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The Vocal Babbling Behavior and Its Sibling Effects in a Wild Parrot

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THE VOCAL BABBLING BEHAVIOR AND
ITS SIBLING EFFECTS
IN A WILD PARROT

A Thesis

by

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

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Major Subject: Biology

THE VOCAL BABBLING BEHAVIOR AND

ITS SIBLING EFFECTS

IN A WILD PARROT

A Thesis
by
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May 2017

ABSTRACT

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Vocal learning is a rare trait in the animal kingdom, defined as the sensorimotor imitation of sounds, and is only found in select groups of birds and mammals. Parrots are a behaviorally complex group of birds, famous for their ability to mimic social companions, but how they develop this ability in the wild has received little attention. The vocal learning period consists of a complex vocal babbling stage, a crucial developmental precursor for imitation of adult vocalizations in humans and songbirds, but has not been described in any of the 360+ parrot species. This project quantifies potential individual variation in vocal babbling of a wild population of Green-rumped Parrotlets (*Forpus passerinus*) in South America, and addresses whether variable sibling presence has an effect on the vocal babbling repertoire. This work exposes a cryptic developmental stage that has never been explored in wild parrots.

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TABLE OF CONTENTS

Page

ABSTRACT ………………………………………………………………………………. iii

ACKNOWLEDGMENTS ……………………………………………………………… iv

TABLE OF CONTENTS ……………………………………………………………….. v

LIST OF TABLES ……………………………………………………………………… vii

LIST OF FIGURES …………………………………………………………………….. viii

CHAPTER I. INTRODUCTION ………………………………………………………. 1

  Vocal Learning ……………………………………………………………………. 1

  Vocal Learning Origins …………………………………………………………… 3

  Vocal Development ……………………………………………………………….. 6

  Social Environment ……………………………………………………………….. 9

  Neurobiology of Vocal Learners …………………………………………………. 10

  Project Goal ……………………………………………………………………….. 11

CHAPTER II. HYPOTHESES ………………………………………………………… 13

  Hypothesis 1. Parrots show individual variation in vocal babbling repertoires ……… 13

  Hypothesis 2. Brood size helps explain possible vocal babbling variation ………….. 13

  Hypothesis 3. Hatch sequence helps explain possible vocal babbling variation ……. 13

CHAPTER III. MATERIALS AND METHODS ……………………………………..... 15

  Study Population ………………………………………………………………….. 15

  Audio-Video Recordings ………………………………………………………….. 15

Project Design ………………………………………………………………... 16

Spectrographic Extracting and Measuring Babbles ………………………………….. 16

Statistical Analysis ………………………………………………………………… 17

Classification of Babble Types ……………………………………………… 17

Individual Nestling Diversity ………………………………………………… 18

Brood Size and Hatch Sequence Effects ……………………………………... 19

CHAPTER IV. RESULTS ………………………………………………………………….. 21

Babbling Data …………………………………………………………………... 21

Spectrographic Measurements ……………………………………………………. 24

Individual Variation ………………………………………………………………. 24

Identification of Call Types ………………………………………………………. 26

Brood Size Effects ………………………………………………………………… 28

Hatch Sequence Effects …………………………………………………………… 30

CHAPTER V. DISCUSSION ……………………………………………………………….. 32

Vocal Babbling in Parrotlets ……………………………………………………… 32

Vocal Complexity ………………………………………………………………… 33

Vocal Rule Learning ……………………………………………………………… 36

Vocal Play-like Behavior …………………………………………………………. 40

Conclusion ………………………………………………………………………… 41

REFERENCES ……………………………………………………………………………. 42

BIOGRAPHICAL SKETCH ………………………………………………………………... 51

LIST OF TABLES

Page

Table 1: Babbling Data Showing Nest Number, Brood Size Category, Nestling Hatch Sequence, Days Of Development Within The Nest, And Observed Days Of Babbling ………………………………………………………………………. 23

Table 2: Summary Statistics Of Seven Spectrographic Measurements That Were Used For Analysis Of Babble Elements ……………………………………………….. 24

Table 3: One-Way Analysis Of Variation Showing Significant Correlation Between Nestling's "Days Of Development" And "Brood Size." ……………………………. 26

Table 4: Individual Variation, Using 2-Level Nested Analysis Of Variance Of Nestlings' S-W Index Within 10 Nests ………………………………………………………… 26

Table 5: Number Of Call Types Found In Each Nest, Based On The Multivariate K-Means Clustering …………………………………………………………………. 26

Table 6: Analysis Of Mixed Effects Variation, With Nestlings As Random Effects (REML Variance Component Estimates), And Brood Size As A Fixed Effect …….. 29

Table 7: Two Way Analysis Of Variance, Using Brood Size And Hatch Sequence. Effect Tests Of Brood Size And Hatch Sequence (Age) Interactions, Showing No Significance In The Interaction …………………………………………………… 31

LIST OF FIGURES

Page

Figure 1: Hypothetical Distributions Of Two Behavioral Phenotypes ……………………… 2

Figure 2: The Evolution Of Vocal Learning Hypotheses …………………………………… 4

Figure 3: A Scheme Of Developmental Vocal Learning ……………………………………. 9

Figure 4: Songbird And Parrot Neural Pathways For Vocal Production ……………………. 11

Figure 5: Two Factor Nested ANOVA Design ……………………………………………… 19

Figure 6: Examples Of Short Babble Elements, As Seen On A Spectrogram ………………. 22

Figure 7: Examples Of Long Babble Elements, As Seen On A Spectrogram ……………….. 22

Figure 8: Days Of Development And Brood Size Correlation ………………………………. 25

Figure 9: Variation Of The S-W Index And Evenness Of That Index In Each Of
The 10 Nests ………………………………………………………………………... 25

Figure 10: K-Means Clustering Showing Number Of Call Types (Indicated By Circles
And Colors) In Each Nest, With Nest ID And Brood Size In Parenthesis. Axis
Are First 2 Principal Components Of The Data.…………………………………… 27

Figure 11: Brood Size Leverage Plots Showing Significance ……………………………….. 29

Figure 12: Hatch Sequence Means Plotted With The Diversity Index And Evenness ………. 30

Figure 13: Hatch Sequence And Nestling Diversity Leverage Plot ………………………….. 30

CHAPTER I

INTRODUCTION

Human language is infinitely complex in its ability to take units of speech and use them as building blocks in combinations of meaning (Youn et al. 2016). This linguistic complexity has been historically perceived to be unique among the animal kingdom, granting human ability a special path to the evolution of language complexity. But recent research into avian abilities has challenged the theories that set human language apart from other vocal species (ten Cate, 2014; Bolhuis, Okanoya, & Scharff, 2010).

Vocal Learning

Most mammalian and avian species use vocalizations to communicate between individuals, but there are differences in ability, complexity, and the development of the ability. "Vocal learning" is defined as the ability to acquire new vocalizations during a period of development, or throughout life. In contrast, "vocal non-learners" are species that do not have the ability to acquire new vocalizations, and communicate using innate vocalizations, without a critical learning period or adult tutors (Petkov & Jarvis 2016). Songbirds are considered vocal learners, yet there is variation between bird species in this ability. For example, the zebra finch (*Taeniopygia guttata*) learns one song during development, while the mockingbird can learn hundreds of songs, including mimicking the songs of other birds (vocal imitation).

Vocal learning is required in human speech, but also occurs in four other mammalian groups that are phylogenetically distant (cetaceans, bats, elephants, and pinnipeds) and three groups of birds (hummingbirds, songbirds, and parrots) (Colbert-White et al. 2014). Most other vertebrates are not capable of vocal learning, because the acquisition of novel vocalizations is evolutionarily complex, and it requires both an auditory and sensory-motor vocal learning components (Jarvis 2004). Auditory learning alone is the understanding of a sound without the ability to reproduce it, such as how pets understand commands. Sensory-motor production is more complicated, since it involves the physical production of that sound, and neural connections that drive behavior. The combined role of the two components evolved the complexity and variation of vocalizations.

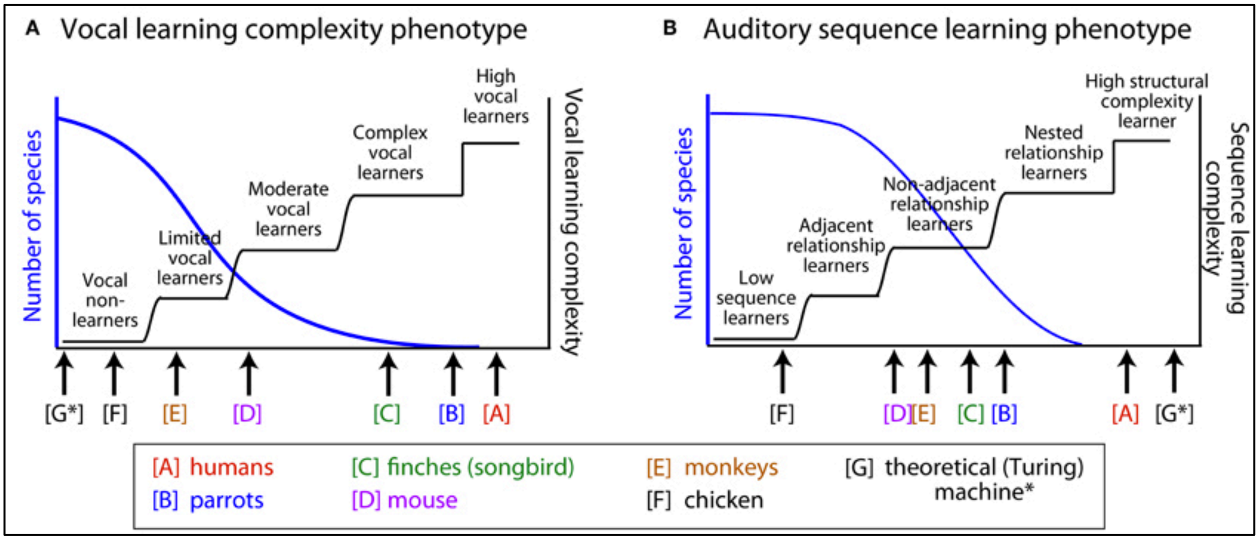


Figure 1. Hypothetical Distributions Of Two Behavioral Phenotypes: Vocal Learning And Sensory (Auditory) Sequence Learning. Figure Taken From Petkov And Jarvis 2016.

For many years, non-human primates were studied to uncover their ability to learn vocalizations, but so far there's been lack of evidence that their vocal learning production ability compares to the other proficient vocal learners (Petkov & Jarvis 2016). The comparative vocal models, in turn, has turned to more distantly-related groups, and how vocal learning as communication has evolved across taxa (Figure 1).

To understand the origins of linguistic complexity across taxa, birdsong has been studied both in captivity and in the wild, in different groups of birds. The songs of birds around the world have striking similarities to human language, which has captivated scientific research in the areas of cognition, behavior, development, evolution, and genetics (Konishi et al. 1989). Birdsong is made up of learned vocal elements that are strung together into a meaningful output for referential communication with other individuals. While songs are species-specific, there is also variation between individuals within a species. This variation could explain the cognitive mechanisms needed for a bird to perceive vocalizations, identify specific vocal units, and to combine them into a categorical sequence. Possible parallels between human speech and birdsong could explain the evolutionary origins of human language, and the biological comparative mechanisms that have allowed complexity of language.

Vocal Learning Origins

How did these separate taxa converge on a similar vocal learning behavior over time? Due to the rare occurrence of vocal learning abilities in animal groups, it is assumed this behavior was not from an ancestral descendant, but rather a convergent solution to a similar problem of communicating in a changing environment (Hauser et al. 2002). The obvious differences in brain region structures (discussed later) between these distant taxa, such as songbirds and humans, support the theory of convergent evolution for auditory-vocal learning. Bolhuis et al. (2010) gives some perspective:

> *"The fact that such similar details of vocal learning arose in distinct evolutionary branches that parted ways some 300 million years ago underscores that evolutionary selection pressure can result not only in similar morphological adaptations but also in similar behavioural adaptations."*

Nowicki and Searcy (2014) present five hypotheses on the evolution and selective benefits of vocal learning (Figure 2). The hypothesis are the (1) vocal dialect hypothesis, (2) sexual selection hypothesis, (3) information sharing hypothesis, (4) environmental adaptation hypothesis, and (5) individual recognition hypothesis.

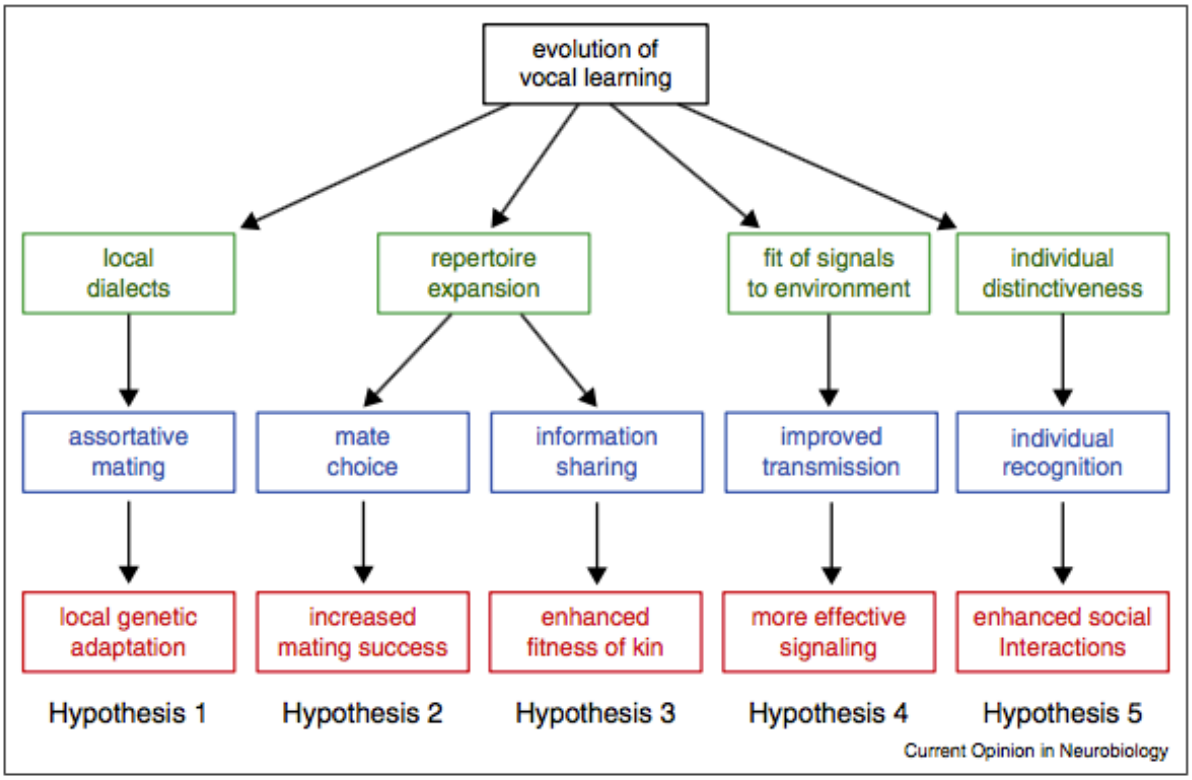


Figure 2. The Evolution Of Vocal Learning Hypotheses Are The (1) Vocal Dialect Hypothesis, (2) Sexual Selection Hypothesis, (3) Information Sharing Hypothesis, (4) Environmental Adaptation Hypothesis, And (5) Individual Recognition Hypothesis. Figure Taken From Nowicki And Searcy 2014.

Learning allows for building flexibility or complexity in the signals of an individual, and an opportunity for variation between individuals. Any learning of communication behavior is considered as social learning in animals (Janik & Slater 2000). In vocal communication, there are two ways to learn the meaning of a signal: (1) *contextual learning*, where an existing signal gains new meaning from a new experience, or (2) *production learning*, where an individual modifies a signal for a new message (Janik & Slater 2000). Production learning is what allows variation of signals even between individuals of the same species, and what may create complex strings of communication, depending on the cognitive ability of the species and the learning pressures of its environment. The definitions can get complicated when trying to separate what defines a signal or a recombination of signals in different taxa.

An important finding on the origin of vocal production learning comes from work by Lipkind et al. (2013), where three species of vocal learners (zebra finches, Bengalese finches, and human infants) were compared for their ability to learn novel combinations of vocal sequences. Their results show that both songbirds and babbling infants use a stepwise manner of adding these new combinations to their repertoire, creating a new model of vocal acquisition across taxa. They suggest that vocal babbling is an important part of the evolution of diversifying vocal transitions: “Collectively, these results point to a common generative process that is conserved across species, suggesting that the long-noted gap between perceptual versus motor combinatorial capabilities in human infants may arise partly from the challenges in constructing new pairwise vocal transitions” (Lipkind et al. 2013, pg. 104).

Vocal Development

Understanding how different taxa develop the ability to learn vocalizations can provide valuable insights into why these groups converged on vocal imitation as a solution for communicating. In most of these vocal learning species, the onset to vocal imitation is preceded by a complex, and poorly-known, *vocal babbling stage* (Doupe & Kuhl 1999).

Vocal babbling is one of the first vocal stages of juvenile individuals that use vocal imitation for communication. Across species, vocal babbling bouts seem to have no set length, are given at low amplitudes, and include an acoustically diverse set of signals. The behavior is still elusive as to its adaptive significance because these bouts are often given without any obvious context or an audience, during a ‘sensitive period’ in development (Nelson & Marler 1994).

Young vocal-learning animals may be better subjects for the study of the evolution of learning, since they are in the developmental stages of these behaviors. The vocal ontogeny has been extensively studied in songbirds and human infants (Soha & Peters 2015, Goldstein et al. 2003). In birds, the initial juvenile vocal output, called the “sub-song”, is quiet and variable, not resembling the adult song elements yet. Later this stage is followed by “plastic song” with louder elements that start to resemble a mature repertoire, but also retain variability and overproduction. The stage of “vocal overproduction” takes place before crystallization into an adult repertoire, where variety starts to diminish through both environmental and social selections. It’s been shown that overproduction serves an adaptive function to a specific dialect of the population, since migratory species have shown to have a greater overproduction repertoires than nonmigratory species (Nelson et al. 1996). The extent and time period of overproduction depends on the bird species as well.

Are there similarities in mechanical development across taxa? Sub-song or plastic song have been considered analogous to babbling in human infants. In infants, babbling is a precursor to spoken words that usually appears around 7 months of age, is also observed in deaf children, and is correlated with the first words that the child produces (Fitch, 2010). Babbling is considered part of the social imitation that infants engage in as a method of learning, and apparently infants as young as 42 minutes engage in facial imitation (Meltzoff & Moore, 1983).

Vocal babbling is the early stages of imitation with the vocal apparatus, an important ability in a social and highly-linguistic species such as humans (Goldstein et al. 2003). The critical period of babbling onset has been studied for correlations with developmental disorders, where children with lower rates of canonical vocal babbling were more likely to later be diagnosed with autism spectrum disorder (Patten et al. 2014). Similar results are found in songbirds, where temporarily deafened individuals during their critical period of vocal learning, can never learn a “normal” song (Fitch, 2010). These results are critical in a disorder such as autism, where early intervention in its development can create positive outcomes, but early detection is still difficult. Vocal babbling models may have similarities in neurological pathways and developmental timelines across species, just as vocal learning is a convergent behavior between birds and humans.

Most of what we know about vocal development comes from songbirds and captive populations (Doupe & Kuhl 1999), but one of the most prolific of vocal imitators, the parrots, have mostly been ignored. The domesticated budgerigar (*Melopsittacus undulatus*), a parrot species, has been studied for its vocal learning of “contact calls” (Brittan-Powell et al. 1997, Tu et al. 2011). Signature contact calls are used for identification of individuals in a social group, group cohesion, and group movement (individual recognition hypothesis, Nowicki and Searcy 2014). In these contact call studies, the behavior seems to retain individual variation of the caller, and as Berg et al. (2012) has shown, these contact calls are socially acquired in the nest during development. But studies on natural development of parrots in the wild have been limited.

Parrots differ from songbirds in several important ways, and may provide additional insight into the learning abilities of birds. For example, parrots exhibit the ability to learn throughout life, have large vocal repertoires, long-term pair bonds (Bradbury & Balsby 2016), male and female warbling songs, significant sibling size hierarchies, and longer nestling developmental periods (Beissinger & Waltman 1991), during which they engage in social learning of signature contact calls (Berg et al. 2012).

Models of language development include not only the ability of vocal imitation, but other factors in development that influence the endpoint of learning, such as social environment, self-feedback, adult feedback, diet, stress, and genetics (Figure 3). Since vocal babbling is the precursor to adult vocalizations, it may play part in many of these developmental effects, as well as be affected by the other developmental factors.

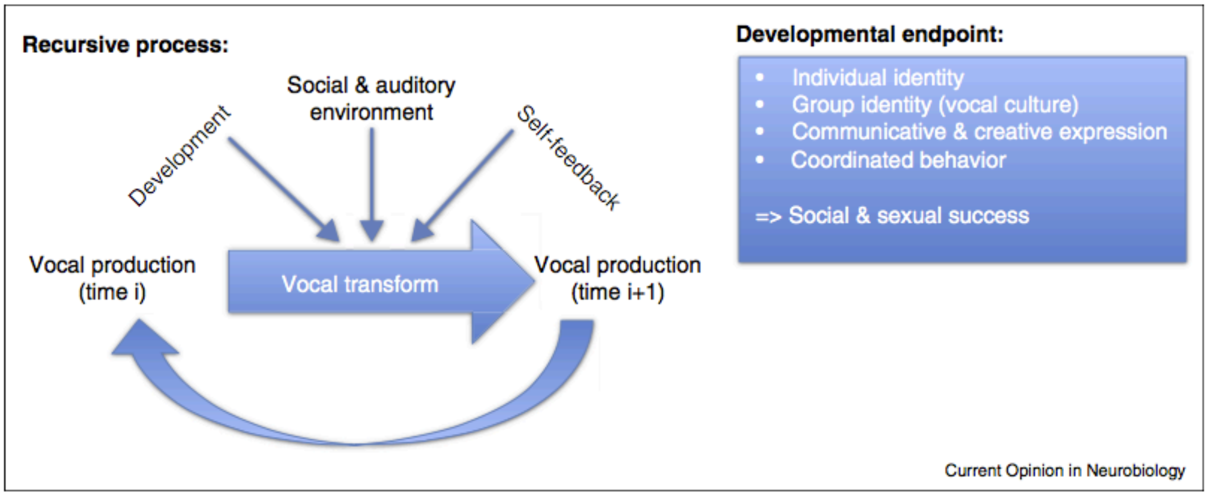


Figure 3. A Scheme Of Developmental Vocal Learning, Figure Taken From Tchernichovski & Marcus (2014).

Social Environment

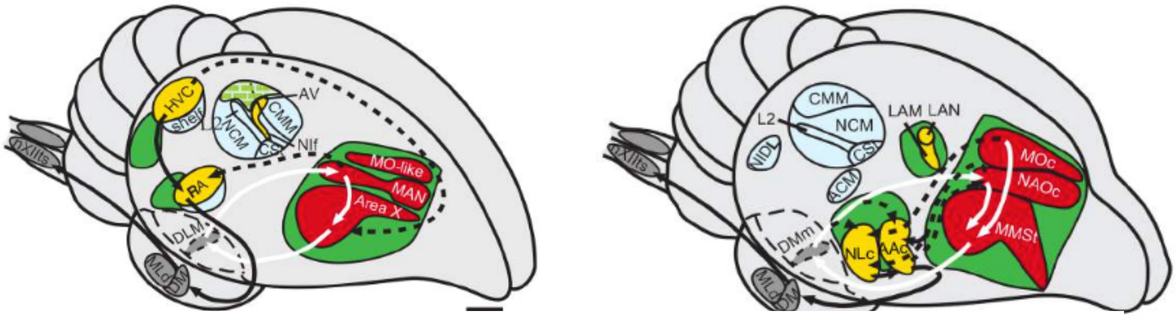
Social interactions have shown to be crucial during the critical learning period in human infants, where adult tutors provide visual and acoustic information to infants to enhance attention to speech sounds. Individuals with developmental disabilities that affect speech acquisition also lack normal social behaviors in adulthood (Chen et al. 2016). The connection between social environment and vocal learning is fundamental in humans, and human infants need social interaction and vocal feedback to fully develop language (Bolhuis et al. 2010).

Social environment during development is important for future mature vocalizations in songbird studies too, where lack of adult tutors in development results in a limited adult repertoire, indicating the importance of imitating adult tutors during development (Doupe & Kuhl 1999; Soha & Peters 2015). For example, in a zebra finch study it was found that adult tutors alter their song when in the presence of juvenile birds in a similar way that humans alter their speech around infants (Chen et al. 2016). Social interactions may promote vocal learning in this way by enhancing certain attention mechanisms, reflecting a role of the nervous system.

Highly social species are thought to have social living as the driver of intelligence (Emery 2006), and vocal calls play a significant part in how these species communicate in the wild. Vocal babbling may be the early stages of these necessary solutions to acquiring enough variation in repertoire, in order to deal with future social demands. It's known that the brains of parrots are relatively as large as those of chimpanzees, gorillas, and orangutans (Emery 2006), giving reason to consider that vocal behaviors, such as babbling, can play as important of a role in parrots as in primates.

Neurobiology of Vocal Learners

Neural pathways of different taxa of vocal learners have been explored in molecular biology, especially those of humans, non-human primates, songbirds, and parrots (Bolhuis et al. 2010, Petkov & Jarvis 2012). The neural circuits for vocal behavior appear to be wired differently in all taxa, even in the three groups of vocal learning birds (songbirds, hummingbirds, and parrots), supporting the theory of independent evolution of neural pathways for converging on the vocal behavior. Specialized brain nuclei have been identified as correlated with vocal learning, and the same nuclei are absent in vocal non-learners (up to seven cerebral telencephalic vocal nuclei, yellow and red in Figure 4). An additional neural difference has been found in parrots, who have an additional region called the "shell" system, within the "core" system that is found in songbirds and hummingbirds, and both systems play a role in producing vocalizations (Chakraborty et al. 2015).



Passeriformes (songbirds)

Psittaciformes (parrots)

Figure 4. Songbird And Parrot Neural Pathways For Vocal Production, Figure Taken From Chakraborty et al. (2015).

Project Goal

The current study describes for the first time the vocal babbling stage of a wild parrot species, the Green-rumped parrotlet (*Forpus passerinus)*, as it develops naturally within a wild population of parrots that have taken to using artificial nest cavities. This study can start explaining the behavior by first looking at its variation, and then whether siblings and brood size have any effects on the individual's babbling variation. Individual variation and early social environments can have important consequences for cognitive function later in life, since clear imitation of adult notes immediately follows the babbling stage.

This project aims to quantify individual variation and diversity of vocal babbling in the Green-rumped Parrotlets using 3000 hours of existing audio-video recordings made inside 45 nests of varying brood sizes at Hato Masaguaral, a 7000 ha field research station in the state of Guarico, Venezuela (data from the Berg Lab, University of Texas Rio Grande Valley). Babbling sequences of individually marked nestlings as captured on video were extracted as sound files and spectrographically and statistically analyzed, with individual differences of nest brood size and hatching sequence. The goal was to define call groups in babbling bouts, identify the repertoire size of each individual, and to calculate call diversity in each individual based on call richness.

This work defines a cryptic developmental stage that has been little explored in wild parrots. The availability to closely examine the developmental behavior of a wild population at this long-term field research station gives unique access to quantify a complex vocal behavior of a social species, which relies on vocal communication in large social groups. Individual variation in babbling behavior and early social environments can have important consequences for cognitive function later in life.

CHAPTER II

HYPOTHESES

Hypothesis 1. Parrots show individual variation in vocal babbling repertoires.

Individual variation of vocal babbling will be defined here by the Shannon-Wiener Diversity index of vocal repertoire of each nestling. If nestlings show individual variation in their babbling, then environmental factors (brood size, hatch sequence, parent influence) during development could be the driving force of vocal diversity. Lack of any babbling variation between broods or siblings would suggest either a genetic template or parental influence for vocal acquisition.

Hypothesis 2. Brood size helps explain possible vocal babbling variation.

Brood size varies between nesting attempts, therefore the size of the brood is a possible direct social effect on developing nestlings, and can be a significant effect on babbling repertoire. If sibling social interactions drive babbling diversity, then individuals raised in larger broods should have significantly different diversity indices from individuals in smaller broods.

Hypothesis 3. Hatching sequence helps explain possible vocal babbling variation.

All parrotlet broods hatch asynchronously over several weeks, and vocal development may be affected by age of hatching in the nest, since it changes the social dynamic and the number of developed siblings within a close-knit nest environment. If hatching sequence has an effect on vocal babbling of a nestling, then the diversity index will be significantly different between nestlings of different ages, with later hatched chicks showing a higher diversity index, regardless of which brood size category they fall into.

CHAPTER III

MATERIALS AND METHODS

Study Population

The wild Green-rumped Parrotlet population is the smallest New World parrot species (25 g.), socially monogamous, have long-term pair bonds, close-knit groups where they breed nearby each other, and lay large clutches that hatch asynchronously (Beissinger & Waltman 1991). The Green-rumped Parrotlet population at Hato Masaguaral, a 7000 ha field research station in the state of Guarico, Venezuela, is a good model to study parrot vocal babbling. This color-banded population has been monitored at the field station since 1988, where 106 artificial nest boxes have been placed and continue to be maintained. The parrotlets breed inside the artificial nest boxes during the wet season of June and December, producing one or two broods per season, with varying brood sizes. The chicks inside the nest have asynchronous hatching over the span of two to three weeks, presenting staggering sibling ages during development within the cavity, and nestlings fledge the nest around 30 days after hatching.

Audio-Video Recordings

With the facilitation of artificial nest boxes, a nonintrusive audio-video arrangement has been developed to film the cryptic nestling development of these cavity nesters in the wild. Concealed camcorders (Sony HDRCX160) and microphones inside nest tubes unobtrusively record nest activity for 3-4 hours per day. The Berg Lab, led by Dr. Karl Berg, has created a digital library of these audio-video recordings, containing over 45 nests to date, in order to closely observe these hidden behaviors.

Project Design

I calculated a babbling diversity index for each individual by analyzing spectrographic measurements of recorded babbling bouts. A sample of 10 nests with 60 nestlings total were selected from the Berg Lab library (recorded during the 2011 to 2014 field seasons) for babbling behavior analysis. The sample consisted of five brood sizes (4, 5, 6, 7, and 8 nestlings in each nest), with two nests of each brood size. Vocal babbling behavior from each nestling was collected from watching daily recordings during nestling development, and individual babbles were spectrographically detected and measured. Detected elements were grouped into call types in each nest, and a babbling diversity index was calculated for each nestling in the study.

Spectrographic Extracting and Measuring Babbles

Daily babbling bouts and vocalizing nestlings were visually identified in Adobe Audition (version 9.2.1). Nestlings were identified from one another by a unique color-band combination attributed to each individual. Babbling bouts were extracted as wave files (48 kHz, 16-bit sample rate) for processing of vocalization elements.

Spectrograms of all babbling bouts were created in Raven Pro, with a 256-point Fast Fourier Transform, a Hann window, (version 1.5B, Cornell Lab of Ornithology), for batch detection and digital measurements of babbles. The bouts were band-filtered to a frequency range of 500-12500 Hz to remove noise that was outside of the parrotlets' hearing range (Elie & Theunissen 2016). The detections were set to separately capture and measure all individual babble elements, and all batch detections were manually checked for accuracy and false batch detection by Raven. To describe acoustical properties of the babbles, relevant parameters that describe the information of the sound from the spectrogram included duration, entropy, energy, time-frequency slope, number of inflection points (time-frequency derivative sign changes), and frequency measurements. These measurements were chosen to capture the multi-dimension of babbles, and methods found in Berg et al. (2011 and 2013).

Statistical Analysis

Classification of Babble Types

Each nestling's repertoire was represented with 900 random babble elements out of all collected babbles (spanning several days of development for each nestling) using a random function in Microsoft Excel, and all but six out of 60 nestlings had over 900 elements to choose from (one individual did not babble). The sample size of 900 was used because the average number of babble elements per nestling was 3434 elements. Calculating with a confidence level of 99% and a margin of error of 4%, the minimum sample size needed is 798 elements per nestling.

Seven spectrographic measurements explained significant variation in the babbles (Average Entropy, BW 90%, Center Frequency, Energy, Length, PFC Average Slope, PFC Number of Inflection Points), and were supported with a principal component multivariate analysis. Average entropy is defined as the entropy for each frame in the babble selection and then taking the average of these values, which describes the amount of disorder for a typical spectrum within the selection. Bandwidth 90% (BW 90%) is the difference between the 5% and 95% frequencies. The frequency 95% divides the selection into two frequency intervals containing 95% and 5% of the energy in the selection, and similarly with frequency 5%. Central frequency divides the selection into two frequency intervals of equal energy. Energy captures the total energy of the selection. Length is the time duration of the selected element. Peak frequency contour (PFC) measures frequency in each frame, to create the peak frequency pattern of the selected element. PFC average slope (vector, Hz/ms) traces this frequency contour, and PFC number of inflection points is the number of times the contour measurement changes concavity.

Each nestling's babbles were grouped by acoustic similarity into call types with a *k*-Means multivariate clustering analysis (JMP Pro 13.0), indicating that each cluster is a call type due to sharing similarities of sound (Tu et al. 2011). Each nest was analyzed separately to identify the number of call types within each nest. Each babbling element was identified as a call type, and was assigned to the nestling's repertoire to calculate the diversity index.

Individual Nestling Diversity of Babble Types

To assess possible variation in the babbling repertoire of each nestling, the Shannon-Wiener (S-W) Diversity Index was calculated for each nestling, using previously-identified clustered call type (cluster number) and call abundance (number of calls within cluster number) as indicators of diversity. The following Shannon-Wiener Diversity Index formula was used:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where p_i is number of calls (call abundance) belonging to each call type (Da Silva et al. 2000). To calculate evenness of the diversity results, the Pielou's Evenness equation was used:

$$J' = \frac{H'}{H'max}$$

where H' is the diversity index, and H' max is the maximum possible value of H', or $\ln S$, where S is the total number of call types. A two factor nested ANOVA between nestlings, within nests, was performed to calculate individual variation in the S-W index between groups of siblings.

Brood Size and Hatch Sequence Effects

Nestling babbling diversity was tested for significant differences between the effects of brood sizes and hatching sequence using linear mixed effects model in JMP. Brood size effects required a two-level nested ANOVA with S-W diversity measurements as the predicted variable, and nestlings (nested within brood size) as random effects, tested with a Wald random test effect, because the focus was the effects found between brood sizes (Figure 5). Brood size was also compared to each nestling's "number of development days" within the nest with a one-way ANOVA, for the possible correlation that the number of siblings within the nest would result in a longer span of development per individual.

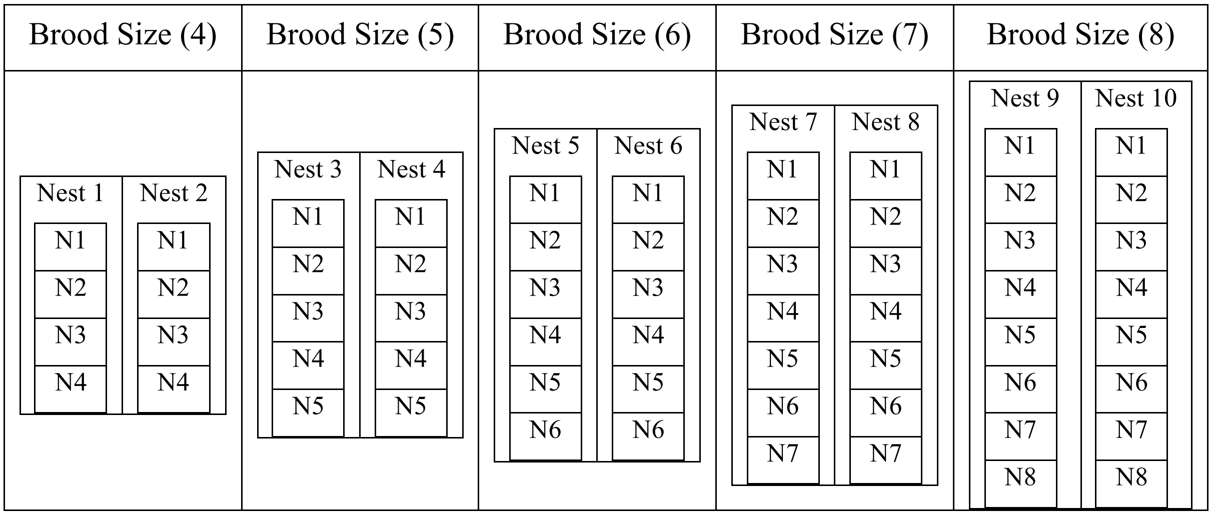


Figure 5. Two Factor Nested ANOVA Design.

The hatch sequence was coded so that each nestling was labeled between the age range of 1 to 4, to normalize ages in nests with varying sibling numbers (4 to 8 nestlings). To assess whether older and younger siblings of different hatch sequences had significant differences in babbling diversity, a two-way ANOVA with interaction of brood size and age was performed.

CHAPTER IV

RESULTS

Babbling Data

Babbling selections were sampled from each individual over their entire babbling development, which ranged from one day to nine days of babbling, with the exception of one nestling that did not babble (Table 1). Babble elements varied in duration, low and high frequency, slope, noise, and usually lasted less than half a second, among other natural variations of sound (examples are shown in Figures 6 & 7). Most babbling bouts were made up of short babble elements, with occasional long elements. There was some repetition of babbles, but it was impossible to qualitatively predict any repetition, due to variation in each individual and even each babbling episode. Variation was also seen in babbles that looked similar, but had minor changes each time they were vocalized. Occasionally, two nestlings were observed to be babbling at the same time, and these babbling bouts were not included in analysis because it was impossible to match the individual identity to each babbling call. The entire collected set of babbling selections to represent the study for all nestlings was at 206,900 elements, from 60 nestlings and 10 nests. Out of 60 nestlings in the study, only six did not have enough elements for the 900 random sample model, with one nestling that did not babble.

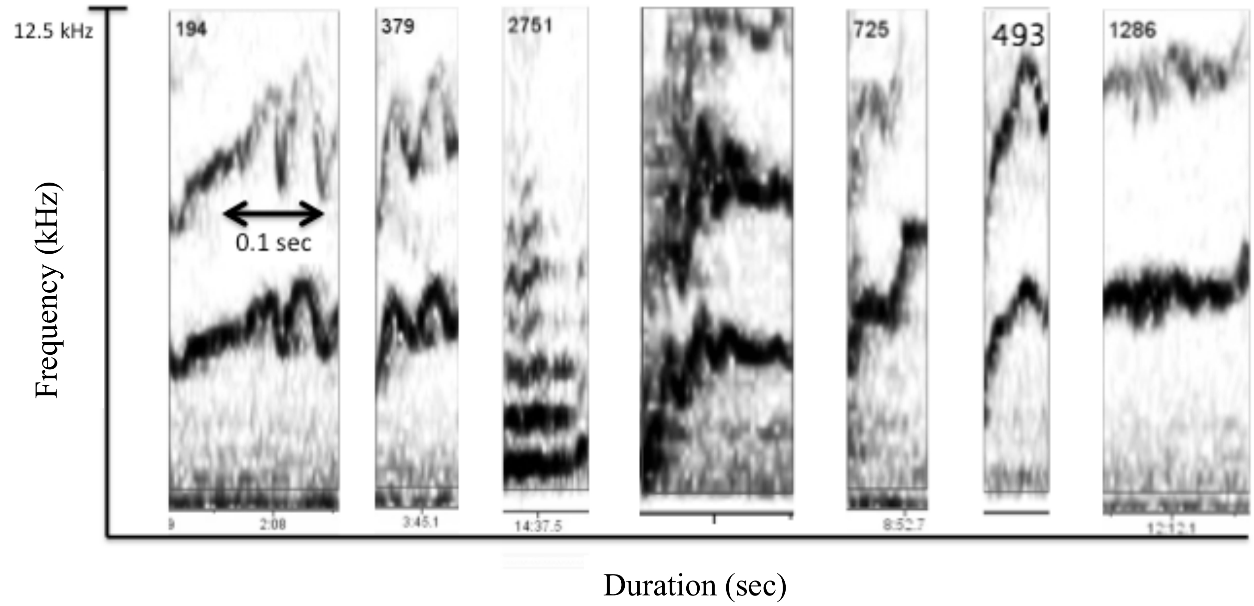


Figure 6. Examples Of Short Babble Elements, As Seen On A Spectrogram.

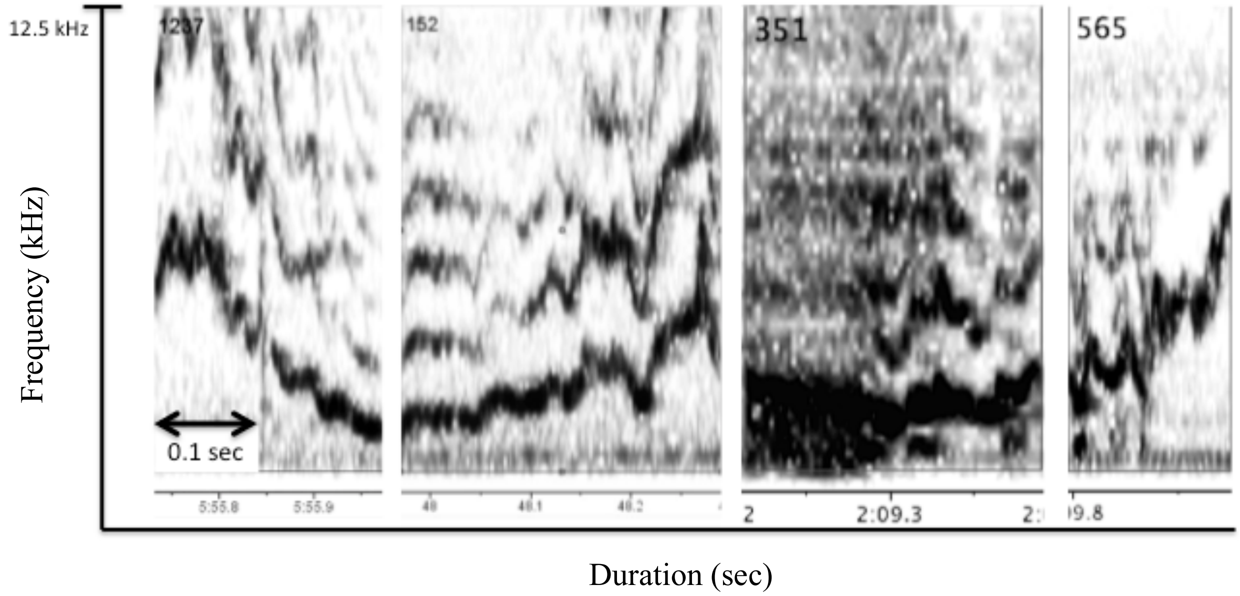


Figure 7. Examples Of Long Babble Elements, As Seen On A Spectrogram.

Table 1. Babbling Data Showing Nest Number, Brood Size Category, Nestling Hatch Sequence, Days Of Development Within The Nest, And Observed Days Of Babbling.

Nest	Brood size	Hatch Seq	Develo -pment	Days of babbling
13B35A	4	1	31	8
13B35A	4	2	30	6
13B35A	4	3	32	3
13B35A	4	4	32	4
11B41A	4	1	32	4
11B41A	4	2	31	5
11B41A	4	3	30	4
11B41A	4	4	33	4
12B91A	5	1	30	2
12B91A	5	2	31	6
12B91A	5	3	30	3
12B91A	5	4	29	3
12B91A	5	5	33	4
14B8A	5	1	32	3
14B8A	5	2	34	3
14B8A	5	3	34	3
14B8A	5	4	36	6
14B8A	5	5	36	3
13B75A	6	1	31	5
13B75A	6	2	31	3
13B75A	6	3	29	2
13B75A	6	4	34	3
13B75A	6	5	30	2
13B75A	6	6	32	4
14B75A	6	1	28	1
14B75A	6	2	30	5
14B75A	6	3	28	7
14B75A	6	4	30	4
14B75A	6	5	30	4
14B75A	6	6	31	6
13B85A	7	1	31	2
13B85A	7	2	33	4
13B85A	7	3	33	4
13B85A	7	4	33	7
13B85A	7	5	32	7
13B85A	7	6	35	9
13B85A	7	7	36	9
12B14A	7	1	31	0
12B14A	7	2	30	5
12B14A	7	3	31	2
12B14A	7	4	31	2
12B14A	7	5	30	1
12B14A	7	6	34	4
12B14A	7	7	30	5
14B87A	8	1	33	5
14B87A	8	2	32	2
14B87A	8	3	32	2
14B87A	8	4	32	3
14B87A	8	5	34	6
14B87A	8	6	34	2
14B87A	8	7	36	2
14B87A	8	8	36	2
12B12A	8	1	36	4
12B12A	8	2	33	7
12B12A	8	3	33	5
12B12A	8	4	33	2
12B12A	8	5	34	3
12B12A	8	6	33	2
12B12A	8	7	34	2
12B12A	8	8	30	1

Spectrographic Measurements

Seven relevant spectrographic measurements acoustically represented the babbling elements of each nestling. Their multivariate principal component eigenvalues were greater than 0.99 in the first three principal components, and explained over 75% of the variation present (Table 2).

Table 2. Summary Statistics Of Seven Spectrographic Measurements Used For Analysis Of Babble Elements (Average Entropy, Bandwidth 90%, Center Frequency, Energy, Length, Peak Frequency Contour Average Slope, and Peak Frequency Contour Number Of Inflection Points).

Measurements	Mean	Std. Dev.	Min	Max
Average Entropy (bits)	2.75	0.54	1.15	5.227
BW 90% (Hz)	3320.45	2256.51	187.5	11812.5
Center Frequency (Hz)	2834.35	1429.13	187.5	11062.5
Energy (dB)	94.72	9.46	59.9	120.5
Length (frames)	22.72	13.89	3	284
PFC Average Slope (Hz/ms)	8.57	48.78	-1371.1	1757.8
PFC Num of Inflection Pts	6.43	5.58	0	124

Individual Variation

Nestlings babbled toward the end of their development inside the nest, up to the last day before fledging. The nestlings that were sampled fledged the nest between days 28 and 36 of development. Results showed that days within the nest increased with increased brood size (Figure 8), with significant differences (Table 3).

In order to explain individual variation, the individual diversity index showed to be different in each group of siblings (Figure 9), and analysis showed significant variation between the 10 nests (Table 4). The evenness of the repertoire diversity remained the same among individuals, on the other hand. There are different factors that could explain this variation, and nest's *brood size* and a nestling's *hatch sequence* were tested in this study.

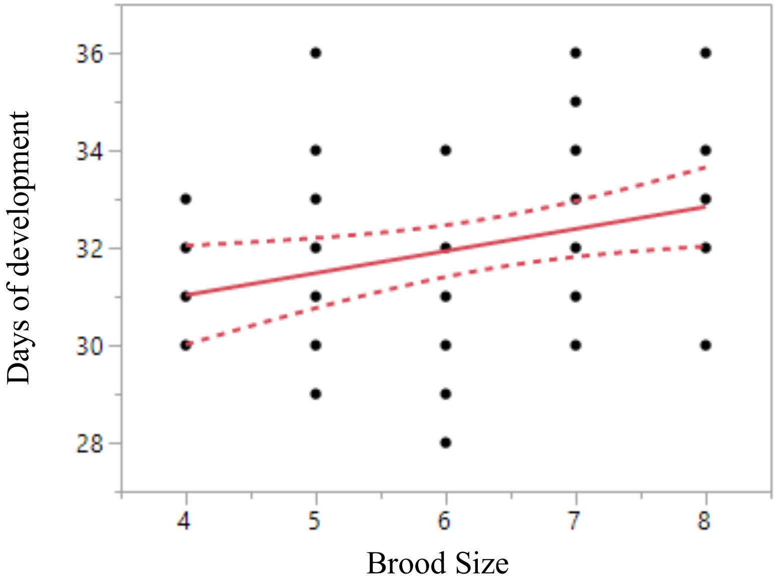


Figure 8. Days Of Development And Brood Size Correlation, Points Show Days Of Development From 60 Nestlings In 5 Brood Sizes. Central Line Is Best Linear Fit (R^2=0.091, p=0.0189).

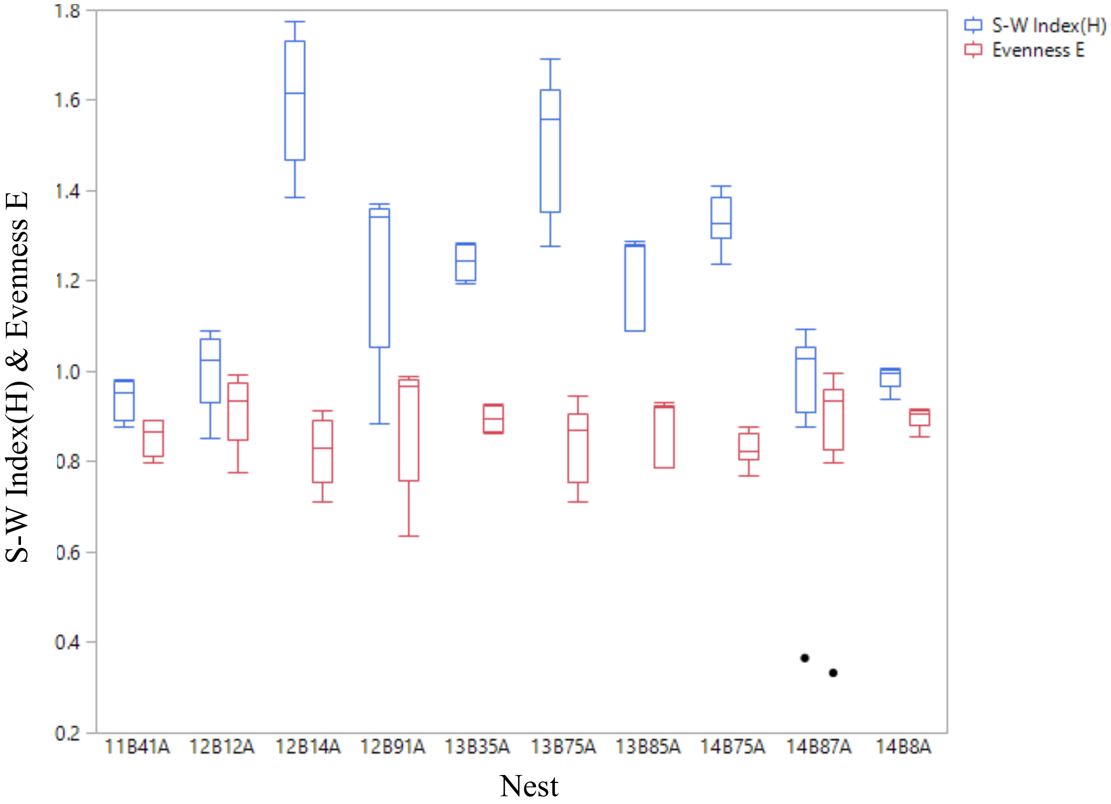


Figure 9. Variation Of The S-W Index And Evenness Of That Index In Each Of The 10 Nests.

Table 3. One-Way Analysis Of Variation Showing Significant Correlation Between Nestling's "Days Of Development" And "Brood Size."

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	23.25098	23.2510	5.8295
Error	58	231.33235	3.9885	Prob > F
C. Total	59	254.58333		0.0189*

Table 4. Individual Variation, Using 2-Level Nested Analysis Of Variance Of Nestlings' S-W Index Within 10 Nests.

Random Effect	Var Ratio	Var Component	Std Error	95% Lower	95% Upper	Wald p-Value	Pct of Total
Nestling[Nest]		0.0188997	0.0038183	0.0131879	0.0293484	<.0001*	100.000
Total		0.0188997	0.0038183	0.0131879	0.0293484		100.000

Source	Nparm	DF	DFDen	F Ratio	Prob > F
Nest	9	9	49	17.7380	<.0001

Identification of Call Types

Using the select measurements of 900 random babbling elements from each nestling, clustering results showed that each nest varied in the number of call types present in sibling groups (Table 5), Clustering analysis revealed that siblings shared call types, but there was variation in how each nestling weighted the repertoire (Figure 10).

Table 5. Number Of Call Types Found In Each Nest, Based On The Multivariate K-Means Clustering.

Nest	Brood Size	# Call Types
11B41A	4	3
13B35A	4	4
14B8A	5	3
12B91A	5	4
14B75A	6	5
13B75A	6	6
13B85A	7	4
12B14A	7	7
12B12A	8	3
14B87A	8	3

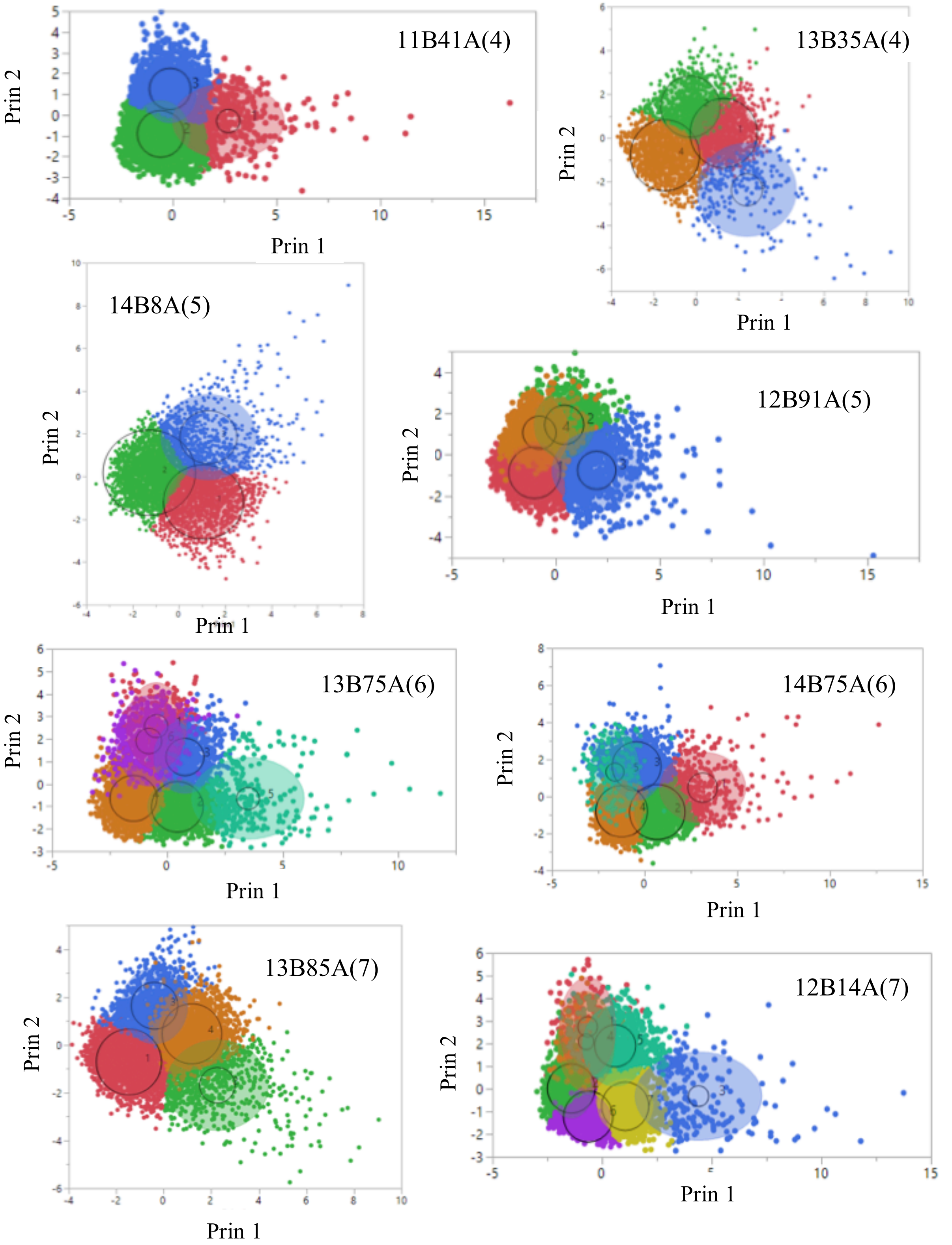


Figure 10. K-Means Clustering Showing Number Of Call Types (Indicated By Circles And Colors) In Each Nest, With Nest ID And Brood Size In Parenthesis. Axis Are First 2 Principal Components Of The Data.

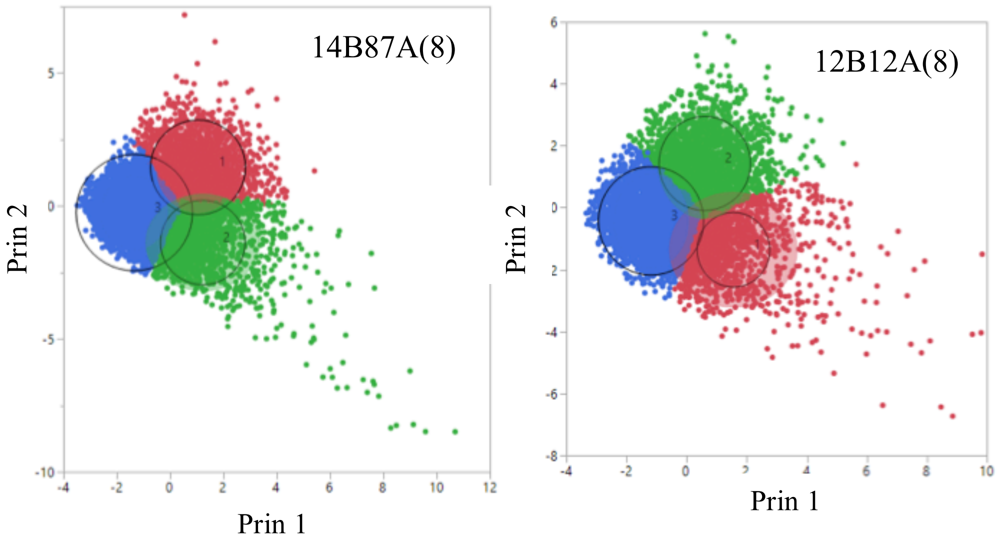


Figure 10 (Cont.). K-Means Clustering Showing Number Of Call Types (Indicated By Circles And Colors) In Each Nest, With Nest ID And Brood Size In Parenthesis. Axis Are First 2 Principal Components Of The Data.

Brood Size Effects

The babbling diversity of nestlings revealed significant differences with increasing brood size of the nest (Figure 11). As sibling numbers increased in the nest, babbling diversity also increased within the individuals of the nest, with the exception of the brood size with 8 nestlings, where the diversity index fell back down again. Analysis of linear mixed effects tested nestlings as a random effect within brood size as a fixed effect. Nestlings showed a significant Wald test p-value (0.0442, df=4, Table 6), and brood size was significant in the effects tests ($p<0.0001$, Table 6). The evenness of the diversity index did not show to have significant differences between brood sizes.

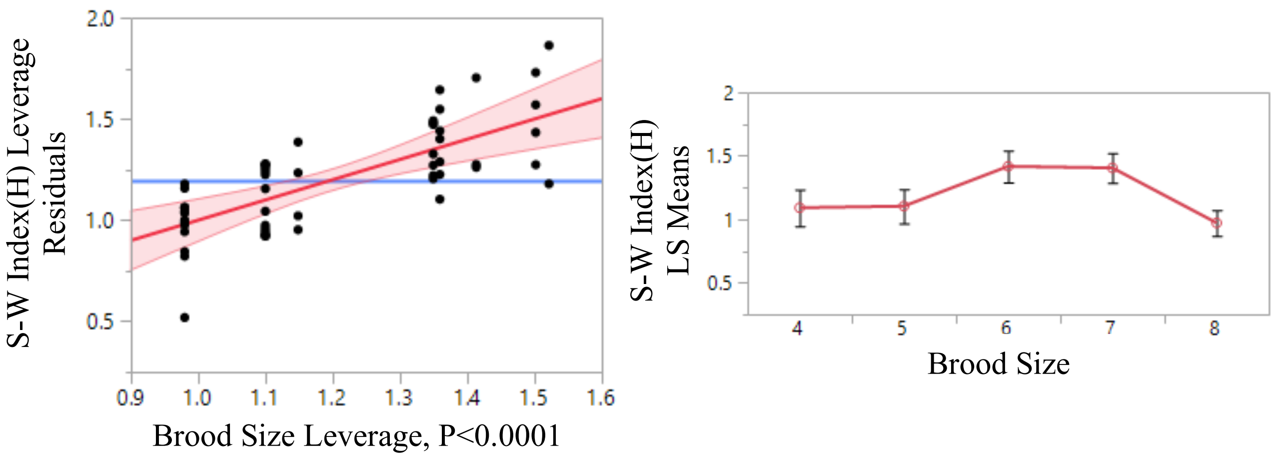


Figure 11. Brood Size Leverage Plots Showing Significance, And Least Squares Means Plot Of Brood Size And S-W Index.

Table 6. Analysis Of Mixed Effects Variation, With Nestlings As Random Effects (REML Variance Component Estimates), And Brood Size As A Fixed Effect.

Random Effect	Var Ratio	Var Component	Std Error	95% Lower	95% Upper	Wald p-Value	Pct of Total
Nestling[Brood Size]	-0.297588	-0.013928	0.0069214	-0.027494	-0.000362	0.0442*	0.000
Residual		0.0468025	0.0124138	0.029566	0.0851585		100.000
Total		0.0468025	0.0124138	0.029566	0.0851585		100.000

Fixed Effect Test	Nparm	DF	DFDen	F Ratio	Prob > F
Brood Size	4	4	23.39	28.3112	<0.0001*

Hatch Sequence Effects

The hatch sequence results showed that while the diversity index had a large range, evenness remained about the same between nestling ages (Figure 12). The hatch sequence categories (1-4) did not appear to be significant in driving any additional diversity to the babbling repertoire, meaning that later-hatched nestlings did not differ in diversity from those that hatched earlier (Figure 13), regardless of brood size category.

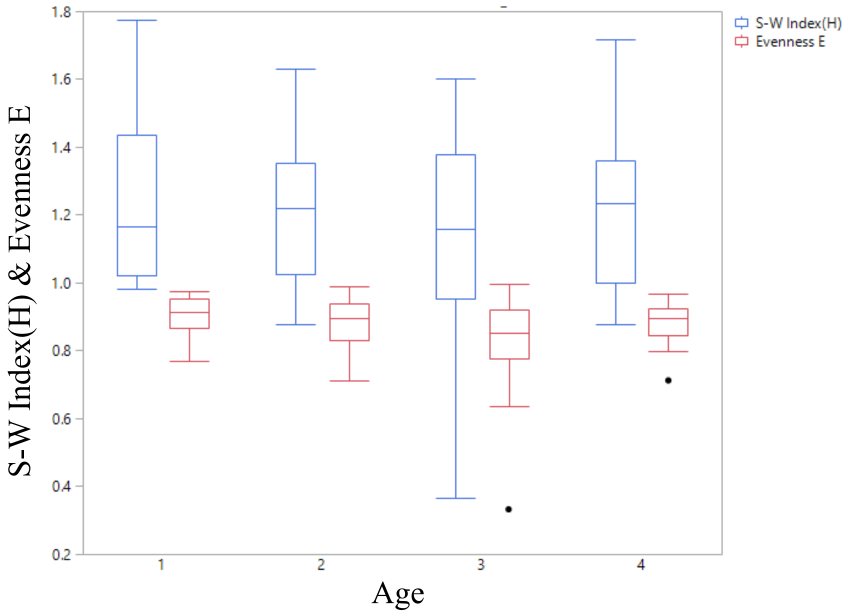


Figure 12. Hatch Sequence Means Plotted With The Diversity Index (Blue) And Evenness (Red).

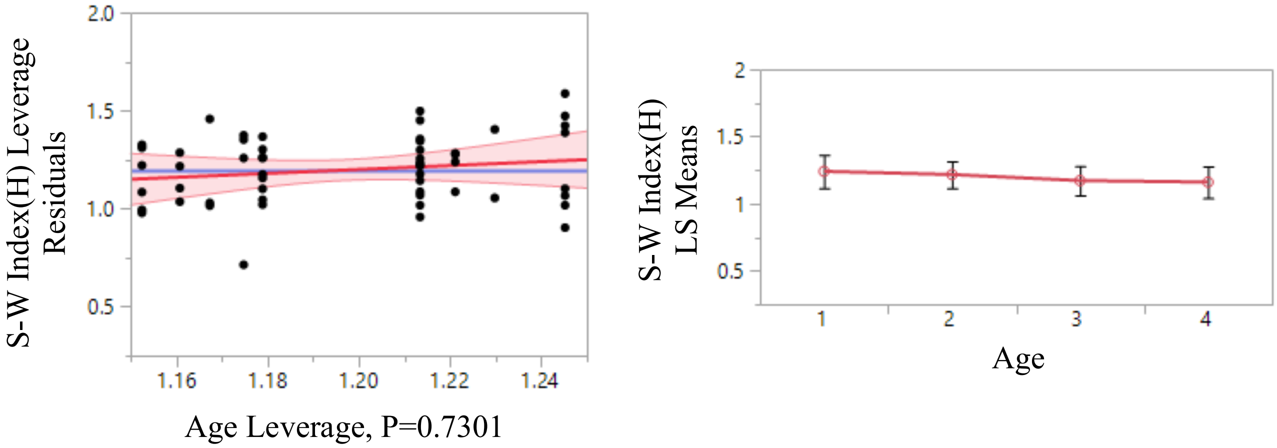


Figure 13. Hatch Sequence And Nestling Diversity Leverage Plot On The Right, And Least Squares Means Plot On The Left.

Table 7. Two Way Analysis Of Variance, Using Brood Size And Hatch Sequence. Effect Tests Of Brood Size And Hatch Sequence (Age) Interactions, Showing No Significance In The Interaction.

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	19	2.3528205	0.123833	3.0365
Error	39	1.5904570	0.040781	Prob > F
C. Total	58	3.9432776		0.0016*

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Brood Size	4	4	2.0149932	12.3525	<.0001*
Age	3	3	0.0530484	0.4336	0.7301
Brood Size*Age	12	12	0.1779882	0.3637	0.9687

CHAPTER V

DISCUSSION

Vocal Babbling in Parrotlets

This is the first study to describe and quantify the vocal babbling behavior based on the acoustical properties of vocalized babbling bouts recorded within nest cavities of a wild parrot. The results provide the first evidence of individual variation and brood size effects in parrot babbling. Individuals varied in how they babbled inside the nest by the number of call types and call richness. The size of the brood where nestlings were developing significantly influenced a nestling's call diversity, as nestlings in larger broods had higher call diversity than nestlings in smaller broods.

This study also tested whether the asynchronous development of nestlings (lasting over 30 days) had any effect on the development of their babbling vocalizations, in regards to call diversity. Results showed that hatch sequence of individuals does not significantly affect babbling diversity, rejecting the hypothesis that younger siblings may have a larger repertoire than older siblings due to more babbling exposure in their development. It's still unknown why this parrot species has asynchronous broods, but hatching asynchrony is often related to larger brood sizes (Beissinger & Waltman 1991). As the cited study proposes, this could be due to the *limited breeding-opportunities hypothesis*, where nest cavities are limited, so females defend their cavities with constant occupancy. But this doesn't explain a connection to development, and the results of this project support that lack of connection. These results conclude that a larger number of siblings influences the individuals' babbling repertoire more than their hatch sequence within the nest.

Brood size also influenced the nestling's length of stay within the nest, with larger broods extending the number of days the birds developed inside the nest. These were results that happened additionally to the proposed hypotheses on babbling, but may play a role in babbling development. The extended development in relation to brood size could help explain the increased babbling repertoire of individuals, since increased time spent in the nest among siblings, in later development, will increase the exposure time of babbling for each sibling.

Brood size influences would lead to the hypothesis that there is an optimum brood size for gaining diversity in vocal babbling. Results showed that brood sizes of 6 and 7 were the highest in babbling diversity (among the tested range) and the highest brood size of 8 actually dropped in their babbling diversity. Parrotlets lay very large clutches, with a mean of 7 eggs, and a range of 3-14 eggs (Beissinger 2008), but not all eggs hatch or fledge. From the 2011-2014 data, a 9-nestling brood size was the biggest clutch that successfully developed and fledged the nest. It may be that broods this large actually compromise diversity in babbling, since larger broods require more resources from the parents for healthy development. If these resources are lacking in any way during the critical time of vocal development, diversifying the behavior may be minimized to focus on the necessary vocal repertoire, without additional variation.

Vocal Complexity

Studies on budgerigars, another parrot species, describe their adult vocal repertoire as composed of contact calls and "warble songs," the latter a "melodic, multi-syllabic, non-stereotyped vocalization that can last well over several minutes" (Tu et al. 2011). Budgerigars that live together also seem to share a higher proportion of similar warble elements in their repertoire than those living apart (Brittan-Powell et al. 1997), although these results are from domesticated individuals, not in their natural setting. Although similarity of sibling vocal elements was not tested in the parrotlets, the current results of increasing repertoire diversity may also reflect that the same siblings are sharing elements of their repertoire.

The warble call of the budgerigar adults could be the adult stage to the vocal babbling behavior of juveniles, because the two vocal outputs share similarities in their length and melodic rambling (Tu et al. 2011). Babbling could be the onset of the warble song in parrot species, but studies on the parrotlet warble song in the wild is needed for a comparison. Songbirds have been shown to have a “plastic song” that precedes their crystalized adult song (Soha & Peters 2015), and babbling could be linked as the “plastic warble song” of parrots, with all of its multi-syllabic variation.

Whether a higher vocal babbling diversity also results in a higher adult repertoire is yet unknown. This study focused on the developmental stage that precedes adult vocalizations, an important behavior that is most likely linked to adult communication and social success. It is known that crystallization of adult vocalizations in songbirds includes loss of acoustic variability to stabilize on a species-specific form or dialect, including learning the specific local language for human infants (Goldstein et al. 2003).

It may be that starting with a higher babbling repertoire allows for a better adaptation to the local dialect. On the other hand, a vocal repertoire that is too diverse may be disadvantageous to a species, because vocal diversity requires that other individuals in the population understand the signals that an individual is transmitting. This is a step that would evolve after vocal learning is already present in a species. Jarvis (2004) and Okanoya (2002) argue that there are pressures that suppresses the possible variation of vocalizations, such as predatory pressure. Just as vocal complexity is attractive to females, it may be attractive to predators by drawing new attention in the acoustical background of an environment (i.e. making an individual stand out). This pressure may be large enough that species do not develop vocal learning as a solution to communication.

The evolution of vocal learning must have been as influenced by an uncertain social environment as its function today is also shaped by social pressures. Jarvis (2004) outlines the possible influential factors that select for learning vocalizations in a species: (1) individual identification; (2) semantic communication; (3) territory defense; (4) mate attraction; (5) complex syntax; and (6) rapid adaptation to sound propagation in different environments. When combined, the above factors could explain the evolution or selection of the vocal learning trait in a species. Individuals withstand necessary adaptations while building vocal complexity throughout life and in changing environments, all while under pressure to retain mate attraction, social cohesion, and predatory avoidance (Sasahara et al. 2012).

Parrotlets babble within the isolated environment of a cavity nest, where their immediate interactions are only with siblings and parents. Of course social learning requires social interactions for it to take place, so the presence of parrotlet siblings could be an important factor in their vocal learning. The extreme hatching asynchrony of parrots produces differences in nestling ages by up to three weeks, creating the opportunity for social interactions between older and younger nest-mates during development (Beissinger & Waltman 1991). The effects of social dynamics and social organization of a species, for its development of social learning, is likely more fundamental than its phylogeny (Galef & Laland 2005).

Vocal Rule Learning

The aim of looking at animal communication for specific mechanisms may be useful for building comparative models among species. The structure of language that gives it infinite complexity can be defined by two characteristics: (1) *phonology*, which is to take meaningless sounds and arrange them into meaningful units, such as words, and (2) *syntax*, which is to take individual sounds that have meaning and arrange them into a larger sequence of meaning, such as sentences (Collier et al. 2014). The rules of phonology and syntax interactions give language its large variation power. Phonology and syntax have been used in research on birdsong to understand the abilities and limitations of these rules in avian communication. The structure and rules of language could be a universal system of communication not limited to humans.

Noam Chomsky proposed his Universal Grammar theory about 50 years ago, which states that children are born with an innate sense of grammar and syntax, and its computational power in language, called *recursion* (Kliesch, 2012). Recursion is typically defined as "the embedding of a unit of a particular category inside a larger unit of the same category" (van Heijningen, de Visser, Zuidema, & ten Cate 2009, p. 20538). The theory describes language to be an innate behavior, and not learned, because our infinite grammar is too complex to be learned. The ability of any normal human child for vocal imitation may represent a novel capacity that evolved in our recent evolutionary history (Hauser, Chomsky, & Fitch, 2002). In recent years the theory has been modified to include social interaction during development, stating that it is a key timeframe where syntactic grammar is modified or polished (Kleisch, 2012), but the focus remains that recursion evolved as a uniquely human ability to construct complex language.

Chomsky's theory has recently been challenged by research on animal abilities with grammatical structures (studies on primates, birds, and rats) (Chen et al. 2015). Because songbirds are vocal learners, have a sensitive vocal learning period, and need adult tutors to learn their species-specific songs, they have been a group of interest for the field of biolinguistics. But understanding the construction of bird songs is difficult without a clear understanding of the message in each song type. To solve this problem, researchers have employed the *artificial grammar paradigm*, which has tested the cognitive ability of abstract thinking in animals (Chen et al. 2015; Suzuki et al. 2016; van Heijningen et al. 2009; ten Cate 2014). If animals show abstract thinking or analogous reasoning in experiments, then this ability is not strictly human and is an example of parallel evolution in other animals as their basis to complex communication.

Support for the idea that abstract thinking has an evolutionary origin prior to human language comes from a key study by Marcus, Vijayan, Bandi Rao, & Vishton (1999), where 7-month infants were tested with artificial grammar learning experiments. They showed that infants can detect the underlying structure of strings of meaningless sounds, which means infants can pick out the grammatical rules of sounds, and then use the same pattern in sounds they've never heard before. Having such an ability in a pre-lingual infant is indication of its evolution before language. It begs the question: is this cognitive ability of detecting abstract patterns also shared with other animals?

To address this question, some studies have looked into rule learning abilities of birds. The first study to address artificial grammar abilities in birds was on European starlings (*Sturnus vulgaris*), and claimed to have found that starlings have recursion (Gentner, Fenn, Margoliash, & Nusbaum, 2006). They reported that starlings accurately recognize a recursive, self-embedding, context-free grammar, meaning that the birds learned a rule from an artificial sequence and applied it to a new artificial sequence of elements by generalization. Starlings are songbirds known for their complex learned songs and social behavior, making them a good candidate for a comparative linguistic model to language. But a study later challenged this conclusion (van Heijningen et al. 2009) by pointing out that the starlings were only tested with familiar song elements that were in different categories (rattles vs. warbles), and not on novel elements, so it could not be concluded that rule learning was the reason for the results. Rather, the acoustic similarity of elements could have been used by the starlings to discriminate between these artificial strings (the phonetic pattern).

After the starling study, the artificial grammar paradigm was redesigned to use novel items within a string, in order to specifically test birds on structural understanding in a sequence of elements (abstract or analogous reasoning). A study on Zebra Finches tested the degree to which the birds can detect and generalize *rule abstractions* by testing both birds and human adults to detect the difference between an XYX and a XXY structure (Chen, van Rossum, & ten Cate, 2015). This kind of string structure allows for interchanging categories of elements, testing between training items and novel items while keeping the structure the same. The authors introduced two different abstraction abilities: (1) *the simple rule abstraction*, which identifies the particular position of the element in the string (first or last notes), and (2) *the complex rule abstraction*, which identifies the underlying structure, even when elements switch to novel elements. Results showed that Zebra Finches could only pass the simple rule abstraction test with familiar song elements, while human subjects passed the complex rule abstraction test with novel elements. These results point towards some sort of ability of abstract thinking in a songbird.

But songbirds are not the only group of birds to have vocal learning and extensive repertoires of songs. Parrots have been an understudied group of birds, and recent research (Colbert-White, Corballis, & Fragaszy, 2014) has revealed important differences: they are lifelong vocal learners, have more vocal variation in their adult songs, which vary in both sequences, shape, and duration of elements within songs, and have large social groups. By contrast, songbirds only have a sensitive song-learning period in development, are limited to a few species-specific adult songs, and many songbird species are territorial.

Budgerigars were tested for rule learning abilities in an artificial grammar paradigm by Spierings and ten Cate (2016), along with zebra finches to compare species-specific learning strategies. In this study, both species had to first distinguish that X and Y are different items in the XYX and XXY sequences, identify the pattern, and then to apply this same abstract pattern when presented with novel items. They identified that parrots showed analogical reasoning because they used the grammatical structure of novel items, without needing to be familiar with the sounds. Zebra finches, on the other hand, could only detect the ordinal position of the items they were familiar with, but could not detect the structure of novel items. The songbird did not have analogical reasoning in the same capacity as parrots, but did respond to similarities of item position in the sequence, indicating that they understand where the elements are (first or last call), but not the actual structure of the sequence.

Different bird groups have evolved different strategies of rule learning, or different levels of abstract thinking, when presented with vocal sequences (Spierings & ten Cate, 2016). The structural strategy employed by the parrots indicates they are more cognitively advanced in solving learning tasks. As the Social Complexity Hypothesis states: the bigger the social group, the more cognitively advanced the species (Freeberg, Dunbar, & Ord, 2012). Applicably, parrots travel and forage in large groups, and need a high social intelligence between all the individuals within the group. In 2006, Gerken tested whether 9-month-old infants also have different strategies in an artificial grammar experiment and found that infants can do both of the strategies shown by the birds (ordinal and structural), and can alternate between them. The presence of these strategies in a parrot species may be an example of parallel evolution with solving communication rules between humans and parrots.

Syntax in communication of other species challenges the universal grammar theory that states there is a given set of properties for all languages. Instead, an evolved flexible vocal solution in several animal species supports that languages develop and die over time in a variety of animal clades (it is estimated that there have existed 500,000 human languages over time) (Kliesch 2012). Bird research has already begun to uncover the possible evolution of language, and the hidden mechanisms of this evolved solution to communication.

Vocal Play-Like Behavior

In humans, babbling is identified as a play behavior expressed during development for the acquisition, or learning, of variable adult vocalizations (Soha & Peters 2015). Play behavior can describe any behavior that expands flexibility and repertoire, especially in juveniles (Dubbeldam, 2001). The definition of vocal play in birds is repetitive and variable vocal patterns, experimentation of adult systems, mostly without negative feedback by adults (Pepperberg 2010). A model that predicts for the evolution of play behavior is that birds engage in social play if (1) they belong to a relatively large-brained, altricial order, (2) they live in complex, stable social groups, and (3) they mature slowly and maintain an extended post-fledging association between juveniles and adults (Diamond et al. 2006).

The above qualifications fit with the social structure of highly-social parrots, such as the species of the current study, the Green-rumped parrotlets. Categorizing vocal diversity prior to maturity as “vocal play” is interesting and naturally open-ended in definition, but it is a new perspective on animal behavior that can yield new observations of the complexity of other animals, especially juveniles.

Conclusion

This work exposes a cryptic developmental stage that has never been explored in wild parrots. Avian research has gaps in how we understand vocal communication and its development in one of the most prolific groups of vocal imitators, the parrots. This project builds the groundwork for the significance of vocal babbling in juvenile parrots. Parrots are one of the most endangered groups of birds in the world, so it is crucial to parrot conservation efforts and wildlife managers that we understand basic developmental biology, especially the life-long impacts of early cognitive nuances. The impacts of this study can build a more wholesome model of the vocal developmental stages, and can be compared across vocal learning species.

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BIOGRAPHICAL SKETCH

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