physical contest (Allen & Krofel, 2017). Signals of RHP communicate traits that are associated with fighting ability, such as body size, condition, and weaponry (Batchelor et al., 2012).

Body size displays

An important way that RHP is signalled in agonistic contexts is with displays of body size. Relative body size is often the greatest predictor of victory in an escalated agonistic encounter in species with variable size (Parker, 1974). Body size advantage has been demonstrated in a variety of species such as the green sunfish (*Lepomis cyanellus*; Greenberg, 1947; Hale, 1956), crayfish (*Orconectes virilis, Procambarus allen*; Bovburg, 1953, 1956), varied tit (*Paris varius*; Yamaguchi & Kawano, 2001), and New Forest pony (*Equus fetus caballus*; Tyler, 1972).

An animal will signal their body size before or during agonistic encounters to encourage their rival to submit before escalation. Body size can be assessed without a specialized signal, but ritualized signals such as a posture displays can emphasize size differences.

For example, kangaroos (*Macropus rufus*) fight by standing upright and boxing with their forelegs, which enables a comparison of size (Croft & Snaith, 1990). The "broadside display" is a common signal of body size in which an animal orients its body to present the largest possible visual image to a rival. When the American bison (*Bison bison*) performs the broadside display, the bison faces perpendicular to a rival, arches his back, and keeps his tail stiff. If he moves, it is in slow, stiff steps that maintain his broadside orientation to the rival (Lott, 2002). The broadside display is made more effective by the bison's shaggy fur that increases its profile. The helmeted basilisk (*Corytophanes cristatus*) also uses broadside displays in agonistic contexts, similarly aided by crests on its head and throat to increase its broadside profile (Pough et al., 2016).

Body size can also be signalled through the frequency of acoustic signals. Low sound frequencies are a reliable indicator of body size because lower frequency sounds require a larger vocal apparatus and resonance chamber. Frogs are a classic example of this widespread phenomenon. In 136 species across 4 clades of anurans, vocalization frequency is negatively correlated with larger body size (Gingras et al., 2013).

Signals of condition

RHP can be also signalled in agonistic contexts with signals of condition, which display how hard and long an animal can persist in an energetically demanding fight. Condition is a summary of the general health and vigour of an organism, and is narrowly defined as the acquired resources available for allocation to various fitness-enhancing traits (Tomkins et al., 2004). An animal in better condition can invest more energy into fighting harder and longer. Signals of condition display whole-organism performance traits which are consistently higher for contest winners than losers. In field crickets (*Teleogryllus commodus*), for example, bite force, jumping strength, and head-butting force are all consistently higher in contest winners than they are in losers (Hall et al., 2010). Reliable signals of condition can reveal asymmetries and stimulate the lower condition contestant to back down (Bradbury & Vehrencamp, 2011).

Signals of condition may include morphological structures, such as the comb crest of red junglefowl (*Gallus gallus spadiceus*). The size and chroma of a rooster's comb is an indicator of its current testosterone level and immune system activity (Lignon et al., 1998; Zuk et al., 1995). A signal of condition may also demonstrate physical ability directly. For example, many iguanid lizards perform an agonistic "lateral compression display" in which they elevate their body, extend their dewlap, and compress their thorax for extended periods of time. Studies in the side-blotched lizard *(Uta stansburiana*) reveal that thoracic compression is energetically costly because it interferes with respiration, and causes the lizard to accumulate an oxygen debt (Brandt & Chappell, 2004). A signaller's ability to maintain this posture is highly correlated with their physical condition and fighting ability.

Weaponry displays

Whereas signals of condition are about movement abilities, weaponry displays indicate fighting ability by showcasing the animal's weaponry (e.g., teeth, claws, horns, spines, and bills). Animals use weaponry to signal fighting ability by mimicking movements used in fights, such as when a ram lowers its horns (Bradbury & Vehrencamp, 2011). If the weapon is not normally visible, the act of revealing the weaponry may be a signal of RHP, such as when a wolf pulls back its lips to bare its teeth. A common weaponry display is the "mouth-gaping display" in fish and lizards, in which the signaller opens its mouth to reveal its jaw size (Huyghe et al., 2005; Lailvaux & Irschick, 2007). Male collared lizards

(*Crotaphytus collaris*) have evolved white skin patches inside their mouths that highlight jaw-abduction structures, further amplifying the display (Lappin et al., 2006).

Weapon size itself can be an index of fighting ability. For example, male northern sandy dung beetles (*Euoniticellus intermedius*) use their horns to grapple with conspecifics during agonistic encounters, and a greater horn size is "by far the most important predictor of victory" even when controlling for body size (Pomfret & Knell, 2006). Horn size in this species reliably signals fighting ability, as shown by Lailvaux & Irschick's (2006) finding that large horn size in these male dung beetles accurately predicted attributes that are important to the outcome of a fight: grasping strength and stamina.

1.1.3 Signals of Aggressive Motivation

RHP is not everything when it comes to winning resources. An animal's decision to participate in a conflict over a resource is also based on its level of motivation (Bradbury & Vehrencamp, 2011). Signals of aggressive motivation are used to broadcast an individual's motivation to enter, persist in, or escalate an agonistic encounter. Level of motivation is a predictor of victory, because an individual that stands in greater need of a resource will tolerate more risk and fight harder to obtain it (Arnott & Elwood, 2008). For example, in a conflict over a food source, a hungry individual will fight harder and is more likely to win, as seen in species such as house crickets, (*Acheta domesticus*; Nosil, 2002), bald eagles, (*Haliaeetus leucocephalus*; Hansen, 1986), and dark-eyed juncos (*Junco hyemalis*; Cristol, 1992).

Besides hunger, an individual may be motivated by other internal states to obtain resources, such as by their current reproductive phase to obtain mating opportunities, or by their territory quality to obtain more territory. By broadcasting their level of motivation, an individual can reveal an asymmetry of motivation between combatants. In the face of this information, less-motivated combatant may be less willing to tolerate the risk of escalation and therefore more likely to cede control of the resource to the highly-motivated combatant (Waas, 2006). Three important classes of aggressive motivation signals communicate general aggressive motivation, motivation to engage with a targeted receiver, and intention to escalate, respectively.

General aggressive motivation signals

Signals of general aggressive motivation often take the form of a continuously variable behaviour. Most commonly, motivation is signalled by adjusting the display rate of a signal such that higher display rates signal higher motivation. For example, hermit crabs (*Pagurus bernhardus*) signal aggressive motivation by the rate of their "cheliped extension display" (Elwood et al., 2006; Laidre & Elwood, 2008), and electric fish *(Apteronotus leptorhynchus*) signal motivation with the rate of their rate of electric "chirps" (Triefenbach & Zakon, 2008). These general signals of aggressive motivation are used throughout the agonistic encounter.

Challenge signals

Early in an agonistic encounter, animals can also signal aggressive motivation with a challenge signal. A challenge signal identifies an opponent. It is a directed 'pointing' signal that singles out the rival and indicates the sender is willing to escalate (Bradbury & Vehrencamp, 2011). These signals typically occur at a distance. The directionality of challenge signals can be accomplished by the directional beaming of an acoustic signal, such as the highly directional call of the sage grouse (*Centrocercus urophasianus*; Dantzker et al., 1999). Challenge signals may also be visual, such as the little blue penguin's (*Eudyptula minor*) "pointing" and "directed flipper spread" displays (Waas, 2006), or the agonistic "zebra" skin pattern display in Caribbean reef squid (*Sepioteuthis sepioidea*) which is selectively displayed on the part of the squid's body closest to the rival (Mather, 2016). Challenge signals allow the challenged individual to respond by withdrawing or escalating the agonistic encounter with further signals of aggressive motivation (Hinde, 1981).

Signals of aggressive intent

Once an aggressive encounter has escalated to the point that a physical fight is likely, the sender can use signals of aggressive intent to communicate that they are likely to escalate, conditional on the receiver’s response to the signal (Searcy et al., 2006). Because signals of aggressive intent are followed by attack, we should expect the signaller to be close to the receiver.

Searcy and Beecher (2009) write that signals must fulfil three criteria to be considered signals of aggressive intent (which they call “aggressive signals”). The context criterion states that the signal must increase in aggressive contexts. All agonistic signals should fulfil this criterion. Additionally, signals of aggressive intent should fulfil the predictive and response criteria. The predictive criterion states that the signaller will tend to attack after it produces the signal. The response criterion says the receiver must respond to the signal appropriately. Relevant responses include moving away, de-escalation signals, or further aggressive signals (Logue, 2021).

Signals of aggressive intent are often pre-attack postures or movements. The form of the posture depends on the fighting tactic employed by the species. For example, the ears-back bared-teeth display in carnivores and many mammals, bill-forward postures in birds (Bradbury & Vehrencamp, 2011), and horns-lowered foot-stamping displays in ramming bovids (Caro et al., 2003) reflect fighting postures in those systems. Aggressive intent may also be signalled through a combination of multiple signals, such as in the smooth-billed ani (*Crotophaga ani*) which uses a combination of “hoot” calls with a visual throat-inflation display to signal imminent attack (Grieves et al., 2015).

1.1.4 Dominance Signals

Experience and learning are also important factors when it comes to the outcome of an escalated agonistic encounter. Dominance signals reflect an animal’s past fighting experience and position within a social dominance hierarchy. An individual who has accumulated more victories or has attained a position of social dominance is more likely to win an escalated encounter with an individual who does not have this experience (Dugatkin & Druen, 2004).

Badges of status

Badges of status are correlated with dominance status. A classic example of a status badge is the black patch of plumage on the chest of male house sparrows (*Passer domesticus*). Larger chest patches signal higher dominance status. Male sparrows tend to avoid risky conflicts with males that have larger patches and prefer to engage in conflict with smaller-patch males. Instances of escalated conflict are most common between males of similar patch size (Møller, 1987). Visual badges of status are found in other birds, such as the plumage patches of the European siskin (*Carduelis spinus*; Senar et al., 1993) and eagle owls (*Bubo bubo*; Penterani et al., 2007). Similar visual patches are used as badges of status in several lizard species (Whiting et al., 2006). Badges of status can also be olfactory, the best examples coming from decapod crustaceans, who excrete urine during agonistic encounters. In response to the odour of a dominant male's urine, dominant males respond aggressively, but subordinate males quickly retreat (Gherardi & Daniels, 2003; Katoh et al., 2008).

Victory displays

Victory displays are a post-encounter signal of dominance given by the victor. These signals reinforce the dominance relationship between the victor and loser and advertise the outcome to potential rivals. A good example of this is the visual and vocal "triumph ceremony" of geese and swans (Lorenz, 1966).

1.1.5 De-escalation signals

"De-escalation signals" are a distinct category of agonistic signals that indicate submission or non-aggression. Ending a conflict before it escalates by withdrawing or ceding victory to your rival is a crucial tool in navigating the risks of agonistic encounters. De-escalation signals may take a form that is antithetical to aggressive signals, putting the signaller into a position that leaves them vulnerable to attack or at least less able to mount an attack (Bradbury & Vehrencamp, 2011; Darwin, 1899). For example, the American bison holds its head high and pointed forward during head-butting contests and broadside displays, but its de-escalation signal is a grazing-like posture with the head held very low and to one side, fully exposing its neck and flank. This display will even stop a charging rival (Lott, 2002). In wolves (*Canis lupus*), an upright body and high tail position signals dominance, whereas a lowered tail and lowered body indicates submission. To signal complete de-escalation, a wolf will tuck its tail between the legs and roll onto the back to expose its belly; a form completely antithetical to the aggressive, dominant posture (Mech, 1999).

1.2 Song as an agonistic signal in songbirds

Bird song can be an agonistic signal in the context of territory defense (reviewed by Catchpole & Slater, 2003; Searcy & Beecher, 2009). Singing behaviours that have been hypothesized to function as agonistic signals include song rate, vocal performance, low amplitude song, song overlapping, song type switching, song type matching, and the use of rare song types (reviewed by Byers, 2017; Logue, 2021; Searcy & Beecher, 2009). It is important to note that a given singing behaviour can function differently in different species (Collins, 2004).

1.2.1 Song rate as an agonistic signal

The rate that a bird delivers songs may function as an agonistic signal. Signallers can vary song rate continuously, so song rate is suited to signalling aggressive motivation or RHP. On the other hand, song rate is not suited for signalling categorical conditions that require discrete signals, such as signals of dominance, challenge signals, or de-escalation signals.

If song rate is an agonistic signal that signals motivation or RHP, we would expect birds to sing at higher rates in agonistic contexts. Many species exhibit this pattern, singing at higher rates in agonistic contexts. Canyon wrens (*Catherpes mexicanus*), and song sparrows (*Melospiza melodia*) increase their song rates during simulated territorial intrusions (Benedict & Warning, 2017; Nelson & Poesel, 2010). Other species show that elevated song rates signal aggressive intent, such as in black-capped chickadees (*Poecile atricapillus*; Baker et al., 2012) as well as wood warblers (*Phylloscopus sibilatrix*). Wood warblers also respond more aggressively to playbacks of high song rates, as required by the response criterion (Szymkowiak & Kuczyński, 2017).

On one hand, there is good evidence that increased song rates signal aggressive motivation or willingness to escalate in a number of species, but on the other hand, this pattern is far from universal among songbird species. There are a number of species which don't seem to change their singing rate at all in agonistic contexts. For example, neither banded wrens (*Thryophilus pleurostictus*; Trill & Vehrencamp, 2005), nor swamp sparrows (*Melospiza georgiana*; Ballentine et al., 2008) change their song rates during agonistic encounters. Contrary to other studies of song sparrows, Akcay et al.'s (2011) study population did not change their song rate in agonistic contexts. An absence of significant change in song rate in agonistic contexts is evidence that it is not an agonistic signal.

Some species even lower their song rate in agonistic contexts. For example, black-bellied wrens (*Thryothorus fasciatoventris*) marginally reduce their song rate in response to simulated territorial intrusions (Logue & Gammon, 2004). It is possible that a low song rate is not an agonistic signal, even if it occurs in agonistic contexts. Other agonistic behaviour may suppress song, such as aggressive displays, close-proximity signals, cryptic behaviours, or combat. Without additional evidence about the sender and receivers' behaviour around the time of the drop in song rate, it would be premature to conclude that low song rate functions as an agnostic signal.

1.2.2 Vocal performance as an agonistic signal

Avian vocal performance is the "degree of challenge to the motor system, the respiratory system, or other physiological processes involved in singing" (Cardoso, 2017). Singing requires rapid, precise adjustments in the bird's vocal tract and respiratory system (Catchpole & Slater, 2003; Nowicki et al., 1992; Podos & Nowicki, 2004). The speed, precision, or coordination of these physiological adjustments are constrained, limiting song structure (Hoese et al., 2000; Plummer & Goller, 2008; Podos & Nowicki, 2004). Vocal performance can be measured as the approach to this physiological limit (Podos & Sung, 2020). There is emerging evidence that females prefer higher-performance songs in some species (Dunning et al., 2020; Podos, 2017). Due to the physiological constraints of their sound production systems, only high-quality males should be able to produce high-quality songs, making it a reliable index of male quality (Ballentine et al., 2008; Forstmeier et al., 2002).

Although a song's performance is limited by the singer's quality, male songbirds can still modulate their vocal performance. Males may sing with higher performance in agonistic encounters to signal fighting ability and motivation (Enquist, 1985). There is evidence in the dark-eyed junco, swamp sparrow, and the banded wren that song performance signals increased motivation in agonistic contexts (Cardoso et al., 2009; DuBois et al., 2009; Vehrencamp et al., 2013). An increase in song performance in agonistic encounters should be taken as evidence that it is used as an agonistic signal, most likely as a signal of aggressive motivation or RHP.

1.2.3 Low-amplitude song as an agonistic signal

In a few species, an increase in amplitude is associated with agonistic contexts. Nightingales (*Luscinia megarhynchos*), for example, sing louder during agonistic countersinging exchanges. In addition to improving overall signal transmission, an increase in amplitude may signal the singer's quality or motivation to defend the territory (Brumm & Todt, 2004). On the other hand, the use of low-amplitude "soft song" during agonistic contexts, is a well-studied and widespread phenomenon. A review found that soft song was present in over half of 749 songbird species (De Rosa et al., 2021). Soft song has a smaller active space than normal broadcast song and seems to be used in close-proximity signalling. In agonistic encounters, it is reserved for situations in which the rival is nearby.

There is robust evidence that the use of soft song increases in agonistic contexts. Experiments found this to be the case in song sparrows (Akçay et al., 2011; Searcy et al., 2006), swamp sparrows (Ballentine et al., 2008), and white-crowned sparrows (*Zonotrichia leucophrys;* Nelson & Poesel, 2010) among others. There is also a good body of experimental evidence that soft song is predictive of subsequent attack in a number of species such as song sparrows (Akçay et al., 2011), Bachman's sparrows (*Peucaea aestivalis;* Ali & Anderson, 2018), savannah sparrows (*Passerculus sandwichensis*; Moran et al., 2018), and black-throated warblers (*Amphispiza bilineata*; Hof & Podos, 2013). In these species, it is likely that soft song functions as a signal of aggressive intent.

In other species, soft song is associated with agonistic contexts, but may have other functions besides signalling aggressive intent. Specifically, soft song may be used as a 'locator signal', as shown by Jakubowska & Osiejuk's (2018) playback experiment in ortolan buntings (*Emberiza hortulana*). Using two speakers to simulate a moving intruder, they found that territory owners use low-amplitude song after the simulated intruder changes location, but soft song did not predict attack. In this case, territory owners may use soft song to probe a rival's location — an attempt to provoke a response and determine if they are still nearby. Species such as dark-eyed juncos and Eurasian blackbirds (*Turdus merula*) use soft song for functions outside agonistic contexts. They use certain kinds of soft songs in both intersexual courtship interactions and intrasexual agonistic interactions (Dabelsteen et al., 1998; Rice et al., 2013).

Low-amplitude song is a widespread phenomenon among songbird species. Though its use as an agonistic signal is not universal, there is considerable evidence that many species use soft song as a signal of aggressive intent in agonistic encounters.

1.2.4 Song overlapping as an agonistic signal

Many songbirds display a phenomenon known as "song overlapping" in which one bird sings, and a second bird begins singing before the first bird has finished their song. In this scenario, the second bird has "overlapped" the first. Being overlapped impedes signal transmission. Birds can adjust the timing of their songs to avoid being overlapped, not only by conspecifics but also by heterospecifics and abiotic sounds (Brumm & Todt, 2004; Wilson et al., 2016). But is overlapping itself an agonistic signal? For some time, the scientific community accepted song overlapping as a signal of aggressive intent on the part of the signaller (Todt & Naguib, 2000), but more recent work challenges this idea.

Song overlapping is expected to happen by chance if birds do not expressly avoid overlapping. There is not compelling evidence that song overlapping occurs above chance levels, as we might expect if it serves a signalling function (Searcy & Beecher, 2009). Further, song overlapping does not satisfy Searcy & Beecher's (2009) predictive criterion for signals of aggressive intent.

Recent studies have found little evidence that song overlapping is an aggressive signal. There is now evidence that some species that were previously held up as examples of aggressive overlapping do not use song overlapping to signal aggressive intent. These species do not overlap at rates above chance nor does overlapping predict escalation (Akçay et al., 2020; Baker et al., 2012; Wilson et al., 2016). Generally, studies of song overlapping have not found evidence of it as a signal of aggressive intent in most species.

Although song overlapping has mostly been studied as a signal of aggressive intent, some species may use song overlapping to navigate agonistic encounters in other ways. In banded wrens, song overlapping appears to function in territory defense. In natural territorial disputes, defending males overlap the intruder's song at higher rates as they approach the intruder (Vehrencamp et al., 2014). There is also evidence in banded wrens that overlapping is a de-escalation signal – high rates of song overlapping predicts retreat from an agonistic encounter (Vehrencamp et al., 2007). In black-capped chickadees, song overlapping is associated with dominance status – dominant males are more likely to overlap songs than are subordinate males. Because chickadees avoid song overlapping when they are close to a rival, researchers suggest that overlapping may function as a de-escalation signal or as a challenge signal directed at a specific rival (Baker et al., 2012).

There is significant evidence that song overlapping is not a signal of aggressive intent in most species, as was previously thought. However, overlapping may serve other agonistic signalling functions. In these cases, song overlapping may signal dominance, the intention to de-escalate, or direct a challenge toward a specific rival. These other agonistic signalling functions of song overlapping warrant further investigation.

1.2.5 Repertoire Use

The next few singing behaviours that may function as agonistic signals concern the various ways a songbird uses its song types. Song types are discrete, stereotyped song structures that birds learn by listening to adult conspecifics (Marler, 1970). In approximately 72% (155/215) of songbird species, males sing more than one song type (Macdougall-Shackleton, 1997). The set of songs that an individual can sing constitutes their "song type repertoire." Repertoire size ranges from the single song type of a chipping sparrow (*Spizella passerina*; Liu & Kroodsma, 2006), to the moderate 7-11 song types of a song sparrow, (Beecher et al., 1997), to the repertoire of the brown thrasher (*Toxostuma rufum*), which can sing over 1,100 song types (Boughey & Thompson, 1981). Song type repertoires introduce additional avenues of behavioural variation that may be used by birds as signals in agonistic contexts. Birds may vary the rate at which they switch between song types, "match" their rival's song types, or use specific song types as agonistic signals.

1.2.6 Song type switch rate

Song type switching rate refers to the frequency with which the singer switches between song types. This is usually measured as the number of switches per opportunity to switch (Searcy et al., 2000). Some birds change their song type switch rate during agonistic contexts, although the pattern varies by species. For example, Bachman's sparrows (*Peucaea aestivalis*) and song sparrows switch their song types more often in agonistic contexts (Ali & Anderson, 2018; Kramer et al., 1985; Searcy et al., 2000). In song sparrows, evidence indicates that higher rates of song type switching signal higher motivation and a willingness to escalate. This makes sense considering that large repertoire size seems to signal male quality and fighting ability in that species (Searcy & Beecher, 2009), and large repertoires can intimidate rivals (Krebs et al., 1978; Yasukawa, 1981). However, this pattern does not always hold for other species. In chaffinches (*Fringilla coelebs*), lower switch rates are associated with agonistic contexts (Deoniziak & Osiejuk, 2020). In banded wrens, a higher switch rate predicts the signaller will retreat, not attack (Vehrencamp et al., 2014). It seems probable that song type switching is an agonistic signal in many species, but patterns of switching vary greatly between species, so the agonistic function of song type switching likely varies between species as well. Also, song type switch rates would be affected if certain song types are used in agonistic contexts. For example, if a small subset of songs are used only in agonistic contexts, switch rate may decrease even if it is not a signal per se.

1.2.7 Song Type matching

When two birds share parts of their song type repertoires with one another, they can engage in "song type matching". Matching occurs when one bird sings a song, and another bird responds by immediately singing a song of the same type (Akcay et al., 2013). It is a common interactive singing behaviour in many song birds who learn small- to moderately-sized song type repertoires, and has mostly been studied as a signal of aggressive intent (Krebs et al., 1981).

In some species, song type matching is used more often when individuals are working out their territorial boundaries. In natural interactions, song sparrows and great tits (*Parus major*) song-type match more often with their neighbours during the early breeding season, when territories are being negotiated (Michael D Beecher et al., 2000; Krebs et al., 1978). In another observational study, both intruding and defending banded wrens used song type matching more often in the early stages of territorial conflicts (Vehrencamp et al., 2014).

Song type matching may be important in differentiating between neighbours and strangers, as many species song type match more when a stranger's song is heard from a neighbour's territory, such as western song sparrows (Stoddard et al., 1992), western meadowlarks (*Sturnella neglecta*; Falls, 1985), and great tits (Hutfluss et al., 2021). A stronger response to strangers than to neighbours is in line with the 'dear enemy' hypothesis, which assumes that known neighbours are less threatening than strangers (Jaeger, 1981).

Song type matching seems to be a directed signal, which could be a challenge signal inviting the receiver to escalate, or simply an attempt to identify a specific receiver but not necessarily signal aggressive intent. It may be a probe for more information or a signal (Todt & Naguib, 2000). In any case, there is evidence that song type matching is associated with territorial interactions and may be used more often in agonistic contexts by some species, such as banded wrens, great tits, and song sparrows. It may be an agonistic signal used to acknowledge a rival at an early stage of aggression and signal aggressive intent.

1.2.8 Use of rare song types

Birds with song type repertoires do not sing all their song types an equal number of times. It is common for birds to display preference toward certain song types in their repertoire, while using other song types rarely. This may be because different song types serve different signalling functions. Some species are known to have functional song type categories; for example, many birds in the wood-warbler family (Parulidae) divide their song type repertoire into two distinct functional categories. Certain song types are specialized for male-female interactions and others for male-male interactions, called type I and type II songs respectively (Spector, 1992).

Some species use a rarer subset of their song types in agonistic contexts. Great reed warblers (*Acrocephalus arundinaceus*), for example, produce two structurally distinct kinds of song types: “short songs” and “long songs”. Short songs are the rarer of the two; they are used in the territorial interactions between males (Catchpole, 1983). If some song types are used more rarely, perhaps those song types serve a function that is only needed rarely, like escalated agonistic encounters. Chestnut-sided warblers (*Setophaga pensylvanica*) reserve their rarest song types for agonistic encounters, but the use of rare types does not predict that the singer will attack (Byers, 2017). If rare songs do not predict attack, they must not be signals of aggressive intent. However, the strong association between rare songs and agonism suggests that rare song types are some type of agonistic signal, such as a signal of aggressive motivation, a challenge signal, or a de-escalation signal.

1.3 Discussion

In summary, agonistic signals are integral to animal communication. This diverse set of signals fulfils a number of strategic functions, from signalling directed attention and motivation, to displaying fighting ability or experience, to indicating the intent to attack or withdraw (Bradbury & Vehrencamp, 2011). Agonistic signals assume many forms across animal taxa. Ultimately, all these signals function to manage conflict (van Staaden et al., 2011).

Songbirds can modulate their singing behaviour to fulfil many agonistic signalling functions. The use of songs as agonistic signals varies enormously among species and sometimes even among populations, as in the case of song rate in the Seattle Discovery Park and Puget Sound populations of song sparrows (Akçay et al., 2011; Nelson & Poesel, 2010). There is strong evidence that variation in song rate, amplitude, and vocal performance are agonistic signals in some songbird species (Searcy et al., 2006). Some agonistic signalling involves the use of song type repertoires, using certain subsets of song types, matching an opponent’s song types, or adjusting the rate at which they change their song type to fulfil agonistic signalling functions.

The study of these signalling behaviours in song birds is mostly accomplished through two methodological approaches: playback experiments and observational studies. In playback experiments, birds are exposed to acoustic stimuli and their response is measured (De Rosa et al., 2021). These experiments often take the form of simulated territorial intrusions in which speaker playback and sometimes a taxidermic mount to represent an intruding rival. Playback experiments are remarkably flexible in implementation. Any sounds can be used as stimuli, and the response variable can ostensibly be any measurable behavioural response from the focal bird. This has made playback studies popular in the study of birds' singing behaviour (De Rosa et al., 2021). The vast majority of studies I have mentioned as evidence of agonistic signalling in songbirds are playback studies.

Observational studies, on the other hand, can test hypotheses by observing animals in their natural context without manipulation. Observational studies are important because they contribute external validity. External validity is the extent that findings may be generalized from the context of the study to other situations and populations. Playback studies and other experiments tend to have higher internal validity because the experimental method is designed to identify causal relationships (Altmann, 1974). As a core ideal of ethology is that observed behaviour prompts questions and hypotheses, these two approaches to research naturally inform and complement one another (Tinbergen, 1963).

Remarkably few studies link singing behaviour to agonism in unmanipulated, natural systems. The present study characterizes song use during natural agonistic encounters to test hypotheses of agonistic signalling that have largely been supported using experimental approaches. Examining continuous patterns of singing behaviour relative to agonistic encounters is a novel approach that will help fill the gap between hypotheses and experimental evidence. It may serve as a basis for further theoretical and experimental refinement.

CHAPTER 2: TESTS OF SINGING BEHAVIOURS AS AGONISTIC SIGNALS IN ADELAIDE'S WARBLER (*SETOPHAGA ADELAIDAE*)

2.1 Introduction

2.1.1 Agonistic signals

Animals use agonistic signals to negotiate conflict over resources while avoiding escalated physical fights (Bradbury & Vehrencamp, 2011). Agonistic signals may occur before, during, or after an agonistic encounter. These signals are not only used to signal aggressive intent, but also fill other agonistic signalling functions such as signalling level of motivation, submission, dominance, and victory. How male songbirds use their songs around the time of intrasexual conflicts has been a topic of study for many years. Most of this work addresses the hypothesis that song is a signal of aggressive intent (Briffa, 2015; Laidre & Vehrencamp, 2008; Searcy et al., 2006). However, the broader role of birdsong as a signal in agonistic contexts remains poorly understood.

Searcy and Beecher (2009) write that signals must fulfil three criteria to be considered signals of aggressive intent (which they call "aggressive signals"). The "context criterion" states that the signal must increase in aggressive contexts. Importantly, all agonistic signals should fulfil this criterion. Additionally, signals of aggressive intent should fulfil the predictive and response criteria. The predictive criterion states that the signaller will tend to attack after it produces the signal. The response criterion says the receiver must respond to the signal appropriately. In this study, I use the context criterion to identify agonistic signals.

Most studies on the agonistic function of bird song involve acoustic playback experiments. Playback studies can be divided into two basic approaches. "Sender side" studies test how signing behaviour changes in response to a simulated intrusion. These studies can test both the context criterion ("does singing behaviour change in an agonistic context”), and when paired with a taxidermic mount presentation, the predictive criterion (“does singing behavior predict escalation”; Searcy et al., 2006). “Receiver side” studies measure responses to playback to test the response criterion. Both sender side and receiver side playback studies can be used to test hypotheses about agonistic functions of song, but only observations of free-living birds can reveal how birds use song during natural agonistic encounters. In the present study, I used an observational approach to characterize changes in three singing behaviours during agonistic encounters in Adelaide’s warbler (*Setophaga adelaidae*). Previous studies have linked these three behaviours – song type switch rate, within-repertoire song type frequency, and song rate – to agonistic functions in other species.

2.1.2 Song Type Switch Rate

Song type switch rate is a measure of how often a bird changes their song type. Switch rate is usually measured as the number of switches per opportunities to switch (Searcy et al., 2000). By rapidly switching song types, the signaller displays the size of its repertoire, which may be constrained by the individual's cognitive ability and therefore a signal of male quality (Potvin et al., 2015). Large song type repertoires are more effective at deterring rivals from invading the territory in some species. The classic example concerns great tits (*Paris major*). Playbacks of a large repertoire on an empty territory prevented takeover by neighbouring males longer than playback of smaller repertoires, indicating that the display of many song types has a deterrent effect (Krebs et al., 1978).

Experimental approaches reveal different song type switch rate patterns in agonistic contexts in different species. On one hand, both Bachman’s sparrows (*Peucaea aestivalis*) and song sparrows (*Mesospiza melodia*) switch song types more often in response to simulated intrusions, and they both respond more intensely to playbacks of high-switch rate singing (Akçay et al., 2011; Ali & Anderson, 2018; Searcy et al., 2014; Searcy & Beecher, 2009). These results contribute both sender- and receiver-side evidence that high switch rate is an agonistic signal. On the other hand, Red-winged blackbirds (*Agelaius phoeniceus*) and chaffinches respond more strongly to low-switch rates than high-switch rates (Deoniziak & Osiejuk, 2020; Yasukawa, 1981), which suggests that lower switch rates are an agonistic signal in these species. The mixed responses from different species suggest that song type switching plays a role in agonistic signalling in at least some songbirds, but whether high or low rates function as an agonistic signal depends on the species.

Compared to the large number of playback studies, there are relatively few observational studies of song type switching. In one such study, song sparrows' song type switch rate corresponded to the intensity of the agonistic context (Kramer et al., 1985). Song switch rate was lowest during normal "broadcast" singing, higher when males were singing interactively ("countersinging") with neighbours, and highest immediately before and after fights. An observational study in banded wrens (*Thryophilus pleurostictus*) also found that higher rates of song type switching are associated with agonistic interactions, but in this case, higher levels of song type switching predicted the singer was more likely to retreat. Male banded wrens who switch their song types more often seem to be signalling submission (Vehrencamp et al., 2014). Another exemplary descriptive study was conducted on western meadowlarks (*Sturnella neglecta*; Horn & Falls, 1991). Male meadowlarks increased their switch rate at the initiation of a territorial encounter with another male. The authors speculate that "the timing of a male's song switches, and what songs he sings," might be an important signalling behaviour (p. 262).

Many species display variation in song type switch rate and respond to song type switch rate around agonistic encounters, indicating that it may signal aggressive motivation, intent to de-escalate, or RHP (Logue, 2021). The main signalling function that has been studied is aggressive intent, but there is little evidence to support that idea (Searcy & Beecher, 2009). The patterns of song type switching vary tremendously from species to species, so the agonistic signalling functions of changes in switch rate probably varies with species.

2.1.3 Within-repertoire song type frequency

Individual birds sing some song types more often than others, and song type preferences vary by individual (Catchpole, 1983; Spector, 1992). Birds may reserve "rare" song types for special social contexts, such as escalated agonistic encounters (Byers, 2017). Studies of within-repertoire song type frequency (hereafter "song type frequency") can reveal functional song type categories.

Some species use a rarer subset of their song types in agonistic contexts. For example, great reed warblers (*Acrocephalus arundinaceus*) produce "short songs" and "long songs". Short songs are used in the territorial interactions between males and are the less-frequently used of the two categories (Catchpole, 1983). Likewise, the chestnut-sided warbler (*Setophaga pensylvanica*) reserves its rare songs for agonistic encounters during both experimental intrusions and natural interactions (Byers, 2017). Although the role of song type frequency in agonistic signalling has not been studied extensively, there exists some evidence that birds sing rare song types around the time of agonistic encounters, fulfilling the context criterion. If rare song types are used in agonistic contexts, this may indicate that they function as an agonistic signal such as a challenge signal (particularly if the rare song types are shared with a rival), a signal of general aggressive motivation, or a signal of aggressive intent. If rare songs are used after an agonistic encounter, they may function as victory or submissive signals.

2.1.4 Song Rate

Song rate is a measure of an individual's song output, measured as the number of songs produced per unit of time. The display rate of a signal is a good indicator of aggressive motivation (i.e., willingness to escalate) in many animals (Bradbury & Vehrencamp, 2011). Song rate is well-suited to signal a continuous trait like motivation. If it does signal aggressive motivation, song rate should increase in the time approaching an agonistic encounter. Signals of motivation can be used at any time before an agonistic encounter, but should be more frequent around the time of the encounter.

Elevated song rates are indeed associated with motivation in agonistic contexts in several species. In response to receiver side playback experiments on black-capped chickadees (*Poecile atricapillus*), house wrens (*Troglodytes aedon*), and wood warblers (*Phylloscopus sibilatrix*), males respond most strongly to high song rates. In each species, the subject's own song rate positively predicted subsequent attack on a taxidermic mount, fulfilling the predictive criterion (Baker et al., 2012; Barnett et al., 2014; Szymkowiak & Kuczyński, 2017). In these systems, increased song rate probably functions as a signal of aggressive intent and aggressive motivation.

In other species, however, song playback induces males to reduce their song rates. The black-bellied wren (*Pheugopedius fasciatoventris*) marginally reduces its song rate in response to simulated territorial intrusions (Logue & Gammon, 2004). Birds that reduce their song rate during agonistic contexts are not necessarily using the low song rate as an agonistic signal. They may instead be engaging in other agonistic behaviour that results in a reduced song rate (e.g., preparing to attack, attempting to remain undetected). If song rate is suppressed because of other agonistic behaviours, low song rate may be an environmental cue of interest to a receiver, rather than a signal that has evolved for the function of influencing the receiver. Without additional evidence that low song predicts subsequent behaviour from the sender as well as a response from the receiver, the evidence is weak that low song rates function as an agnostic signal .

Other species do not vary their song rate at all in agonistic contexts. Neither banded wrens (*Thryophilus pleurostictus*) nor swamp sparrows (*Melospiza georgiana*) for example, significantly change their song rate in response to simulated intrusion (Ballentine et al., 2008; Trillo & Vehrencamp, 2005). An absence of significant change in song rate in agonistic contexts is evidence that it is not an agonistic signal.

Observational studies that describe song rate in natural contexts are rare. One example is a description of singing in the Puget Sound white-crowned sparrow (*Zonotrichia leucophrys pugetensis*). Males increase their song rate when engaged in a territorial conflict with another male. The highest song rates were observed in males that continued to engage in the encounter. High song rates predicted further escalation, offering support for the hypothesis that song rate signals aggressive motivation during intrasexual territorial conflicts (Nelson & Poesel, 2010).

2.1.5 Experimental and Observational Approaches

In a typical field playback experiment, the researcher places one or more speakers near or within a bird's territory, plays a stimulus sound and measures the bird's response. This kind of experiment is intended to simulate a territorial intrusion or close approach by another male. Playback experiments are a well-established method to collect data on the behaviour of wild birds. Part of their appeal is the inherent flexibility of the experiment design. Any sort of sound can be used as a stimulus, and the response variable can ostensibly be any measurable behaviour from the focal bird. Playback experiments have a long history in the bird song literature, so reviewers and journal editors are comfortable interpreting them. Another reason that playback experiments are popular is the fact that they are experimental. In an experiment, the researcher manipulates one or more independent variables. This study design allows strong claims about causality (Altmann, 1974). The ease of use of playback studies, their flexibility in implementation, and their power to infer causation have made playback the "go-to" design to test song functions.

Playback experiments are simulations of natural behaviour, but often the mechanics of natural territorial interactions are not well-understood. If researchers do not understand the signalling system that mediates territory intrusion and defence, it is not possible to design a realistic simulation. Good descriptive work should inform the designs of playback studies from the ground-up. Observations of behaviours in natural context should inform which behaviours are tested in playbacks as well as methodological details like speaker placement and stimulus design.

A core ideal of ethology is that observed behaviour prompts questions and hypotheses (Tinbergen, 1963). Observational studies of song behaviour and agonism are crucial for understanding birdsong's function in these contexts. Currently, a substantial portion of the bird song literature is directed to testing hypotheses of song as a functional signal. A better understanding of how birds behave during aggressive interactions will inform the selection of hypotheses that should be tested experimentally.

2.1.6 Objectives

In this thesis, I describe changes in song type switch rate, within-individual song type frequency, and song rate during natural agonistic encounters in male Adelaide's warblers (Figure 2.1). These behaviours are hypothesized to function in agonistic contexts in other species, but few studies have attempted to measure them during natural interactions, and even fewer provide detailed descriptions of their timing relative to agonistic events. Adelaide's warbler is an ideal species for studying singing behaviour around the time of agonistic encounters because they sing moderately-sized song type repertoires, sing at high rates, frequently engage in aggressive encounters, and maintain territories year-round. Adelaide's warbler is a non-migratory tropical songbird, a group that has been historically underrepresented in the birdsong literature.

To the best of my knowledge, this is the first study to estimate continuous changes in these singing behaviours around the time of natural agonistic encounters while controlling for covariates and non-independent data.

Hypotheses and Predictions

In addition to describing singing behaviour around the time of agonistic conflicts, I tested the hypotheses that song rate, the rate of song type switching, and the within-repertoire song type frequency function as agonistic signals in Adelaide's warbler. If these singing behaviours do function as agonistic signals, I predict that they will vary as a function of time to agonistic encounter. I based these predictions on the 'context criterion' in Searcy and Beecher's (2009) review of aggressive signalling in songbirds, which states that agonistic signals tend to occur in agonistic contexts. Hypotheses 1-3 concern the specific functions of the putative agonistic signals. The corresponding predictions specify the expected direction and timing of changes in song delivery under each functional hypothesis.

My hypotheses are in part based on the phenomenon of song categories in the wood warbler family (Parulidae), of which this study species is a member. Many wood warblers divide their song into two functional categories. These categories are characterized by distinct delivery patterns, and each category contains a subset of the song type repertoire (Beebee, 2004; Kaluthota et al., 2019; Spector, 1992; Staicer, 1992). Categories are also used in different contexts. Type 1 song is delivered at a lower song rate and with eventual variety (i.e., infrequent song type switching). Adelaide's warblers sing Type 1 song all year long, after dawn as the male moves around its territory. Type 2 singing is used during the "dawn chorus," an intense period of singing at dawn, during which songs are delivered with immediate variation (frequent switching) at a high rate from a single location. There is limited evidence that Type 2 singing is used primarily in male-female interactions, and Type 2 songs are associated with male-male interactions.

Hypothesis and Prediction 1: Song Type Switching

I test the hypothesis that increased song type switch rates signal general aggressive motivation. I base this hypothesis on evidence in canyon wrens (*Catherpes mexicanus*), and song sparrows (*Melospiza melodia*), which increase their song rates during simulated territorial intrusions (Benedict & Warning, 2017; Nelson & Poesel, 2010), and wood warblers (*Phylloscopus sibilatrix*), which respond more aggressively to playbacks of high song rates (Szymkowiak & Kuczyński, 2017). Also, high switch rate in this species is typical of "Type II" singing, which is hypothesized to function in territorial interactions between males in this species (Staicer, 1992). If a high rate of song type switching is a signal of aggressive motivation in Adelaide's warblers, I predict that males will increase their rate of song type switching in the time leading up to an agonistic event and drop back to baseline levels after the event.

Hypothesis and Prediction 2: Song Type Frequency

I also test the hypothesis that less-frequently used song types in individuals' repertoires signal general aggressive motivation. I base this hypothesis on the findings that chestnut-sided warblers (*Setophaga pensylvanica*) use rare song types during escalated agonistic encounters, but not immediately before attacking (Byers, 2017), and that some wood warblers (Family: Parulidae), including the focal species have two categories of song types, Type I and Type II. There is limited evidence that these song type categories are used in interactions with females and males, respectively (Hof & Podos, 2013; Spector, 1992). Male Adelaide's warblers use Type II song types in the dawn chorus and perhaps in male-male interactions (Staicer, 1992). Because I did not include the dawn chorus in my calculation of within-repertoire song type frequency, Type II song types should be rarer than Type I songs in my sample. If male Adelaide's warblers use either rare song types per se, or Type II songs to signal aggressive motivation, I predict that song type frequency will reach its lowest point before agonistic encounters.

Hypothesis and Prediction 3: Song Rate

The final hypothesis I test is that Adelaide's warblers signal aggressive intent with high song rates. This hypothesis is based on findings in many other songbird species, which respond more aggressively to playback of high song rates and increase their own song rate before attacking. I predict that if high song rate is used as a signal of condition or aggressive intent, it will increase in the time leading up to an agonistic encounter, peak immediately before the encounter, and return to normal levels after the encounter.

Figure 2.1: A male Adelaide's warbler (Setophaga adelaidae). Photo credit: Peter C. Mower.

2.2 Methods

2.2.1 Study System

Adelaide's warbler (Figure 2.1) is a socially monogamous, insectivorous wood-warbler endemic to the tropical islands of Puerto Rico and Vieques. Mated pairs defend all-purpose territories of 0.93 ± 0.32 hectares year-round (Fig. 2.2; Krause, 2023). While most pairs retain their territories from year to year, territory borders frequently shift. Neighbours negotiate borders with territorial skirmishes. These skirmishes manifest as territorial intrusions in which the competitors perform aggressive wing-waving displays and emit chitburst calls, neither of which signals are observed outside of agonistic contexts. Escalated agonistic encounters between males include chases and occasionally physical fights (Staicer, 1992; present study). Females sometimes participate in aggressive encounters alongside their mates, but males take the primary role in territory defense (Staicer, 1992). Females rarely sing, but males sing at high rates throughout the year (Staicer, 1992).

Male Adelaide’s warblers sing repertoires of discrete song types (Staicer, 1992). All songs are frequency-modulated trills. Variation in the pattern of frequency modulation within and among notes defines the different song types. Each male’s repertoire contains 22.6± 2.6 song types, all of which are frequency modulated trills (Figure 2.3; Staicer, 1992). Male Adelaide’s warblers share some of their song types with other males in the population (Staicer, 1992), but for the present study I did not attempt to determine which song types were shared across individuals.

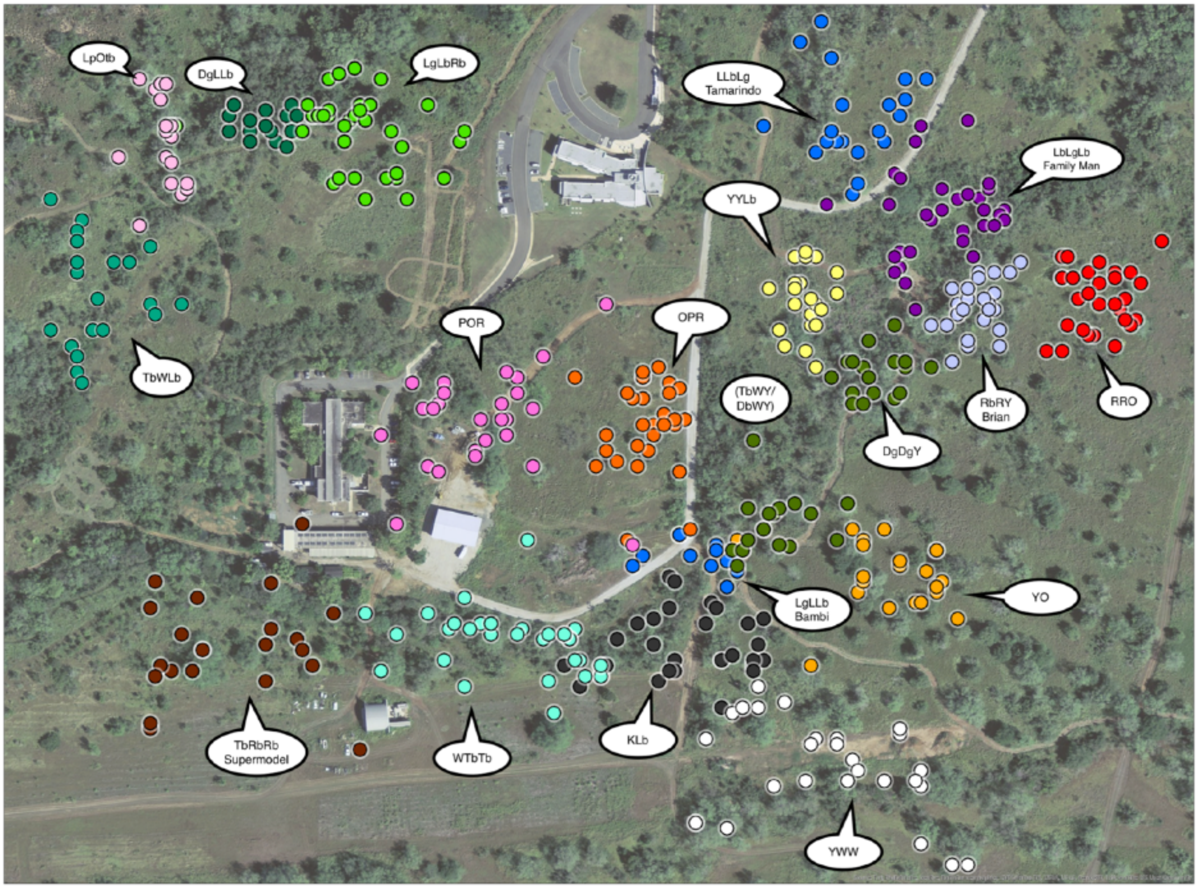

Figure 2.2: Territory map of the field site in 2018. Different-coloured dots are the observed singing locations of different males, which are named in the speech bubbles.

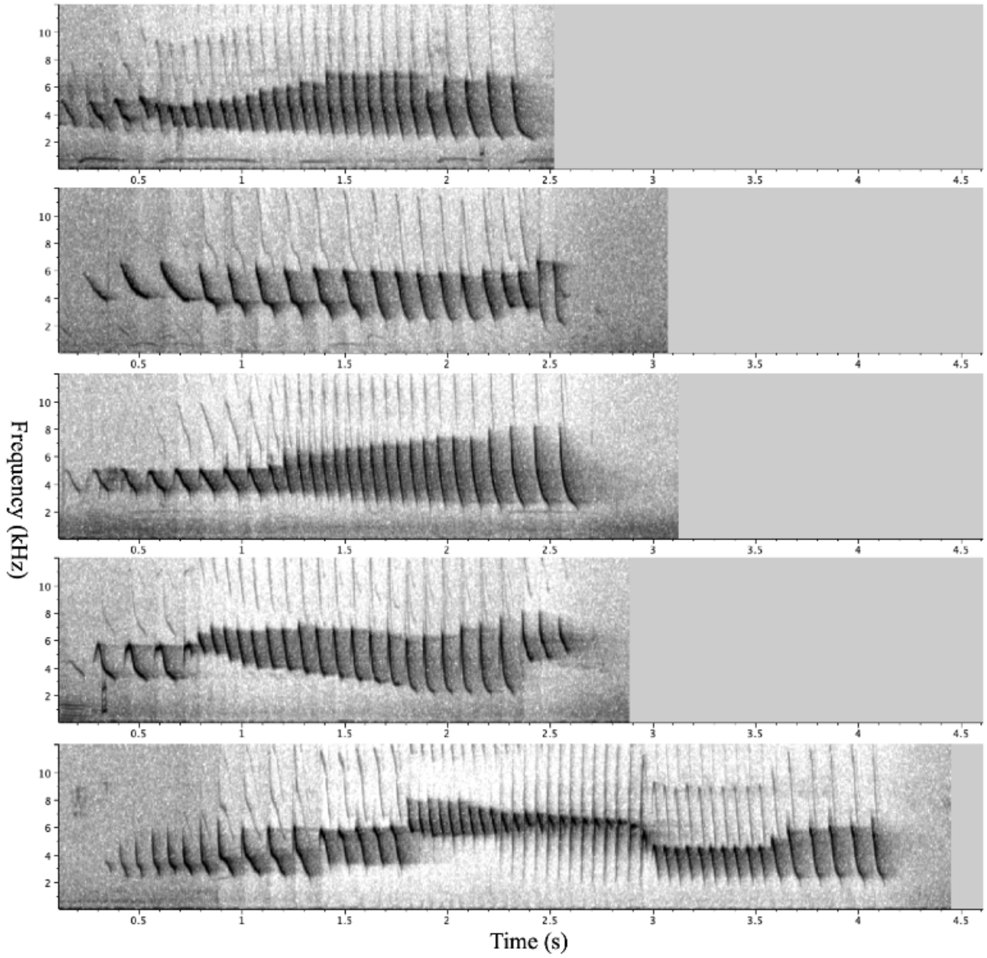

Figure 2.3: Spectrograms of five distinct song types taken from the repertoire of a male Adelaide's warbler. Spectrograms were generated using Raven 1.6.3 (window shape: Hann, window size = 512, overlap = 50%, high-pass filter = - 3dB, 124 Hz).

Study Population

We collected the data for this study from a population of Adelaide's warblers at the Cabo Rojo National Wildlife refuge in southwestern Puerto Rico (Latitude: 17.975° N, Longitude: 67.168° W). The refuge is a tropical dry forest, with densely vegetated arroyos in a matrix of savannah-like open spaces. Adelaide's warblers are abundant in the refuge, especially near the arroyos. The dominant plants on Adelaide's warbler territories include mesquite (*Prosopis juliflora*), tamarind (*Tamarindus indica*), Jerusalem thorn (*Parkisonia aculeata*), shrubs (*Lantana*, *Melochia*, *Waltheria*), vines (*Stigmaphyllon*, and *Tournefortia*), and epiphytes (*Tillandsia spp*.; Staicer, 1992).

Figure 2.4: Pictures of the habitat at the field site at Cabo Rojo Wildlife Refuge that display typical vegetation and mist-netting technique.

We used mist nets and acoustic lures to capture males prior to observation. All males used in this study were fitted with Fish and Wildlife Service numbered metal bands and a unique combination of three coloured plastic bands on their legs for individual identification. Males establish their territories in second-growth vegetation comprised of open canopies with an understory of grasses and shrubs (Figure 2.4). All subjects were mated and held territories.

Dawn Chorus

Male Adelaide's warblers participate in the dawn chorus during their breeding season. During the dawn chorus, they sing Type II songs at an elevated rate, switch song types after almost every song, and rarely change locations (Gil & Llusia, 2020). After the dawn chorus, the birds begin to patrol their territory. They reduce their song rate and song type switching rate and use song types that they did not sing during the dawn chorus (Type I songs). I followed a previous study of Adelaide's warblers which operationally defined the end of the dawn chorus as 700 sec after sunrise, which is the time that the average song rate drops to baseline levels (Kaluthota et al., 2019).

I excluded the dawn chorus from my analyses because agonistic encounters during this period are rare. Once the dawn chorus ends, males sing mostly Type I songs, and they repeat one song type several times before switching to another song type. I sampled from this period because this is when males actively patrol their territory and engage their conspecifics in territorial conflict.

Animal Ethics

This study adheres to ethics guidelines from the Institutional Animal Care and Use Committee at the University of Puerto Rico, Mayagüez (September 17, 2010) and the Animal Welfare Committee at the University of Lethbridge (protocol #1605). Field work was conducted with permission from the U.S. Fish and Wildlife Service (permit 2012-01, 41521-2016-11) and the Departamento de Recursos Naturales y Ambientales (permits 2016-IC-068-1). Bird handling was conducted under David M. Logue's USGS master bird banding permit (no. 23969).

2.2.2 Data Collection and Processing

Field work was conducted from April 13 to May 6 in 2017 and from March 12 to April 26 in 2018, periods that correspond to the height of Adelaide's warblers' breeding season (Toms, 2020). Trained recordists (D. Logue, S. Krause, O. Medina, S. Luyando, E. Rivera, and P. Mower) conducted continuous focal observations beginning with the first song of the day, until approximately two hours after sunrise. Recordings were made with Marantz PMD 661 digital recorders and Sennheiser ME67 shotgun microphones (file format = wav; sampling rate = 44.1 kHz; bit depth = 16 bits). Recordists attempted to record all sounds produced by the focal male, and made verbal annotations of behaviour, movements, and interactions with other birds. Recordists visually confirmed the focal male's leg band combination during every recording session. In 2018, eight males and their mates were fitted with LB-2X Holohil radio transmitters (0.38 g, which corresponds to 5.4% of average body weight) and tracked with H-antennae and R1000 radio receivers (Communications Specialist).

Recordings were reviewed for behaviours and scored by five trained annotators (L. Heatlie, N. Gooding, Sam B, P. Mower, S. Krause) with the acoustic analysis software Raven Pro v 1.5 and 1.6.1 (Center for Conservation Bioacoustics, Raven Pro: Interactive Sound Analysis Software, 2019). The program allowed annotators to listen to and visually inspect spectrograms of the recordings, including comments from the recordist (Hann window size: 512, brightness: 60, contrast: 60, low-band filter: 124Hz, 256 samples, 50% overlap). They scored the sound files for songs and other behaviours, including calls, agonistic behaviours, and territorial interactions with neighbours (Appendix 1). I excluded observation days from my analysis that did not contain any agonistic behaviour, as well as those in which the identity of the focal individual was uncertain.

Song Type Classification

To ensure consistent classification of songs into robust song type categories, song type scoring occurred in two phases: first, individual repertoires of song types were categorized during the annotation process. Annotators scored song types by listening to each recording. When the annotators encountered a song, they compared its spectrogram to spectrograms of the known repertoire of the focal bird, and either assigned the song to an established song type, or created a new song type if it did not match any types in that male’s repertoire. I supervised this process and reviewed the decisions made by annotators.

Individual differences between annotators necessitated a second phase of song type categorization. Three trained reviewers reviewed all song type repertoires once the recordings had been annotated and songs initially categorized into song types. According to an established protocol, song type categories were consolidated if they were judged to be 80% similar in a) overall frequency contour, b) note shape, and c) number of notes in each phrase. Each repertoire was reviewed by two of the three reviewers. If two reviewers disagreed, they evaluated the spectrograms together until an agreement was reached. In the case of disagreement, the third reviewer's judgement settled the song's classification. I trained and oversaw all song type categorization and subsequent repertoire refinement efforts, and also made the final song type categorization decisions (for song type categorization protocol, see Appendix 2).

2.2.3 Variables

Time to Agonistic Encounter

This study is about singing behaviour around the time of agonistic encounters, so it is important to define agonistic encounters. I used three aggressive behaviours to define agonistic encounters: "chitburst" calls, aggressive posture, and chases. Chitburst calls are loud, broad-frequency "chit" calls delivered in an extended series (Figure 2.5). Adelaide's warblers give chitburst calls only during agonistic territorial encounters (Staicer, 1992), and territory holders will fly across their territory to approach chitbursts (pers. obs.).

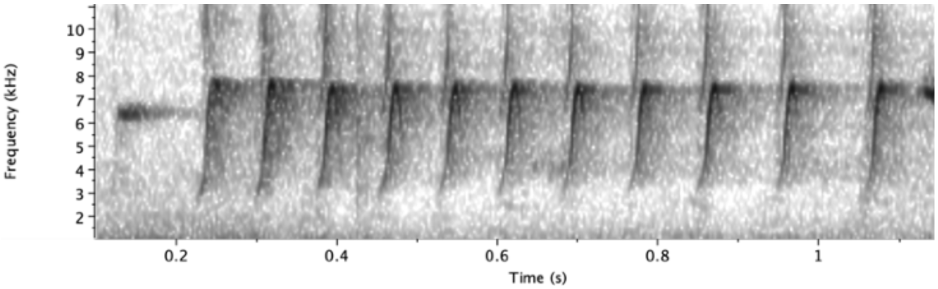

Figure 2.5: Spectrogram of an aggressive "chitburst" call, one of the aggressive behaviours that was used to identify agonistic encounters. This example was generated using Raven 1.6.3 using the Hann window type, a window size of 160 samples, and 50% overlap.

In aggressive posture, the male assumes a distinctive low hunched position with the beak pointed forward. He vibrates his wings, which are held slightly depressed and spread (Figure 2.6; Anderson et al., 2013). These displays can be evoked by simulated territorial intrusions using song playback, and are associated with chitburst calls (Staicer, 1992). Chases occur when one bird pursues the other closely in the air. The occurrence of any of these behaviours was taken as evidence of an agonistic encounter. I identified agonistic behaviour by reviewing the recordings for aggressive calls and the recorder's observations of aggressive posture and chases.

Figure 2.6: A male Adelaide's warbler in an aggressive posture display, one of the behaviours that indicate involvement in an agonistic encounter. Photo credit: Jay Gowan.

Male Adelaide's warblers often exhibit multiple aggressive behaviours during a single agonistic encounter. If aggressive behaviours occurred within 30 seconds of one another, I grouped them into a single "agonistic state". If no further agonistic behaviour occurred within 30 seconds, the agonistic state was ended at the last observed aggressive behaviour. Combining aggressive behaviour into agonistic states mitigates the risk of pseudoreplication because agonistic behaviours that occur in close succession are usually not independent. I assigned each agonistic encounter a unique identifier, *EncounterID*, so that I could include it in my models to account of the non-independence of singing behaviour around a given agonistic event. Defining agonistic encounters in this way allowed us to calculate each observed song's time relative to agonistic encounter (*TimeRelState*), which is the distance in time to the nearest agonistic encounter. This value is negative in the time leading up to the agonistic encounter, and positive in the time following it (Figure 2.7).

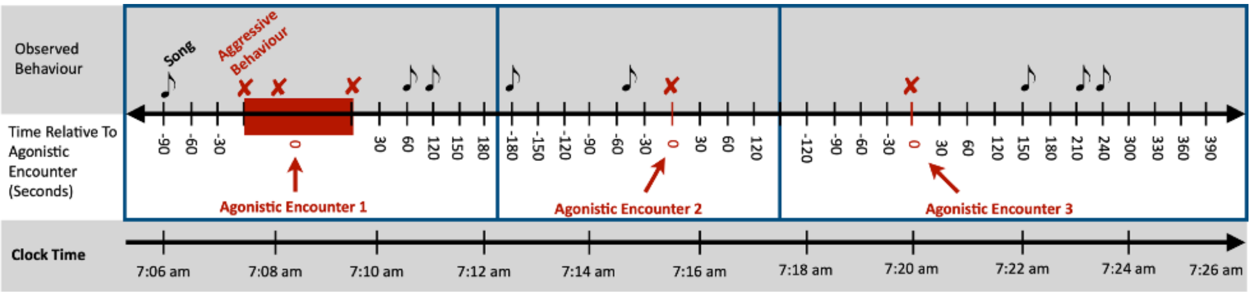

Figure 2.7: A hypothetical timeline of a ten-minute recording segment, showing agonistic encounters and songs. Aggressive behaviours are grouped into "agonistic states" (red bar) if they occur within 120 seconds of each other. The figure shows how time-to-agonistic-encounter is assigned to song observations as the distance to the nearest agonistic encounter.

Time Since Sunrise

Because these birds are known to shift their singing behaviour over the course of the day, I included the number of seconds since sunrise (Time since sunrise) in my models (Schraft et al., 2017; Staicer, 1992; Vazquez-Cardona et al., 2023). I used "apparent sunrise," which is when the centre of the Sun is positioned 50 arcminutes below the horizontal plane. I chose this sunrise time because it accounts for atmospheric refraction (U.S. Navy, n.d.). Sunrise times were retrieved from timeanddate.com and verified using the Solar Calculator Global Monitoring Laboratory of the National Oceanic and Atmospheric Administration (Thorston, n.d.; U.S. Department of Commerce, 2005).

Song Type Switching

I scored this variable 0 if the song type was the same as the previous type, and 1 if it was not. Averaging this variable gives a proportion of songs that were song type switches.

Song Type Frequency

Song type frequency is the within-individual proportion of occurrence of a given song type. For example, if Male X sang 1000 songs, and 300 of those belonged to Song Type Y, Song Type Y would have a song type frequency of 0.3 for Male X.

Song Rate

I divided recordings into 60-second bins from the beginning and end point of agonistic encounters. The bins were named by the EncounterID of the nearest agonistic encounter as well as their distance in seconds to the encounter. To calculate song rate, I counted the number of observed songs in each bin. Partial bins were excluded from the analysis.

2.2.5 Inferential Statistics

All data analysis took place using the statistical programming suite R x64 4.1.0. (R Core Team, 2018). Statistical analysis followed Richard McElreath's workflow for Bayesian analysis (McElreath, 2019). I used the package DAGitty to create directed acyclic graphs (Textor & Van der Zander, 2016), and brms to fit the Bayesian mixed-effects models (Bürkner, 2018). I standardized all independent variables by mean-centering and scaling them with the base R function "scale" prior to analysis.

DAGs

Directed acyclic graphs (DAGs) are a way of representing variables and their causal relationships as a network. They are useful for specifying causal hypotheses and avoiding statistical confounds (Westreich & Greenland, 2013; McElreath, 2019). Variables are represented by nodes and the causal relationships between them form directed edges. I made DAGs for each of the three hypothesized agonistic singing behaviours to reflect my assumptions about the systems. The independent variables I included were JulianDate (ordinal date), *TimeRelState* (seconds to nearest agonistic encounter), and *TimeRelSun* (seconds since sunrise). I assumed that JulianDate could affect both singing behaviour and *TimeRelState*. This assumption about JulianDate attempts to capture the effect of seasonal variation in agonistic behaviour (Staicer, 1992), for example, variations in testosterone that are associated with the breeding season. I assumed that *TimeRelSun* could affect the *TimeRelState* as well as the dependent variable. Both of these assumptions come from the observation that singing behaviour and agonistic behaviour vary over the course of the day. Finally, I included the causal relationship between *TimeRelState* and singing behaviour, because that relationship is the focus of this study.

I used the *DAGitty* package (Textor & van der Zander, 2016) in R to create and evaluate the *DAGs* and to refine my variable selection for the models (Figure 2.8). Following the advice of *DAGitty* ensures that models will estimate the direct causal influence of *TimeRelState* on singing behaviour, while blocking other suspected causal paths (Westreich & Greenland, 2013; McElreath, 2019). I used *DAGitty's* "*impliedConditionalDependencies*" function to identify possible dependencies between variables when conditioned on the other variables. No conditional dependencies were found, so no further refinement was necessary. I used the function "adjustmentSets" which identifies the independent variables to include in a model to estimate the direct effects of *TimeRelState* upon the response singing behaviour. The results from these functions indicated that I should include both *TimeRelSun* and *JulianDate* in all models.

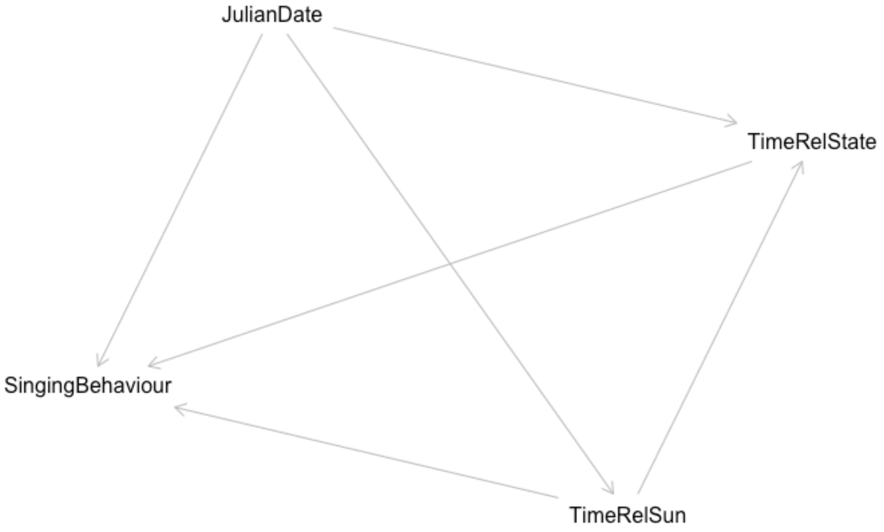

Figure 2.8: A directed acyclic graph (DAG) describing the hypothesized patterns of causality for variation in singing behaviour.

Sparse data limit the ability of models to make accurate estimations, so I omitted songs that were far away from the time of the agonistic encounter where data were sparse. I selected the data to be used in the models by evaluating the distribution of data and selecting a sampling cut-off that preserved the bulk of the data while excluding the sparsely populated extremes. This resulted in two truncated datasets for the models, which I subsampled from the larger dataset of all recordings.

The independent sampling unit for both *song type switch* and *song type frequency* is the individual song observation, so I created the first dataset that only included song observations. I selected a subsample that maximized the sample size of songs while excluding songs with very high or very low *time to agonistic encounter*. I chose 25 total songs in a 60-second bin as the threshold for sparse data. A 25-song threshold resulted in a low cutoff of -1,860 seconds and a high cutoff of 2,520 seconds. The remaining dataset contained 75.3% of all recorded songs (Figure 2.9).

Song rate required a different dataset because the sampling unit was not songs, but time bins. I set a minimum sampling threshold of 30 recordings, resulting in a low cutoff of -1860 seconds and a high cutoff of 3300 seconds. The remaining dataset contained 79.2% of all time bins (Figure 2.10).

The *brms* package uses a Markov Chain Monte Carlo (MCMC) conditioning engine to estimate posterior distributions. I used four chains with 3500 iterations each. Based on the results of my DAG, I chose the following independent variables for inclusion in my models: *Julian Date*, *Time Relative to Sunrise*, and *Time to agonistic encounter*.

I included *Year* within *BirdID* as a nested random term in my models. *Year* accounts for the differences between years that affect all individuals; such as changes in environmental factors as well differences in data collection methods (e.g., the use of radio tracking in 2018). *BirdID* accounts for the individual differences between birds. I chose to nest *Year* within *BirdID* rather than cross them because many birds were recorded in both years and experienced changes between years that were idiosyncratic to the individual and

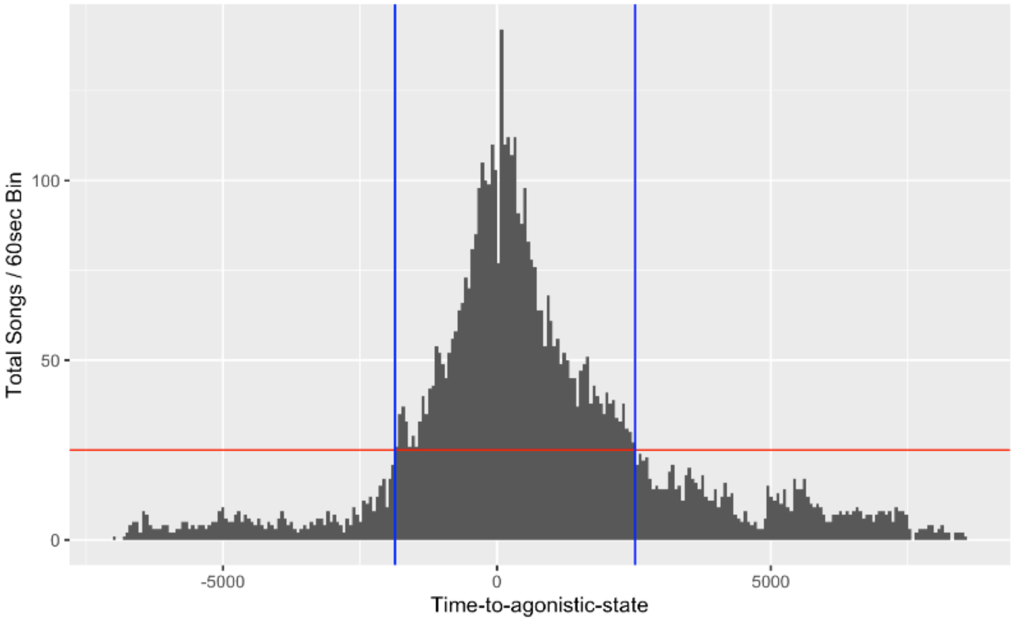

Figure 2.9: The distribution of all sampled songs across time to agonistic encounter, used to form the data cut-off for Song Type Switch and Song Type Frequency models. The red line shows the sampling threshold of 25 songs/60sec bin. Excluding times with lower song samples than 25 resulted in time cutoffs before and after the agonistic encounter, showed by the vertical blue lines. and had a range around agonistic encounters from -1860 to 2520secs.

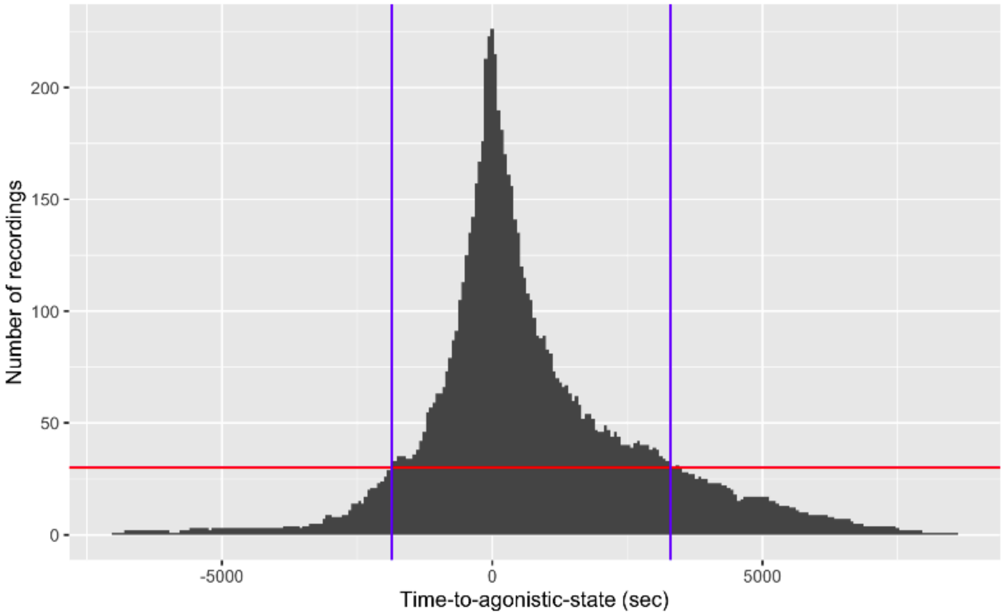

Figure 2.10: The distribution of all recordings associated to an agonistic encounter across time to agonistic encounter. The maximum sample was 254, the number of unique observation bins. The horizontal red line shows the sampling threshold of 30 recording samples/60sec bin. Excluding times with lower recording samples than 30 resulted in time cutoffs before and after the agonistic encounter, showed by the vertical blue lines. This dataset was used in the Song Rate model and had a range around agonistic encounters from -1860 to 3300secs.

not broadly applicable to all birds. For example, changes in mate status or territory ownership, or changes in condition like disease or injury, which occur at the individual level from year to year. These differences are important to capture because recordings of the same individual from different years are not independent. I also included *EncounterID* as a random term, which prevents pseudo-replication between agonistic events. Because of these random terms, results should be interpreted as occurring at the level of agonistic events with an individual bird.

Bayesian Models

I built Bayesian multi-level models to estimate the influence of *Time to agonistic encounter* on three singing behaviours. A Bayesian approach allows us to accurately estimate parameters in complex models, which can be a challenge with frequentist models (MacElreath, 2016). In particular, the Bayesian framework facilitates the use of splines to characterize effects. Splines are well-suited to non-linear descriptions of behaviour over time. Bayesian models require the user to input prior estimates of the model parameters. I used weakly-informative priors that were centered on zero. This approach sets the model's initial state to assume that the independent variables have no effect on the dependent variable.

I used the brms package to construct one model for each of the three dependent variables (s*ong type switch, song type frequency, song rate*). Each model contained the same independent and random variables, but they differed in the distribution family and dependent variables. *Song rate* is a count (songs per 60-second bin), so I used a Poisson distribution. *Song type switch* required a Bernoulli distribution because the variable was binary (each song is either a switch or not; 1 or 0). I chose the Beta distribution for *song type frequency* because data were represented as proportions. All independent variables were fitted as splines, which allowed them to vary non-linearly.

I validated the fit of my models by plotting their posterior predictive checks with the function *pp_check* from the *brms* package (Bürkner, 2017). This function compares the distribution of the observed data (*Y* in Figure 2.11) with samples of the posterior predictive distribution (i.e., replicated data; Y_{rep}). If *Y* and Y_{rep} show a similar distribution, it means that the model fit the observed data well (Gelman & Hill, 2018). The closer the lines converge, the better the model fits the data.

Posterior predictive checks of the *song type switch* and *song rate* models show that their predictions fit the data well (Figures 2.11 A, 2.11 C, respectively). The *song type frequency* model shows that there is remaining variation in the data that is unaccounted for by the model (Figure 2.11 B). A poor model fit indicates that there is variance in the birds' song type frequency that is unexplained by the predictor variables, but does not necessarily indicate that the results of the model are inaccurate.

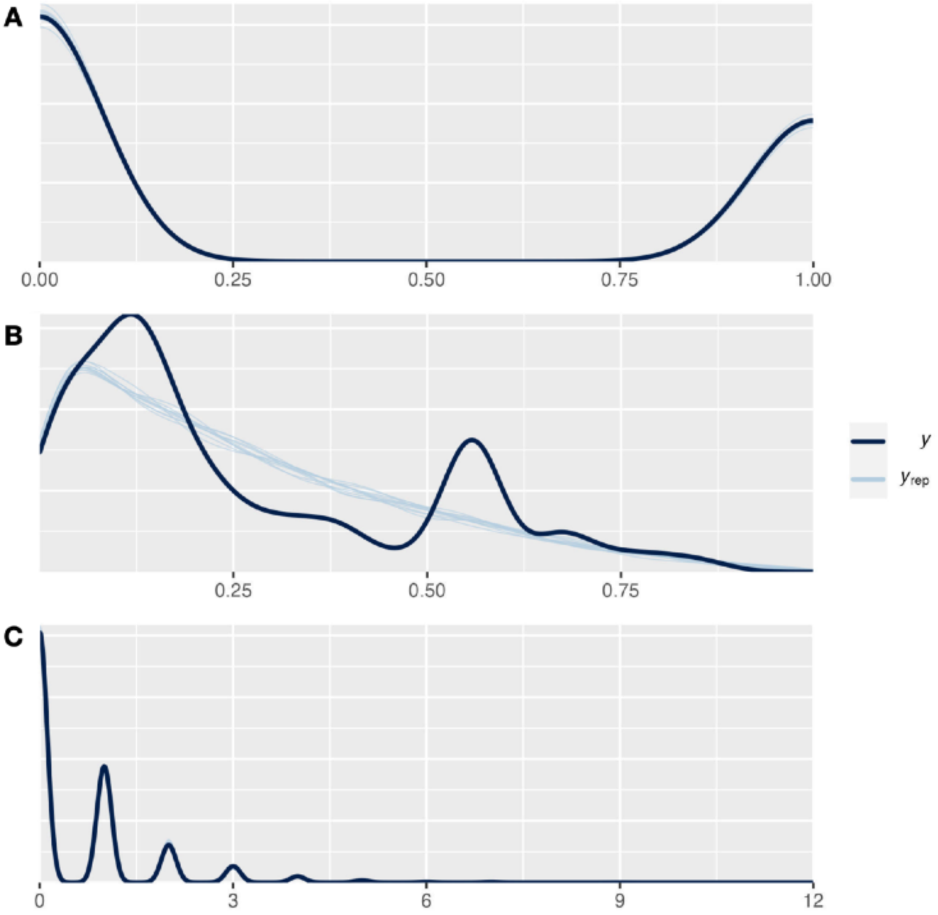

Figure 2.11: Posterior predictive checks showing how well the models fit the data. In these plots, the distribution of the dependent variable is shown in dark blue (*y*). The lighter blue lines behind it represent simulations from the model (y_{rep}). **A** shows prior predictive checks of the song type switch model, **B** shows the song type frequency model, and **C** shows the song rate model.

To further validate my models' predictions I used the function *sample()* to randomly reorder the values of the dependent variable (within *Bird* and *Date*), and then I fit the model to the randomized data. I repeated this four times for each model and compared the results of the randomized data to the observed data. If the estimated effects from the randomized data are consistently flatter than the effects from the observed data, I can be more confident that the models' predictions based on the observed data represent real patterns in the data.

2.3 Results

2.3.1 Descriptive Statistics

I analyzed data from recordings of 23 individual male Adelaide's warblers from 2017 and 2018 (19 individuals in 2017, 17 in 2018, 13 in both field seasons).

This dataset contains a total of 145.84 hours of behavioural observations and 5,803 songs from 83 individual recording sessions. We collected 3.61 ± 1.82 recording sessions per bird, allowing 7.21 ± 4.82 days between recording sessions of the same individual. Recording sessions were 1.89 ± 0.51 hours in length and on average contained 68.98 ± 76.39 songs. There were a total of 239 agonistic encounters, which consisted of 621 observations of aggressive behaviour (averaging 2.78 ± 2.21 agonistic encounters per recording session).

Male Adelaide's warblers switched their song types at an average proportion of 0.36 ± 0.48 switches per song. The within-individual song type frequency of the average song was 0.26 ± 0.23, and their average song rate was 0.66 ± 1.00 songs per 60 seconds. See Table 2.1 for a collection of summary statistics.

Table 2.1: Summary Statistics

Variable	**Summary statistic**
Total song observations (song type models)	4351 songs
Total song observations (song rate model)	4608 songs
Recording Date	18 April ± 14 days
Recording Sessions	83 total 3.61 ± 1.82 recording sessions / individual
Days Between Recording Session	7.21 ± 4.82 days
Individual Song Type Repertoire Size	11.1 ± 7.1 distinct song types / individual
Agonistic Encounters	254 total agonistic encounters 3.05 ± 2.25 encounters / recording session
Song type switch	0.37 ± 0.48
Within-repertoire song type frequency	0.26 ± 0.23
Song rate	0.66 ± 1.00 songs/60 secs
Time to nearest agonistic encounter (of observed songs)	265.7 ± 1037.4 secs
Aggressive behaviours	532 total 6.4 ± 6.2 behaviours / recording session

2.3.2 *Song Type Switch* Rate

The estimated conditional effects show a strong decrease in *song type switch* rate leading around the time of agonistic encounters (Fig. 2.12). *Song type switch* rate begins at 0.57 switches / song at the beginning of our sampling period (- 1860 seconds, or about 31 min, before the encounter), and immediately begin to drop. *Song type switch* levels continue to drop after the time of agonistic encounter to a nadir of 0.29 switches / song at 882 seconds (about 15 minutes) after the encounter. This means that birds decrease their *song type switch* rate from one switch per 1.75 songs to one switch per 3.45 songs, an overall decrease of 49%. *Song type switch* then increases again to mean levels around 2000 seconds (15 minutes) after the encounter.

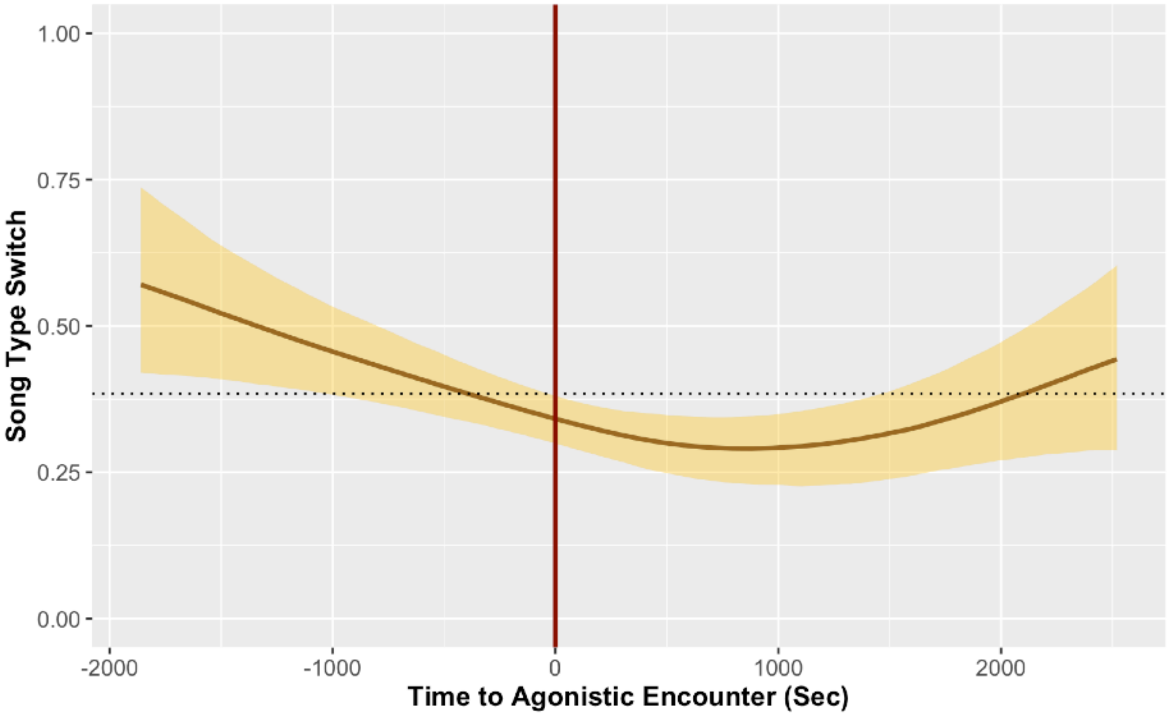

Figure 2.12: Estimate of song type switch as a spline (yellow line) in the time around agonistic encounters (indicated by the red vertical line) derived from a Bayesian mixed-effects model. 95% credible intervals are indicated by the yellow band. The mean level of song type switching is indicated by the horizontal dotted line.

Model predictions of song type switching on 4 iterations of randomly reordered data consistently produce a flat effect compared to the pattern produced by observed data (Figure 2.13).

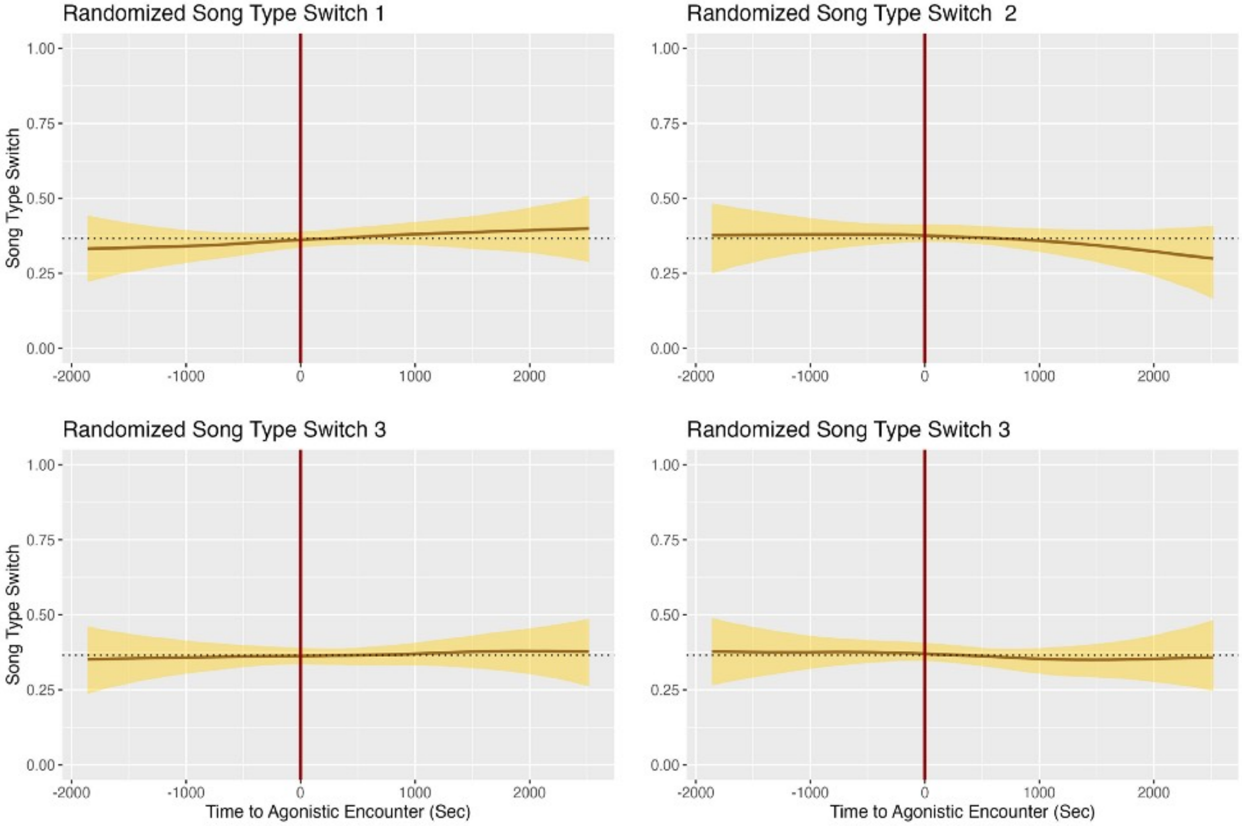

Figure 2.13: Estimated conditional effects (horizontal yellow lines) of Time to agonistic encounter on randomly reordered *song type switch* values, repeated four times to validate the model's estimation of observed data. (horizontal yellow line). Song type switch values were shuffled and fit to the model four times.The consistently flat effects indicate that the strength of the model's predictions based on observed data is a result of patterns in the data.

2.3.3 *Song Type Frequency*

Estimated conditional effects of my model show a modest increase in within-individual *song type frequency* around the time of agonistic encounters (Figure 2.14). The effect is fairly symmetrical around the time of the encounter.

Song type frequency increased from 0.220 at -1860 seconds (about 30 minutes before the encounter) to 0.275 at -135 seconds (about two minutes before the encounter). *Song type frequency* remained at this level for roughly 300 seconds (five minutes) before decreasing by 0.205 at 2520 seconds (42 minutes), the end of our sampling period.

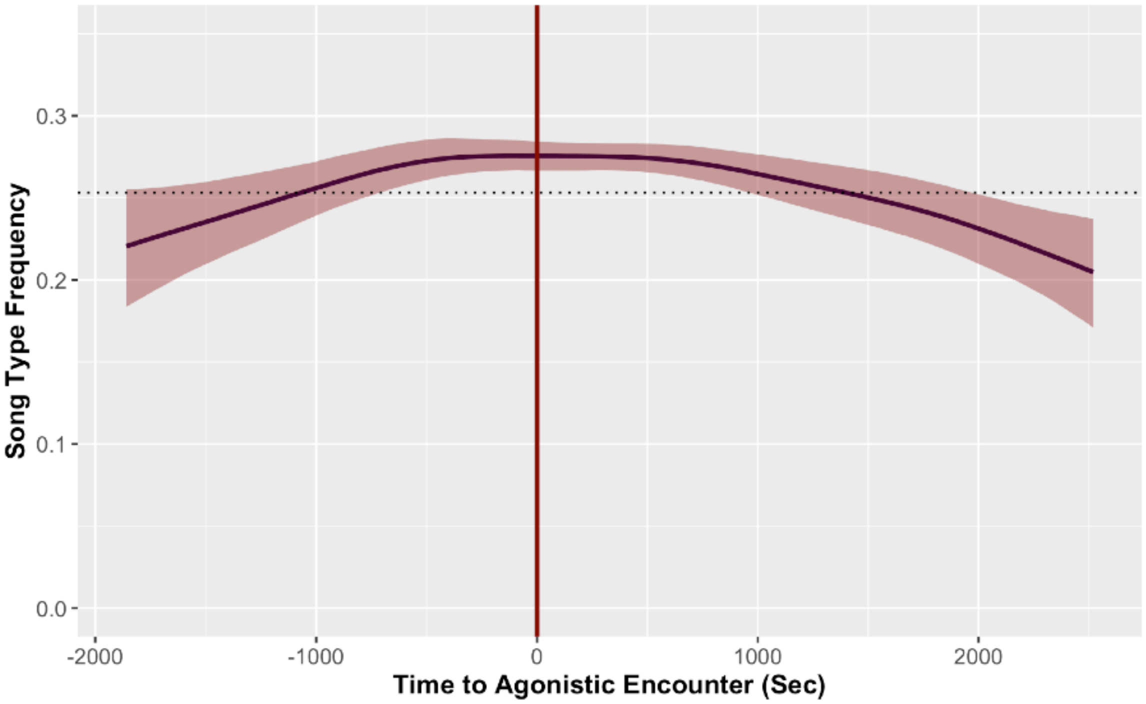

Figure 2.14: Estimate of the *song type frequency* (horizontal red line) of songs used around the time of agonistic encounters (vertical red line) derived from a Bayesian mixed-effects model. Higher song type frequency values indicate that the song type is more commonly used within that individual's repertoire. The mean song type frequency is indicated by the horizontal dotted line.

Comparison with the model's predictions based on randomly-reordered song type frequency values supports the interpretation of a small to moderate effect size (Figure 2.15). Randomly shuffled dependent variables consistently produce a flat estimate over time to agonistic encounter. These results indicate that male Adelaide's warblers tend to sing their more frequently-used song types slightly more often in the minutes before and after agonistic encounters, and slightly favour their less-frequently used song types in times further from agonistic encounters.

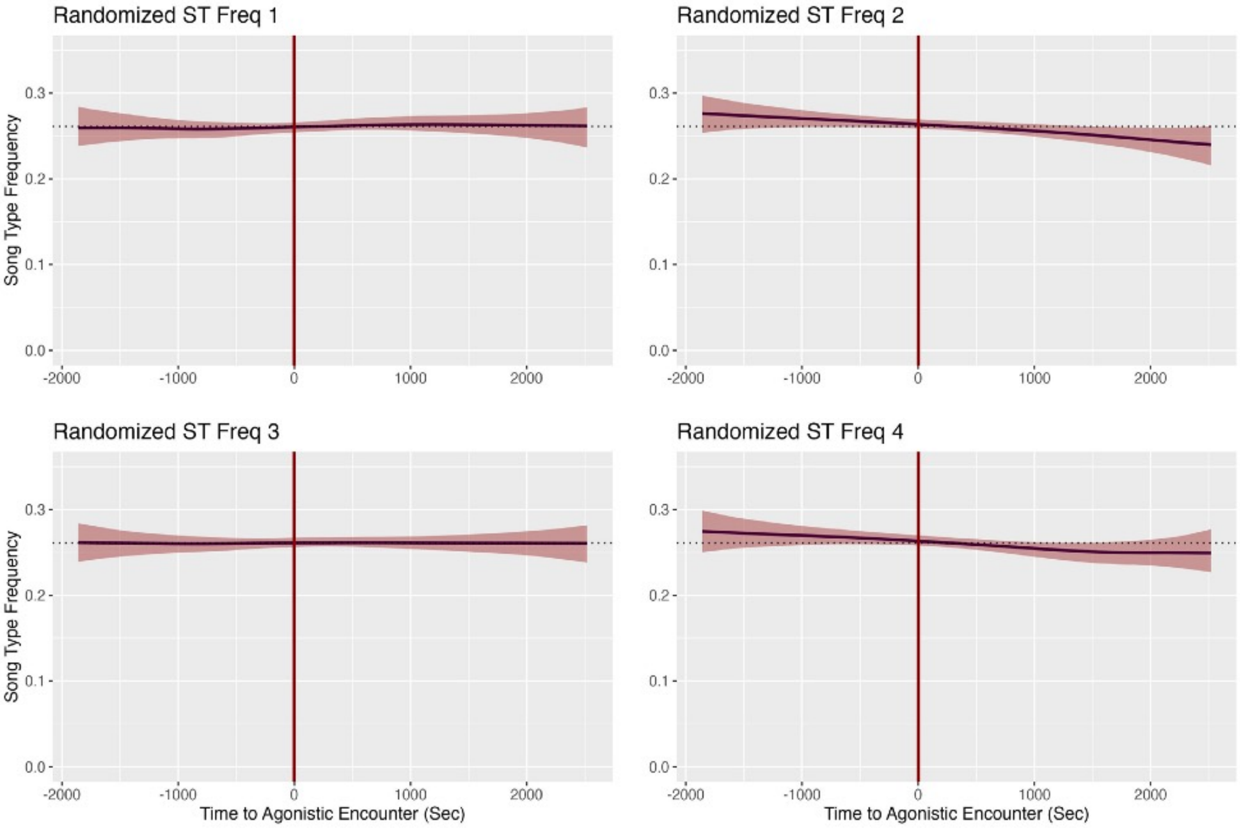

Figure 2.15: Estimated conditional effects (horizontal red line) of *Time to agonistic encounter* on randomly reordered *song type frequency* values, repeated four times to validate the model's estimation of observed data. The consistently flat effects indicate that the strength of the model's predictions based on observed data is a result of patterns in the data.

2.3.4 *Song Rate*

The estimated conditional effects from the Bayesian mixed-effect model of song rate indicate a moderately-sized depression of song rate at the time of and immediately before the agonistic encounter (Figure 2.16). Initially, *song rate* appears to peak at 0.78 songs/min at -1316 seconds (approximately 22 minutes before the agonistic encounter) before decreasing to its lowest point of 0.55 songs/min at -170 seconds (approx. 3 minutes before the encounter), a decrease of 27%. From its lowest point several minutes before the encounter, *song rate* increases by 34% to 0.83 songs/min at 1810 seconds (about 30 minutes after the encounter). At the end of the sampling period (3270 seconds) *song rate* appears to fall from the second peak to 0.39 songs/min.

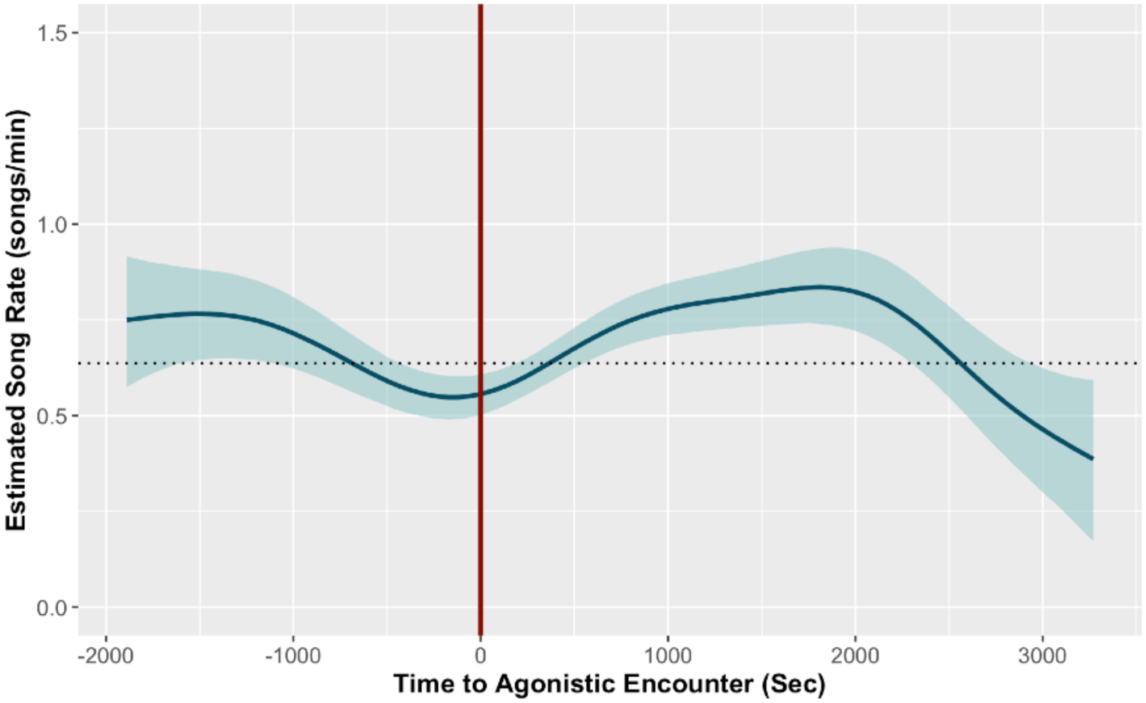

Figure 2.16: Estimate of song rate (blue line) around the time of agonistic encounters (red vertical line) derived from the fitted Bayesian mixed-effects model with a Poisson distribution. Upper and lower 95% credible intervals (blue bands) were derived from the fitted model. Mean song rate is indicated by the horizontal dotted line.

Randomly shuffling *song rate* values before fitting the model consistently produces a flat estimate over time to agonistic encounter. Comparing the results generated by observed data, this supports an interpretation of a moderate effect size (Figure 2.17). These results indicate that male Adelaide's warblers lower their song rate a moderate amount in the roughly 10 minutes around agonistic encounters, reaching its lowest point immediately before the encounter.

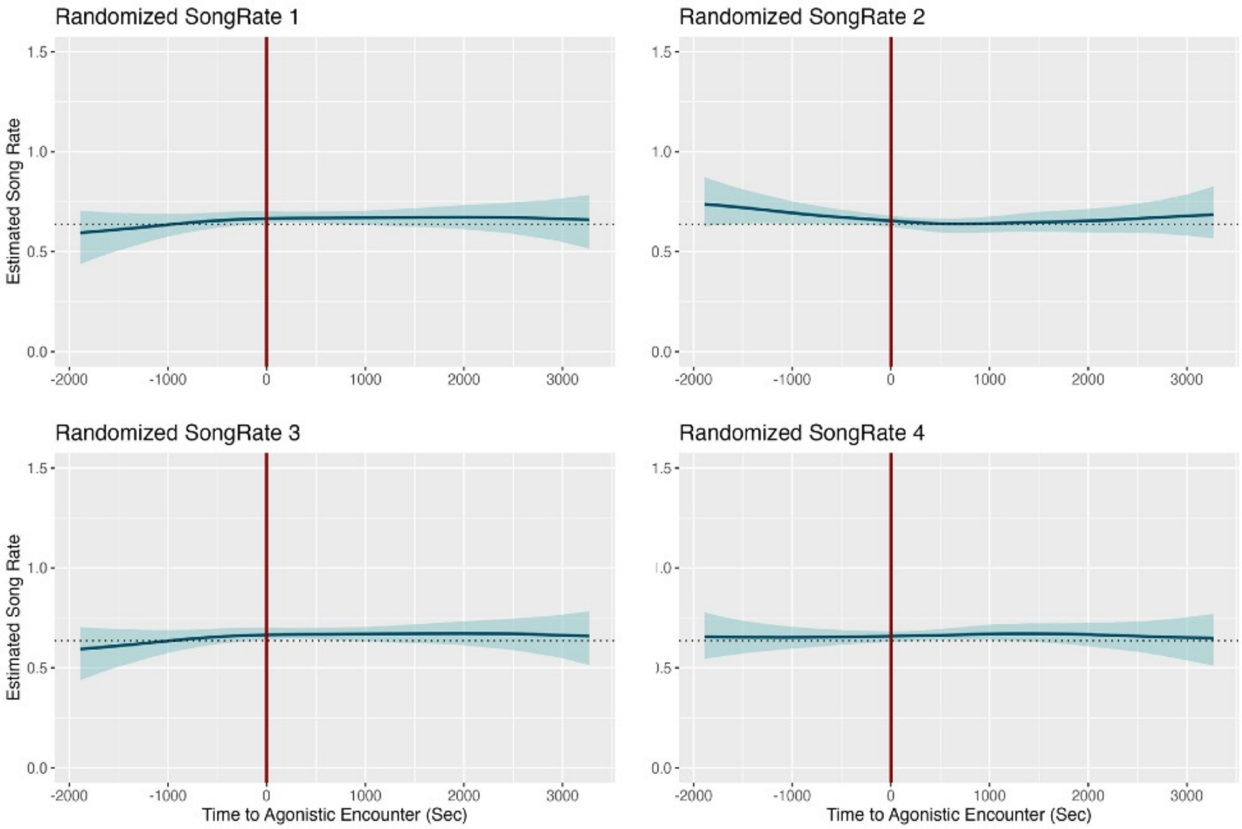

Figure 2.17: Estimated conditional effects (horizontal blue line) and 95% CR (blue band) of *Time to agonistic encounter* on randomly reordered *song rate values,* repeated four times to validate the model's estimation of observed data. The consistently flat effects indicate that the strength of the model's predictions based on observed data is a result of patterns in the data.

CHAPTER 3: DISCUSSION

In this chapter, I review my hypotheses and evaluate if their predictions were supported by my results. First, I review each of my hypotheses, predictions and results in turn. I offer alternative hypotheses where my predictions were not met, interpret the pattern of my results and propose avenues of further research. I then discuss the hypothesis of functional song categories in the family Parulidae, which informed my own hypotheses and provides context for my findings. Finally, I discuss the broader conclusions of this thesis.

I described how male Adelaide's warblers (*Setophaga adelaidae*) use their song in naturally occurring agonistic interactions, and tested hypotheses about the agonistic functions of *song type switch rate*, *song type frequency*, and *song rate*. The pattern of these singing behaviours changed around the time of agonistic encounters. *Song type switch* rate dropped substantially before and after an agonistic encounter, reaching its lowest point several minutes after the encounter. *Song type frequency* increased slightly before an agonistic encounter and returned to baseline well after the encounter was over. Lastly, song rate moderately decreased shortly before agonistic encounters, returned to normal levels shortly after the encounters, and decreased again ~30 minutes after the encounter.

I hypothesized that Adelaide's warblers use three singing behaviours as agonistic signals: the rate that they switch their song types, the use of rare song types, and the rate at which they deliver songs. Based on this hypothesis, I predicted that these behaviours would vary as a function of time-to-agonistic encounter. Model results largely support this prediction, because all three singing behaviours varied as a function of time to encounter and the magnitude of this variation exceed that produced by randomized data. However, effect sizes varied from small (in the case of *song type frequency*) to moderate (*song rate*) to large (*song type switch*) and alternative hypotheses may better explain some of these patterns.

I also made hypotheses about the agonistic signalling functions of the three singing behaviours. First, I hypothesized that (**1**) males signal aggressive motivation with high rates of song type switching. I predicted that if this were true, song type switching would increase around the time of agonistic encounters. Second, I hypothesized that (**2**) males also signal aggressive motivation with song types that are rare in their repertoire. If this hypothesis is true, I predicted that males would use more rare song types around the time of agonistic encounters. Thirdly, I tested the hypothesis that (**3**) high song rates signal aggressive intent. If this were true, I expected song rates to increase and peak in the time just before the encounter. None of these predictions were supported.

1: *Song Type Switch* Rate as a Signal of Aggressive Motivation

Contrary to my prediction that *song type switch* rate would increase around the time of agonistic encounters, my model showed that males decreased their *song type switch* rate in the time leading up to agonistic encounters (Fig. 2.12). Switch rate continued falling after encounters and reached its lowest point at 882 seconds (about 15 minutes) after the encounter, before returning to the mean levels around 2000 seconds (about 33 minutes). These results are contrary to patterns seen in some species of sparrows (Akçay et al., 2011; Searcy et al., 2014; Searcy & Beecher, 2009), but they align with those of chaffinches (*Fringilla coelebs*), red-winged blackbirds (*Agelaius phoeniceus*), and Bachman's sparrows (*Peucaea aestivalis*), which also lower their switch rates in territorial encounters (Ali & Anderson, 2018; Deoniziak & Osiejuk, 2020; Yasukawa, 1981).

Notably, *song type switch* rate reached its lowest point well after the agonistic encounter and persisted at a low level for some time. This pattern suggests an alternative hypothesis that low song type switch rates may signal dominance from the victor, or submission from the loser (Bradbury & Vehrencamp, 2011; Lorenz, 1966). Unfortunately, it was not possible to identify victors and losers in in this study. Further observational work that includes fight outcomes would enable tests of song type switching as victor or loser displays.

Another alternative explanation for the reduced *song type switch* rate around the time of agonistic encounters is that a lower switch rate is not an agonistic signal at all, but a by-product of other agonistic signal(s). Some species use specific song types in agonistic contexts, such as song sparrows (*Melospiza melodia*) which match their rivals' song types (M. D. Beecher et al., 2000; Hughes et al., 2007), or chestnut-sided warblers, which use rare song types in agonistic contexts (Byers, 2017). If Adelaide's warblers also use a subset of songs for agonistic contexts, these song types might be repeated more around agonistic encounters, incidentally lowering the song type switch rate. Many studies suggest that using song types that are shared with a rival may function as directed "challenge signals" that direct attention to the rival. This alternative could be tested by measuring the rate of shared song types around the time of agonistic interactions with a rival.

2: *Song Type Frequency* as a Signal of Aggressive Motivation

Contrary to my prediction, males sang more frequently used song types in the time immediately around agonistic encounters (Fig 2.14). My results indicate that immediately before and after the encounter, males use song types that are slightly more common than usual. *Song type frequency* reaches a plateau from about 500 seconds before, until about 500 seconds after the encounter. Males sang rarer song types further from agonistic encounters at the edges of our model's sampling period. Based on this result, I reject the hypothesis that males reserve rare song types for agonistic encounters to signal their aggressive motivation, as is the case in chestnut-sided warblers (Byers, 2017).

I assumed that the songs associated with agonistic events would be rare. However, if males are navigating frequent threats during the sampling period, it is possible that most song events are associated with territorial encounters. If this is the case, the song types reserved for agonistic encounters would not be rare. Alternatively, one could address the hypothesis that certain song types are used as agonistic signals by observing the effect of time to agonistic encounter on the use of each song type in an individual's repertoire. This is a more direct approach that would control for the frequency of agonistic encounters and could also test the hypothesis that shared song types are used as agonistic signals in this species.

The generalizability of the observed trend in song type frequency may be attributable to sampling bias in my data. We recorded males near dry riverbeds. Territories in these areas were typically smaller, had denser vegetation, and formed denser neighbourhoods compared to those in open habitat. Though I did not attempt to measure territory quality, male survival is associated with foliage density in this species (Staicer, 1992). If small, high-value territories experience more attempted intrusions, agonistic events would be more common. This may contribute to the increased frequency of song types that are associated with agonistic events in my data. In the future, this sampling bias could be corrected for by sampling a greater diversity of habitats and attempting to control for territory size and quality.

Posterior predictive checks that compare the model's simulations to the data show that there is variation in the song type frequency that are not accounted for by the model (Fig. 2.11 B). Unexplained variance doesn't necessarily mean that the model's predictions are inaccurate, but it does indicate that there are additional effects on *song type frequency* in agonistic contexts that are not included in the model. One such effect could be the presence and breeding phase of a female, which influences males Adelaide warbler singing behaviour, such as song rate and song type use (Staicer, 1992). In the future, female presence and behaviour should be considered as a covariate in characterizations of singing behaviours.

3: *Song Rate* as an Agonistic Signal of Aggressive Intent

If high song rate signals aggressive intent, I predicted that *song rate* would increase around the time of agonistic encounter and peak immediately before the encounter. Instead, model predictions indicated a moderate decrease in song rate. *Song rate* reached its lowest point 170 seconds (about 3 minutes) before the encounter before rising to mean levels shortly after the encounter (Figure 2.16). From these results, I reject the hypothesis that high song rate is a signal of aggressive intent.

An alternative hypothesis suggested by these results is that lowered song rate, not a raised song rate, is a signal of aggressive intent in Adelaide's warblers. Black-bellied wrens (*Thryothorus fasciatoventris*) also reduce their song rate in agonistic encounters, but only marginally and in response to simulated territorial intrusions (Logue & Gammon, 2004). To my knowledge there are no other documented species that lower their song rate in agonistic encounters, much less lower their song rate to indicate imminent attack. According to the predictive criterion, a signal of aggressive intent must be reliably followed by an attack (Searcy & Beecher, 2009). In this study, physical attacks were difficult to identify reliably, and the identity of attacker and defender was not recorded. To observationally test the hypothesis that lowered song rate is a signal of aggressive intent, escalated physical attacks must be identified as well as the attacker/defender roles of the opponents. Experimentally, the receiver and sender side could be tested with playback experiments that simulate an escalated territorial intrusion. The receivers' side could be tested with an acoustic stimulus of a suddenly dropping song rate. An appropriate response such as an attack on a taxidermic mount or sudden retreat would support this alternative hypothesis. The sender's side could be tested experimentally with a playback experiment which uses an acoustic stimulus of escalating aggressive signals to prompt the bird into attacking a taxidermic mount. If the attacking bird reduces its song rate more than non-attackers, that would also support the alternative hypothesis of lowered song rate as a signal of aggressive intent.

An alternative explanation for the decrease in song rate around the time of agonistic encounters is that the birds are using other signalling behaviours that suppress song, such as aggressive posture or aggressive chitburst calls. In Adelaide's warbler, chitburst calls and other aggressive displays are rarely used in combination with songs. Staicer (1992, p. 122) described how males use calls and songs in territorial encounters: "Upon approaching a potential territorial encounter males stopped singing and remained quiet until giving the chitburst display. After the encounter, neighbouring males did not sing until moving away from one another." Song is a long-distance signal. Perhaps song is not used as an agonistic signal once competitors are close enough to make visual contact. Of course, if aggressive behaviours do suppress song in this species, a decrease in song immediately around the time of agonistic encounter may not be a signal at all. It may, however, still be a cue to the opponent that the territory owner is aggressive.

The other pattern observed in *song rate* around agonistic encounters was a rise in song rate well above mean levels both before and after the agonistic encounter. These peaks in *song rate* may be too far away from the encounter to be considered related, and they could be interpreted as a statistical artifact. However, it should be noted that at a moderate time away from the encounter, increased song rate could function as an agonistic signal that is at an earlier stage in a hierarchical signalling system. Signals used in less-escalated agonistic contexts could be signals of motivation, a challenge signals, or signals of condition.

Song Categories

Adelaide's warbler uses two different categories of singing. These song categories use specific song types and are thought have specialized functions. My results may also be interpreted regarding a widely-held hypothesis which posits that "Type 1" song is used in interactions with females, and "Type 2" song is reserved for interactions with males (Lein, 1978; Lemon et al., 1987; Spector, 1992). Adelaide's warblers divide the song types in their repertoires into these two categories on an individual level, i.e., different males may assign a given song type to different categories (Staicer, 1992). Type 1 and 2 song types display statistically-significant acoustic differences (Staicer, 1996).

Song categories in Adelaide’s warblers aren’t only distinct in terms of song types, but also in song delivery patterns. Males primarily sing their Type 2 song types during the “dawn chorus,” a period of intense early-morning singing in which males sing at a rapid rate, and with very high rates of song type switching. After the dawn chorus, males switch to primarily Type 1 song as they patrol their territories throughout the day. They sing this different subset of song types at a much lower song rate than the dawn chorus and tend to repeat song types a number of times before switching to a new song type. Thus, relative to Type 2 songs, Type 1 songs are delivered with higher song type switch rates and song rates, although it is not clear whether the difference between the two types is continuous or discrete (Kaluthota et al., 2019). Because I sampled after dawn, I assumed that Type 2 songs would also be rare relative to Type 1 songs.

My results do not support the hypothesis that Type 2 song is used intrasexual territorial interactions in Adelaide’s warblers. In fact, all of the singing behaviours that I found to be associated with agonistic encounters are typical of Type 1 song, not Type 2; low song type switch rate, low song type frequency, and low song rate. These results suggest that the view that Type 1 song functions in intersexual communication while Type 2 song functions in intrasexual communication is probably an over-simplification. Indeed, the hypothesis that Type 2 song functions in intrasexual interactions has received mixed support in this species. Staicer (1992) observed that male Adelaide’s warblers song type match with other males far more with Type 2 songs, but only during the breeding season. They also observed males using Type 2 song in territorial interactions, but only when the female mate is incubating. If Type 2 songs function in territorial interactions, they should be observed year-round, yet they are only observed during the breeding season. Anecdotal accounts from that study also indicated that territorial encounters are preceded and followed by Type 1 song (Staicer, 1992, p. 122).

The assumption that Type 2 song types in wood-warblers should be rare during daytime singing, but used in male-male interactions (Hof & Podos, 2013; Spector, 1992) is partly why I chose to test song type frequency. A more direct way to test the hypothesis that Type 2 songs are used in agonistic contexts would be to identify which song types are used in Type 2 singing, and test for the presence of those song types during agonistic encounters.

Tests outside of my study species also cast doubt on the hypothesis that wood warblers' Types 1 and 2 songs function in inter- and intra-sexual communication, respectively. Playback experiments to yellow warblers (*Dendroica petechia*) have shown that males respond more to simulated territorial intrusions using Type 1 song, not Type 2 (Beebee, 2004). Female yellow warblers also show no preference for either Type 1 or Type 2 song (Beebee, 2004). The oversimplified framework for understanding singing behaviour and the mixed support for the function of Type 2 song is in part why I chose to test these three specific singing behaviours as agonistic signals. More focused hypotheses on specific behaviours as intrasexual signals in specific signalling systems may introduce nuance into our understanding of song categories in the wood-warbler family.

Conclusions

I found evidence that male Adelaide's warblers vary song type switching, song type frequency, and song rate around the time of agonistic encounters. The large decrease in song type switching may indicate its use as a post-conflict agonistic signal like a victory signal, although this could also be due to an interaction with other agonistic signals. Song type frequency showed a slight increase around agonistic events. Though the effect is small, this may indicate that frequently-used song types are being used as agonistic signals, perhaps as a signal of aggressive motivation. Song rate moderately decreased immediately before agonistic encounters. A drop in song rate may be a signal of aggressive intent, but further testing on the receiver side should be pursued to test the possibility that low song rates are a side-effect of other agonistic behaviours.

For future work on this topic, it is also important to note that male singing behaviour may be highly dependent on female behaviour. In this species, unmated males sing at a markedly higher rate and were excluded for this reason (Staicer, 1996). In observational work on male singing behaviour in this species, Staicer (1992) noted that female presence influenced male behaviour. They found that female presence had an inhibitory effect on song rate in males, they she also found a positive correlation between female presence and the amount of aggressive displays. They noted, "female presence had an obviously greater effect on these male behaviours than did male identity" (p.121). For future studies on singing behaviour in social contexts, I advise including female presence or proximity in future analyses to control for this effect.

Analysis of agonistic signals would be strengthened by knowing the winner and loser of a given encounter. However, the outcome of agonistic encounters is difficult to ascertain, in part because this kind of single-individual observational data only records the behaviour of a single individual in a dyadic interaction. Simultaneous observation of both individuals during and after their interaction may help clarify the outcome of the encounter, but the challenge of interpreting the outcome of agonistic encounters also stems from the difficulty of identifying the immediate consequences of a conflict. I should also point out that while these agonistic encounters probably differ in their level of aggressive escalation, I did not attempt to include this in my analysis. The different aggressive behaviours I used to identify agonistic encounters (aggressive vocal calls, posture, and chases) may very well represent hierarchical levels of escalation, but those functions are not well understood in this species.

It is also possible that the agonistic encounters I recorded represent only the most-escalated encounters, and my results could be construed as "failed attempts" to de-escalate a conflict. If this is the case, it is still evidence that these singing behaviours may function as agonistic signals. The occurrence of certain behaviours more in the proximity of escalated conflicts is still evidence that those behaviours may function as agonistic signals. Behaviours that occur in the context of a conflict that does not escalate would be under many of the same selection pressures as behaviours that occur in the context of a conflict that does escalate.

This study provides direction for further testing that was previously unavailable. Song type switch rates reach their lowest after the encounter, so future experiments may test hypotheses of song rate functioning as a victory or loser display by linking switch rate after agonistic encounters to the identity of the victor or loser. The small increase in song type frequency along with unexplained variation in the data warrant future investigation into how specific song types are used in agonistic encounters. Playback experiments may test if receiver responses support the moderate drop in song rate around the time of encounter as an aggressive intent signal or a side-effect of other agonistic behaviour.

This study represents an observational approach that stands to contribute to the rich conversation around agonistic signalling in songbirds. Good experimental design depends on observational research. It is impossible to simulate or interpret behaviour in an experimental setting without first understanding it in a natural context. Allowing a multilevel model to represent my behavioural variables as splines produced unexpected patterns of behaviour. To my knowledge, there are no other studies of agonistic signalling in songbirds that use an approach that allows a continuous response from the dependent variable. It would be highly beneficial for the field of birdsong research to employ observational techniques to test widely-held hypotheses of agonistic signalling.

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APPENDIX 1: RECORDING ANNOTATION PROTOCOL

Data Fields for Song Annotations

Note: Quotes indicate the column name in the selection table.

Bird ID: "Bird"

- XxXxXx - The bird ID specified in the file name. E.g. LbRbLg

Recording Date: "Date"

- YYYMMDD - The date specified in the file name formatted. E.g. 20180413

Breeding Phase: "BPhase"

- S – single
- N – nest building
- I – incubation
- H – hatchling/nestling
- J – juvenile
- NB – not breeding (STILL PAIRED)

On/Off Bird: "On/Off"

- On – bird was actively monitored (this will be selected in most cases).
- Off – when not actively monitoring bird for longer than 5 minutes (e.g. bird flew away and recorder didn't notice until later). Make a selection from the moment the bird was "lost from sight" and mark OFF. Next time the bird is actively monitored make sure to mark ON carrying forward.

Time Mark: "TimeM"

- X – a selection of sound that appears in both recorder's sound files. E.g. walkie-talkie conversation snippit, or actual side-by-side conversation snippit. A Time Mark selection should be approx. 2-3 seconds long and should be selected approx. every 10 minutes.
- (leave blank if not a time mark)

Vocalization: "Vocal"

- S – Songs
- D – Duets
- C – Calls
- Leave blank for recordist or annotator notes.

Location: "Locat"

- 01, 02, 03, etc. – Singing locations of the **focal bird** noted by recorder.
- U – for location unknown due to recorder omission.

Note: any location referring to other birds does not go here. Include those locations in "notes", FeBe, MaBe, or JuvBe fields.

Inter-bird Distance: "IBD"

- ## – number of meters estimated to be between the male and female

Singer: "Singer"

- M – male
- F – female
- B – both male and female sings (duets)
- J – juveniles

Song Quality: “SQual”

- 1 – Lowest quality; background noise is high; many notes are indistinguishable
    - Selection will not be used for further analysis
- 2 – Moderate quality; some sounds in the background; notes are identifiable
    - Selection will likely be used for further analysis
- 3 – Best quality; no background noise; notes are clearly defined and visually obvious
    - Selection will be used for further analysis.

Song/Call Type: “S/CType”

Song Type

- 01, 02, 03, etc. – Within-bird song type number assigned by annotator.
    - Annotator must have 60-70% confidence to assign to a song type.
- xA, xB, etc. – If there are song types that are very similar, use letters behind the song type number to indicate it is related to a preexisting song type.
- U – Unknown song type (if confidence in song type identification less than 60-70%).

Note: See “Saving Song Types”.

Call Type

- P = pip
- B = chitburst
- C = chip
- A = alarm
- T = twitter

Note: Annotating the calls in detail may be done at a future date, and is not necessary at this point. Just select the calls, note they are calls under “Vocalization” and leave this column blank.

Note: If long sections of only calls, highlight whole section for annotating later.

Song Character: “SChar”

- N – normal song
- P – partial song (only a part of the song is visible on the spectrogram)
- D – double song (attempt to identify which song types are used in “notes” section)
- O – odd song (any other unusual song)

IntroNotes: “IntroN”

- Y – call notes are present within 0.5 seconds before the song (and are included in the recording)
- (leave blank if no call notes present)

Matching:

(focal is matching neighbour)

- M – matching (90% similarity between songs)
    - focal begins singing **within 1.5 seconds** of neighbour
    - Songs have identical structure with ≈ number of notes within each syllable set
- MO – matching and overlapping
    - Focal begins singing before the neighbour has finished
    - Songs have identical structure with ≈ number of notes within each syllable set
- PM – partial matching (75% similarity between songs)
    - Focal begins singing within 1.5 seconds of neighbour
    - Songs have ≈ structure, but could have missing syllable set
- PMO – partial matching and overlapping

  - Focal begins singing before the neighbour has finished
  - Songs have ≈ structure, but could have missing syllable set

Matched:

(neighbour is matching the focal)

- M – matched (90% similarity between songs)
  - Neighbour begins singing **within 1.5 seconds** of focal
  - Songs have identical structure with ≈ number of notes within each syllable set
- MO – matched and overlapped
  - Neighbour begins singing before the focal has finished
  - Songs have identical structure with ≈ number of notes within each syllable set
- PM – probably matched (75% similarity between songs)
  - Neighbour begins singing within 1.5 seconds of focal
  - Songs have ≈ structure, but could have missing syllable set
- PMO – probably matched and overlapped
  - Neighbour begins singing before the focal has finished
  - Songs have ≈ structure, but could have missing syllable set

Fight:

A fight is an aggressive interaction between the focal and opponent.
ex. physical fight, chase, aggressive vocal exchange.

- XxXxXx – if a fight occurs and the opponent ID number if known
- Y – if a fight occurs but opponent ID number is not known

Male Behaviour: "MaBe"

- Notes about female behaviour (presence, interactions, etc.)

Female Behaviour: "FeBe"

- Notes about female behaviour (presence, interactions, etc.)

Juvenile Behaviour: "JuvBe"

- Notes about juveniles and behaviour (presence, behaviour, number, etc.)

Notes:

- Any additional information (mentioned by recorder, annotator concerns, etc.) worth noting.
- Indicate if the notes are from the recorder or the annotator.

Recorder: "Rec"

- XX – recorder initials

Annotator: "Ann"

- XX – Annotator initials

APPENDIX 2: SONG TYPE SCORING PROTOCOL

For two song types to be a match, you must be sure of a qualitative similarity of 80% or greater in the following categories:

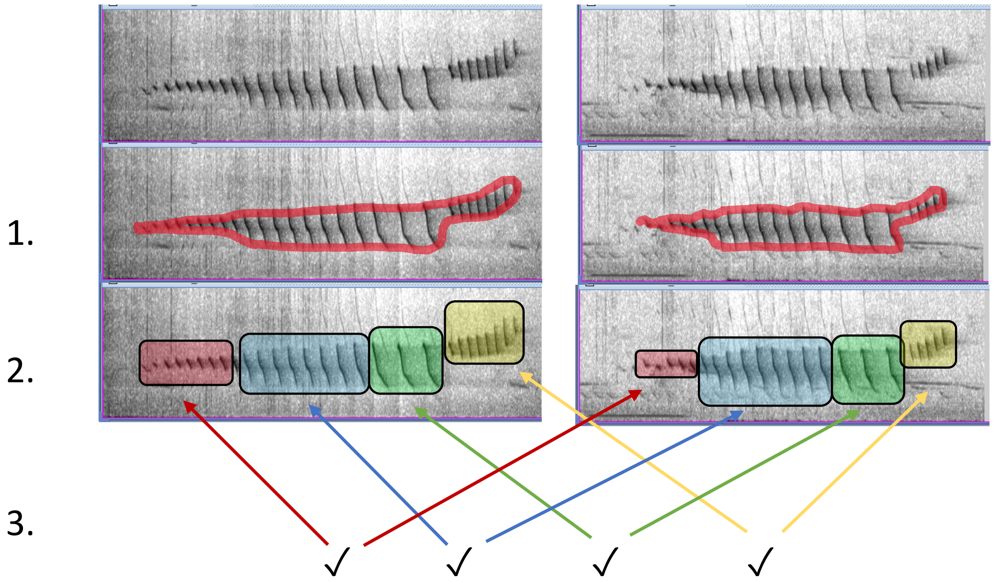
1. **Overall Shape**

2. **Syllable Type**

3. **Number of syllable notes**

4. **Overall "matchiness"**

Matching example:



1. Overall shape:

- These song types have minor differences in shape, mostly in the length of the introductory syllable.
- Similarity is 80% or greater.

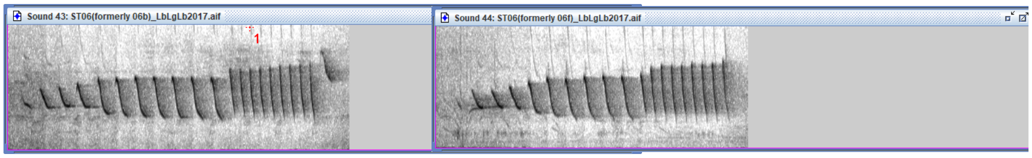
2. Syllable Note type:

- All syllable types present between these two song types.

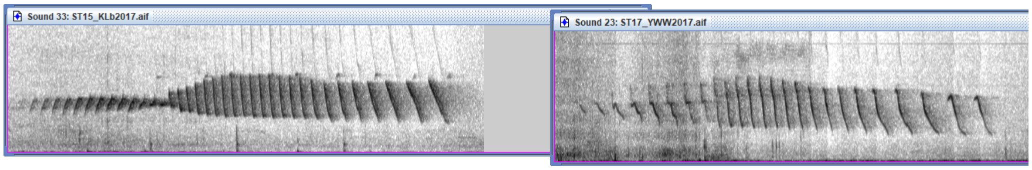
3. Number of syllable notes:

4. Overall impression of similarity

Here’s another match:



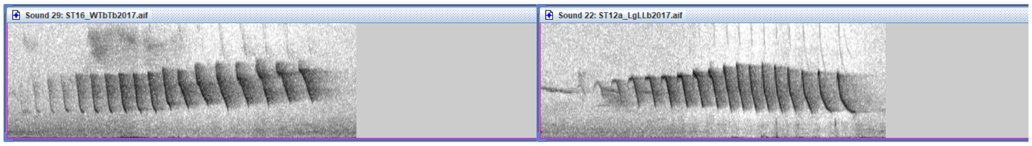
These are close, but not a match:



Shape: match 80%

Syllable type: intro notes do not match, ST17 has distinct ending notes.

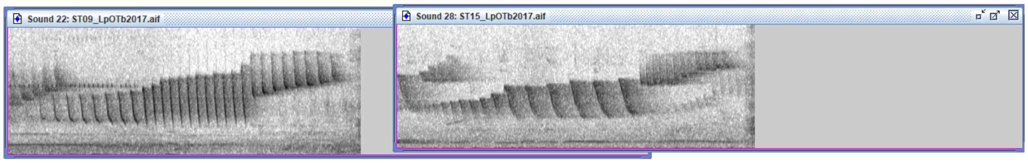
No. of syllable notes: sorta



Shape: slightly under 80%

Syllable type: close, but distinct differences between notes.

No. of syllable notes: sorta similar, but the syllable types are not the same



Shape: general shape match.

Syllable type: nope – intro notes are Totally different, as well as body notes.

No. of syllable notes: main difference in number of body notes. No match.