**A cultural atlas of vocal variation: yellow-naped amazon contact calls exhibit discreet call types throughout their range**

**Molly Genes,1\* Marcelo Araya-Salas,2 Christine Dahlin, 3 Timothy Wright1\***

1Department of Biology, New Mexico State University, Las Cruces, New Mexico, USA

2Centro de Investigación en Neurociencias & Escuela de Biología, Universidad de Costa Rica, San Pedro, San José, Costa Rica

3Department of Biology, University of Pittsburgh at Johnstown, Johnstown, Pennsylvania, USA

\***Correspondence:**

Molly Genes

m\_dupin@aol.com

Timothy Wright

wright@nmsu.edu

**Keywords:vocal learning1, yellow-naped amazon2, vocal dialect3, cultural drift4.**

**Abstract**

The yellow-naped amazon, *Amazona auropalliata,* is a vocal learning parrot species that is native to Mesoamerica. Populations in Costa Rica have been shown to exhibit geographic variation in their contact calls, known as vocal dialects, but little data exists regarding vocal variation trends in populations outside this southern portion of their range. We hypothesized that yellow-naped amazon populations in the northern portion of the range would exhibit similar dialect patterns as those observed in Costa Rica. We recorded yellow-naped amazon contact calls at 47 different sites across the range between 2016 and 2019 and evaluated them for the presence of dialects. We visually classified 14 contact call variants based on spectrographic similarity and used spectrographic cross-correlation along with principal component analysis to assess acoustic similarity. We observed regional separation of variants, with no variants repeating precisely in multiple regions; however, some distinctive structural characteristics are found in multiple variants. Our results indicate that vocal variation covaries with geographic distance. Although our survey was extensive, there are existing unsampled yellow naped amazon populations that should also be investigated and monitored over time. This species can serve as a model for further investigation of vocal learning and the formation and persistence of vocal dialects.

# **1 Introduction**

Vocal learning is a well-studied cognitive trait that is defined as the ability to replicate a sound produced by a conspecific or another species (Bradbury & Balsby, 2016; Tyack, 2020). Cultural transmission of vocal traits occurs when naïve individuals in a population match their vocal behavior to a template observed from conspecifics, such as parents or contemporaries (Whitehead, 2010; Whiten, 2019). Imperfect learning of these traits can lead to changes in the behaviors of a population, a phenomenon known as cultural drift (Podos and Warren, 2007). When acted upon in conjunction with geographic or reproductive isolation, cultural drift in the context of learned vocalizations can produce vocal dialects, a distinct mosaic pattern of geographic variation in acoustic signals (Wright et al., 2008; Martins et al., 2018).

In 1964, Marler and Tamura were the first to identify vocal dialects in a non-human animal, the white-crowned sparrow, *Zonotrichia leucophrys* (Marler & Tamura, 1964). Since their documentation of this occurrence, vocal dialects have been identified in a much wider array of taxa, including whales (Deecke et al., 2000), hummingbirds (Wiley, 1971), seals (Casey et al., 2018), bats (Boughman and Wilkinson, 1998), and parrots (Wright, 1996). Songbirds, however, have remained the main focal point of research regarding both vocal learning (Beecher and Brenowitz, 2005; MacDougall-Shackleton, 2009) and vocal dialects (West and King, 1985; Maney et al., 2003; Pipek et al., 2018; Loo and Cain, 2021) despite their general inability to acquire new songs after crystallization (Brainard & Doupe, 2002). Contrarily, parrot species such as the yellow-naped amazon, *Amazona auropalliata,* are well-known for their vocal mimicry skills and their ability to learn new acoustic signals throughout their lives, known as open-ended learning (Wright and Wilkinson, 2001; Wright et al., 2005).

Yellow-naped amazons are large, social parrots that occur within lowland, seasonally dry tropical forests along both the Pacific and Caribbean coasts of Mesoamerica, ranging from southern Mexico to northern Costa Rica (Wright et al., 2018). They exhibit a fission-fusion flock dynamic, communally roosting in the evenings and departing in smaller groups around sunrise to forage (Wright, 1999). In 1996, Wright documented the first evidence of vocal dialects in a parrot in Costa Rican populations of yellow-naped amazons (Wright, 1996). In 2005, Wright *et al.* resampled contact calls in Costa Rica and found that the acoustic variation discovered in 1996 exhibited both geographic and temporal stability. During both the 1996 and 2005 surveys, birds exhibiting more than one dialect, known as bilingualism, were observed at some sites along dialect boundaries (Wright, 1996; Wright et al., 2008). Genetic analysis showed that yellow-naped amazon vocal dialects are not genetically distinct (Wright and Wilkinson, 2001), suggesting that this species preferentially learns local call types (Wright et al., 2008), a conclusion supported by translocation experiments (Salinas-Melgoza and Wright 2012). No data currently exists on whether yellow-naped amazon vocal dialects extend to portions of the species range outside of Costa Rica. Evaluating their range-wide vocal trends is a necessary step in understanding how and why dialects persist both geographically and temporally.

We hypothesized that vocal dialect patterns observed in the southern portion of the range would also be present in the northern portion. To answer this question, we recorded contact calls from yellow-naped amazon populations in Costa Rica, Nicaragua, Honduras, Guatemala, and Mexico from 2016-2019. We expected to see a mosaic pattern of geographic variation in the contact calls, where calls within populations are more similar in their acoustic structure than between populations (Wright and Dahlin, 2017). Alternatively, variation in yellow-naped amazon contact calls could be graded, or clinal. In this case, we expected to see the acoustic structure of calls progressively diverge from one end of the range to the other (Lee et al., 2019). We used SPCC, PCA, and mantel-based spatial autocorrelations to assess these two alternatives. In addition, we compared the fit of models predicting vocal variation based on our visual dialect classification to a model based on geographic distance alone.

# **2 Materials and methods**

## **2.1 Datacollection**

We recorded the contact calls of unmarked and unsexed yellow-naped amazons occurring in and around the same roost sites surveyed by Dupin *et al.* (2020). We recorded calls during the morning and evening, after individuals had left or as they arrived at the night roost. Contact calls are the most frequently emitted acoustic signal in this species, particularly in and around the roost where we opportunistically recorded birds during morning and evening choruses (Wright, 1996). We recorded flyovers and perched calls as this species is known to use contact calls in both contexts (Wright, 1996). We aimed to record a minimum of 10 calls each from six different birds at each site. Calls were recorded using a Sennheiser (ME67, Wedemark, Germany) shotgun microphone and a Marantz (PMD660, Sagamihara, Japan) digital recorder at sampling rate of 22.05 kHz and an amplitude resolution of 16 bits. Individuals were differentiated in recordings via detailed dictation by the person doing the recording.

## **2.2 Sampling sites**

We sampled contact calls from yellow-naped amazons during June and July of 2016, 2018, and 2019; both are months that fall outside of the species’ breeding season (Matuzak and Brightsmith, 2007). Sites were determined based on previous sampling history, local anecdotes, local organizations working with yellow-naped amazons, and the use of eBird. We attempted to sample birds at all locations where they were known to exist at the time of sampling. In 2016, we surveyed 25 sites in Costa Rica and 19 in Nicaragua, in 2018 we sampled 11 sites in southern Mexico, and in 2019 we resampled 2 sites and sampled an additional 3 new sites in Mexico, as well as 5 sites in Guatemala, and 7 sites in the Bay Islands, Honduras; one site in the Bay Islands was a private location which remains undisclosed at the owner’s request. In total, we surveyed 72 sites across the yellow-naped amazon range (Figure 1). We were unable to sample a reportedly small population on the Pacific coast of El Salvador, and larger populations reported to occur along the Caribbean coast of Honduras and Nicaragua due to safety and logistical challenges.

**2.3 Data processing**

Contact calls were processed digitally and visualized using the sound analysis program Raven Pro version 1.5. Calls from each field site were selected for analysis after a visual assessment of the original sound files and identification of one or more local variants. Contact calls in yellow-naped amazons are typically short (0.2 - 0.5 seconds), monosyllabic, have a dominant frequency around 2 kHz, and are repeated in long strings by birds while perched and in flight; thus, call variants across the range were identified as homologous by looking for these patterns. After all contact calls within each file were identified, the highest quality calls were selected by highlighting the call from start to finish using the cursor in Raven. In 2016, calls were highlighted in the original sound file before being copied and pasted into a blank window and saved as a new sound file. This procedure produced a sound file for each individual contact call. In 2018 and 2019, we selected calls within raw sound files and saved those selections within the original sound file, generating a .txt file selection table in Raven. Each 2018 and 2019 original sound file was therefore accompanied by a selection table which detailed the start and end time of each selected and saved within it. We used the start and end times from the selection table files and individual contact call sound files in our metadata sheet which we used for subsequent analyses.

## **2.4 Visual assessment of call variants**

We visually assessed variation in all the calls from 2016, 2018, and 2019 by creating spectrograms. Selection tables were generated by manually highlighting calls within raw sound files, and then exporting those tables from Raven into R using the function imp\_raven from the package Rraven (Araya-Salas, 2020). All selection tables were combined, and the dataset was used to create a spectrographic catalogue of all calls from each year using the catalog function from the warbleR package in R (Araya-Salas & Smith-Vidaurre, 2017) (code available supplementarily). We used a window length of 512, overlap of 85%, and a bandpass filter with low and high frequencies of 0.5kHz and 2.5kHz, respectively. We chose these frequency limits to filter out low and high frequency background noise such as traffic, cicadas, and other bird species. Calls were organized into visual catalog by site.

Each contact call was categorized as being of low, medium, or high signal quality by a single observer (MG). Low quality calls were those that had high levels of noise interference, overlap with another call, and/or had no visible harmonic bands in the signal; calls of medium quality had some visible bands but lacked higher-frequency harmonics and might contain some noise interference. High quality calls had multiple, dark bands and no noise interference. Each spectrogram was evaluated for the presence of overlap with other calls, and whether a 2.5 kHz upper frequency limit excluded any overlapping signal or background noise. All low-quality calls were removed from the dataset along with calls that overlapped with another signal. Calls that presented with noise even after the bandpass filter was implemented were examined individually to determine whether that noise would interfere with analysis. If noise did not overlap significantly with the call or was mostly excluded as a result of the bandpass filter, it was retained.

After our visual assessment, we evaluated the number of remaining calls per bird at each site, and the number of birds at each site. Birds with less than 3 calls and sites with less than 3 birds were removed from the dataset. We adjusted the start and end times of the remaining calls using the seltailor function from the warbleR package in R (Araya-Salas & Smith-Vidaurre, 2017) (code provided in electronic supplement). Each call was then categorized based on its acoustic structure; calls with noticeably different acoustic structures were categorized as a distinct call variant. This method is subjective but has proven to be useful as a tool to assess the overall degree of difference between variants, as described by Wright and colleagues in their previous studies on yellow-naped amazons (Wright, 1996; Wright et al., 2008). All calls were grouped by country for subsequent analyses to aid in visual assessment of results.

## **2.5 Statistical analyses**

We conducted a spectrographic cross-correlation (SPCC) using the cross\_correlation function from the package warbleR in R (Araya-Salas & Smith-Vidaurre, 2017). Window length was set at 512, overlap was set at 85%, and low and high frequency bounds set at 0.5kHz and 2.5 kHz, respectively. The cross\_correlation function generates a correlation matrix that we used to create classic metric multidimensional scaling (hereafter, MDS) plots as well as Kruskal non-metric MDS plots. The classic MDS plots were created by using the package ggplot2 (version 3.3.5) (Wickham, 2009) to plot all points from the first two dimensions of the cross-correlation matrix in acoustic space. We also created Kruskal non-metric MDS plots (hereafter, kernel plots) using the function isoMDS from the package MASS in R (Venables and Ripley, 2002). The kernel plots we produced showed the distribution of each call using contour lines, with closer lines representing a higher density of calls. The smallest circles indicate high concentrations of calls in one area of acoustic space; we refer to these as centroids of the distribution. In addition to creating plots for each country, we also generated cumulative plots over the entire range for each analysis to assess whether variation appeared to be random or clinal. All code used for SPCC and MDS plots was modelled on code by Smith-Vidaurre *et al*. available online via GitHub (Smith-Vidaurre et al., 2021).

We used a principal component analysis as an alternative approach to measure similarity between call variants across the range. We accomplished this by first using the spectro\_analysis function from the warbleR package in R (Araya-Salas & Smith-Vidaurre, 2017) to measure acoustic parameters across calls, and then using the prcomp function (R Core Team, 2021) to apply the principal component analysis (PCA). We plotted the first 2 principal components for each region as a ground-truthing method to validate the approach. We used the function levene.Test() (R Core Team, 2021) to assess for equal variances, and the function shapiro.test() (Venables and Ripley, 2002) to evaluate the normality of our dataset. We performed Welch’s ANOVA using oneway.test() (R Core Team, 2021) on principle components 1 and 2 from our PCA output to evaluate for differences among variants. To determine which variant comparisons showed significant differences, we conducted a Games-Howell post-hoc analysis on our ANOVA results using the posthocTGH() from the rosetta package (version 0.3.6) (Peters and Verboon, 2021).

Finally, we evaluated the relationship between geographic distance and acoustic similarity of contact calls by employing a mantel-based spatial autocorrelation using the package vegan (version 2.5-7) (Oksanen et al., 2020). Calls were split into distance classes according to a predetermined number and any distance classes where there were not enough observations were removed from the analysis. The first distance class evaluates calls recorded at the same site. We used Holm’s p-value for multiple testing to create a correlogram of the data (Holm, 1979).

**3 Results**

## **3.1 Contact calls and quality assessment**

We surveyed 72 locations in Mesoamerica where yellow-naped amazons are known to occur or have occurred historically. We observed this species at 56 of those sites, and recorded 3 or more individuals at 47 sites. In 2016 our team sampled contact calls at 22 locations in Costa Rica and 9 in Nicaragua. We sampled calls at 10 sites in Mexico between 2018 and 2019. In 2019 we sampled calls at 2 sites in Guatemala and 4 in the Bay Islands of Honduras. We identified and selected 2,561 yellow-naped amazon contact calls from our field recordings and removed 116 of those during quality assessment due to the presence of noise overlap or low signal quality. In total, 26 birds were removed from the remaining dataset due to retention of fewer than three contact calls. Eight birds were removed from Mexico 2018/2019, 4 from Guatemala, 1 from the Bay Islands, Honduras, 2 from Nicaragua, and 11 from Costa Rica. Three sites from Costa Rica (Enseñada, Pelon Bajura, and Palo Verde) were removed as a result of having fewer than 3 birds. None of the other countries surveyed had sites removed during quality assessment.

We retained 2,338 yellow-naped amazon contact calls from our original dataset for analysis. We classified 21.5% of calls as medium quality, and 78.5% of calls as high quality. Contact calls from Mexico represented 23.3% of contact calls in the final dataset; Guatemala 1.5%; the Bay Islands, Honduras 9.3%; Nicaragua 23%; and Costa Rica 43% of all calls.

## **3.2 Call variants across the range**

Our visual classification of yellow-naped amazon contact calls yielded 14 different call variants across the species range (Figure 2). We identified 4 variants in Mexico and 2 variants in Guatemala. In the Bay Islands Honduras, recorded individuals exhibited 2 distinct variants. Previously, Wright *et al.* reported 3 call variants in Costa Rica during a 1994 survey and the same 3 variants and a new subvariant during a second survey in 2005 (Wright, 1996; Wright et al., 2008); our visual analysis of contact calls collected from these same regions during 2016 indicate that birds in Nicaragua give 4 different variants, one of which was previously reported at the northern border of Costa Rica, and birds in Costa Rica give 2 different variants, both of which were reported in the previous surveys. Sixteen percent of the 243 birds in our dataset exhibited bilingualism. Overall, these observations were rare, and primarily concentrated in Costa Rica (N = 16), although bilingual birds were also recorded in Mexico (N = 2) and Guatemala (N = 1). None of the birds in our dataset from Nicaragua or Honduras were bilingual. Additionally, our visual assessment suggested that the mosaic patterns of vocal variation consistent with dialects was present throughout the range, rather than clinal or graded variation of call types. Dialect variatants in this species appear to result from discreet modifications to a basic call structure (Figure 3) that result in superficially similar call variants appearing in different parts of the species range.

**3.3 Spectrographic cross-correlations**

SPCC analyses for each country supported some, but not all of our call classifications for the yellow-naped amazon contact call variants identified across the range (Figure 4). When all identified variants from across the range were plotted in acoustic space, it was difficult to visually detect separate distributions as many overlapped to a significantextent. When we examined acoustic overlap on a country-level basis, we noticed that the variants sampled in the northern portion of the range showed more acoustic separation amongst themselves than did calls in the southern portion of the range, where dialects were first described in this species.

## **3.4 Principal component analysis of spectral measures**

We used PCA on spectral measures as an alternative measure of validation for our visually classified contact call variants. The first 5 loadings from our analysis accounted for 77.38% of cumulative variation (Figure 4). PC1 represented 26.69% of explained variation and primarily accounted for differences in frequency variables such as mean dominant frequency, and mean frequency (in kHz). PC2 explained 17.60% of variation and represented differences in temporal variables such as signal duration and duration of the call in the 75th quantile.

Plots of PC1 and PC2 for variants in each country generally reflected the patterns exhibited in the corresponding SPCC plots. When we created a PC plot for all call variants identified across the range, there was little visual separation among call types. An ANOVA on PC1 and PC2 did indicate significant differences between call variants for both PC1 (F = 294.07, df = 299.41, p = < 2.2-16) and PC2 (F = 53.263.82, df = 300.35, p = < 2.2-16).

## **3.5 Spatial patterns of acoustic similarity**

The Mantel-based spatial autocorrelogram illustrated 3 distinct patterns in our data. First, within 250 km yellow-naped amazon contact calls generally exhibit high similarity (Figure 5). The second pattern we identified was the significant dissimilarity in calls between ??? and ??? km; beyond ??? km there is an almost equal distribution of significant similarity and dissimilarity, with an increasingly neutral significance as geographic distance increases.

**4 Discussion**

Historically, variation in the contact calls of yellow-naped amazons in Costa Rica has been described as dialectical, with a mosaic pattern of variation in which calls within a locale are similar but change dramatically in acoustic structure at dialect boundaries (Wright, 1996). Our visual classification of the 14 different call types observed across this species’ range support this historical trend. Currently wild yellow-naped amazons are isolated into discreet regional populations due to loss of habitat and declining populations (Dupin et al., 2020). In each region we sampled, we observed more than one variant with discreet differences which we were able to detect visually. Our SPCC and PCA analyses validated many, but not all, of our visually identified variants.

## **4.1 Global patterns of vocal variation**

In 1996, Wright identified 3 distinct contact call variants in Costa Rican populations (Wright, 1996), and later confirmed the geographic and temporal stability of those same variants (Wright et al., 2005). Our visual assessment of 2,338 contact calls collected from yellow-naped amazons across their range revealed the presence of 14 distinct call variants, including those identified in 1996. Results from our SPCC analyses and PCA support many of our visual classifications; however, they also indicate that several variants were acoustically similar. This pattern may result from the repetition of similar acoustic structures in different parts of the range, or a lack of resolution in our acoustic analysis approaches.While SPCC is widely-used method of assessing acoustic similarity (Cortopassi and Bradbury, 2000; Sharp and Hatchwell, 2006; Araya-Salas et al., 2019) and has been used in previous yellow-naped amazon dialect studies (Wright, 1996; Wright et al., 2008), the limits of its capabilities should be considered. The cross-corr function from the package warbleR in R generates correlation coefficients by sliding one spectrogram over another and comparing amplitudes across each call (Clark et al., 1987; Araya-Salas and Smith-Vidaurre, 2017; Sawant et al., 2022). Thus, when call variants are similar in the same bandwidths being measured, the cross correlation will indicate that the calls are acoustically similar, even if there are visually detectable differences in the overall structure. Although SPCC is considered to be robust to noise, field recordings do contain acoustic interference like insects, other birds, vehicles, agricultural equipment, and animals. We implemented a bandpass filter to remove high and low frequency noise but were unable to eliminate masking noise within the same range as the calls themselves.

Several other parrot species have been found to exhibit vocal dialects in addition to yellow-naped amazons, including the Australian ringneck parrot, *Barnardius zonariu* (Baker, 2000); galah, *Eolophus roseicapillus* (Baker, 2003); Australian palm cockatoo, *Probosciger aterrimus* (Keighley et al., 2017); Cuban parrot, *Amazona leucocephala* (Reynolds and Hayes, 2010); and invasive populations of the monk parakeet, *Myiopsitta monachus* (but see (Smith-Vidaurre et al., 2021) for evidence of different patterns in native populations)(Buhrman-Deever et al., 2007). There is little understanding as to why parrot species exhibit vocal dialects, but several hypotheses have been formed to explain their function. Podos and Warren (Podos and Warren, 2007) postulate that female preference for local call types is a driver of acoustic divergence. In this case, female sexual preference for males with a local trait would result in some level of genetic divergence between populations (Wilkins et al., 2013). A study by Wright and Wilkinson reported no genetic correlation with yellow-naped amazon contact calls, stating instead that individuals exhibited high dispersal across dialect boundaries (Wright and Wilkinson, 2001). Parrots may also exhibit vocal dialect as a badge or signal of group affiliation and familiarity (Sewall et al., 2016). Alternatively, geographic variation as seen in dialects could be a consequence of cultural drift, when individuals learning calls make copying errors (Podos and Warren, 2007).

Overall, yellow-naped amazon vocal dialect shows evidence of cultural drift. In general, we noticed that yellow-naped amazon contact calls exhibit some similar spectrographic structures in different call variants across the range, like the presence of gaps within a call, frequency shifts, and differences in duration. We observed that neighboring call types exhibit subtle differences in acoustic structure as opposed to whole-structure change. In conjunction, these facts suggest that call variants have a common origin, and that variation is a result of imperfect learning. Previous temporal studies by Wright *et al.* on yellow-naped amazons in Costa Rica also lend credence to the cultural drift hypothesis (Wright et al., 2008) C. Dahlin et al in prep). Additionally, there is support for the social identification hypothesis when call variants are examined on a smaller scale. Previously, Wright found that neighboring dialects exhibited marked differences. If dialects were solely a result of cultural drift, neighboring call types would show a strong tendency to be more similar and show clinal variation across the range. The absence of strong clinal patterns suggest that there is some selection for neighboring populations to produce acoustically distinct call types, consistent with the hypothesis that calls function for group identification. The fission-fusion pattern of distribution in yellow-naped amazons increases the likelihood that individuals mix with neighboring populations during foraging hours. It is highly probable that individuals using different variants would forage together at some point or regularly. In this case, the occurrence of bilingualism supports this theory.

Several birds in our dataset exhibited more than one call variant. In most cases of bilingualism there appeared a dominant call type used with high frequency by an individual, and another type which a bird would emit rarely. Wright reported the infrequent occurrence of bilingual birds in Costa Rica during his 1994 survey, and Wright *et al.* observed them infrequently in Costa Rica during their 2005 survey (Wright, 1996; Wright et al., 2005). Bilingualism may exist in these populations to facilitate individual movement between social groups during fission and fusion. If, during foraging, individuals encounter conspecifics that give a different call type, learning the additional call type might increase foraging success and enhance protection provided by group membership.

**4.2 Regional patterns and implications for cultural evolution**

Yellow-naped amazon populations currently occur in regional clusters across their range with few or no birds in between, due to rapid population declines (Dupin et al., 2020). This geographic isolation may serve to enhance the mosaic pattern of call distribution, however, there is no reason to believe that the current call types have arisen due to this recent isolation. Rather, it sems more likely that call types predate this isolation, as some of the earliest recordings from this region show distinct regional variants (see Wright and Wilkinson 2001). In southern Nicaragua and Costa Rica, where yellow-naped amazon populations are more contiguous, many variants are restricted to a certain geographic area, while others appear are currently more wisespread. In the northern-most country of Mexico, yellow-naped amazons are much more sparsely distributed, which may explain why call types exhibit almost no acoustic overlap.

Though we were able to sample the majority of the native yellow-naped amazon range, there are several regions we were unable to survey due time, manpower, and safety limitations. These regions include the country of El Salvador, the southeastern Caribbean region of Honduras, and the northwestern Caribbean region of Nicaragua. Although we were not able to record birds in these areas, we believe that our data is still an accurate representation of the pattern of vocal variation across the range as we were able to sample populations at the northern- and southern-most bounds. A study by Herrera and colleagues in El Salvador suggest there are an estimated 250 yellow-naped amazons in the country (2020). It is also likely that some healthy populations remain in the large, unsampled regions of Nicaragua and Honduras where forests are relatively intact and human populations are smaller. Future yellow-naped amazon dialect studies should focus on evaluating the temporal and geographic stability of variants across the range, including those unsampled populations.

**4.3 Summary and future directions**

Our catalog of vocal variation in contact calls across the range of the yellow naped amazon supports the idea that vocal dialects are present across the range. This result suggests that the factors that give rise to, and maintain, vocal dialects are inherent to the social structure and communication system of this species. Our observation of repeated structural similarities in geographically distinct acoustic variants suggests that calls may have diversified from a shared basic structure through the occurrence of learning errors and their subsequent cultural transmission in populations. These regional variants may then be maintained by a tendency towards philopatry and selection towards matching regional variants to enhance group identification, as suggested by playback responses of dialect variants of another vocalization type, pair duets (Wright & Dorin 2001). Recent isolation of populations may reinforce these tendencies. Future studies on yellow-naped amazons could examine functional responses to dialect variants of contact calls, potentially in reintroduced populations that lack local dialect types.. Overall, our study contributes to the growing body of evidence that yellow-naped amazons are a useful model species for understanding the functions of vocal learning and the evolution of vocal dialects.

**5 Conflict of Interest**

The authors declare that the research was conducted in absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

**6 Author Contributions**

Molly K. Genes formulated the questions, collected data, analyzed the data, and wrote the paper; Marcelo Araya-Salas analyzed the data; Christine R. Dahlin collected data and supervised the research; Timothy F. Wright collected data and supervised the research

**7 Funding**

This research was funded by the World Parrot Trust (grant date April 2018), and New Mexico State University’s College of Arts and Sciences.

**8 Acknowledgements**

We are very grateful to the colleagues that aided in the collection field data between 2016 and 2019: Alyssa Trimeloni, Dr. Grace Smith-Vidaurre, Dominique Hellmich, Lorena Cabada-Gomez, Carlos Campos, Dr. James Gilardi, Sam Williams and the Macaw Recovery Network, Eric Anderson, Edith Belen Jimenez Diaz, Cristina Contreras Meda, Candelario Giron Montes, Martín Lezama Lopez, and Cara Dunbar. We would also like to extend a thank you to the following organizations which facilitated in data collection via permission to record on their land: Area de Conservación Guanacaste, La Biosfera de la Encrucijada, and Finca Patrocinio and One Earth Organization. Also, thank you to Theodore Muka, Sophia Lasche, and Adam Hopper for providing feedback and editing.

**9 Contribution to the field**

Vocal learning research in wild animals has gained momentum over the last several decades, yet the focus of most studies remains on songbird species. Songbirds, however, are limited in their capabilities when it comes to vocal learning, as there is generally a period after which individuals cannot learn new calls or song. In contrast, many parrot species are known to be open-ended vocal learners, acquiring new calls and additions to song repertoires well into adulthood. Our study on the yellow-naped amazon illustrates the remarkable capabilities of a species to differentiate between populations by using different contact calls. Additionally, our analyses show that the variants we identified across the range show general similarities, meaning that yellow-naped amazons are able to recognize slight differences in call structure. Although songbirds are more easily kept in captive situations, wild parrots have abundant untapped potential to reveal more about vocal learning processes and communication processes than songbirds can afford. Thus, we hope that our study encourages other researchers in the field of vocal learning to consider wild parrot populations, such as the yellow-naped amazon, as model species in the future.

# **10 References**

Araya-Salas, M., and Smith-Vidaurre, G. (2017). warbleR: an r package to streamline analysis of animal acoustic signals. *Methods Ecol Evol* 8, 184–191. doi: 10.1111/2041-210X.12624.

Araya-Salas, M., Smith-Vidaurre, G., Mennill, D. J., González-Gómez, P. L., Cahill, J., and Wright, T. F. (2019). Social group signatures in hummingbird displays provide evidence of co-occurrence of vocal and visual learning. *Proceedings of the Royal Society B: Biological Sciences* 286. doi: 10.1098/rspb.2019.0666.

Baker, M. C. (2000). Cultural diversification in the flight call of the Ringneck Parrot in Western Australia. *Condor* 102. doi: 10.2307/1370319.

Baker, M. C. (2003). Local similarity and geographic differences in a contact call of the Galah (Cacatua roseicapilla assimilis) in Western Australia. *Emu* 103. doi: 10.1071/MU02035.

Beecher, M. D., and Brenowitz, E. A. (2005). Functional aspects of song learning in songbirds. *Trends Ecol Evol* 20. doi: 10.1016/j.tree.2005.01.004.

Boughman, J. W., and Wilkinson, G. S. (1998). Greater spear-nosed bats discriminate group mates by vocalizations. *Anim Behav* 55, 1717–1732. doi: 10.1006/anbe.1997.0721.

Bradbury, J. W., and Balsby, T. J. S. (2016). The functions of vocal learning in parrots. *Behav Ecol Sociobiol* 70, 293–312. doi: 10.1007/s00265-016-2068-4.

Brainard, M. S., and Doupe, A. J. (2002). What songbirds teach us about learning. *Nature* 417. doi: 10.1038/417351a.

Buhrman-Deever, S. C., Rappaport, A. R., and Bradbury, J. W. (2007). Geographic Variation in Contact Calls of Feral North American Populations of the Monk Parakeet. *Condor* 109. doi: 10.1093/condor/109.2.389.

Casey, C., Reichmuth, C., Costa, D. P., and Boeuf, B. Le (2018). The rise and fall of dialects in northern elephant seals. *Proc. R. Soc. B* 285, 20182176. doi: 10.1098/RSPB.2018.2176.

Clark, C. W., Marler, P., and Beeman, K. (1987). Quantitative Analysis of Animal Vocal Phonology: an Application to Swamp Sparrow Song. *Ethology* 76. doi: 10.1111/j.1439-0310.1987.tb00676.x.

Cortopassi, K. A., and Bradbury, J. W. (2000). The comparison of harmonically rich sounds using spectrographic cross-correlation and principal coordinates analysis. *Bioacoustics* 11. doi: 10.1080/09524622.2000.9753454.

Deecke, V. B., Ford, J. K. B., and Spong, P. (2000). Dialect change in resident killer whales: Implications for vocal learning and cultural transmission. *Anim Behav* 60, 629–638. doi: 10.1006/anbe.2000.1454.

Dupin, M. K., Dahlin, C. R., and Wright, T. F. (2020). Range-wide population assessment of the endangered yellow-naped amazon (Amazona auropalliata). *Diversity (Basel)* 12. doi: 10.3390/d12100377.

Herrera, N., Lara, K., and Funes, C. (2020). Estado poblacional de la Lora Nuca Amarilla (Amazona auropalliata) en El Salvador. *Zeledonia* 21.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian journal of statistics* 6.

Keighley, M. V., Langmore, N. E., Zdenek, C. N., and Heinsohn, R. (2017). Geographic variation in the vocalizations of Australian palm cockatoos (Probosciger aterrimus)\*. *Bioacoustics* 26. doi: 10.1080/09524622.2016.1201778.

Lee, J. H., Podos, J., and Sung, H. C. (2019). Distinct patterns of geographic variation for different song components in Daurian Redstarts Phoenicurus auroreus. *Bird Study* 66. doi: 10.1080/00063657.2019.1614144.

Loo, Y. Y., and Cain, K. E. (2021). A Call to Expand Avian Vocal Development Research. *Front Ecol Evol* 9. doi: 10.3389/fevo.2021.757972.

MacDougall-Shackleton, S. A. (2009). The importance of development: What songbirds can teach us. *Canadian Journal of Experimental Psychology* 63. doi: 10.1037/a0015414.

Maney, D. L., MacDougall-Shackleton, E. A., MacDougall-Shackleton, S. A., Ball, G. F., and Hahn, T. P. (2003). Immediate early gene response to hearing song correlates with receptive behavior and depends on dialect in a female songbird. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 189. doi: 10.1007/s00359-003-0441-z.

Marler, P., and Tamura, M. (1964). Culturally transmitted patterns of vocal behavior in sparrows. *Science (1979)* 146. doi: 10.1126/science.146.3650.1483.

Martins, B. A., Rodrigues, G. S. R., and de Araújo, C. B. (2018). Vocal dialects and their implications for bird reintroductions. *Perspect Ecol Conserv* 16, 83–89. doi: 10.1016/j.pecon.2018.03.005.

Matuzak, G. D., and Brightsmith, D. J. (2007). Roosting of Yellow-naped Parrots in Costa Rica: Estimating the size and recruitment of threatened populations. *J Field Ornithol* 78. doi: 10.1111/j.1557-9263.2007.00099.x.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2020). vegan: Community Ecology Package.

Peters, G.-J., and Verboon, P. (2021). rosetta: Parallel Use of Statistical Packages in Teaching.

Pipek, P., Petrusková, T., Petrusek, A., Diblíková, L., Eaton, M. A., and Pyšek, P. (2018). Dialects of an invasive songbird are preserved in its invaded but not native source range. *Ecography* 41, 245–254. doi: 10.1111/ecog.02779.

Podos, J., and Warren, P. S. (2007). The Evolution of Geographic Variation in Birdsong. *Adv Study Behav*. doi: 10.1016/S0065-3454(07)37009-5.

R Core Team (2021). *R: A Language and Environment for Statistical Computing*. Vienna, Austria.

Reynolds, M. B. J., and Hayes, W. K. (2010). Geographic Variation in the Flight Call of the Cuban Parrot (Amazona leucocephala) and its Taxonomic Relevance. *Journal of Caribbean Ornithology* 23.

Salinas-Melgoza, A., and Wright, T. F. (2012). Evidence for vocal learning and limited dispersal as dual mechanisms for dialect maintenance in a parrot. *PLoS One* 7. doi: 10.1371/journal.pone.0048667.

Sawant, S., Arvind, C., Joshi, V., and Robin, V. V. (2022). Spectrogram cross-correlation can be used to measure the complexity of bird vocalizations. *Methods Ecol Evol* 13. doi: 10.1111/2041-210X.13765.

Sewall, K. B., Young, A. M., and Wright, T. F. (2016). Social calls provide novel insights into the evolution of vocal learning. *Anim Behav* 120. doi: 10.1016/j.anbehav.2016.07.031.

Sharp, S. P., and Hatchwell, B. J. (2006). Development of family specific contact calls in the Long-tailed Tit Aegithalos caudatus. *Ibis* 148. doi: 10.1111/j.1474-919X.2006.00568.x.

Smith-Vidaurre, G., Araya-Salas, M., and Wright, T. F. (2021). Individual signatures outweigh social group identity in contact calls of a communally nesting parrot. *Behavioral Ecology* 31. doi: 10.1093/BEHECO/ARZ202.

Tyack, P. L. (2020). A taxonomy for vocal learning. *Philosophical Transactions of the Royal Society B: Biological Sciences* 375. doi: 10.1098/rstb.2018.0406.

Venables, W. N., and Ripley, B. D. (2002). *Modern Applied Statistics with S*. Fourth. New York: Springer.

West, M. J., and King, A. P. (1985). Studying dialects in songbirds: Finding the common ground. *Behavioral and Brain Sciences* 8. doi: 10.1017/S0140525X0001997X.

Whitehead, H. (2010). Conserving and managing animals that learn socially and share cultures. *Learn Behav* 38. doi: 10.3758/LB.38.3.329.

Whiten, A. (2019). Cultural Evolution in Animals. *Annu Rev Ecol Evol Syst* 50. doi: 10.1146/annurev-ecolsys-110218-025040.

Wickham, H. (2009). *ggplot2*. New York, NY: Springer New York doi: 10.1007/978-0-387-98141-3.

Wiley, R. H. (1971). Song Groups in a Singing Assembly of Little Hermits. *Condor* 73. doi: 10.2307/1366121.

Wilkins, M. R., Seddon, N., and Safran, R. J. (2013). Evolutionary divergence in acoustic signals: Causes and consequences. *Trends Ecol Evol* 28, 156–166. doi: 10.1016/j.tree.2012.10.002.

Wright, T. (1999). Vocal Communication In Wild Populations of the Yellow-naped Amazon (Amazona auropalliata). *AFA Watchbird* 26.

Wright, T. F. (1996). Regional dialects in the contact call of a parrot. *Proceedings of the Royal Society B: Biological Sciences* 263, 867–872. doi: 10.1098/rspb.1996.0128.

Wright, T. F., and Dahlin, C. R. (2017). Vocal dialects in parrots: Patterns and processes of cultural evolution. *Emu* 118, 50–66. doi: 10.1080/01584197.2017.1379356.

Wright, T. F., Dahlin, C. R., and Salinas-Melgoza, A. (2008). Stability and change in vocal dialects of the yellow-naped amazon. *Anim Behav* 76, 1017–1027. doi: 10.1016/j.anbehav.2008.03.025.

Wright, T. F., Lewis, T., Lezama-Lopez, M., Smith-Vidaurre, G., and Dahlin, C. (2018). Yellow-naped amazon (Amazona auropalliata) populations are markedly low and rapidly declining in Costa Rica and Nicaragua. *Bird Conserv Int*, 1–17. doi: 10.1017/S0959270918000114.

Wright, T. F., Rodriguez, A. M., and Fleischer, R. C. (2005). Vocal dialects, sex-biased dispersal, and microsatellite population structure in the parrot Amazona auropalliata. *Mol Ecol* 14. doi: 10.1111/j.1365-294X.2005.02466.x.

Wright, T. F., and Wilkinson, G. S. (2001). Population genetic structure and vocal dialects in an amazon parrot. *Proceedings of the Royal Society B: Biological Sciences* 268, 609–616. doi: 10.1098/rspb.2000.1403.

**10 Figure Captions**

Figure 1. (a) A map of all sites sampled during 2018 and 2019. Sites from the Wright et al. study (Wright et al., 2019) conducted in 2016 are also included. The color and shape of each point corresponds to the year the site was sampled. (b) A species range polygon for the yellow-naped amazon provided by BirdLife (BirdLife International and Handbook of the Birds of the World, 2019).

Figure 2. Spectrograms of each identified call variant with the country of origin listed above and the call variant name listed below the image. All images are shown on a 0.6 second timescale at 3.5 kHz frequency.

Figure 3. An image depicting typical structural variants of yellow-naped amazon contact calls and hypothesized routes by which one type might evolve into another through cultural drift.

Figure 4. A multi-panel image with four columns showing SPCC plots (A), PCA plots (B), a geographic map (C), and a legend (D). Rows represent the sampled countries, arranged in order from north to south. The geographic map for Honduras depicts the call type for the undisclosed location using an asterisk (\*). Black circles represent a single site.

## Figure 5. A Mantel-based spatial autocorrelogram depicting the acoustic similarity of calls against increasing geographic distance. Spatial correlation values indicate the significance of each point, with a cutoff value of 0.05.