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DUET PHONOLOGY AND SYNTAX  
OF THE RED-CROWNED PARROTS  
IN SOUTH TEXAS

A Thesis

by

ABIGAIL POZULP

Submitted to the Graduate College of  
The University of Texas Rio Grande Valley  
In partial fulfillment of the requirements for the degree of  
MASTER OF SCIENCE

December 2021

Major Subject: Biology



DUET PHONOLOGY AND SYNTAX  
OF THE RED-CROWNED PARROTS  
IN SOUTH TEXAS

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ABIGAIL POZULP

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December 2021



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## ABSTRACT

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Bird behavioral interaction systems show a preference for temporal precision. This preference is exemplified in the way many species avoid masking of vocal signals. Antiphonal duetting in songbirds suggest that overlapping notes are a sign of poor temporal coordination which can signify a weak pairbond, a possible cue for conspecifics seeking to usurp territories or mates. However, parrots (Psittacidae) are accomplished yet understudied duetters in nature. I recorded antiphonal duets produced by a wild population of red-crowned parrots (*Amazona viridigenalis*) in Brownsville, Texas. Temporal and acoustic variation of signals was assessed within and across a sample of mated pairs. Results suggest element overlap is prevalent in red-crowned parrot duets, even in pairs which were observed to have successfully raised offspring. This may be an indication that partially overlapping notes in parrot duets is not indicative of a weak pairbond or that urban parrot populations are under different selective pressures.



## DEDICATION

This work is dedicated to my most faithful field assistant, Arlowe. For the past ten years you've been riding shotgun as we guided one another through forested canyons and salty lagoons, exploring animal behavior coast-to-coast. The perfect friend for this adventure, so grateful to share it with you. Sincerest thankyou to my father and brother Mikey, as we all work together to honor Jayne Ellen Brophy, the best of us all. My love to cousin Allison and grandma June for getting me to Brownsville. Thank you to the parrot-loving people of Brownsville, Texas, especially Lawrence A. Johnson, and Charles Alexander, whose compassion for the flock of individuals taught me that through knowing we can really love our wild neighbors.



## ACKNOWLEDGMENTS

Researching wildlife in the urban setting of Brownsville, Texas, this study relied on the tolerance of our borderland community. The red-crowned parrots of Brownsville are an endangered species whose claim to this land is disputed and whose future is uncertain in human hands. To properly honor the heritage of this terrestrial community above which flocks of green gems do fly, I must acknowledge the history of this study site; inhabited for centuries by Indigenous groups of the Rio Grande Delta prior to unjust European colonization. I too, am an outsider whose migration to this region is thanks to The University of Texas Rio Grande Valley's Graduate College, who honored me with the President's Graduate Research Assistantship which funded my coursework and supported my thesis research. Thank you to Eagle Scout Zachary Edelstein and Brownsville Boy Scout Troop Six for assembling the nest tubes which provided breeding sites for the parrots. Additionally, I thank the collaboration of Brownsville Public Utilities Board for the installation of the Boy Scout Troop Six nest tubes. This dogged pursuit of parrot phonology was made possible by the generous exchange of ideas, manpower, and equipment of Dr. Karl S. Berg and his UTRGV Avian Ecology Lab team: Caleb Arellano, Michelle Campbell, Soraya Delgado, Rory Eggleston, Stephen Kayota, Celia Maclean, Jessica Majors, Mario Porras, Santana Rodriguez. A special thank you to Herman Ramsden, I can think of no better copilot for the hundreds of hours of parrot patrolling.



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## CHAPTER I

### INTRODUCTION

#### **1.1 Vocal Learning**

Some organisms acquire new vocalizations through imitation in a process known as vocal learning; vocal learners are those that process sounds heard in their environment and vocally reproduce them. Researchers working at the intersection of Sociology, Linguistics, and Cognitive Development have long turned to animal behaviorists to help unravel the complex mechanisms responsible for human conversation [47]. Although many social vertebrates communicate with the use of vocal signals, only a small fraction have been shown to learn and replicate novel vocal signals [41]. Vocal learning has been observed in a number of distantly related animal groups: cetaceans (dolphins and whales), pinnipeds (seals), primates (humans), Chiropterans (bats), elephants and three Avian groups: oscine passerines, parrots and hummingbirds [53, 27]. Vocal learning has likely evolved independently in the above animal groups and this was long thought to be the case in the three avian families known to be capable of vocal learning [53]. Recent phylogenetic studies have found passerines and parrots to be sister taxa, which leaves open the possibility for a vocal learning mechanism originating in their common ancestor, and subsequent loss in the case of some suboscine passerine lineages [66, 30]. A trait as unusual in nature as vocal learning may indicate that the innate vocalizations in most species are able to meet the functional criteria of their life history, allowing them suitable communication systems without the added complexity of needing to learn signals from an external source and then practice them [71]. Among the clades that possess this rare ability, only three vocal learners are known to be proficient enough to reproduce not only the sounds of conspecifics but any sound in their environment: oscine songbirds, humans, and parrots

[37]. Birds, as the most diverse taxa of non-human vocal learners, have long been conscripted by researchers investigating the evolutionary, ontogenetic, functional and mechanistic foundations of vocal learning. Although there are three avian groups associated with vocal learning, the oscine songbirds have formed the bulk of the avian vocal learning model. When one considers more closely the nuanced differences in the life history of these three avian groups, it is clear that narrowly focusing on one taxa limits our broader understanding avian vocal learning.

Songbirds have long been the primary model organism of vocal learning, while very little is known about vocal learning in hummingbirds, and the vocal learning abilities of wild parrots have gained scientific notice only in recent decades [10]. As lifelong learners, parrots tend to readily pick up new vocalizations and behaviors in captivity. Due to this aptitude for mimicry, researchers have been less willing to accept traditional laboratory methods of songbird vocal development as valid representations of wild parrot behavior [16, 17]. With wild parrots being deemed unsuitable for laboratory study, academic interest in this family was largely focused on cognition of domesticated parrots in a laboratory setting (comprehensive contributions by Irene Pepperberg and colleagues; reviewed by Auersperg and von Bayern [4]. The study of vocal learning in wild parrots is a newer field of study, having overcome not only the technological limitations in the durability and portability of recording equipment in the tropical canopy habitat of many psittacine species, but also refuting previous assumptions that mimicry was a mere novelty of captivity and thus exclusive to parrot-human interaction [10]. Along with broadening the academic understanding of psittacine behavior, the conventional understanding of avian vocal learning would benefit from the increased scientific attention on lifelong vocal learners like parrots.

Much of what is known about the ontogeny and function of avian vocal learning comes from studies of oscine passerines. As the model organism for the study of vocal learning, songbirds have generated important insights into the evolution of human speech and language [25]. Many of the foundational comparisons of avian vocal ontogeny focus exclusively on passerine songbirds. For example, Lipkind and co-authors [44] proposed a mechanism of how infant humans learn to talk (the stepwise acquisition analogy) by studying two songbird species. Neither of the species in this

study, the zebra finch (*Taeniopygia guttata*) and Bengalese finch (*Lonchura striata domestica*) have female vocal learning or lifelong vocal learning. It is these caveats that show how the traditional bird model limits the potential analogies made between bird human behavior: human vocal learning manifests itself throughout the life of the individual, is present in both sexes, and is more rapidly interactive than other forms of avian vocal communication [71, 56]. To enhance the current model, other avian groups should be included, especially those whose biology and behavior happens to fulfill many of the aforementioned limitations of the songbird model. Parrots, where both sexes show lifelong vocal learning, may offer more valuable insights into the ancestor of parrots and songbirds [10].

## **1.2 Ontogeny and Sex in Relation to Vocal Learning**

Similar to human babies, birds exhibit a period of development where they produce long strings of seemingly random sounds, referred to as vocal babbling. Following the babbling stage, most songbirds exhibit a brief period during juvenile development in which they must learn the vast majority of their species-specific song – as adults they can no longer add to their repertoire, referred to as close-ended song learners. By adulthood, close-ended song learning species will have lost the ability to learn new vocalizations [15]. Conversely, most parrot species and some songbirds (e.g., Corvids like crows and magpies) retain the ability to imitate and spontaneously combine sounds throughout their life [15, 10, 42]. The precise cause for this difference in vocal learning ability remains unknown. One possible explanation is that vocal learning occurs across a spectrum of close-ended song learners and life-long song learners, rather than a dichotomy of closed versus open-ended [12]. In the close-ended vocal learning model, young males have a set time limit in which to learn song signals and syntax, which the adult females will use to judge their appropriateness as potential mates. Typically, songbird mating systems are such that an ideal song type, in syntax and phonology, is the target of female mate choice. The ability of the male to imitate the ideal song demonstrates to females his cognitive fitness: the ability of an animal's brain to efficiently learn and accurately reproduce vocalizations. Imitative acuity is believed to be a strong indicator that the male's juvenile development was stable; either by virtue of genetic and

environmental pressures including attentiveness of parental care [64, 55].

The overrepresentation of male-exclusive song learning in the traditional avian vocal communication model is since in many songbird species the females are not prolific singers. Ancestrally, vocal learning is thought to be monomorphic (males and females of ancestral songbird species were thought to equally possess the trait) [54]. Although dimorphic (only males can learn) song learning has spread among modern birds, the females of nearly 30 percent of extant songbird species lack the neural architecture necessary to learn new vocalizations [54]. This is not the case for female parrots, which retain vocal learning throughout adulthood. The body of research supporting the traditional model of avian vocal communication is focused on species whose behavior is different than humans: close-ended single sex, usually male learning. This study aims to add to the traditional model of avian vocal communication by investigating vocal behavior in a poorly-known parrot species of *Amazona*, a genus known for their vocal flexibility in captivity but understudied in nature.

### **1.3 Interactivity of Avian Song Behavior**

The differences in various life histories and song learning neurological traits demonstrate parrot vocal behavior could be more comparable to human language than the conventional oscine model. Current models seldom address categories of vocal behavior that are interactive, such as the duet. Perhaps the best-studied, but less interactive, avian signal is the dyad, typically sung by males of the same species in the context of competitive interaction [68]. The dyad's vocal features can be time-specific (ex. counter-singing or overlapping) and pattern-specific (ex. song type matching). In a common form of countersinging, a male songbird matches the song type sung by a rival, the participants in the singing bout will rapidly go through the song types in their mutual repertoire [68, 29] The speed and pattern tends to intensify as tension between participants escalates, while conspecific females and other rival males can eavesdrop on the display and judge the social status of the singers based on their vocal merits [68]. These songs also display the motivations of the singers to the surrounding community, for example, does a singer intend to steal the territory of a neighbor, is he available for extrapair copulation [70, 58]?

Overlapping can occur in dyadic interactions, masking the rival's signal. This would seem

to be a boon for the overlapper as a display of his superiority, but it tends to be reserved for high-conflict dyads because overlapping weakens the communication value of the display to conspecific eavesdroppers [68, 29]. Dyadic songs have two weaknesses as models for human communication. First, dyads have less precise temporal coordination than human vocal interactions (i.e., dialogue). Second, the learned framework of nonrandom associations between signals (grammar) is stricter in human language than in dyads [57]. Although countersinging species do have to learn a song framework to respond quickly with the appropriate song match, the two scenarios have hindered interdisciplinary engagement between the fields of Animal Communication and Human Conversation Analysis [47, 57]. Studies exploring other, more humanlike, avian vocal interactions would benefit a host of disciplines.

The dyad is characterized as a signal display driven by inter-species conflict. In contrast, human vocal communication likely serves a greater diversity of functions in addition to conflicts. Additionally, the interactivity of dyads is somewhat slower than in humans and therefore requires less cognitive sophistication on the part of the listener [57]. The behavioral aspect that is lacking from the traditional avian vocal communication model—interactivity—is best associated with duetting, a complex behavior which many parrots are known to perform [68, 47, 46, 57]. Human vocal communication is thought to be more similar to avian duets, as they both involve coordinated, rapid and precise interactive responses [68], turn-taking rules (the ability to rapidly exchange signals without overlapping) [65]; both socioecological scenarios that often require vocal learning [33]. The development of more sophisticated vocal interaction rules, such as turn-taking has been shown to occur in humans [36] but analogies to bird behavior are lacking [46]. Unlike the non-duetters, which make up most of the traditional models of avian vocal learning, the precise interactive behaviors of duetting species have the potential to reveal similarities in the higher-level vocal interaction rules of humans and birds. Duets are much more precisely interactive in nature and broaden the scope of the avian vocal learning model to address potential analogues of human conversation.

## 1.4 Vocal Duets

Duets are precisely-timed alternating or overlapping vocal signals made by a mated pair. The coordinated displays vary along a spectrum from relatively simple duets to those of high acoustic and temporal complexity [27]. Duetting is the product of two levels of behavioral organization: individual-level and pair-level [46, 33]. The individual behaviors—song initiating and response—are considered to occur independently and dependently, respectively [68]. The phrase initiated by the leading pair member is considered to be independent of the partner, while the pair member's responding phrase depends on the preceding phrase [68]). This interactive process is characterized by a distinct structure involving pattern-specific “answering rules” and time-specific “timing rules” [46]. Answering rules are defined as the individual-level behavior in which a respondent consistently answers a preceding phrase type with a specific phrase type or linking the timing of the response to the timing of the previous phrase [33, 45]. Logue and Krupp [46] isolate phrase timing from answering rules and into the separate “timing rules”. Like song, duetting appears to be multifunctional [63, 31, 19]. Functions can be categorized by the intended receiver(s) as either: intrapair (communication from one pair member to the other) or cooperative (a joint effort by the pair to communicate to the broader social group) [33]. Purported intrapair functions include exchanging information between mates [22] and establishment and maintenance of pair-bonds [60, 3]. Purported cooperative functions include: communicating information about potential danger to the broader social network; to guard a mate from competitors [27]; and to communicate pairbond information to other pairs that compete for breeding sites [31, 63]. The emphasis on territoriality as a correlate of duetting is likely related to duetting being more common among non-migratory tropical species, whose stable climate favors the establishment of year-round territories [33]. The fine-scale temporal coordination of an antiphonal duet is considered an indication of the duetter's attentive ability [63]. The cooperative functions of duetting, mate and territory guarding, must be precisely timed to show extrapair members that the pair is united. Temporal precision functions to minimize lag time due to distance or inattention, displaying to eavesdroppers the appearance of the duetters as proficient territory holders who are unreceptive to solicitations for extra-pair

copulation [63]. Antiphonal duets are finely timed in that the average latency (lag time between a pair-member's production of a signal and the response of the other pair-member) is 24 ms, closely resembling that of human conversational turn-taking (averaging around 200 milliseconds regardless of language) [57]. The time difference between 24 ms and 200 ms would appear dissimilar but human turn-taking had been found to vary with the language spoken; for example, average latency in a Japanese conversation is 7 ms [65]. Not only is duetting a more suitable behavior from which to model vocal learning, but parrots are the ideal family to model considering their specialized language-processing neuroanatomy and characteristic monomorphic, open-ended song learning.

### 1.5 Parrot Duets

Many tropical birds perform antiphonal duets, including parrots (Psittacidae). Balsby and Bradbury [10] reviewed five parrot species representing four separate genera whose duets have been studied. Three of the known duetting parrot species (*Brotogeris versicolor*, *Brotogeris jugularis*, and *Amazona auropalliata*) are found in Central America while the other two are from southern equatorial Africa (*Poicephalus guliemi* and *Agapornis roseacollis*). Parrots found in the tropics of South America and Australasia are likely duetters as well [73]. The life history and ecology of tropical birds is likely related to the suspected higher prevalence of duetting in this region, although this relationship has not yet been supported with phylogenetically-controlled analysis [6, 27]. The relationship between duet structure and function in parrots has been studied in the yellow-naped amazon (*Amazona auropalliata*) [18, 21, 22, 20]. Researchers concluded that the duets of the yellow-naped amazon are performed according to a set of predetermined syntactic rules described in 2009 [21]:

- i. Males and females have different duet note types
- ii. Sex-specific notes can be repeated or alternate in a paired fashion
- iii. Sex-specific note types follow each other in a defined order within the duet
- iv. Females initiate the sex-specific part of the duet

Although this study chose to use the term “syntax” to draw parallels with the framework

underlying human language, syntactic rules can be termed more neutrally as “rules of interaction”. The above rules of interaction for yellow-naped amazon duets fall into three subcategories: (i) the non-random association of notes (which notes are used in which order); (ii, iv) sex-determined roles (who uses which notes and in which order) and (iii) the temporal precision of notes (the duration between notes). These interaction rules were determined by playing recorded duets to pairs of yellow-naped amazons and assessing their reactions. By artificially creating duets that break the syntactic rules and noting that the pairs had a delayed reaction to the rule-breaking duets, researchers concluded that only duets following these interaction rules were perceived by the pairs as authentic [22]). The nature of the interaction rules may be similar in other parrot species but is currently unknown.

### **1.6 Temporality of Duet Interaction**

The yellow-naped amazon duet study focused on the interaction rules that deal with note order, while the study did not explore variation of temporal precision beyond observing that the average inter-note response time was 680 ms for males and 800 ms for females [21]. Duets with overlapping notes (inter-note response time less than 0 s) were excluded from analysis, even though overlapping notes were observed often. Overlapping notes are challenging to work with because the components of each individual’s vocal contribution cannot be analyzed spectrographically since they are occurring simultaneously across temporal-frequency domains. Intuitively, overlapping notes could be similarly challenging for duetting parrots to interpret—like when a conversation is interrupted by multiple speakers. Although difficult to work with, overlapping notes appear to be a part of duet interaction rules of in at least one wild parrot.

To hypothesize how overlap could potentially be related to duet function, it is helpful to review the existing knowledge surrounding avian vocal interruptions and antiphonal duets. Songbirds have long been observed to modify their signal timing when singing to avoid “signal-masking” (when an individual’s vocalization interferes with/overlaps another’s in the time-frequency domains) other vocalizing birds [28] and even urban noise ([61, 62]. Some believe the mechanism of avoidance of signal-masking could be responsible for or related to the temporal coordination in

duetting birds [33]. Similarly, antiphonal duets have long been expected to demonstrate very low overlap of components [27]. Masking avoidance has guided much of the contemporary investigation of antiphonal duetting behavior. A generalization of the masking avoidance theoretical relationship between duet function and overlap is that overlap is considered a detrimental feature in species in which overlap is highly variable and rare overall (uninterrupted notes are more common), or for contexts in which overlapping duets elicit negative or neutral reactions from listeners. This masking avoidance relationship between duet function and overlap has been supported experimentally in a number of species. Previous studies of temporal precision in antiphonal duetters have mostly concluded that any partial overlap is either undesirable [32, 34, 45, 22] or of no significance [24], but that hypothesis has not been evaluated in parrots. Hall's (2006) assessment of temporal precision in duetting Australian magpie-larks (*Grallina cyanoleuca*) found that overlap was absent from duets with precise temporal coordination, and that precise temporal coordination was associated with longer-term, monogamous pair-bonds [32]. Hall and Magrath (2007) further demonstrated that variable temporal precision (which contained overlapping segments) was perceived as less threatening compared to precise temporal coordination in duet playback [34]. These studies show that when magpie larks listen to a duet, the signal's degree of temporal precision relates social cues about those duetters to the listener. The social cue from a highly coordinated duet could be that pairs which have been together longer and have practiced and perfected their duet are also more experienced at defending their territories. These studies imply that overlap is an undesirable indicator of poor duet temporal precision. This conclusion has been supported by studies of temporal precision in warbling-antbirds (*Hypocnemis peruviana*) and black-bellied wrens (*Pheugopedius fasciatoventris*) [67, 45]. Logue and co-authors (2008) found duetters to be so sensitive to their own duet coordination that a gap or overlap in notes would cause the duetters to halt their display [45]. Signal-masking avoidance is a concept that originated in observations of conflict between conspecific males. Since duets are multifunctional, there may be more options than this one function which stems from a narrow context of same-sex conflict rather than a broader context of mated pair coordination.

In consideration of duet multifunctionality and mated pair coordination, overlap does not necessarily have to be detrimental to duet quality but could be a feature that enhances duet quality. A pair-member overlapping their partner could be the overlapper's demonstration of their attentive commitment to the partner's duet. A relationship of attentive enhancement between duet function and overlap posits that overlap is considered an enhancing feature for species in which overlap is highly variable and overlapping notes are more frequent, or for contexts in which overlapping duets elicit positive or neutral reactions from listeners. This attentive enhancement theoretical relationship between duet function and overlap has yet to be experimentally tested. Duetting behavior is not a strict dichotomy of precise antiphonal or overlapping. As a multifunctional signal there may even be contexts in which antiphonal precision is employed while other contexts employ equally valid polyphonic functions. For species whose duet behavior appears largely antiphonal but with variable temporal precision, the masking avoidance concept would deem the entire species to be incompetent duetters. Reexamining the incidence of overlap in these incompetent duetters from the perspective of attentive enhancement could lead to evidence that temporal precision is unimportant or that overlap itself serves a very different function in these species.

## **1.7 Study Species and Population**

Red-crowned parrots, *Amazona viridigenalis*, are about the size of an American crow (500 g). The primarily green parrot is distinguishable from other *Amazona* parrots by a red patch on the crown of the head that is trimmed by a blue edge and bright green cheeks. Adults have golden iris and their red crowns are more prominent in males. Juveniles tend to have less red on the crown which makes males harder to distinguish from the females. Juveniles have brown irises for approximately 6 months post-hatching which make them distinguishable in the field from the adults during recruitment.

Although red-crowned parrot vocal behavior has never been systematically studied, the species belongs to a diverse genus within which some congeners' wild vocalizations have been characterized (*Amazona amazonica*, [23]; *Amazona finschi*, [1]; *Amazona vitatta*, [48]; *Amazona farinosa*, [35]. However, the majority of these studies attempt to categorize vocalizations of the

functional repertoire rather than examine syntax-scale interactive vocal dyads. The exception being the previously mentioned *Amazona auropalliata*, a congener in which antiphonal vocal duets have been extensively documented by Christine Dahlin and Timothy Wright. Notably, overlapping notes in the duets of this species are considered common [21]. Overlapping notes themselves contradict the conventional definition of “antiphonal” duetting as established in Passerine models, but the overlapping observed in yellow-naped parrot duets is not the kind of synchronized duetting where pair-members sing all their notes while overlapping one another as found in some other Passerine species [33]. Documentation of red-crowned parrot duet behavior could render more clearly the nature of duets in *Amazona*.

Red-crowned parrots are native to a bird conservation region comprising the brushlands extending from southern Texas into the northern parts of the Mexican states of Tamaulipas, Nuevo Leon, and Coahuila [69]. The population has been declining for over 30 years, estimated to consist of a few thousand birds in a range of less than 8,000 square kilometers [9]. They are considered by the ICUN Red List of Threatened Species as globally endangered with extinction in their native habitat. North of the historic red-crowned parrot range exists a population suspected to at least partially consist of introduced individuals. It is currently unknown to what extent this population is isolated from the native populations of Mexico or if red-crowned parrots were extirpated from the Lower Rio Grande Valley (LRGV) during colonial times. The LRGV population has been established in the suburban landscape of South Texas for over 50 years [51, 14]. The current population size is estimated to be under 700 individuals [40]. This study focuses on the Easternmost portion of the LRGV population in Brownsville, TX.

The Brownsville study area is located throughout the southern portion of Cameron County, TX. The study area is known to host a resident population of approximately 250 red-crowned parrots [39]. In Brownsville, the red-crowned parrot appears well suited to the suburban landscape, foraging on golf courses and in backyards, communally roosting in the trees of a public park and nesting in close proximity to human development [14]. This study is focused on an area consisting of 20 active natural nest sites and an additional 40 artificial polyvinyl chloride (PVC)

nesting cavities having been installed by researchers at the University of Texas Rio Grande Valley in collaboration with Texas Parks and Wildlife and the local community as part of an endangered species habitat-enhancement effort.

## **1.8 Objectives of Study**

The primary objective of the study is to establish a baseline of knowledge of the acoustic dynamics of red-crowned parrots' duetting behavior. Several questions will be addressed. Are the notes used in the duet used only in the context of duetting or are elements of the duet also found in other parts of the functional repertoire of vocalizations (e.g., contact calls)? Are notes used interchangeably by both sexes or are there sex-specific rules? Which sex's note structure is more variable within and between pairs? Do the sexes vary in temporal precision (temporal response) within a duet? Which sex's temporal precision is more variable within and between pairs? Secondly, I will determine whether overlap in pair duets is a reliable indication of coalition quality. If overlap is associated with poor duet coordination, pairs whose nests fail should perform duets with overlapping signals more frequently, while overlapping signals should be infrequent in the duets of pairs who succeed in maintaining a nest site throughout the breeding season and rearing chicks to fledging age. To investigate this hypothesis, I audio-video recorded naturally-occurring duets in a sample of pairs throughout successive breeding seasons to obtain metrics of individual participant's roles in duets and how this varies across pairs, while estimating their nesting success and behavioral context.

## CHAPTER II

### METHODS

#### **2.1 Methodological Approach**

The primary objective of this study established a baseline of knowledge of the acoustic dynamics of red-crowned parrots' duetting behavior. In order to fully address all the facets of this question, I quantified multiple acoustic variables associated with duet notes, with a specific focus on the presence and duration of overlap from duets produced by free-living red-crowned parrots (unprompted by experimental playback) and determined whether there is a significant relationship between overlap and coalition quality. My methodological approach can be summarized as: I observed pairs throughout successive breeding seasons in 2019 and 2020, while taking note of their nesting success and behavior and making high quality audio-video recordings of their naturally-occurring duets to measure spectrographic structure of notes and the presence and duration of overlapping signals.

#### **2.2 Data Collection**

. Audio-video recordings were made of duetting and contact-calling by breeding pairs at 17 nests throughout the 2019 and 2020 breeding season. Audio-Video recording was performed with a Cannon XF Professional Handheld Camcorder, wired and mounted with a Sennheiser MKH 70-1 unidirectional shotgun microphone. Video was recorded in HD (1280 x 720 resolution) at 59.94 frames per second (FPS) and audio recorded 48 kHz 16-bit sampling rate and saved as MPEG2 files. Study nests were chosen based on whether the researcher was granted property-owner permission and whether there was a clear field-of-view to the nest for filming. To capture beak movements of individuals, the filming distance was between 20-40m from the vocalizing pair. To

minimize disruption to the parrot's behavior, filming was performed from a blind. Blinds consisted of structures that were pre-existing to the landscape near the nest site, such as cars, gravestones, brick walls, and dumpsters. Nests surrounded by dense vegetation or near heavily trafficked roads were excluded from study due to visual and noise disruption.

Throughout the breeding season (February 30 to July 30), nesting pairs of red-crowned parrots were filmed during bouts of duetting. Four pairs were filmed in 2019 and 13 pairs were filmed in 2020. A bout may consist of more than one duet. Individual duets were determined following methods established by Dahlin and Wright [18] as being a sequence of rapidly alternating signals separated by greater than two seconds of silence. Duets were identified as having a minimum of three notes alternating between pair members (male-female-male or female-male-female). Repetitive sequences by the same pair-member were included as part of the duet as long as they were within the predefined two second note interval threshold.

Video footage was used to identify the sex of the duetting parrots. Duets in which the sex of the duetter(s) could not be identified with observer confidence, or duets with three or more participants, were omitted. The sex of the duetters was determined with observer confidence in 205 duets. To eliminate the confounding variable of unequal distance between the microphone and each of the duetters (causing sound to reach the microphone at different times due to distance instead of temporal precision between duetters), all of the duets in the study are from stationary pairs in which both duetters are visible in the video frame, less than 5 meters apart, the distance from the pair to the microphone varied but both parrots were more-or-less the same distance ( $\pm 30$  m) from the microphone when duetting. By maintaining a visual line of sight to the duetters when filming, there were no large objects blocking the path of sound from the birds to the microphone.

The video footage and audio spectrograms were examined frame-by-frame simultaneously in Adobe Audition (2018). Whenever duets with the previous criteria (proper distance, ability to determine which individual is vocalizing, sex identification confidence, clear audio) were detected, the sex of the duetters was marked and duet notes were selected (Figure 2.1).

### **2.3 Duet Note Length**

Using the two seconds of silence cutoff rule established by Dahlin and Wright [18] to determine what notes are part of any single duet, I recorded duets ranging in length from 3 notes to 13 notes. Duets more than 8 notes in length were uncommon, only occurring 22 times out of 205 duets. This uneven variation in duet length made it difficult to accurately categorize and standardize the sequence of notes within a duet. Rather than exclude the longer duets entirely, it was decided to limit analysis to only the first six notes of every duet. Duets with fewer than seven notes were included in their entirety.

### **2.4 Spectrographic Analysis**

With the use of Raven 1.6 software, spectrograms were generated from the audio of 205 duets. The spectrograms were made with a Hann window size of 512 samples, a 3 dB Filter Bandwidth of 124 Hz, with 50 percent overlap, and a hop size of 256 samples. In order to quantify the acoustic structure of duet elements, individual notes were selected from each duet ( $n = 1305$  notes). Raven has many measurements available, however some (like amplitude) were not relevant to this study because they cannot be accurately measured with this experimental design, while other measurements are largely redundant. This study intended to investigate temporal qualities with as much consideration as acoustic qualities, so it was important to include delta time (total note duration) and other interval parameters. A temporal quality of particular interest was the time it takes for the partner to respond its mate during the duet, termed the inter-note interval, and was measured as the difference in time from the end a note and the beginning of the following. From all the possible measures of frequency available, eight were selected that seemed to be the most accurate representatives of note variation. The first is entropy which can be measured as averaged or aggregated across the timescale of the note. Entropy quantifies the disorder of the acoustic energy across frequency spectra; low entropy notes have energy in fewer frequencies at any given time, while high entropy notes have energy dispersed among many frequencies. The second was bandwidth 90% (BW 90%) which depicts the distribution of energy across the 90% of the bandwidth

of frequencies of the whole note. A BW 90% of zero indicates the note is a pure tone from start to finish, while larger BW 90% values indicate energy is distributed across more frequency bands. The third, fourth and fifth are center frequency, frequency 5% and frequency 95%, which depict, respectively, the region of the notes' most intense energy and the minimum and maximum energy in the note excepting 5% at both extremes. The final two measurements, the average slope and number of inflection points were both derivatives of the peak frequency contour, which is similar to a coordinate graph marking the changes in the note's most intense energy (usually the fundamental frequency) over time (Figure 2.2). The average slope consolidates the coordinates into a single numeric representation of the general tendency to decline or increase in frequency along the course of a note. A note with a peak frequency contour that begins low but escalates in pitch will have a large positive average slope, while a note whose pitch begins high but descends in pitch will have a large negative average slope. A note whose pitch is flat and does not change over time will have an average slope closer to zero. Figure 2.2's blue dotted line shows a gradually descending peak frequency contour, with a slightly negative average slope. The final measurement was the number of inflection points of the peak frequency contour which is a count of the number of times the "pitch" of the note changes direction across time. A note that is a flat clear tone with no variation in pitch would have fewer or no inflection points compared to a note whose pitch rises and falls multiple times. The inflection points of the note in Figure 2.2 are occurring in the beginning of the note, there orange highlights each inflection point, meaning there are 5 times that the note's average slope changes direction. Both of these measurements, average slope and number of inflection points are only valuable for notes with low entropy, because notes with high entropy have diffusely dispersed acoustic energy in the frequency domain and therefore tend to lack a contoured area of higher energy. For example, in figure 2.1, the first note of the duet has high entropy as noted by the way the note is fuzzy gray and lacks any dark contoured lines; notes with high entropy like this one will not have meaningful measurements of Peak Frequency Contour because there basically is no peak frequency contour. In contrast, the second and third notes of the duet in figure 2.1 have distinct peak frequency contour that starts at a higher frequency, has a single downward inflection point, and ends

at a lower frequency. In notes such as these, there is clearly a negative average slope and a single inflection point.

## **2.5 Statistical Analysis**

In attempt to determine whether sexes used different types of notes, and which notes are at the beginning vs end of the duet, Generalized Linear Mixed Modeling (GLMM) was used in SAS (version 9.3). First, GLMM was employed to evaluate the influence of eight acoustic variables on the acoustic variation across a subset containing only duets without overlapping syllables (Table 3). Three different models were built to see which best explains the variation and empirical support. All three models included pair identity as a random effect to control for repeated observations of the same individuals. The first model included sex as a fixed factor, second model included pair and sex as fixed factors, and the third model included interaction between pair and sex. Secondly, GLMM was employed to evaluate the influence of sex, pair, and duet structure as fixed effects on the temporal variation of the notes in duets (dependent variable). Three models were tested, all with pair identity included as a random effect. The first model controlled for sex differences, the second model controlled for variation in note order, the third model accounted for interaction between variation in sex and note order. Akaike Information Criterion (AIC) was conducted in order to compare and rank various models according to their AIC weights (w); lower AIC scores are considered better fitting (higher weight) among models included. Significant P-values for individual model terms are indicated by an asterix.

## **2.6 Visual Note Sorting**

Visual methods were employed to qualitatively categorize the note spectrograms. First, every note of total 205 duets were categorized by visually assessing the contour of the spectrogram for each note. Common spectrogram contours were grouped together and their similarities were further confirmed by listening to the audio recording of each note.

As previously mentioned, due to the limitations of spectrographic measurement, overlapping notes were excluded from analyses described in Section 2.4 and 2.5. A benefit of visual categoriza-

tion of notes is that the overlapping notes often differed, allowing the individual notes to be isolated from one another and be categorized into discrete note types. In this age of artificially intelligent techniques for categorizing data visual note categorization may seem outdated, however, a trained human observer often performs more reliably than the suite of available autonomous computer-aided vocalization classification softwares [13]. Visual categorization allowed the inclusion of overlapping notes in the dataset. This technique can be considered as the human eye analyzing the shape of the spectrogram which captures all the dimensions of acoustic variation simultaneously and then the human brain processes the images and sorts them into categories based on visual similarity.

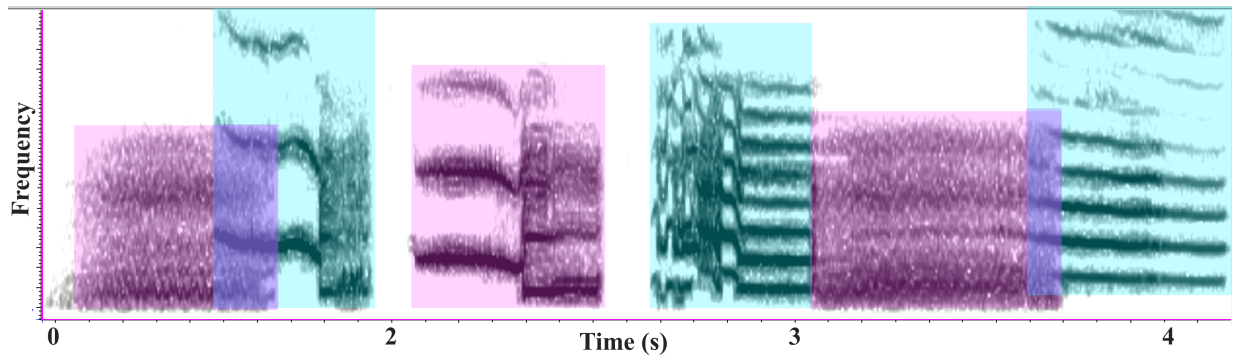


Figure 2.1: Example Red-Crowned Parrot Duet Spectrogram. The above spectrogram depicts a single duet sung by a mated pair of red-crowned parrots in Brownsville, TX in the spring of 2019. Spectrograms are visual representations of a sound where frequency is on the y-axis and time is on the x-axis. The darkness of the spectrogram image represents amplitude, the blackest features have the highest amplitudes. Notes sung by the male pair-member are highlighted in blue and notes sung by the female pair-member are highlighted in pink. Spectrograms were generated in Raven 1.6 with a Hann window size of 512 samples, a dB Filter Bandwidth of 124 Hz, with 50 percent overlap and a hop size of 256 samples.

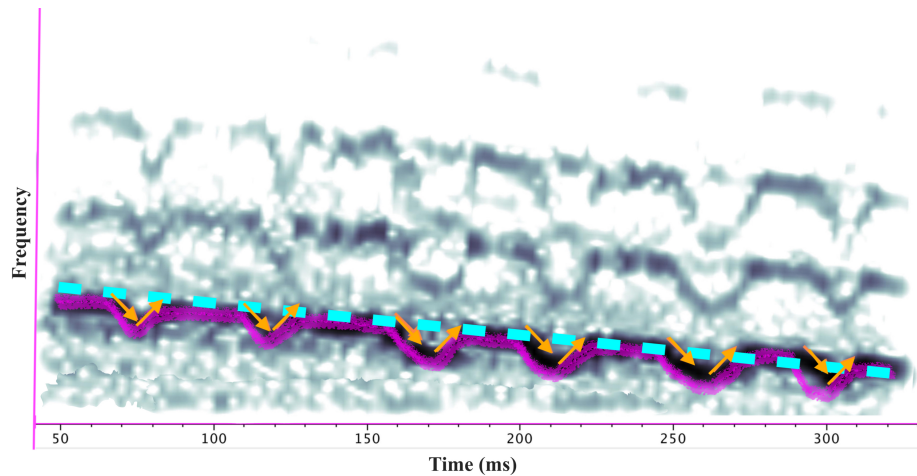


Figure 2.2: Example of Spectrographic Acoustic Measurements. Pictured is a spectrogram of a single note from a red-crowned parrot. The peak frequency contour is highlighted in pink. The inflection points are denoted by orange arrows. The average slope is dotted blue line.

## CHAPTER III

### RESULTS

#### 3.1 Ecology of Duetting

For two consecutive nesting seasons, 17 mated pairs of red-crowned parrots were recorded at nesting sites across Brownsville. The nesting sites were either in artificial nest tubes, natural cavities in palm snags (*Washingtonia spp.* and *Sabal spp.*) and living oak (emph~~Quercus~~ *Quercus spp.*) trees, or in walls of buildings. Duetting behavior began in January or February and became more predictable and vigorous in March; egg laying occurs in early March in Northeast Mexico (Enkerlin 1995). Duetting often continued daily until fledging had culminated in late July (Fig 3.1). Duetting typically occurred within an hour after sunrise and again an hour before sunset (Fig. 3.2). Duetting was typically performed when pair members were on or within ca. 5 m of the nest.

Duetting was at times performed in an apparent aggressive response to conspecifics as well as other cavity nesting species, such as Black-bellied Whistling-ducks (*Dendrocygna autumnalis*), European Starlings (*Sturnus vulgaris*), Green Parakeets (*Psittacara holochlorus*) and Red-lored Parrots (*Amazona autumnalis*). In the case of other conspecifics, pairs would counter duet, which usually resulted in a larger number of duets given by the focal pair. During March-May, when females were incubating or brooding throughout the day and night, duets were given upon arrival of the male and after the female had ascended to the entrance.

The number of duets recorded per pair averaged 12.0 (range = 3-40,  $n = 205$  duets). More than half of all duets had overlapping components (53%). The number of notes per duet averaged 6.2 (range = 3-15,  $n = 1305$  notes) (Table 3.1, 5th column). Males and Females alternated notes during the duet (i.e., antiphonal), and females were the majority duet initiator in 35% of pairs ( $n$

= 17 pairs) (Table 3.1, 8th column). The majority of pairs were successful in raising offspring to fledging age; one nest was poached before nestlings could fledge, one pair's nest was destroyed in a storm—killing the nestlings, while only one pair's nestlings were never observed and presumably died from unknown causes prior to fledging (Table 3.1, 9th column).

### **3.2 Acoustic Structure of Duets**

Spectrographic analysis indicated that the acoustic structure of duet notes varied between sexes and the order of notes within a duet (Table 3.2). AICc analysis indicated that the complex model (sex, order and their interaction) was the top-ranked model predicting 5 of 8 acoustic variables ( $w = 0.76$ -1.0; Table 3.3). For the three remaining acoustic variables, duration, average slope and average entropy, the complex model was second-ranked model. Note order was the top model predicting duration and average slope of notes ( $F_{1,494} = 6.84$ ,  $P < 0.0092$ ,  $F_{1,496} = 9.68$ ,  $P < 0.002$ , respectively) ( $w = 0.74$ ,  $0.45$ , respectively; Table 3.3). Sex was the top-ranked model for average entropy ( $F_{1,496} = 12.77$ ,  $P < 0.0004$ ) ( $w = 0.63$ ; Table 3.3).

### **3.3 Acoustic Structure and Sex**

Marked sex differences were detected in the acoustic structure of the notes' aggregate entropy and number of inflection points (Figures 3.3 and 3.4, respectively). Notes sung by females had a significantly higher aggregate entropy (Females =  $3.6 \pm 0.44$ , Males =  $3.4 \pm 0.46$ ), and a greater mean number of inflection points (Females =  $30 \pm 9$ , Males =  $23 \pm 9$  inflection points).

### **3.4 Acoustic Structure and Note Order**

Only 16% of notes were same-sex repeats, meaning that the male or female repeated themselves instead of taking turns with their mate in the typical alternating duet fashion. The alternating of sexes and note types was demonstrated in the acoustic structure of the notes by the means of that note order for the acoustic parameter of aggregate entropy and number of inflection points. (Figures 3.5 and 3.6, respectively).

### 3.5 Temporal Variation of Duets

Of the 205 duets, 53% contained note overlap (Table 2.1). Regardless of duet overlap, as the duet progressed, the inter-note interval of duets tended to decrease in time (Table 3.4). However, overlapping notes occurred nearly as frequently at the beginning of duets (first note 12% overlapping, sixth note overlapping 14%; Table 3.4). AICc analysis indicated that the complex model was the top-ranked model predicting variation in inter-note interval ( $F_{1,801} = 14.37$ ,  $P < 0.0002$ ) ( $w = 63\%$ ).

### 3.6 Qualitative Duet Variation

Manual note categorization resulted in approximately 30 different note types, some notes occurring as many as 100 times, while others only occurring once or twice. Some notes showed sex-specificity and some other notes showed note order-specificity (Figure 3.7). The manually categorized notes also demonstrated the alternating sexes of the notes and the variety of syntax between and across pairs (Figure 3.7).

### 3.7 Overlapping Notes

The overlapping notes had to be excluded from the cross-correlation and GLMM analysis because it is not possible to tease apart two complex sounds that overlap in the frequency-time domain. However, the visual note categorization was able to determine the identity of overlapping notes (Figure 3.7).

Table 3.1: Summary of Nests and Duetting Behavior

Year	Pair Name	Nest Type	Filming Days	Total Duets	% Duets with Overlap	Avg # of Notes	%Female-Initiated Duets	Nesting Attempt Success
2020	Acacia Lake	Palm	3	13	38	7.2	84%	yes
2019	BlueBonnet	Palm	2	10	70	5.9	70%	yes
2020	Cobblehead's	Palm	2	11	73	6.5	27%	yes
2019	DantePilar	Bank	2	12	33	6.1	67%	no
2020	Davita	Palm	3	23	17	6.1	43%	no*
2020	Dean Porter	Oak	3	9	56	7.3	55%	yes
2020	Don Quixote	Palm	3	15	47	5.6	13%	yes
2020	Hole13VICC	Palm	3	9	44	7	2%	yes
2020	Honeydale	Palm	3	3	100	7	33%	yes
2020	La Plaza Apts	Palm	2	16	25	7.3	53%	yes
2020	Lonestar Bank	Bank	1	6	0	5.8	33%	yes
2019	P2Library	Nest Tube	1	6	0	4.8	0%	no*
2020	P25 Oliveira	Nest Tube	1	28	96	6.9	25%	yes
2019	P29 Lincoln	Nest Tube	3	17	47	4.6	50%	yes
2020	P34 Bike Trail	Nest Tube	2	8	0	6.8	100%	yes

Table 3.2: Summary of Duet Acoustic Structure. Each row indicates a different acoustic variable, the columns display the mean  $\pm$ standard deviation for that acoustic variable within the indicated note order.

NoteOrder:	First	Second	Third	Fourth	Fifth	Sixth
FEMALES <i>n</i> :	30	40	34	38	43	33
Avg. Entropy	3.7 $\pm$ 0.44	3.8 $\pm$ 0.30	3.6 $\pm$ 0.45	3.4 $\pm$ 0.49	3.6 $\pm$ 0.46	3.6 $\pm$ 0.44
BW 90%	2819 $\pm$ 899	2827 $\pm$ 660	2545 $\pm$ 716	2470 $\pm$ 763	2658 $\pm$ 784	2446 $\pm$ 756
Center Freq.	2047 $\pm$ 530	2135 $\pm$ 517	1958 $\pm$ 266	1961 $\pm$ 328	1982 $\pm$ 275	1835 $\pm$ 373
Delta Time	0.32 $\pm$ 0.09	0.32 $\pm$ 0.09	0.36 $\pm$ 0.11	0.44 $\pm$ 0.13	0.40 $\pm$ 0.09	0.48 $\pm$ 0.09
Freq. 5%	1022 $\pm$ 343	1134 $\pm$ 316	1180 $\pm$ 292	1261 $\pm$ 330	1147 $\pm$ 283	1065 $\pm$ 264
Freq. 95%	3841 $\pm$ 1000	3961 $\pm$ 795	3725 $\pm$ 824	3730 $\pm$ 879	3805 $\pm$ 836	3511 $\pm$ 848
Avg. Slope	0.60 $\pm$ 3.5	0.66 $\pm$ 3.1	-0.85 $\pm$ 1.8	-0.30 $\pm$ 1.7	-0.13 $\pm$ 1.6	-0.50 $\pm$ 1.3
Inflection Pts.	29 $\pm$ 9	28 $\pm$ 9	28 $\pm$ 8	29 $\pm$ 8	31 $\pm$ 12	40 $\pm$ 26
Note Interval	0.32 $\pm$ 0.38	0.21 $\pm$ 0.15	0.13 $\pm$ 0.13	0.25 $\pm$ 0.25	0.12 $\pm$ 0.11	0.20 $\pm$ 0.20
MALES <i>n</i> :	62	52	58	49	40	32
Avg. Entropy	3.3 $\pm$ 0.46	3.5 $\pm$ 0.55	3.4 $\pm$ 0.6	3.5 $\pm$ 0.5	3.5 $\pm$ 0.5	3.6 $\pm$ 0.5
BW 90%	2381 $\pm$ 823	2430 $\pm$ 970	2578 $\pm$ 866	2531 $\pm$ 908	2667 $\pm$ 843	2868 $\pm$ 875
Center Freq.	2028 $\pm$ 365	1837 $\pm$ 301	1919 $\pm$ 294	1929 $\pm$ 307	2093 $\pm$ 431	2054 $\pm$ 464
Delta Time	0.31 $\pm$ 0.13	0.29 $\pm$ 0.15	0.35 $\pm$ 0.17	0.34 $\pm$ 0.17	0.39 $\pm$ 0.12	0.42 $\pm$ 0.12
Freq. 5%	1234 $\pm$ 365	1082 $\pm$ 309	1143 $\pm$ 319	1150 $\pm$ 329	11309 $\pm$ 243	1166 $\pm$ 268
Freq. 95%	3615 $\pm$ 924	3512 $\pm$ 984	3721 $\pm$ 906	3681 $\pm$ 899	3797 $\pm$ 868	4034 $\pm$ 911
Avg. Slope	0.41 $\pm$ 2.5	-0.51 $\pm$ 3.3	0.07 $\pm$ 2.5	-0.13 $\pm$ 4.7	-1.2 $\pm$ 2.6	-0.36 $\pm$ 1.7
Inflection Pts.	24 $\pm$ 12	25 $\pm$ 15	27 $\pm$ 17	25 $\pm$ 14	27 $\pm$ 13	31 $\pm$ 15
Note Interval	0.44 $\pm$ 0.46	0.20 $\pm$ 0.20	0.22 $\pm$ 0.23	0.10 $\pm$ 0.15	0.05 $\pm$ 0.10	0.03 $\pm$ 0.04

Table 3.3: AICc Analysis of GLMM Models. Lowest AICc score indicates the model which best fits the variation, weights indicate the strength of the model.

Dependent Variable	Model	AICc	AIC	w
Average Entropy	Sex	747.60	0.00	0.63
	NoteOrder	762.12	14.52	0.00
	Sex + NoteOrder	754.35	6.75	0.02
	Sex + NoteOrder + Sex*NoteOrder	748.76	1.16	0.35
Bandwidth 90%	Sex	8271.38	31.49	0.00
	NoteOrder	8274.66	34.77	0.00
	Sex + NoteOrder	8262.97	23.08	0.00
	Sex + NoteOrder + Sex*NoteOrder	8239.89	0.00	1.00
Center Frequency	Sex	7421.00	29.33	0.00
	NoteOrder	7422.88	31.21	0.00
	Sex + NoteOrder	7414.09	22.42	0.00
	Sex + NoteOrder + Sex*NoteOrder	7391.67	0.00	1.00
Delta Time	Sex	-576.97	55.73	0.00
	NoteOrder	-632.70	0.00	0.74
	Sex + NoteOrder	-630.58	2.12	0.26
	Sex + NoteOrder + Sex*NoteOrder	-451.51	181.19	0.00
Frequency 5%	Sex	7154.02	13.32	0.00
	NoteOrder	7157.22	16.52	0.00
	Sex + NoteOrder	7148.26	7.56	0.02
	Sex + NoteOrder + Sex*NoteOrder	7140.70	0.00	0.98
Frequency 95%	Sex	8286.42	29.69	0.00
	NoteOrder	8289.23	32.50	0.00
	Sex + NoteOrder	8278.08	21.35	0.00
	Sex + NoteOrder + Sex*NoteOrder	8256.73	0.00	1.00
Average Slope	Sex	2502.43	3.76	0.07
	NoteOrder	2498.67	0.00	0.45
	Sex + NoteOrder	2498.94	0.27	0.40
	Sex + NoteOrder + Sex*NoteOrder	2500.87	2.20	0.15
Inflection Points	Sex	4084.76	17.15	0.00
	NoteOrder	4081.34	13.73	0.00
	Sex + NoteOrder	4069.97	2.36	0.23
	Sex + NoteOrder + Sex*NoteOrder	4067.61	0.00	0.76

Table 3.4: Summary of Duet Temporal Structure. The first row displays the occurrence of overlapping notes, following rows display the mean and standard deviation of temporal parameters of overlapping notes of males and females are displayed in the note order within the duet.

Note Order:	First	Second	Third	Fourth	Fifth	Sixth
<b>FEMALES</b>						
<i>n</i> (overlap)	82(14%)	90(13%)	79(19%)	66(11%)	47(11%)	38(18%)
Note Duration	0.39±0.12	0.3±0.08	0.34±0.11	0.39±0.13	0.38±0.1	0.43±0.1
Inter-note Interval	0.14±0.27	0.15±0.14	0.1±0.16	0.17±0.22	0.1±0.11	0.12±0.19
<b>MALES</b>						
<i>n</i> (overlap)	89(11%)	87(23%)	82(15%)	74(13%)	59(17%)	29(9%)
Note Duration	0.38±0.16	0.46±0.18	0.41±0.12	0.38±0.17	0.4±0.12	0.45±0.15
Inter-note Interval	0.26±0.28	0.11±0.24	0.12±0.23	0.09±0.19	0.07±0.27	0.02±0.08

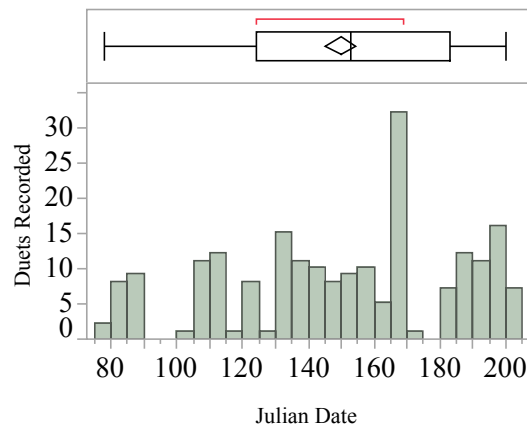


Figure 3.1: Julian Date of Duets. Distribution of 205 duets recorded between March-July 2019-2020. Horizontal axis is Julian date.

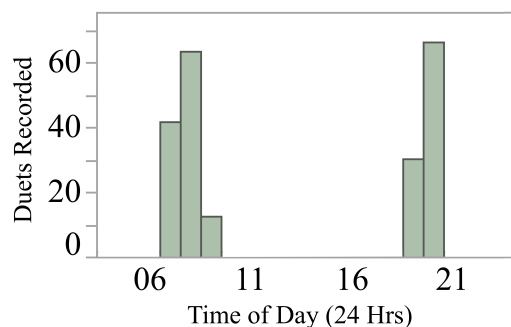


Figure 3.2: Time of Day of Duets. Distribution of time of day that duetting occurred. Horizontal axis is 24-hr period.

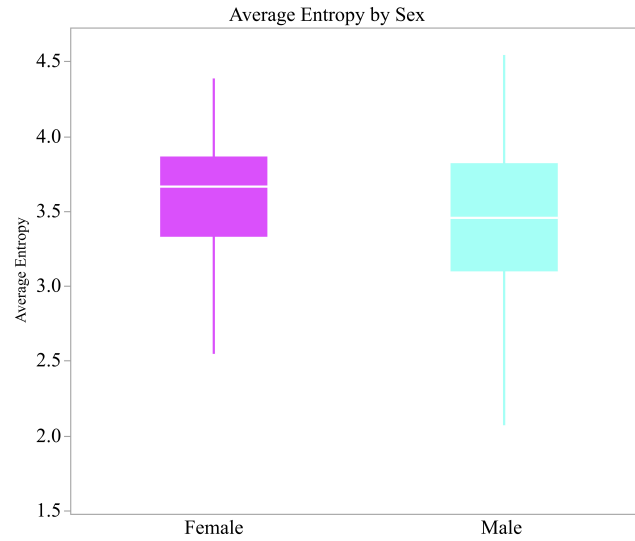


Figure 3.3: Average Entropy. For only the non-overlapping notes, average entropy for each sex is displayed as variation about the mean. The white line in the middle of the box plot indicates the mean, the upper and lower boxes denote the third and first quartile, respectively. The upper and lower whiskers denote the maximum and minimum of the dependent variable, respectively. Females are in pink, males are in blue. (Females = 30, Males = 23 inflection points).

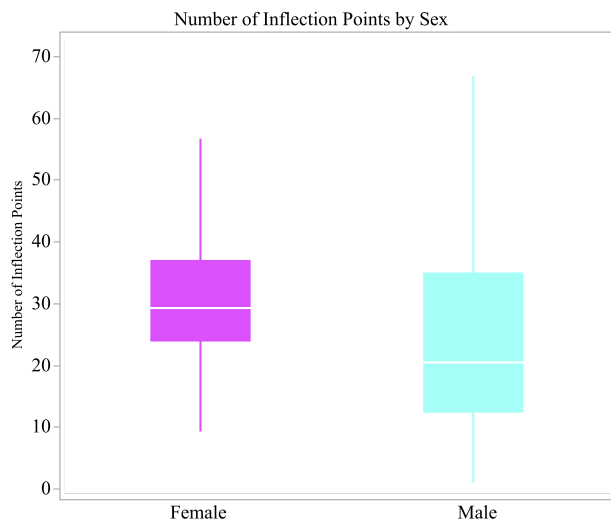


Figure 3.4: Number of Inflection Points. For only the non-overlapping notes, number of inflection points for each sex is displayed as variation about the mean. The white line in the middle of the box plot indicates the mean, the upper and lower boxes denote the third and first quartile, respectively. The upper and lower whiskers denote the maximum and minimum of the dependent variable, respectively. Females are in pink, males are in blue. (Females = 3.6, Males = 3.4 bits)

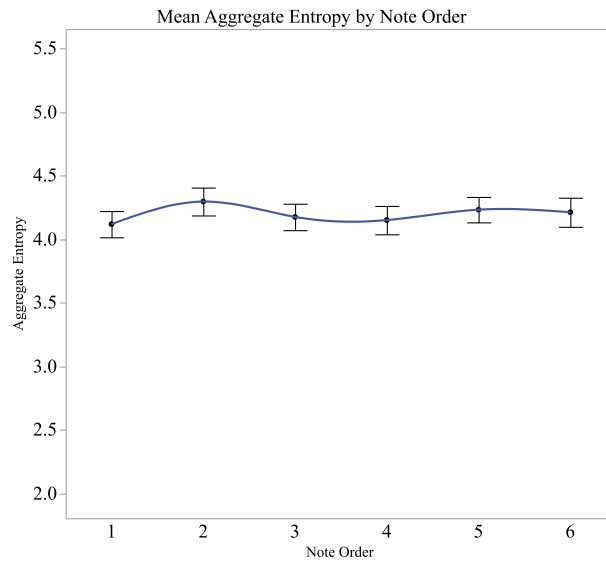


Figure 3.5: Aggregate Entropy by Note Order. For non-overlapping sex-alternating notes only, mean of Aggregate entropy by note order, with standard error bars.

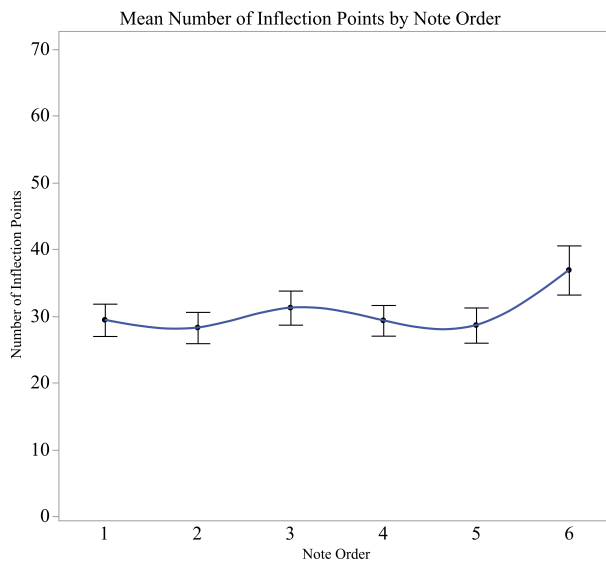


Figure 3.6: Number of Inflection Points by Note Order. For non-overlapping, alternating notes only, mean of number of inflection points by note order, with standard error bars.

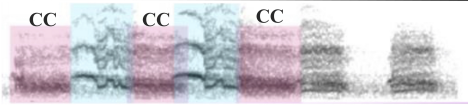

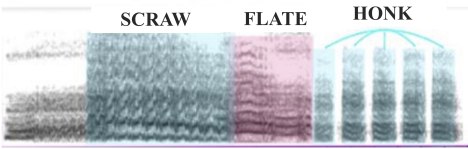


Note Type	<i>n</i>	% Sung by Female	Occur in % of pairs <i>n</i> =17	Occur in % of duets <i>n</i> =205	Example of Note Type Incorporated into a Duet	
CC	134	42.5	100	25.3		
CHELLO	49	34.7	64.7	11.7		
HONK	149	1.3	70.5	16.6		
FLATE	80	98.7	94.1	37		
SCRAW	113	6.2	100	53.2		
BING	47	95.7	88.2	21.9		
HELLO	52	63.5	52.9	17.5		
YEW	54	14.8	88.2	25.9		
BAH	79	88.6	100	35.6		
DING	48	97.9	82.3	22.9		
YOOHOO	59	96.6	94.1	94.1		

Figure 3.7: Visually-Sorted Note Types. Displayed are the top 11 most common notes out of the 30 note categories. Each note is depicted within a duet, highlighted in pink for female singer, blue for male singer. Note types not within the top 11 most common notes are not highlighted.

## CHAPTER IV

### DISCUSSION

#### 4.1 Ecology of Duetting

Duetting in free-ranging red-crowned appears to have an important reproductive function. Duetting was frequently observed during the breeding period and around breeding sites, and only rarely heard outside of the breeding period (Figure 3.1). Duetting was observed in aggressive interactions with other cavity nesters, both conspecifics, congeners and other cavity nesting birds. Duetting also occurred in response to duetting of other conspecific breeding pairs (i.e., counter-duetting). Duetting tended to occur within an hour of sunrise and within a hour of sunset (Fig. 3.2), as is the case for the dawn and dusk chorus' performed by many songbirds and other species. Whereas the reproductive functions of song are usually related to territory defense and mate attraction, parrot duetting appears to be used to defend small areas around nest sites and given the antiphonal nature of duetting pairs, long-lived nature of *Amazona* parrots and life-long pairbonds in many parrots [10], a less clear role for the functions of duetting in mate attraction. Thus duetting shares many similarities with seasonal song production known to coordinate reproductive functions but with some interesting differences related to cavity nesting and mating systems.

Females initiated nearly half of duets (43%,  $n=205$ ; Table 3.1), suggesting that initiation of the duet is void of predetermined sex-specific roles. Previous studies of the duetting of yellow-naped amazon parrots concluded that females were predetermined as the duet initiators based on the observation that they initiated 51% of the total 171 duets studied [18]. Although our observation of female red-crowned parrots initiating about half of the duets is more-or-less similar to the previous study, the opposite could be argued: given that parrot vocal behavior is more sexually egalitarian

(with females retaining lifelong vocal learning), it would be possible that these results of both studies support the hypothesis that sex roles in parrot duets are be more flexible than in many Passerines. However, it would be most conservative to interpret this result as inconclusive. A more thorough methodology for teasing out sex-specific initiation roles in antiphonal duets is to measure the frequency at which each pair-member vocalizes and the frequency at which their mate engages in a reply and a duet ensues [33]. As our study was the first to focus on recording the duets of free-ranging red-crowned parrots, and the primary goal was to discover “what is a duet” versus other vocalizations, it was not feasible to measure the call rates of pairs in this way. With our study having established the baseline of note categories most often observed at the beginnings of duets, this information will inform the design of future playback experiments to investigate whether male or female red-crowned parrots are more likely to initiate a duet and in what context.

Chicks surviving to fledging age were observed in most cases (Table 3.1), suggesting that most pairs were established and successful in parenting ability. Over half of all duets had overlapping components, but two pairs did not produce any overlapping duets, and some pairs produced almost exclusively overlapping duets (Table 3.1). This may lead one to wonder if the sample sizes of duet behavior were too small for these pairs. My sample sizes ( $n=17$  pairs, 205 duets, 1,305 notes/vocalizations) conforms within the range of other contemporary works characterizing vocalizations in congeners: 171 duets from 7 yellow-naped amazon pairs [22]; 27 duets from 11 orange-winged amazon pairs [23]; 462 vocalizations from Puerto Rican parrot individuals [48]; 8,622 notes from lilac-crowned amazon individuals [1]; 150 vocalizations from mealy amazon parrots [35]. Thus, there is considerable variation in temporal overlap across pairs, which might reflect differences in age or strength of pair-bond, however this will require more work.

Within this study’s dataset of arguably reasonable sample size, note overlap is an event far beyond what could be considered poor coordination skills on behalf of the pair-members. Overlap incidence was greatest in pairs with the largest duet sample sizes (Table 3.1), thus pairs with no overlap may have been under-sampled. Excluding natural disasters, over 90% of the pairs studied demonstrated sufficient parenting skills to successfully rear offspring—an observation

which contradicts the suspicions that overlapping notes are a mistake made by inexperienced pairs. Given that note overlap does occur so commonly, and most chicks did survive, overlap did not seem to be connected to poor coalition quality in my analysis (Table 3.1).

## 4.2 Acoustic Structure of Duets

Due to the confounding influence of overlapping notes on acoustic measurement accuracy, and the high occurrence of overlap in red-crowned parrot duets, acoustic structure analysis was limited to a portion of total duets recorded. The most complex GLMM model of the interaction of sex and note order was the top-ranked model predicting variation in the majority of the acoustic measurements (Table 3.3). This could be due to the complex model best capturing the differences in note types. Red-crowned parrot duet note types are quite variable and it does appear that sexes prefer certain note types and that certain note types tend to occur in either the beginning, middle, or end of a duet. Therefore, when the model includes note order, sex and their interaction it suggests that sexes tend toward different signals depending on the order in which they are used. Is this result the first example of duetting pairs who are able to share note types and deftly switch note types in adherence to a conceptual framework of predetermined note order rules? Logue (2016) described female black-bellied wrens (*Thryothorus fasciatoventris*) choosing her response note based on the preceding note sung by the male, but males and females of this species have sex-specific note types [46]. Wright and Dahlin (2007) observed this strict adherence to note order in duetting yellow-naped amazons and termed it “combinatorial syntax”, but they also found this species to have sex-specific note types [18]. The antiphonal duets of Australian magpie-larks (*Grallina cyanoleuca*) do show sex flexibility. Hall (2007) observed that both sexes could use all the types in the pair’s repertoire and would reply with contrasting types [34]. However, the duet structure in Australian magpie-larks is quite different, instead of being a sequence of discrete notes alternating between pair-members, the pair-member picks a repeating “motif” and begins the duet, then the partner layers his or her own responding motif in between the silences of the initiating mate’s motif, resulting in an antiphonal duet with repetitive elements which offset one another [34]. While Australian magpie-larks do possess sex-inclusive repertoire abilities on par

with parrots, their resulting duets do not closely resemble discrete turn-taking elements that make parrot duets more attractive as a model of human vocal interaction. Combinatorial syntax abilities along with sex-unspecific note type within the context of a highly-coordinated antiphonal duet may be a behavioral strategy not previously described in nature. Taken literally, the interpretation of the results of this study's complex model implies a degree of sexual vocal flexibility and strict adherence to note order in parrot duets, one which has not been documented in other wild duetting bird species, neither Psittacine nor Passerine. It is irresistible to draw comparisons to human vocal behavior, conversations in which participants of either sex take turns creating discrete responses and these responses are in reaction to the meaning of the utterance which precedes it in a structure known as syntax. For the human model of vocal interaction word order is important, turn-taking is also important, and both participants of any sex can use any of the word types while adhere to the order. Given their behavioral plasticity and vocal diversity, it does seem, at least superficially, within the capability of parrots to perform duets in this way. Captive parrots have demonstrated similar capacity for learning human vocal syntax, when taught by humans via operant conditioning [38].

I observed some agreement to the model's literal conclusion in prioritizing note order above sex from the manual note categorization. For example, a note that almost always occurred as the first note in the duet sequence, "Greet" was used by males or females but regardless of sex it was usually the first note. However, "Greet" was the exception, most note types were predominantly preferred by either males or females and that preference superseded note order. For example, a note type "Honk" was exclusively used by males, in some duets "Honk" was the 2<sup>nd</sup> or 3<sup>rd</sup> note, and in other duets "Honk" was the 5<sup>th</sup> note, regardless only males honked no matter the note order. Although AICc analysis results are promising, a more conservative perspective that accounts for the model's result is that note types are markedly diverse in acoustic structure and there is a notable tendency for the duetters to respond with a note type that is structurally different from the note before it. When one considers that manual note categorization found almost 30 note types, most of which are predominately sung by one sex or the other, combined with the tendency for sexes to alternate note order in the duet, it could be that the complex model was simply the best way for

this analysis to capture the alternating notes being sung by different sexes that prefer to reply with note-types containing acoustic structures which differ from the preceding note in the sequence.

### **4.3 Temporal Variation of Duets**

Sex differences in inter-note interval suggests that males overlap females more often than females overlap males (Table 3.4). The AICc analysis modeling the variation in inter-note interval included the interaction effect, which further supports the notion that different note types are used at different times in the duet by different pair members. This is also supported by the distinct manner in which acoustic features change based on note order (Figures 3.5 and 3.6).

Inter-note interval decreases in duration later in the duet, superficially suggesting that overlapping is more likely to occur towards the end of the duet. However, overlap occurs at the beginning of the duet just as much as the end (Table 3.4). However, it is unclear whether overlap tending to occur at the beginning indicates the rest of the duet is going to overlap or how overlap is involved in duet function? Future work could conduct playback experiments using baseline information provided by this study.

### **4.4 Visual Note Categorization**

As mentioned earlier in this chapter (Discussion: Acoustic Structure of Duets), note types were observed to have sex-specificity and note-order specificity with one or the other predominating. “Greet” was predominately the first note and was used by either sex. “Honk” was predominately used by males and occurred at any sequence within the duet (Figure 3.7). Some notes showed both sex-specificity and note-order specificity. For example, “Bah” was a note mostly sung by females and it almost always was the last note in the duet, no matter if the duet was three, six, or nine notes in length (Figure 3.7). Alternatively, the note type “Chello” showed note-order specificity at the scale of the couplet, not the duet. For example, towards the middle or end of the duet, a male or female would sing a “Chello” note and usually it led the mate to reply with their own “Chello” note.

#### **4.5 Reconsidering Note Order**

The aforementioned trends of some visually-sorted note types like “Honk” to be sung by the same sex but at any sequence within the duet does call to attention a challenge in the methods this study employed to define the singular unit of a “duet” from other vocalizations. Duets were defined as rapidly alternating note sequences with less than 2 seconds of silence, this resulted in a broad range of duet note lengths (3-13). This range in length is similar to the yellow-naped amazon duet behavior in which Wright and Dahlin (2007) found duets to be in pairs of notes containing 1-18 note couplets [18]. The fact that red-crowned parrot duets ranged in note length from 3-13 notes is a reflection of how diverse and dynamic this behavior is, when a pair is duetting they are interacting in real time and their internal states are able to change even during the course of the duet itself which might influence a pair-member’s decisions to change a note type of their reply or to cut short a duet. To properly compare duets to one another in a balanced statistical analysis, all duets longer than 6 notes were cut off at a length of six notes. The cutoff method presented two main challenges. Firstly, if a duet had three repeating notes at the beginning, followed by six alternating notes, the cutoff parameters would mean that only half of the alternating notes were included in analysis. Secondly, another confounding factor to cutting off the duets at six notes is that the analysis still included some duets were only 3-5 notes long. After considering the way in which the cutoff method limits the interpretation of the analysis, it leads me to reframe the basic unit of measurement of a duet to not focus on individual notes but instead on pairs of notes.

#### **4.6 Future Analysis**

Justification for implementing a couplet coding system instead of classic note order. When duets are described as antiphonal, therefore resulting from each pair-member taking turns, it might be more accurate to focus attention on the turn, i.e. the unit consisting of two notes contributed in sequence from both participants. This would shift the significance of note order off singular notes and onto couplets (defined as pairs of notes). Couplet-scale note order might resolve the issues of same-sex repeats (which could be considered as part of the same couplet only weighted heavier on

the pair-member who is repeating themselves), this would significantly reduce the range of notes in the duets and could even eliminate the need for a 6-note cutoff because most duets would be between 2 and 5 couplets in length. I have already implemented a couplet coding system for the dataset and am interested in how analysis might differ from the note order already tested. This is not to undermine what was learned from the previous method of 6 note cutoff and scale of focus on order of individual notes. The results of that method did expose some interesting trends in the relationship between alternating sex and note type within the order of the duet that still deserve consideration. It is because of these results that I feel drawn to further investigate the syntax-level dynamics at play within those trends.

Furthermore, the trends found in the beginning and ends of the duet, regardless of duet length (such as either sex singing the “Greet” note type initiating many duets, or the “Bah” note type always being sung by females and almost always at the end of a duet) could be refined by coding in a “start” and “end” datapoint to the beginning and end of each duet.

Alternatively, it might be helpful to explore the opposite perspective, completely ignore the unit level of “duet” and analyze the datapoints as simple pairs. Assuming red-crowned parrot notes can be arranged many different ways within a syntactical framework, the information encoded within each duet is different with a different arrangement of notes (out of 205 duets, the visually-sorted note types contained within each were arranged in 147 different ways). Due to the vast number of possible combinations within the syntactical potential, analyzing duet-level variation can be challenging. The reason Linguistics focuses so heavily on syntax is because the underlying hierarchical framework of how words can and can’t be arranged in order to symbolize meaning is foundational to the ability of sequences of words to communicate abstract ideas [59]. This is why it would be interesting to focus on the pairwise note sequences in order to try to tease out which notes tend to be found together which might suggest a predetermined lexical relationship.

I believe some note types are more likely to overlap, to test this theory future research should conduct Monte Carlo randomization test to calculate the expected inter-note interval and compare it to the observed note interval [2]. If coordination scores can be attributed to specific note types or to

the beginning/middle/end of the duet it might suggest that some amount of overlapping could be an intentional way to enhance some quality of the duet. Overlapping does not have to be a negative outcome of poor coalition quality.

## CHAPTER V

### RESEARCH JUSTIFICATION

#### **5.1 Parrots, Duets and the Avian Vocal Learning Model**

The traditional themes of the songbird model of vocal learning are insufficient as a comparison to vocal learning in general because of the limitations (dimorphic vocal learning, close-ended vocal learning, reduced interactivity of non-duetters) of vocal learning demonstrated by most songbird species. Parrots possess neither a biological restriction on female vocal learning nor the narrow window of juvenile development in which learning is possible [26]. Parrots, and some other oscine passerine species, are monomorphic lifelong vocal learners. By focusing this study on a species unhindered by the limitations of the traditional songbird vocal learning model, the subsequent knowledge may be more applicable to non-avian groups of vocal learners. Additionally, studies of the mechanics of human speech, have recently become more interested in the way in which parrots use their tongue to control their formation of sounds, which other vocal learning birds do not. Humans and parrots are the only vocal learners known to use their tongue in sound production [5]. Studies of some kinds of parrot vocal behavior like contact calls and subsong (the vocal process by which nestlings develop adult vocalizations) have already begun to broaden the avian vocal learning model [11, 8, 7, 17, 49, 50]. However, a psittacine vocal behavior that has received less attention, the duet, with its characteristic temporal precision and turn-taking interactivity may be just as valuable. Although the qualities that make parrots uniquely human-like vocal learners do extend to all parrot vocalizations, the temporal features found in duets make this category of vocal behavior in this species particularly apt for further study. Researchers specializing in parrot vocal behavior have proposed that parrots are an ideal candidate as a model organism for vocal learning

[10]. Researchers specializing in duetting have proposed that duet behavior is the ideal model for human conversation [57]. Combining the suggestions of these two distinct sub-fields of avian communication, this study of red-crowned parrot duets intends to focus on the ideal behavior in the ideal organism.

## **5.2 Interpreting Temporal Structure and Function of the Parrot Duet**

Overlap in most studies of antiphonal duets was often omitted from analysis [22, 18, 32] either because it was deemed unimportant, undesirable, or because of challenge of overlapping signals negating analysis of the acoustic features of the individual notes. Omitting overlap because it is an inconvenient feature to acoustically analyze is not unlike the omission of recordings with a low signal-to-noise ratio; it is a decision that is made in hopes of assembling a dataset that best captures the behavior of interest without the interruption of irrelevant acoustic variables that were difficult to control. However, in the case of low signal-to-noise recordings, new studies focusing on this inconvenient variable have found that background noise is actually an important environmental factor that birds deal with in previously unknown ways [52]. My study explored potentially adaptive functions of overlap, rather than ignore it altogether.

## **5.3 *Amazona* as an Evolutionary Model of Speciation via Vocal Learning**

The genus *Amazona* is the most diverse of the Psittacine family, with over 30 of the 350 recognized parrot species and 31 subspecies. This genus is known for extensive ability in imitation and vocal learning behavior, but these abilities have only been studied in a few species (*Amazona auropalliata* [21]; *Amazona amazonica* [23]; *Amazona finschi* [1]; *Amazona vitatta* [48]; *Amazona farinosa* [35]). Dialect occurrence had been demonstrated in the yellow-naped parrot [72]. The prolific vocal learning capabilities of this genus is hypothesized to contribute to its rapid speciation, and could result in reproductive isolation via dialect differences [20]. Recent work by Hellmich et. al. (2021) found little contact call divergence between populations of genetically-divergent southern mealy amazons (*Amazona farinosa farinosa*) [35]. These researchers questioned whether lifelong learning might make *Amazona* less apt to form dialects since individuals are capable to

mimic new call types throughout life. This untested conclusion was tampered by the admission that their study contained methodological and sampling limitations. Adaptation of call type is of serious conservation concern for *Amazona* as many species are in danger of extinction. There are 4 known populations of Puerto Rican parrots (*Amazona vittata*), two wild and two captive. Martínez and Logue (2020) found vocal divergence in all four populations, suggesting it to be due to rearing practices, cultural drift, and physical separation [48]. Species conservation efforts aim to preserve species in their natural state, special consideration must be given as to how best to preserve not just the genetic diversity but the behavioral diversity as well. A more thorough understanding of avian vocalizations is of particular significance to conservation planning, especially in ex-situ recovery, how to best maintain natural behaviors in captivity and in training natural behaviors to engender successful translocation [43]. Furthermore, the dynamics of dialect formation are important to consider with in-situ conservation planning. Red-crowned parrot populations are vulnerable to habitat fragmentation, a conservation problem which could lead to differential vocal drift in the separated populations [43]. Although the scope of this study does not extend to red-crowned parrot populations beyond the LRGV, the first step to further studies in dialect formation comes from this proposed work to characterize the phonology and syntax of this one population of red-crowned parrot in the LRGV.

#### **5.4 Human Impact on Duetters and Vocal Learners**

The population we are researching is living differently than the majority of their native wild Mexican counterparts, as an urbanized resident population. It would be interesting to know if this different habitat could influence the dialect formation/development of red-crowned parrots. As landscapes across the world are more progressively altered by anthropogenic activity, the way in which the behavior of wild species changes to habituate themselves is of relevant concern. It could be that vocal learning is especially helpful for species to adapt rapidly to a habitat that is changing much more rapidly than natural ecological succession: the anthropogenic soundscape [61, 62, 52]. With more foundational studies of species found both in wilderness and urbanized environments, comparative studies could then examine the ways those environments influence the vocal behavior

of vocal learners. The LRGV population of red-crowned parrots shares its range with a number of invasive parrot species (chiefly, *Amazona autumnalis*, *Amazona finschi*, *Amazona albifrons*, among others) which may contribute new sources of selective pressure like competition in the acoustic landscape or vocal change through acoustic adaptation [43]. Red-crowned parrots are endangered and understudied; my thesis contributes new information that can be used in future focal studies or comparative studies which may address these theories about the selective advantage of vocal learning.

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