

Vocal interactions and song performance in Adelaide's warbler (*Setophaga adelaidae*)

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Abstract

Vocal interactions are very common in songbirds. Song-type matching is a kind of vocal interaction in which an individual matches the song-type that his neighbor sang. Traditionally, song-type matching has been considered a signal of aggressive intent, but recent studies fail to support this hypothesis. An alternative hypothesis states that song-type matching facilitates female eavesdroppers' comparison of song performance. This hypothesis predicts that matching songs should be higher performance than non-matching songs, and that non-matching answers should be lower performance than non-answers. I tested these predictions in a population of Adelaide's warbler (*Setophaga adelaidae*). Nine territorial males were recorded four times each, for three and a half hours during morning singing. A linear mixed model was done, testing four metrics of performance. Both predictions of the 'facilitating comparison' hypothesis were supported, but effect sizes were small. In addition, I characterized the song-type repertoires of the subjects, described their vocal duets, and tested the joint territory defense hypothesis of duet function. The hypothesis states that female song answering (the behavior that generates duets) signals cooperative territory defense. I found support for the joint territory defense hypothesis: duets were temporally associated with fights between males, and were particularly common after fights. This research represents novel methods and support for key hypotheses in this group of new world warbler.

Resumen

Las interacciones vocales son muy comunes en aves. El emparejamiento de tipo de canción es uno de estos comportamientos vocales. En el mismo un individuo iguala la canción que acaba de cantar un ave vecina. Se pensaba que este comportamiento vocal estaba relacionado a agresión; sin embargo, investigaciones científicas recientes han demostrado que no es así. Una hipótesis alternativa plantea que el emparejamiento de tipo de canción es una herramienta para facilitar la elección de la hembra. Los machos podrían estar utilizando este comportamiento vocal como una estrategia para presentarse más atractivos a las preferencias de la hembra. Se puso a prueba esta hipótesis en una población de la reinita mariposera (*Setophaga adelaidae*). También se describió la estructura vocal de sus duetos y se puso a prueba la hipótesis de defensa en conjunto. La misma plantea que el propósito de los duetos es demostrar que el territorio está ocupado y defendido por una pareja. Esta es la primera vez que esto se pone a prueba en el grupo de las reinitas del nuevo mundo. Se grabó a nueve machos en sus respectivos territorios cuatro veces por tres horas y media en las mañanas. Todos los posibles comportamientos vocales y físicos se anotaron y luego se procesaron. Los datos apoyaron parcialmente la hipótesis de que el emparejamiento de canción es un medio para facilitar la elección de un macho por las hembras. Más aun, el dueto fue descrito con éxito y la hipótesis de defensa en conjunto fue apoyada también. Los duetos están estrechamente relacionados con las peleas entre machos, lo que sugiere una función de defensa de territorio en conjunto. Esta investigación representa nuevas metodologías y apoyo a hipótesis primarias en el grupo de reinitas del nuevo mundo.

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Dedication

To my family and friends for all their support in this project. Especially, my love Josiris and my chairman David M. Logue, for always believing in me.

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Song-type Matching

Introduction

Natural selection is a process in which one class of replicating entities reproduces more than another class, because of their properties. Selection can cause a population of individuals to adapt to its environments. Sexual selection is a special type of natural selection that acts on individuals' abilities to access gametes of the opposite sex (Andersson, 1994; Eberhard, 1996). There are several mechanisms of sexual selection including male-male competition, sperm competition, and the topic of this report: mate choice (Andersson, 1994). Mate choice occurs when individuals choose sex partners based on the partners' characteristics. The chosen sex often displays conspicuous 'ornaments' that influence the choice process. If, as is typical, males display ornaments and females choose, the process is called 'female choice'. Over evolutionary time, sexual selection can modify ornaments such that their bearers are more attractive to the opposite sex (Kokko, 2003). Songs, colors, and displays are some examples of ornaments that evolve in response to female choice (Kokko, 2003).

If preferences vary among females, and are heritable, and if females with certain kinds of preferences consistently have higher fitness than females that lack those preferences, adaptive patterns of choice are expected to evolve. For example, choosier females will benefit from choice if they can accurately assess male quality, and so produce more or better offspring than their less choosy competitors (Kempnaers, 1997). If, however, male quality cannot be accurately assessed, then the costs of preference will exceed the benefits, and the genes underlying female preferences will go extinct in the population, unless they are preserved for some other function (i.e., they are pleiotropic).

Mate choice is widely believed to be the principal selection pressure that shapes the evolution of songs, display and other ornaments (Andersson, 1994). In songbirds, female choice is believed to influence song structure and singing behavior. Honest signaling theory states that the only kinds of signaling systems that are expected to be evolutionarily stable are those in which signals consistently covary with male characteristics that influence female fitness (i.e., signals are

‘honest’). Further, signal honesty (and thus evolutionary stability) can be maintained only if signals are costly (Zahavi, 1975; Gil and Gahr, 2002) or constrained (Podos, 1997). Costly signals will be honest because low quality (e.g., stressed, weak, sick) males will not be able to invest as much in signals as will high quality males. Constraints guarantee honest signals because there is a physical or physiological limitation that cannot be cheated, so only high quality (e.g., vigorous, well-developed) males will be able to produce a particular signal (Podos, 1997). Many aspects of song performance could be costly or constrained, meeting the requirements of an honest signal (Gil and Gahr, 2002). I discuss signal variation in further detail in the Background. First, however, I consider how females compare signals from two or more males, and how this comparison may influence male singing interactions.

Studies on humans (*Homo sapiens*) and other animals have shown that choice is based on ‘comparative evaluation’ (Bateson and Healy, 2005), rather than ‘absolute valuation’. Choices that are based on comparative evaluation are affected by the set of items that the chooser has observed, both in the present and in the past. Comparative evaluation can be contrasted with ‘absolute valuation,’ in which choosers assign absolute values to each option independently, and choose the most valuable option in the set. It is important to note that comparative evaluation, but not absolute valuation, can result in violations of mathematical rationality. For example, a chooser using comparative evaluation might choose *A* over *B* in a two-choice test, but then switch their preference to *B* in a three choice test between *A*, *B*, and *C*. Several studies have shown that non-human animals use comparative evaluation to make foraging decisions (Shafir, 1994; Bateson et al., 2002). A few studies also indicate that comparative evaluation is also important in mate choice.

One of the first studies to address this phenomenon showed that female swordtails (*Xiphophorus helleri*) use comparative evaluation to make mating decisions. In that study, the addition of a low-quality ‘decoy’ shifted females’ preference away from the common male phenotype toward a rare phenotype (Royle et al., 2008). The finding that an irrelevant option shifted the preference pattern demonstrates that females do not use absolute valuation. Similarly, a recent study on guppies (*Poecilia reticulata*) showed that males prefer to position themselves near drab rivals, which increases their attractiveness to females (Gasparini et al., 2013). The fact that the females are influenced by the immediate competitive context is consistent with comparative evaluation,

but not with absolute valuation. A study on fiddler crabs (*Uca mjoebergi*) produced similar results (Callander et al., 2012). Five robotic ‘males’ were simultaneously presented to live females. Two of the males had small claws, one had a medium-sized claw, and two more had large claws. Consistent with the hypothesis that mate choice is comparative, females were more likely to choose the medium-clawed male when it was standing close to the small-clawed males than when it was standing close to the large-clawed males. Thus, there is emerging evidence that female choice is affected by the competitive context in which males are evaluated, and that males might benefit from managing the context of competition.

One important effect of comparative evaluation in humans concerns the ‘structural alignability’ (SA) of options. Structural alignability describes the structural similarity of items that are being compared. For example, in the comparison between a camera and a camcorder an alignable difference is that the camera takes pictures and camcorders take moving pictures. A non-alignable difference is that cameras do not record sound and camcorders do (Markman and Medin, 1995). Psychologists have shown that SA affects several aspects of choice in human beings (Markman and Gentner, 1993). Importantly, people find it easier to choose and make more accurate choices when options are highly alignable (Lindemann and Markman, 1996; Zhang and Fitzsimons, 1999; Zhang et al., 2002). Alignability effects have never been demonstrated on non-human animals, but theory suggests that all choosing systems are affected by SA. As Markman and Medin (2002) explained, “to evaluate an alignable difference, it is only necessary to know which value is better... to evaluate a non-alignable difference, it is necessary to know the value of an attribute on an absolute scale” (pp. 444-445). The process of converting values to an absolute scale requires cognitive and time resources (making choice harder and slower), and introduces additional error into the decision process (reducing the accuracy of choice). In spite of the obvious relevance of SA to behavioral ecology, there are no published tests for SA effects on animal communication. A model by Logue and Forstmeier (2008) predicts that animal advertisers should signal alignably with respect to their rivals only if they can produce a higher quality signal than the rivals. This strategy would make it easier for choosers to discern their superior quality. Inferior advertisers should signal non-alignably to make the choice less accurate.

In many song birds, females evaluate males based on their songs and singing behavior (Catchpole and Slater 2003). For example, female canaries (*Serinus canaria*) are attracted to a special syllable in the male songs, and give more copulation solicitation displays when they hear those songs than when they hear songs without these so-called ‘sexy syllables’ (Leitner and Catchpole, 2002). Female dusky warblers (*Phylloscopus fuscatus*) prefer males that maintain high sound amplitude in their songs (Forstmeier et al., 2002). In brown-headed cowbirds (*Molothrus ater*), the singing of many song-types in succession is the attractive component (Hosoi, 2005). Female sedge warblers (*Acrocephalus schoenobaenus*) also prefer males with large repertoires size (Buchanan and Catchpole, 2000). So, females will be attentive to the song itself and potentially attend to particular song features depending on the species.

Vocal interactions between male songbirds are common. Males of many species sing repertoires of distinct ‘song-types’. When two males sing back-and-forth, a behavior known as ‘countersinging,’ one male may ‘match’ the other’s song-type. It has been suggested that song-type matching influences female choice by increasing signal alignability (Logue and Forstmeier, 2008). Males who match songs may be making it easier for female eavesdroppers to compare their singing quality to that of their opponents (Logue and Forstmeier, 2008). If this is the case, males should only match when they assess their songs to be of higher quality than those of their opponents.

Background

Sexual Selection and Birdsong

Display performance (or motor performance) is a physical representation of an individual’s attributes in the form of a visual, acoustical or behavioral action (Byers et al., 2010). The performance of a given signal represents how close that signal comes to a population-wide performance constraint. Signals that are close to the constraint are said to be ‘high performance’ signals. Theory predicts that choosers will evolve to attend to performance, because it is constrained, ensuring honesty (Gil and Gahr, 2002). In the present study, I looked at an aspect of song performance known as ‘trill performance’.

Podós (1997) discovered a constraint in trilled sparrow songs. Plotting the frequency bandwidth (maximum frequency – minimum frequency) against the trill rate (notes / sec), he found a triangular distribution with a negatively sloping upper boundary. Birds can produce fast trills, or trills with broad frequency bandwidths, but they cannot do both. A given song's deviation from the upper boundary limit describes its performance relative to the population-wide constraint, with lower deviations corresponding to higher levels of performance (Fig. 1). This deviation from the upper bound limit is called 'vocal deviation' (VDev).

Studies on swamp sparrows (*Melospiza georgiana*) show that males are constrained by the frequency bandwidth trill rate trade-off. Further, individual males vary with respect to performance level (Ballentine et al., 2004). Female swamp sparrows give significantly more copulation solicitation display to high trill-performance songs versus low trill-performance songs (Ballentine et al., 2004), indicating a female preference for high performance. Female canaries (*Serinus canaria*) give more copulation solicitations displays to songs that contain a special 'sexy syllable' (Vallet and Kreutzer, 1995). The sexy syllable, which is believed to demand high performance, is necessary for a female sexual response (Vallet et al., 1998).

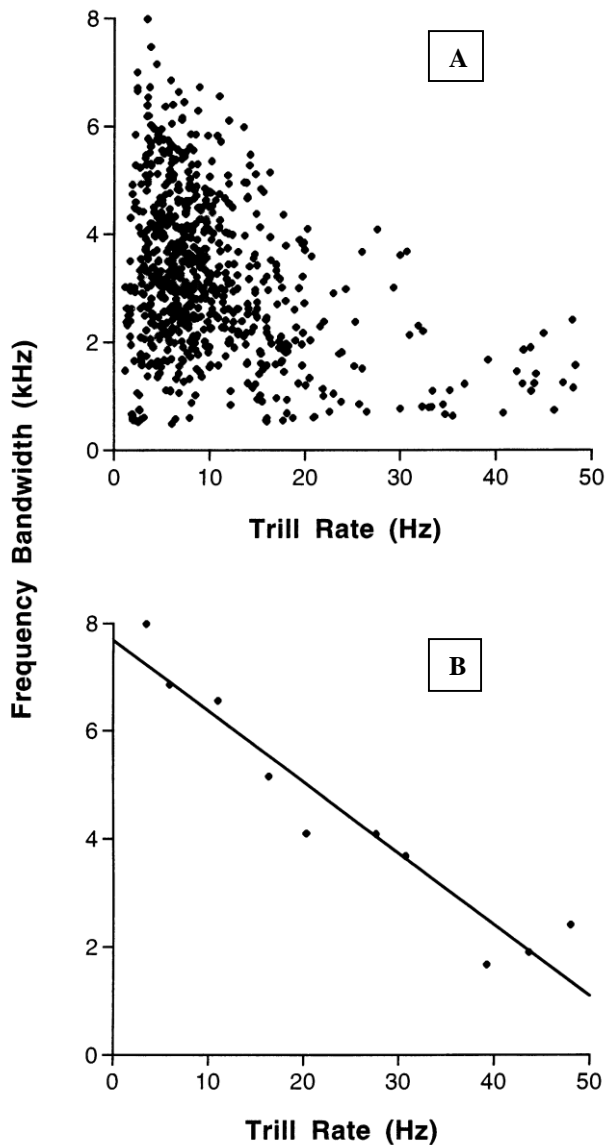


Figure 1: Frequency bandwidth and trill rate trade-off of songbird species (A) (Podos, 1997). Line represents the upper bound limit (B).

Vocal deviation (VDev) has proven to be a useful tool for measuring song performance, but it fails to account for variation in note structure, other than overall bandwidth. Structural features such as frequency modulation within a note may also encode performance. Further, notes within a song often vary in both bandwidth and duration (the inverse of trill rate). It was for this reason that Podos et al. (in prep) developed the new metric ‘frequency excursion’ (FE). Frequency

excursion measures the rate of frequency change in a song, including change that occurs during silent gaps between notes. It thus attempts to estimate the rate at which the singer modulates its vocal apparatus as a metric of performance. FE is particularly useful for the present study species, Adelaide's warbler, which exhibits a great deal of within-song variation in frequency bandwidth and within-note frequency modulation.

Song-type Matching

Song-type matching is a common vocal behavior in songbirds. It occurs when a bird chooses to sing the same song-type that its neighbor has just sung. The prevailing hypothesis for several decades was that song-type matching signals aggressive intent (Vehrencamp, 2001). However, in a study with song sparrows (*Melospiza melodia*) song-type matching was not a significant predictor of aggression or attack (Searcy et al. 2006). Searcy and Beecher (2009) reviewed the evidence and found that song-type matching may be a signal of low levels of aggression escalation but not of attack. Akçay et al.'s (2014) study of song sparrows (*Melospiza melodia*) found support for this 'hierarchical signaling' hypothesis. Males that song-type matched in the early stages of simulated intrusions, and continued to match as the simulated intruder 'escalated' by moving into the territory center, were more likely to attack a taxidermic mount than those that either failed to match or quit matching during the escalation phase. Searcy et al. (2013) conducted a similar experiment with a different population of the same species. They did not find any relationship between song-type matching and other aggressive behaviors.

Logue and Forstmeier (2008) proposed an alternative to the aggressive intent hypothesis. It stated that type matching facilitates accurate comparison by eavesdroppers. Suppose a male can assess the quality of a song he hears and evaluate whether he can sing it at a higher performance. Suppose also that females are likely to be eavesdropping on this interaction (as in Mennill et al. 2003), and that high structural alignability (i.e., matching) facilitates accurate comparison of song quality. In these circumstances, it would be beneficial for males who can sing higher performance songs to match their rivals, and so facilitate accurate assessment by eavesdropping females. If, however, a male cannot sing a song as well as his opponent, he should choose a different song-type to reduce the accuracy with which females compare the songs. Thus,

matching could represent a strategy that high performance singers use to influence female choice.

Pereira et al.'s (in prep) experiments on Adelaide's warbler support key predictions of this hypothesis. They digitally manipulated songs to produce high-performance (sped up), control, and low-performance stimuli (slowed down). They then did a playback experiment with those songs to free-living males. As predicted by the 'managing alignability' hypothesis, males matched high-performance stimuli at the lowest rates and low performance stimuli at the highest rates. I am following up on this work by using observational data recorded from free-living Adelaide's warblers to test predictions of the hypothesis that males match song types to influence female preferences (Logue and Forstmeier, 2008).

Adelaide's warbler

Adelaide's warbler (*Setophaga adelaidae*) is endemic to the island of Puerto Rico. It is socially monogamous and maintains an all-purpose territory of ~ 0.3 hectares throughout the year (Staicer, 1991). The breeding season peaks from March to June, but may vary depending on rainfall patterns (Toms, 2010). The occurrence of extra-pair copulation is suggested by a study in which females were observed to venture into neighbor's territories, but genetic paternity data are lacking (Toms, 2010). Each male's repertoire includes approximately 24 song-types (Staicer, 1991). Many of the songs in their repertoire are shared among neighbors. Males use their songs to engage in a variety of vocal interactions, including song-type matching, non-matching answering, and temporal overlapping (Staicer, 1991). Songs are divided into two classes, which are delivered in distinct ways. So-called 'B songs' are only sung prior to sunrise during the breeding season and during certain social interactions, whereas 'A songs' are sung throughout the day during the entire year (Staicer, 1996). Males sing B songs at a high rate and with 'immediate variety,' which means they constantly change song-types. They sing A songs at a much lower rate, and with eventual variety, meaning they repeat a song-type many times before switching. The two classes are structurally similar, but not identical (Staicer, 1996).

Closely related yellow warblers (*Dendroica petechia*) also have A and B songs. Beebe (2004a) tested the hypotheses that B songs are directed at male receivers and A songs are directed at

female singers. In apparent support of these hypotheses, he found that A songs had higher average trill performance than B songs. In a follow up study, he found that males responded to the song classes the same way, but were more likely to answer with A type songs (Beebee, 2004b). Beebee (2004b) also injected females with a hormone to promote copulation solicitations and found that females were equally receptive to both singing modes. Modes of singing may have similar functions, but their differences in vocal performance suggest the opposite.

Duets

Introduction

Vocal duets occur when a pair of individuals sings in synchrony or alternatively with one another (Thorpe et al., 1972). Duetting is common among birds, and also occurs in frogs, insects, and primates. In a given species, one or both sexes may initiate a vocalization, and one or both may answer the mate's vocalization to form a duet. Birds that answer have to be attentive to their partner's vocalizations. Many species use the same songs types to sing alone and to duet, but some reserve certain vocalizations for duets. Duets may comprise alternating syllables (e.g., male syllable – female syllable – male syllable, etc.), alternating songs (e.g., male song – female song – male song, etc.) or overlapped or synchronous vocalizations (e.g., male song overlapped by a female call; Hall, 2009). Duets with an initiation and two or more answers are called 'duet trains' (Brown and Lemon, 1979).

Duet structure is a function of the vocal behavior of the birds that are participating in the duet. Specifically, it depends on how birds temporally coordinate their vocalizations with those of the mate, and what type of vocalization they contribute to the duet. Both properties vary among species and among individuals within a species (Hall, 2009). Birds can answer their mates during the mate's vocalization (overlapping), immediately afterward, or after a silent gap. The details of duet timing have been described for three species of wren (Logue et al., 2008; Templeton et al., 2013; Rivera-Caceres, 2015). Birds with song-type repertoires combine their vocalizations non-randomly when duetting (Logue, 2006; Hall, 2009). Some species have been shown to abide by 'duet codes,' which are sets of rules that govern which song type a bird will use to answer each

of its mates' song types (Logue, 2005, 2007). In black-bellied wrens, females follow a strict set of rules in order to make a duet. Males follow the rules but not as strictly as females (Logue, 2006, 2007).

There exists support for several functional explanations for duetting suggesting that duet participation serves multiple functions, which probably vary among species (Hall 2004, 2009). Duetting may be thought as a developmental achievement in which participants need to be attentive and follow learned rules to produce a good duet (Wickler, 1980). If only attentive or long-tenured individuals can master the rules that structure the duet, coordination and responsiveness could be an honest indicator of commitment and cooperation (von Helversen, 1980; Hall, 2009). Furthermore, there is evidence suggesting that duets with high temporal coordination are perceived as more threatening than those with low temporal coordination (Hall and Magrath, 2007). It may be the case that birds that are more coordinated in their duet represents a stronger relationship and more commitment in territory defense.

The joint resource defense hypothesis is the best supported functional hypothesis for duetting. It states that duets convey the message that the territory is occupied and that two individuals are willing to defend it (Hall, 2000; Logue, 2007; Logue et al., 2008). In a study by Logue and Gammon (2004) they put a novel design, a stereo duet playback to pairs. This consists of two speakers simulating a duet where each speaker represents an individual of the pair. They found evidence to support a variation of the contact-maintenance hypothesis, the 'identity hypothesis'. However, Logue and Gammon mentioned that the territory defense hypothesis is plausible with their model. In a similar experiment by Mennill (2006) with rufous-and-white wrens (*Thryothorus rufalbus*), he found support for the territory defense hypothesis. Pairs were presented with a similar design as Logue and Gammon's (2004), with a stereo duet playback and responded at higher levels than normal. Additionally, female aggression was directed equally to the male speaker and the female speaker of the duet event, supporting a territory defense function instead of a mate guarding function. It may be advantageous for birds that are socially monogamous and that defend territories all year-round to develop this kind of vocal strategy. In migratory species, one should expect that the presence of migration has a negative effect on duetting behavior since it will be more difficult to develop a well-coordinated duet each year. In their study of duet evolution in songbirds, Logue and Hall (2014) found that birds that migrate

tend not to duet and birds that do not migrate tend to duet. They propose that migration limits the duration of pair bonds, which in turn affects the costs and benefits of duetting.

The mate guarding hypothesis of duet function states that males or females vocally demand the response of the mate to prevent copulation with other individuals (Langmore, 1998; Hall and Magrath, 2000). In a study by Grafe and Bitz (2004), male tropical boubous (*Laniarius aethiopicus*) used some of their duetting vocalizations in territory defense cooperation and some in what appears to be a variation of mate guarding. In a playback experiment, males ‘jammed’ the male playback song. However, most studies that have tested this hypothesis found little evidence to support it (Hall and Magrath, 2000; Gill et al., 2005).

Finally, the contact maintenance hypothesis states that birds use their mate’s duet contributions to localize their mates. Brown and Lemon (1979) observed that paired happy wrens (*Pheugopedius felix*) approached their partner after they duet. Also in support of this hypothesis, female Steere’s liocichlas (*Liocichla steerii*) answered their mates more often in visually dense habitats than females living in visually open habitats (Mays et al., 2006). Logue (2007) found direct support for mate localization in a radio telemetry study of black-bellied wrens (*Pheugopedius fasciatoventris*). The initiator of the duet approached the mate more often when the mate answers than when it does not. Similarly, rufous-and-white wrens (*Thryothorus rufalbus*) approach their mates during bouts of duetting (Mennill and Vehrencamp, 2008).

My aim is to describe duetting behavior in Adelaide’s warblers in terms of vocal structure and to test the territory defense hypothesis to see if there is a relation between fights and duets. Using observational data, I will identify duet events and fights between neighbors. Following the territory defense hypothesis, I predict that duets will be temporally related to fights. A duetting behavior related to fights would suggest that at least one of the uses of duets is to defend the territory as a pair. In this case a duet will show that two individuals are willing to defend a territory together, so pairs might use this vocal strategy to maintain their territory more efficiently.

Background

Duetting in warblers

Duetting research has focused on wrens, shrikes, and a few other groups of songbirds, but very little is known about the phenomenon in new world warblers (Family: Parulidae). The literature on duetting in new world warblers is therefore limited to basic description in species accounts. My research assistants examined published species accounts of warblers to determine the extent of duetting in that group. They also recorded information on migration to see if duetting is associated with the absence of migration in this group (Logue and Hall 2014). What follows is a complete list of the resources they examined:

- The Handbook of the birds of the World Vol. 15 (Del Hoyo et al., 2010)
- The Audubon Society Encyclopedia of North American Birds (Terres, 1991)
- A Guide to the Birds of Panama: With Costa Rica, Nicaragua, and Honduras (Ridgely and Gwynne, 1992)
- A Guide to the Birds of Costa Rica (Stiles and Skutch, 1989)
- Birds in Brazil (Sick, 1993)
- Birds of Peru (Schulenberg et al., 2010)
- Birds of Venezuela (Hilty, 2002)
- New World Warblers (Curson et al., 1994)
- Birds of the West Indies (Arlott, 2010)
- National Geographic Field Guide to the Birds of North America (Dunn and Alderfer, 2006)
- A Guide to the Birds of Puerto Rico and the Virgin Islands (Raffaele, 1989)
- A Field Guide to the Birds of Mexico and Adjacent Areas: Belize, Guatemala, and El Salvador (Edwards, 1998)

This survey of the literature revealed evidence of duetting in only 9 out of 125 warbler species. Masked Yellowthroat (*Geothlypis aequinoctialis velata*) pairs duet with a series of slowly delivered harsh grating sounds (Del Hoyo et al., 2010). Likewise, Painted Whitestars (*Myioborus pictus*) duet, but we could not find any description of their duet (Del Hoyo et al., 2010). The

female Two-banded warbler (*Basileuterus bivittatus*) sings in response to male song (Del Hoyo et al., 2010). Citrine warbler (*Basileuterus luteoviridis*) just has one record of a duet (Del Hoyo et al., 2010). The Buff-rumped warbler (*Phaeothlypis fulvicauda*) female occasionally gives a short warble in response to male songs (Del Hoyo et al., 2010). I have observed of Adelaide's warbler (*Setophaga adelaidae*) duets, and my colleague D. Logue has recordings of Elfin-wood warbler (*Dendroica angelae*) duets. There is also mention and a brief description of the Adelaide's warbler duet in Staicer (1991). There is no description whatsoever of the duet for the last two warblers, the Russet-crowned warbler (*Basileuterus coronatus*) and the Wrenthrush (*Zeledonia coronata*), although there is mention of its occurrence (Del Hoyo et al., 2010). Most of these warblers (n=7) do not undergo long distance migration, consistent with Logue and Hall's (2014) findings, but two duetting species migrate in part of their range. It is not clear whether the duetting individuals also migrate. The estimate that only nine species of warbler duet is almost certainly an underestimate, given the paucity of research on tropical birds (Stutchbury and Morton, 2001).

Adelaide's warbler is a non-migratory songbird that duets (Staicer, 1991). Their duets consist of a male song, overlapped by a female 'pip' call (Staicer, 1991). The female gives three or more pip calls during the last part of the male song and it is as if it were punctuating the male song (Staicer, 1991). The context and functions of the duet are not known. Here, I present the first detailed description of the Adelaide's warbler's duet and the context in which it is produced. I will also test a prediction of the hypothesis that duetting is used to cooperatively defend the shared territory. According to this hypothesis, we predict duets will be temporally associated with fights between neighbors.

Objectives

- 1) Characterize song type repertoires in this population.
- 2) Test for a performance constraint in Adelaide's warbler songs by plotting trill rate against average frequency bandwidth, and conducting a quantile regression analysis.
- 3) Compare frequency excursion, vocal deviation, average frequency bandwidth and trill rate, to better understand the relationship among these putative metrics of performance.
- 4) Test two predictions of the hypothesis that song-type matching is an adaptation for facilitating female choice. These predictions are based on Logue and Forstmeier's (2008) model, which suggests that birds should only match when they can perform at a higher level than their rivals.
 - a. Prediction 1. Songs used for matching a rival should have higher performance than those that are not, accounting for variation attributable to individual, song type, and other variables.
 - b. Prediction 2. Songs that answer a rival but do not match should have lower performance than those that do not, accounting for variation attributable to individual, song type, and other variables.
- 5) Describe the structure of duet song in this species.
- 6) Test if duets are associated with fighting, as predicted by the joint territory defense hypothesis.

Methods

Site:

Fieldwork was conducted in Southwestern Puerto Rico at the Cabo Rojo National Wildlife Refuge (17°59'N, 67°10'W), a semidry tropical forest with peak precipitation in April and May (Staicer, 1996). The population of Adelaide's warblers at the refuge had been studied continuously for two years prior to the current study. We captured birds with mist nets and took measurements of each bird's beak, tarsus, wing and tail. Three colored bands and one numbered aluminum band were put on each bird's tarsus for individual identification. Territories were mapped by visual observation of song posts. The present study included nine males from two neighborhoods: one with three territories and the other with six territories. I chose these males based on their proximity to each other and ease of observation (Figure 1).



Figure 2: Focal birds and neighborhood structure in Cabo Rojo Fish and Wildlife Refuge. Red dots represent the centers of focal males' territories, and blue ovals define the two neighborhoods used in the study. Map from Google Maps, 2014.

Recordings:

My field assistants and I observed and recorded birds from March 2 to June 19, 2012. Pairs were breeding throughout the duration of our observation. I chose this time of year because males exhibit pre-dawn (B type) singing only during the breeding season. We went to each territory and recorded from half an hour before sunrise until three hours after sunrise. After recording all males one time, we repeated the cycle three more times for a total of 36 recordings. Observers used binoculars (Eagle Optics Ranger Series 8x42; Eagle Optics; 2120 W. Greenview Dr. Middleton, WI 53562) to see colored leg bands and confirm the identity of the focal male several times during the observation period. We made audio recordings with Marantz PMD661 solid state digital audio recorders attached to Sennheiser ME67 'shotgun' microphones. Recordings were saved as 16 bit wav files, with 44,100 samples per second. In addition to recording all vocalizations, observers recorded the date, time of the beginning of the recording, time of sunrise, information of pairing status, breeding status when possible, and fights, and noted the occurrence of song-type matching, overlapping and other vocal interactions.

Data processing:

We used the computer program SYRINX-PC (John Burt, www.syrinxpc.com) to view spectrograms of the field recordings (Settings: Blackman window, transform size = 1024 points, temporal resolution = 12 ms). Four trained assistants and I transcribed all recordings. One assistant and I transcribed 28 / 36 recordings. I conducted a repeatability test between myself and the primary assistant. The two of us independently transcribed a randomly selected recording and compared our scores based on song occurrence and interaction of each of those songs. Overall repeatability was 91% (88% before dawn, 93% after dawn). I conducted a song-by-song review of transcriptions (n = 8) from the other scribes to ensure proper transcription. Finally, I reviewed all interactions that were scored as 'ambiguous'.

Observers listened to field recordings and entered the data into a Microsoft Excel 2010 (Microsoft) spreadsheet. They were blind to the identity of the focal males. Observers recorded the occurrence and timing of all songs and calls, as well as song-type matching, non-matched answering, song overlapping, territorial intrusions, fights, and other observed behaviors.

Broadly speaking, human hearing is similar in sensitivity to songbird hearing (Doupe and Kuhl, 1999). Therefore, if the observer could hear the other song clearly, we assumed the bird could as well, regardless of whether it emanated from an immediate neighbor or a more distant neighbor. We scored a song-type match when a bird sang the same song-type as his neighbor within two seconds. A non-matched answer was scored if non-matching countersinging occurred within 1.5 seconds. This is a conservative cutoff point; birds may be answering after 1.5 seconds, but it is impossible to know for certain if the interaction was triggered by a specific male. We scored overlapping when at least a third of one song was sung overtop of another (Foote et al., 2008). Song-type matching, answers and overlapping were labeled to indicate whether the focal male was the initiator or the responder. Difficult-to-score interactions were noted as ambiguous. Fights were scored only when there was visual confirmation of a fight. Aggressive ‘chip burst’ calls are strongly associated with fighting (personal observation, O.M.), so we noted these as well to support any indication of a fight.

Each song recording from a focal male was saved as a separate file and assessed for recording quality. Song recordings were classified into three categories based on their quality: 1) high amplitude, clear recording, no overlapping, 2) some overlapping, noise, or recording problems and 3) poor quality recordings. Only recordings from the first category were used for song measurements (see below).

I used a reduced set of recordings for the structural analyses (Objectives 2-4). In total, 2825 recordings were of sufficient quality (high amplitude, low noise, not overlapping with other loud sounds) for structural analysis. I further reduced the dataset by eliminating incomplete songs (N = 42), ‘double songs’ (two songs sung in rapid succession; N = 2), and all songs belonging to song-types with 10 or fewer exemplars (N = 55 songs). The rationale for eliminating rare song-types is that the linear mixed model, which includes song-type as a random factor, would have little information with which to estimate parameters for rare song-types. For the linear mixed model, I also eliminated the first songs of each day because they lacked a ‘latency since prior song’ (N = 9).

Data analysis:

Acoustical analyses:

Collaborator Jesse McClure analyzed high quality song recordings ($n = 2823$) with his custom software FEX (Podos et al. in prep), which calculates the performance metric ‘frequency excursion’ (FE; see Background). Laboratory assistants entered the same set of songs into the program Luscinia v2.14 (Lachlan, 2007) to measure the average frequency bandwidth and trill rate for each song (settings: max. freq. = 10kHz, frame length = 5ms, time step = 1ms, dynamic range = 35 dB, dynamic equalization = 100ms, dereverberation = 100%, dereverberation range = 100ms, highpass threshold = 1.0kHz, noise removal = 10dB).

Song-types were then classified. During the data scoring, scribes classified each song-type based on its appearance on a spectrogram. At that point, songs were classified within individual, but classifications were not valid between individuals. My colleague, Paloma Sánchez, and I printed spectrograms of the best recordings of each song-type from each male. We laid them on a large table and visually grouped structurally similar song-types. Song files were played acoustically to aid in classification. A total of 75 song-types were classified. Another colleague, David Logue, then consolidated the song types with the help of the program Luscinia (Lachlan, 2007). Luscinia measures acoustic features of songs and performs cluster analyses based on their structures. Logue ran two cluster analyses on the 75 song type exemplars using the following variable weightings (1. Time = 1, peak frequency = 1, peak frequency change = 1, gap between elements = 1; 2. Time = 5, relative position = 1, peak frequency = 1, peak frequency change = 1). Song-types that clustered together were visually reviewed for structural similarity. Using this technique, Logue merged four song-types with other song-types, reducing the number of song-types to 71. Finally, Logue inspected all song files in Syrinx ($n = 9499$ songs), and corrected all classification errors.

Objective 1: Song type repertoires

I made collector’s curves with the song-types for each male to estimate repertoire size. A collector’s curve is a graph in which cumulative song-types are on the vertical axis and the

number of songs analyzed is on the horizontal axis. The curve reaches a stable asymptote when a male's entire repertoire has been obtained.

Objective 2: Performance constraints

We plotted the average frequency bandwidth against the trill rate for all songs that were measured in *Luscinia*. We then performed a 90th quantile regression to test for a limit to performance. Once this limit was established, we measured the orthogonal distance from each song to the regression line, to determine songs' VDev. Vocal deviation scales negatively with performance.

Objective 3: Comparison of performance metrics

We conducted Pearson's correlations to characterize the relationships among the putative performance metrics FE, VDev, average frequency bandwidth and trill rate. We consider *trill rate* and average *frequency bandwidth* partial measures of performance, because they represent components of FE and VDev.

Objective 4: Performance as a function of matching, answering rivals.

This analysis is part of a collaborative project on variation in performance in Adelaide's warbler. Here, I focused on the results pursuant to the social context of singing. The complete analysis is in preparation for publication (Schraft, Medina, McClure, Pereira, and Logue, in prep).

The models used in this analysis include the following explanatory variables: *ID*, *day* (*within ID*), *song-type*, *time*, *order*, *latency since prior song*, *singing mode*, *matching*, *answering*, and *run number*. *Time* (sec) represents the time relative to sunrise, so negative values represent times before sunrise. *Order* is the sequential order of the songs for that male, on that day. For example, (*order* = 1) for the first song that a male sings in the morning, (*order* = 2) for the second song he sings, and so on. *Latency* is the time elapsed since the subject's previous song. *Singing mode* separates Type I and Type II singing (Staicer, 1996). Singing modes in Adelaide's warblers differ with respect to several variables, including time of day, time of year, patterns of song

switching (immediate versus eventual variety), song structure, and social context (Staicer, 1996), but there are no published diagnostic criteria to assign singing modes to individual song-types. According to Staicer (1996), Type II songs are sung primarily during the dawn chorus and secondarily during vocal interactions with neighbors. Treating song-type within male as an independent sampling unit (because different individuals can assign a given song type to different modes; Staicer, 1991), we built a histogram of median time of delivery. The histogram revealed a bimodal distribution, with a pronounced gap shortly after sunrise. I therefore assigned songs in the left lobe of the distribution to Type II and those in the right lobe to Type I. Songs were scored positive for *matching* if they were the first song that the focal male sang after a neighbor sang the same song type. *Answering* describes non-matching songs sung within 1.5 sec of an audible neighbor song. *Run number* is the song's order within a run of the same song-type.

My colleagues and I built linear mixed models (LMMs) to study variation in song performance (Winter, 2013). Model selection is a controversial topic. We tried three model selection procedures: No model selection (full models), model averaging using Akaike's information criterion (AIC), and reduced models based on relative AIC. All three approaches produced qualitatively similar results with respect to both effect sizes and significance tests. Here I report the reduced models based on relative AIC, because that approach yielded the most concise results. For each dependent variable (FE, VDev, frequency bandwidth, and trill rate), we began with a full model that included all main effects (*time*, *order*, *latency*, *run number*, *matching*, *answering*, *singing mode*) and random intercepts for *ID*, *day within ID*, and *song-type*.

Covariates (*time*, *order*, *latency*, and *run number*) were standardized and centered by subtracting the mean and dividing by two standard deviations. We did not include interactions because we had no *a priori* predictions related to interactions. Each full model was subjected to the dredge function in the R package MuMIn (Barton, 2015), to rank all sub-models with respect to AIC (Burnham and Anderson 2002). Terms that were in all models with $\Delta AIC \leq 2$ were included in the reduced models. We did not include random slopes, which would have further complicated the analyses. Estimates of the relationships between the raw covariates and performance variables were obtained by dividing the slopes by two times the standard deviation of the unscaled variables. Residuals were approximately normally distributed and homoskedastic.

We used the ‘anova’ function to conduct likelihood ratio tests of statistical significance for each variable, while accounting for variation attributable to all other variables. Effect sizes were estimated with the REML method, but likelihood ratio tests were based on the ML method (Meyer, 1991). The critical tests for this thesis were whether the terms *matching* (Objective 4a) and *answering* (Objective 4b) influence performance. Based on Logue and Forstmeier’s (2008) model, we predicted a positive influence of matching on performance, and a negative influence of answering on performance.

Objective 5: Describe duets

Duets were described in terms of their structure and the timing of male and female components. Duets were visualized in SYRINX. Temporal measurements were made with a transform size of 256 points, for a temporal resolution of 1ms. I measured the timing of the beginning and end of the male and female vocalizations. I also counted the number of notes in the female’s vocalization and described the structure of the male song and female call for each duet.

Objective 6: Test whether duets are associated with fights.

We studied the association between duetting and fighting at two scales: between days and within days. The between days analysis uses a linear mixed model to predict *duet frequency* over an entire observation period based on the occurrence of fights. *Fight occurrence* was treated as a binary variable here, because fights within a day appear to be strongly non-independent (they are clustered, such that several fights often occur in a short period of time). *Individual* was treated as a random variable. I was interested in the relationship between fights and female vocalization more generally, so I ran a second version of the model using the sum of *female songs and duets* as the dependent variable.

We used a Monte Carlo approach to test whether duets occurred more closely to fights than would be expected by chance alone, within days. The 17 days that included both fights and duets contributed to this analysis. We conducted an omnibus analysis, which weighted all pairs equally, as well as separate analyses for each pair.

We began by coding the variable *songs to fight*, for all male songs (including duets). That variable describes the distance in songs to the closest fight on the same day. For example, the 100th song before a fight was coded “+100” and the 10th song after a fight was coded “-10”. We then determined the absolute value of *songs to fight* for all duets (*absolute songs to fight*), and averaged that value for each day. Day averages were averaged for each pair to arrive at the test statistic *average absolute songs to fight*, which describes the average distance in songs between duets and fights for each pair. Duets were then shuffled within day to produce a distribution of simulated *average absolute songs to fight*. For the omnibus test, we averaged *average absolute songs to fight* over all pairs to arrive at a single estimate of the population’s *absolute songs to fight*. This approach gives equal weight to all pairs, regardless of their number of duets or fights, or the number of days that they fought and duetted. The pair-by-pair tests compare each pair observed *absolute songs to fight* (averaged over all days they fought and duetted), to pair-specific random distributions.

Transcriptions and basic data analyses were conducted in Microsoft Excel 2015 (Microsoft) and InfoStat (InfoStat, 2015). Quantile regressions were conducted in R (R Core Team 2012) using the *quantreg* package (Koenker, 2008). Linear mixed models were constructed in R using the *lme4* package (Bates et al., 2012). Alpha levels were set to 0.05. Monte Carlo tests were conducted in Microsoft Excel 2013 (Microsoft) running the PopTools add in (Hood, 2010).

Results

We obtained a total of 9499 songs, of which 2823 were of high enough quality to get frequency excursion (FE) values (Table 1). We used 2727 values of FE for the performance constraints analysis after eliminating extreme values (outliers), coding errors and rare song types.

Table 1: Basic statistics for all nine males.

Bird ID	Hours	Songs	Songs w/ FE	Song types	Duets	Matches	Answers
DDLb	14.57	1221	603	27	20	46	365
KYK	14.05	756	90	33	12	21	237
LgRLg	14.32	954	255	24	5	124	271
LgWV	14.29	1107	251	23	4	41	337
OWO	13.93	1197	457	28	4	16	269
PDP	14.33	1152	151	31	4	63	337
RbRbO	14.29	1350	423	31	13	114	410
RDY	12.84	954	477	34	14	31	239
ROLb	13.67	808	116	31	12	16	270
total:	126.29	9499	2823	71	88	472	2735
Average:	14.03	1055.44	313.67	29.11	9.78	52.44	303.89
SD:	0.52	199.27	182.28	3.86	5.76	40.77	60.54

Objective 1: Song type repertoires

The collector's curves for three (DDLb, LgWV and RbRbO) of the nine subjects showed stable asymptotes, suggesting that all song types were recorded (Figure 3). The average number of song types in these birds' repertoires is 27 ± 4 . A collector's curve for all the songs obtained from all males appears to be close to an asymptote at 71 song-types (Figure 4).

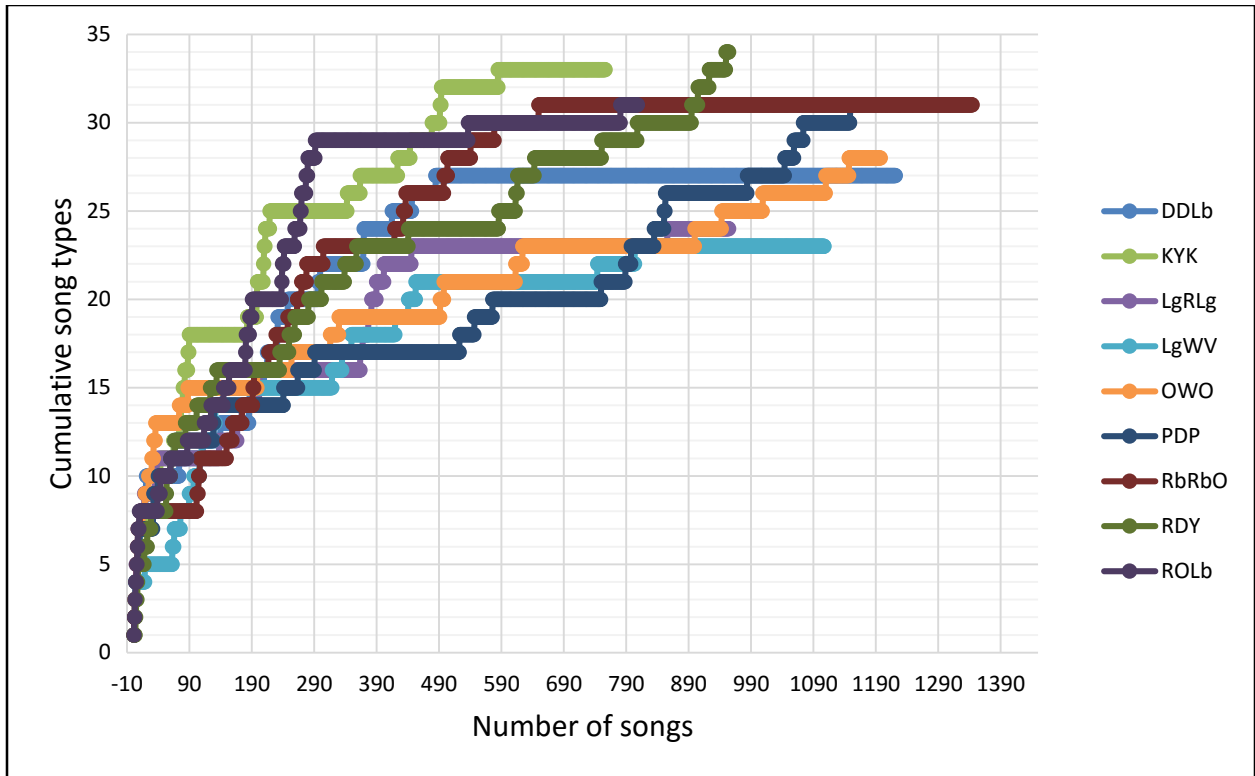


Figure 3: Collectors curve of song-types for all nine males.

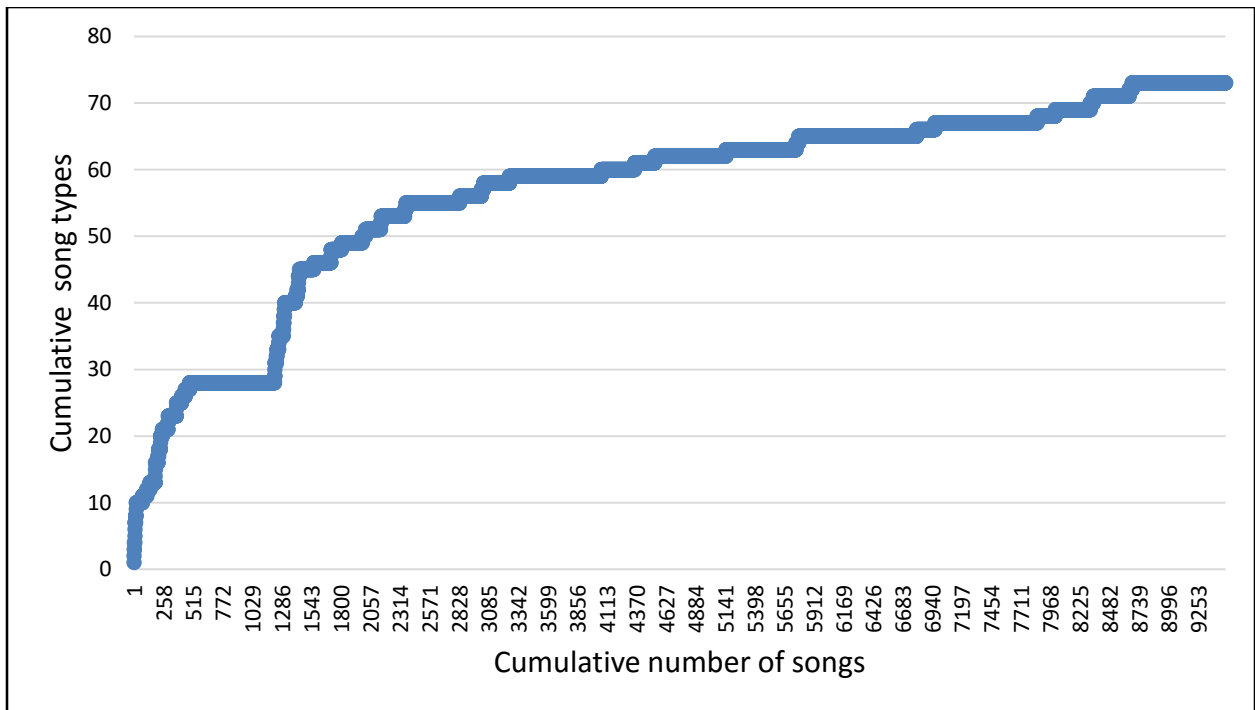


Figure 4: Collectors curve for all song-types overall.

Objective 2: Performance constraints

The performance constraint analysis was based on 2727 songs. The distribution of trill rate (Hz) vs. average frequency bandwidth (kHz) showed a negatively-sloping upper edge (Fig. 5). The 90th quantile regression line is negative and statistically significant ($y = -0.14x + 5.12$; $t_{\text{slope}} = 24.7$, $p_{\text{slope}} < 0.00001$).

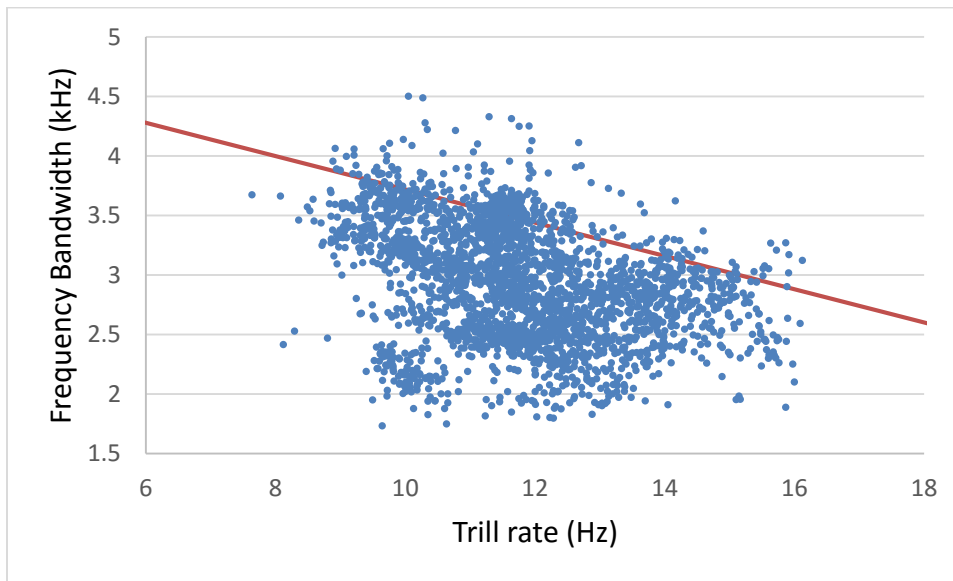


Figure 5: Plot of average frequency bandwidth vs. trill rate for 2717 Adelaide's warbler songs. Orange line represents the 90th quantile regression line.

Objective 3: Comparison of performance metrics

The performance metrics, FE and VDev were strongly correlated. FE was more correlated to frequency bandwidth than to trill rate. Vocal deviation was much more strongly correlated to frequency bandwidth than trill rate (Table 2).

Table 2: Pearson's correlation coefficients among putative performance metrics (n = 2717).

		r
Freq. band.	Trill rate	-0.36
FE	VDev	-0.84
FE	Freq. band.	0.64
FE	Trill rate	0.32
VDev	Freq. band	-0.90
VDev	Trill rate	-0.08

Objective 4: Performance as a function of matching, answering rival.

Independent variables were highly correlated (Table 3). No pair of variables exhibited $|r| > 0.7$, however, limiting the risk of multicollinearity (Dormann et al., 2013).

Table 3: Pearson's correlation coefficients among independent variables.

	Matching	Answer	Order	Run Number	Mode	Time
Answer	-0.15					
Order	-0.10	-0.19				
Run Number	-0.05	-0.13	0.29			
Mode	0.06	0.17	-0.45	-0.43		
Time	-0.08	-0.20	0.67	0.33	-0.58	
Latency	-0.04	-0.06	0.22	0.10	-0.25	0.30

The linear mixed models were based on 2717 songs, sung by nine males (four observation days per male), and representing 40 song-types. All random variables (ID, day within ID, and song type) were highly significant ($p < 0.0001$) in all models (Tables 4-7). Effect sizes should be interpreted as if all other terms in the model were held equal. Covariates reported in the text were back-transformed and scaled up to biologically relevant units (*time* as the effect per hour, and *order* as the effect per 100 songs). The model for *FE* showed a strong positive effect of *order* (2.69 FE points / 100 songs), and negative effects of *time* (-1.67 FE points / hour) and *answer* (unmatched answers were 0.55 FE points lower than other songs; Table 4).

Table 4: Results of a linear mixed model for the dependent variable ‘frequency excursion’.

term	type	estimate	lower 95% CL	upper 95% CL	chi ²	df	p
Intercept		66.13	62.37	70.47			
Answer	Fixed	-0.55	-1.06	-0.083	5.54	1	0.019
Order	Fixed (Cov)	5.07	4.29	5.96	131.65	1	< 0.0001
Time	Fixed (Cov)	-3.31	-4.25	-2.48	51.33	1	< 0.0001

Estimates of random terms and residuals represent standard deviations. Covariate (Cov) estimates refer to centered, scaled data. See text for unscaled estimates and model construction. ($\sigma_{ID} = 4.13$, $\sigma_{Day\ w/in\ ID} = 2.85$, $\sigma_{Song-type} = 9.97$, $\sigma_{Residual} = 5.42$; all $p < 0.0001$)

The other ‘holistic’ performance metric, *VDev*, is an inverse measure of performance, so lower values indicate higher performance. The *VDev* model revealed negative effects of *order* (-0.043 *VDev* points / 100 songs), and *matching* (matching answers were 0.04 *VDev* points lower), and positive effects of *answer* (unmatched answers were 0.02 *VDev* points higher) and *time* (+0.041 *VDev* points / hour; Table 5).

Table 5: Results of a linear model for the dependent variable ‘vocal deviation’.

term	type	estimate	lower 95% CL	upper 95% CL	chi ²	df	p
Intercept		0.58	0.42	0.75			
Answer	Fixed	0.02	0.0040	0.040	5.84	1	0.016
Matching	Fixed	-0.04	-0.076	-0.0055	5.20	1	0.023
Order	Fixed (Cov)	-0.08	-0.11	-0.050	27.30	1	< 0.0001
Time	Fixed (Cov)	0.08	0.052	0.12	24.80	1	< 0.0001

($\sigma_{ID} = 0.14$, $\sigma_{Day\ w/in\ ID} = 0.08$, $\sigma_{Song-type} = 0.42$, $\sigma_{Residual} = 0.19$; all $p < 0.0001$)

Trill rate was positively affected by *order* (0.34 Hz / 100 songs). *Trill rate* was the only dependent variable that showed an effect of singing *mode* (A-type songs were 0.2 Hz faster than B-type songs, Table 6). *Average frequency bandwidth* was affected negatively by *time* (-0.044 kHz / hour, Table 7) and positively by *matching* (matching answers had a 0.049 kHz broader bandwidth than other songs).

Table 6: Results of a linear model for the dependent variable ‘trill rate’.

term	type	estimate	lower 95% CL	upper 95% CL	chi ²	df	p
Intercept		11.99	11.39	12.48			
Mode	Fixed	-0.20	- 0.31	-0.088	14.59	1	0.0001
Order	Fixed (Cov)	0.64	0.57	0.71	303.74	1	< 0.0001

($\sigma_{ID} = 0.44$, $\sigma_{Day\ w/in\ ID} = 0.38$, $\sigma_{Song-type} = 1.43$, $\sigma_{Residual} = 0.68$; all $p < 0.0001$)

Table 7: Results of a linear model for the dependent variable ‘frequency bandwidth’.

term	type	estimate	lower 95% CL	upper 95% CL	chi ²	df	p
Intercept		2.89	2.73	3.06			
Matching	Fixed	0.049	0.014	0.087	6.47	1	0.011
Time	Fixed (Cov)	-0.088	-0.11	-0.066	65.95	1	< 0.0001

($\sigma_{ID} = 0.10$, $\sigma_{Day\ w/in\ ID} = 0.08$, $\sigma_{Song-type} = 0.43$, $\sigma_{Residual} = 0.21$; all $p < 0.0001$)

Objective 5: Describe duets

Males start to sing first followed by females answering with a series of high frequency notes (Fig. 6). On average, the female overlapped the last 56% of the male’s song (Table 8). Female duet contributions range from 3 to 10 notes (avg. = 6 notes), with an average duration of 1.37 seconds. The female vocalization is usually at a higher frequency than any part of the male song (Staicer, 1991). I identified two female note types. On a spectrogram, one appears p-shaped and the other appears arch-shaped (Fig. 7). Females answer the males later in the song when male songs are longer ($r^2 = 0.18$, $F = 18.95$, $p\text{-value} = <0.0001$; Fig. 8).

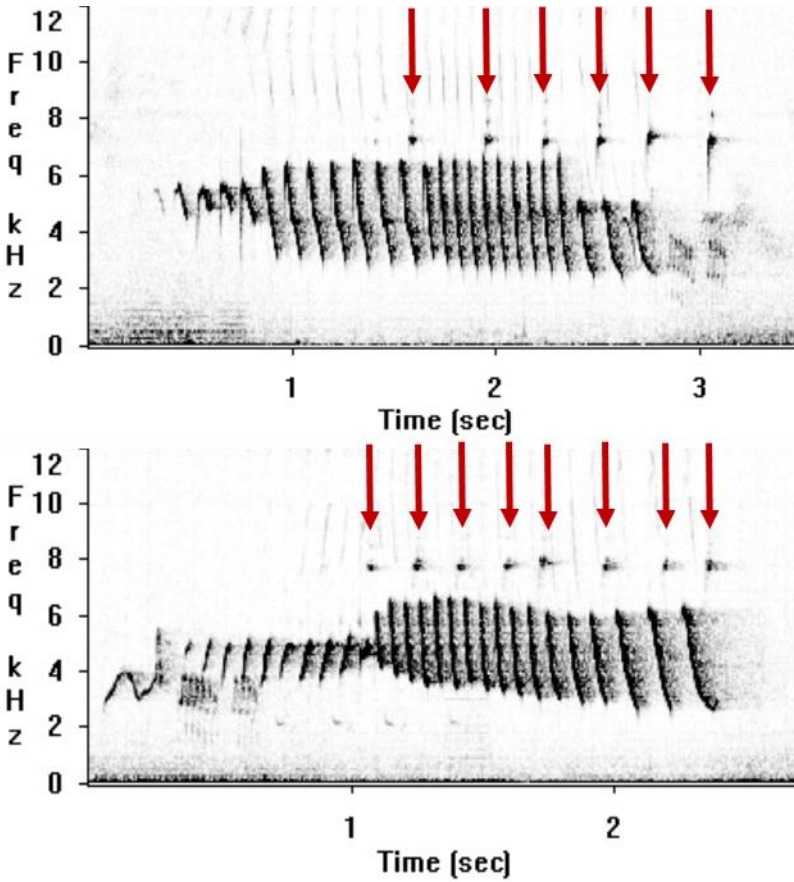


Figure 6: Spectrograms of typical Adelaide's warbler duets. Red arrows indicate the female's contribution.



Figure 7: Example of female note shapes. P-shape note (left), arch-shape note (right).

Table 8: Average lags between the beginning of the male song and the beginning of the female song in Adelaide’s warbler duet, as a percentage of the male song length (n=9).

Males	Start of female vocalization into male song (average %)
DDLb	52.60
KYK	51.34
LgRLg	54.75
LgWV	54.85
OWO	83.43
PDP	76.72
RbRbO	54.06
RDY	37.54
ROLb	42.55
Average:	56.43
SD:	14.76

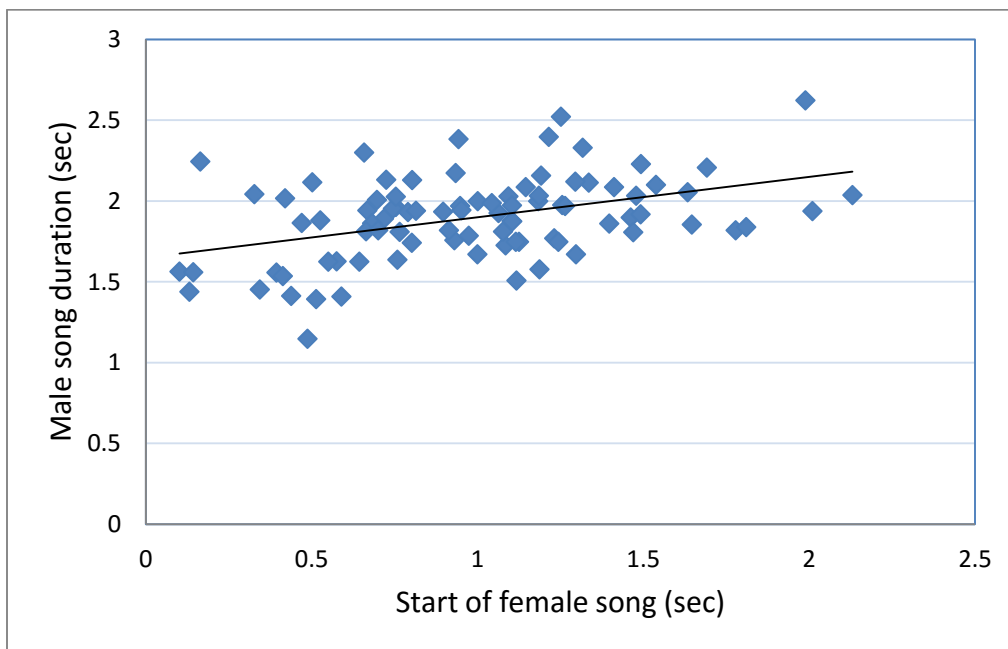


Figure 8: Relationship between male song duration and the start of the female song in a duet.

Objective 6: Test whether duets are associated with fights.

The between-days analysis revealed a positive and marginally significant effect of *fight occurrence* on *duet frequency*, while accounting for the effect of ID (effect of fight occurrence = +2.21 duets; $\text{Chi}^2 = 3.84$, $\text{df} = 1$, $p = 0.050$). Using the sum of *female song* and *duets* as the

dependent variable resulted in a higher estimated effect and a lower p-value (effect of fight occurrence = 3.23 female vocalizations; $\text{Chi}^2 = 6.16$, $\text{df} = 1$, $p = 0.013$).

A graph of female answering rate relative to fights indicates that duets clustered around fight events, and were particularly common in the period after fights (Fig. 9). The outlier at -100 songs is attributable to three duets given in rapid succession by one pair. The omnibus within-day analysis indicated that duets occur closer to fights than would be expected by chance alone (Monte Carlo test: *absolute songs to fight*_{Obs.} = 49.58, *absolute songs to fight*_{Exp.} = 86.89, realized $p = 0.0018$). The within-pair tests revealed that duets were more closely associated with fights than would be expected in seven out of eight pairs, and significantly so in four pairs (Table 9).

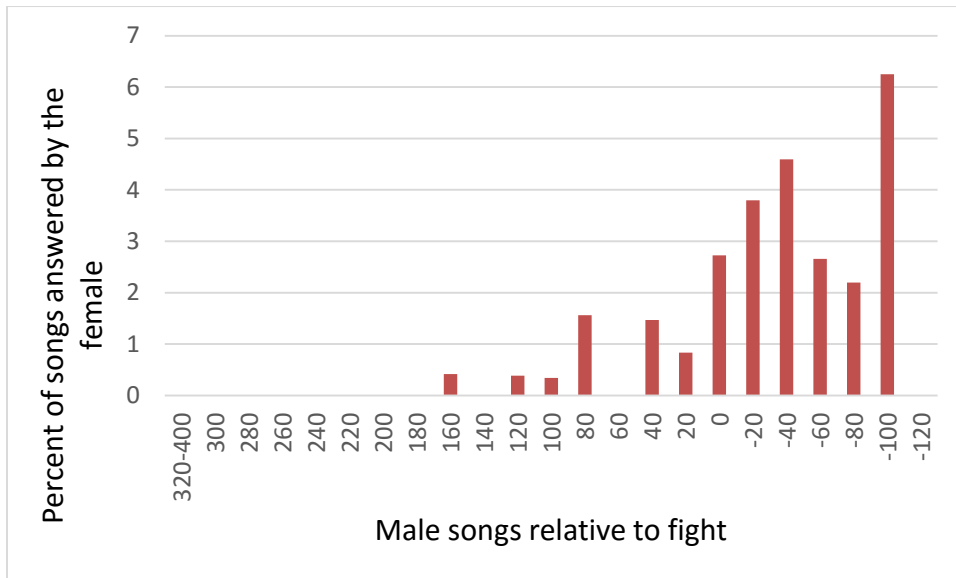


Figure 9: Distribution of duets (female answers) with respect to fights.

Table 9: Monte Carlo within-pair test (n=8).

Pair	Absolute songs to fight (observed)	Absolute songs to fight (expected)	Realized P
DDLb	51.45	58.66	0.31
KYK	7.5	77.26	< 0.0001
LgWV	177	151.91	0.58
OWO	50	81.68	0.21
PDP	22	49.80	0.31
RbRbO	54.9	122.13	0.0052
RDY	21.75	93.45	< 0.0001
ROLb	12	61.87	0.031

Discussion

This observational study of Adelaide's warbler in South Western Puerto Rico allowed me to describe song use and duetting behavior, and to test hypotheses about the functions of song-type matching and female song answering (duetting).

Males song-type repertoires comprise approximately 30 song types. I obtained full repertoire of three males, and incomplete, but near asymptotic, repertoires for the other six, for an average observed repertoire size of 29.1 songs (Fig. 3, Table 1). At the population level, I found 73 song types, which appears to be slightly below the true number based on the nearly asymptotic collector's curve (Fig. 4). Studying the same population more than 25 years earlier, Staicer (1991) found a total of 63 distinct song types ($n=16$ males). The small difference in our estimates may be attributed to (1) different ways of classifying songs types, (2) different sampling intensity, or (3) an actual change in the number of song types in the population.

I observed substantial among-males variation in repertoire size (Fig. 3). Although some of this variation could be attributable to sampling error, the slopes of the curves in Figure 3 suggest that much of it is real. The variation could be due to factors such as the age of the birds (Nowicki et al., 2000; Cosens and Sealy, 1986; Nicholson et al., 2007), nutrition (Nowicki et al., 1998 and 2000), or genetic differences. Repertoire size is important for female choice in some species (Searcy, 1984; Buchanan and Catchpole, 1997; Reid et al., 2004), but not others (Byers and Kroodsma, 2009). Future studies could address the causes and consequences of variation in repertoire size.

In the test for constrained vocal performance, the distribution of average frequency bandwidth versus trill rate showed a negatively sloping upper boundary, as expected (Fig. 5). This means that Adelaide's warblers trade-off between frequency bandwidth and trill rate, like some other trill-singing species (Podos, 1997; Ballentine, 2004). Thus, males apparently cannot sing with both a very high trill rate and a very high frequency bandwidth. This constraint suggests that songs in this species meet the conditions of an honest signal and that females should have evolved to be attentive to them in order to obtain information about direct and/or indirect benefits (Podos, 1997; Byers et al., 2010). There are two methodological issues worth mentioning, with respect to this plot. First, we made the plot using the quantile regression

method instead of the traditional upper boundary regression method. The quantile regression method is a better way to obtain an upper-boundary limit because it is less biased (Wilson et al., 2014). Second, the use of automated acoustic analysis (Luscinia) allowed us to average the frequency bandwidth over the notes in the song (a first, to the best of our knowledge) and to generate a dataset that is both large and unaffected by human measurement bias.

A comparison of four putative performance metrics revealed interesting patterns. Frequency excursion and vocal deviation attempt to estimate performance in a more-or-less general sense, and some studies use them as measures of whole song performance (Podos, 1997; Ballentine, 2004; Illes et al., 2006; Cramer and Price, 2007; Podos et al., in review). On the other hand, trill rate and average frequency bandwidth are song components that are associated with performance, and contribute to FE and VDev. The strong negative correlation between FE and VDev (an inverse metrics of performance) indicates that they measure similar features, which was expected based on the way that these features are obtained. The strength of their relationship is nevertheless reassuring, given VDev's history of use and FE's lack thereof. I found that FE scales with both average frequency bandwidth and trill rate (Table 2). Frequency bandwidth exhibits double the strength of correlation as trill rate, meaning that FE is more influenced by variation in frequency bandwidth than it is by variation in trill rate in this population. However, trill rate is still considerably correlated with FE.

I expected to find a similar pattern with VDev. However, although average frequency bandwidth was strongly related to VDev, trill rate was not. Vocal deviation is only very weakly influenced by trill rate, although the tendency is in the expected direction (Table 2). Because VDev is based only on trill rate and bandwidth, I conclude that VDev is almost completely a function of frequency bandwidth, at least in this species. This is interesting because VDev attempts to measure performance in a general sense, but it almost entirely ignores trill rate, which is known to affect female choice in some species (Ballentine et al., 2004; Ballentine, 2009; Byers et al., 2010). Thus, vocal deviation appears to be a poor general metric of performance. FE appears to be a better model since it accounts better for trill rate and frequency bandwidth, as well as frequency modulation within notes and frequency jumps between notes (Geberzahn and Aubin 2014). I recommend using FE, and not vocal deviation, as a model of performance because it better accounts for performance-implicated components in birdsong.

I found limited support for the hypothesis that song type matching is an adaptation for facilitating female choice. FE and VDev showed a significant effect on non-matching answers and VDev and average frequency bandwidth showed a significant effect of matching. Importantly, all effects were in the predicted direction. With respect to FE and VDev, non-matching answers are significantly lower in performance than non-answers. This finding is consistent with the structural alignability hypothesis: Males should answer without matching when they are not able to produce high performance songs (Logue and Forstmeier, 2008). With respect to VDev and average frequency bandwidth, matching answers are higher performance than non-matches. This finding is also consistent with the structural alignability hypothesis: Males should match only when they are able to produce high performance songs. We propose that males do this to make the signal alignable, facilitating evaluation to the actor's benefit (Logue and Forstmeier, 2008). It appears that frequency bandwidth, but not trill rate, is associated with matching behavior.

Even though the matchings and answering effects are statistically significant, their effects are rather weak. Whether they represent biologically significant variation remains an open question. The critical question is whether females can detect and attend to the effects. Perception mechanisms are very sensitive in some animals (Romo et al., 2003). Future studies of female birds are necessary to see if subtle changes in frequency bandwidth affect preferences.

Although my predictions were partially met, FE, which I believe to be a better metric of overall performance, was not affected by song type matching events. Perhaps this lack of effect occurs because matching is entirely contingent on frequency bandwidth, which is less strongly weighted by FE. We did find a strong effect for other variables like order, song-types and time, suggesting novel explanations like a warm-up function. Order, for example, has a big effect on performance. It appears that males sing increasingly better and that this could drive the dawn chorus. However, this will be the topic of another publication (Schraft, Medina et al., in prep). Future studies could compare the influence of frequency bandwidth and trill rate on matching decisions by digitally altering these properties and playing them back to birds to measure their effects on matching behavior. Also, recordings of two neighbor males at the same time can be done to compare both performances in matching interactions.

Our overview of duetting in new world warblers revealed that this group is badly understudied in terms of duet descriptions and experimental research (Background). This oversight is probably due to the fact that most non-migratory warblers (those that are most likely to duet) live in the tropics, where ornithological research is less common (Stutchbury and Morton, 2001). Our observation that nine warbler species duet is therefore almost certainly an underestimate.

I presented the first detailed description of duet structure in Adelaide's warbler, which is also the first detailed description of any new world warbler duet. Adelaide's females answered males at a low rate; just 0.9% of male songs were answered to form a duet. Duets comprise typical male songs, and a series of high frequency female notes beginning, on average, 56% of the way through the male song. In other species, the contributions of the two sexes also occur at different frequencies (Mennill and Vehrencamp, 2005; Grafe et al., 2004; Logue, 2007). Being higher in frequency may be an adaptation to avoid masking the male song.

Females adjusted the timing of their vocalization in anticipation of the male song duration. This demonstrates that females pay attention to the male vocalization to produce a coordinated answer rather than simply overlapping haphazardly. There were two principal female note shapes, p-shaped notes and arch-shaped notes. This difference may serve a function in the duet, or it may be a product of the sound distortion in the environment (Bradbury and Vehrencamp, 1998). It could also be dependent on the male song type as in the first steps into a duet code (Logue, 2006). We could test this in the future by grouping the similar female note shapes together and see if they correlate with fights in a certain way. For example, some note shapes may happen before fights and others after fights. Alternatively, some note shapes may be dependent on the male song characteristics, like frequency bandwidth or trill rate.

I found that females answer songs to produce duets in the context of territory defense. This hypothesis has been supported in other species as well (Mennill, 2006; Logue and Gammon, 2004), but never in a new world warbler species. Adelaide's warbler duets tend to cluster around fights, especially after fight events (Fig. 9). Pairs appear to give a statement, mainly after a fight, that there are two individuals willing to defend the territory. This may function as a victory display (Grafe and Bitz, 2004). Our data support the hypothesis that one of the function of duetting in this species is to mutually defend a territory. This hypothesis is thought to be the primary function of duets. Duets may serve multiple functions in the same population, such as

mate guarding, and contact maintenance. However, the fact that they happen in such relation to fights make at least the contact maintenance not likely. It is the first time that such a key hypothesis is tested and supported in new world warblers. This is also the first time this method was used to test this hypothesis. A dual taxidermic intrusion design can be used in future studies to further test the hypothesis that duets relate to fights or serve additional functions. I hope this work motivates further research on duets in warblers, since there is a lack of scientific research on duetting in this group.

Conclusions

I characterized the vocal repertoire of nine male Adelaide's warblers. A trade-off was shown between frequency bandwidth and trill rate. The hypothesis that song type matching is a mean to facilitate female choice was partially supported with our data. The vocal behavior of song type matching in the Adelaide's warbler seems to be strategically displayed in order to facilitate female choice to some extent.

Additionally, I described the Adelaide's warbler duet. The joint defense hypothesis was supported by the data. Duets occurred in close proximity to fights than was expected by chance. Individuals in a pair appear to use this vocal behavior as a mean to defend the territory together. This represents a novel finding for this species.

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