

A cultural atlas of vocal variation: yellow-naped amazons exhibit contact call dialects throughout their Mesoamerican range

Molly K. Genes,^{1*} Marcelo Araya-Salas,² Christine R. Dahlin,³ Timothy F. Wright^{1*}

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:**

Timothy Wright
wright@nmsu.edu

Keywords: contact call, cultural atlas, geographic variation, vocal dialect, vocal learning, yellow-naped amazon.

Abstract

Vocal dialects are a taxonomically widespread phenomenon which are typically only studied in a portion of a species' range. Thus, it is difficult to infer whether geographic patterns of vocal dialect that are observed in one part of a species' range are typical across the range or whether local conditions influence their presence or absence. We examined the yellow-naped amazon, *Amazona auropalliata*, a parrot species with remarkable vocal learning capabilities. Although this species' native range spans across Mesoamerica, only Costa Rican populations have been evaluated long-term. Previous studies have shown that these populations exhibit geographically and temporally stable vocal dialect patterns. Without data on populations outside of Costa Rica, it is impossible to know if vocal dialects are present in northern range populations, and whether or not they exhibit similar geographic structure to southern range populations. 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 types based on spectrographic similarity and used spectrographic cross-correlation, principal component analysis, and Mantel-based spatial autocorrelations to assess acoustic similarity and evaluated the robustness of our findings using simulated data. The results from our study show that the vocal patterns previously seen in Costa Rica are also present in northern range populations, supporting our hypothesis. Call types were regionally specific (e.g., vocal dialects) across the range, and no call types were repeated across multiple regions. We did, however, observe distinctive structural characteristics that are found in multiple call types, suggesting that different call types stem from a common origin. Vocal dialect in this species is likely maintained through a tendency toward philopatry and matching call types to enhance social identification.

1 Introduction

Vocal learning, defined as the ability to replicate a sound produced by a conspecific or other species based on social experience (Bradbury & Balsby, 2016; Tyack, 2020), can generate high levels of variation in acoustic structure. 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). Research on vocal dialects in wild populations is usually limited to a portion of a species' range (but see Kroodsma et al., 1999). Thus, it is generally unclear whether vocal dialect formation is intrinsic to a species or dependent on local conditions.

Since vocal dialects were first documented in the white-crowned sparrow, *Zonotrichia leucophrys* (Marler & Tamura, 1964), they 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). Despite this wide taxonomic distribution, songbirds have remained the 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). Parrots are well-known for their vocal mimicry skills in captivity and there is increasing evidence that under natural conditions this open-ended learning results in a number of different patterns of variation, including vocal dialects, clinal variation, and individually-specific vocal signatures (Wright and Dahlin, 2018; Smith-Vidaurre et al., 2021).

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). The first evidence of vocal dialects in a parrot was documented in Costa Rican populations of this species (Wright, 1996). In 2005, Wright *et al.* (2008) recorded contact calls at the same sites as previously recorded 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, some birds were recorded using multiple dialects, known as bilingualism, 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). In addition, playback experiments showed this species is less responsive to playbacks from different dialects (Wright & Doring 2001). These data indicate that yellow-naped amazon dialects may be maintained because utilization of the proper dialect provides social benefits to individuals (Wright and Dahlin 2018).

At present, there is little data to indicate whether yellow-naped amazon vocal dialects occur only in Costa Rica and neighboring populations or extend throughout the species' range. Furthermore,

it remains unclear whether patterns of geographic structure exist above the dialect level in this species. We hypothesized that vocal dialect patterns observed in the southern portion of the range would also be present in the northern portion. To address 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, 2018). Alternatively, variation in yellow-naped amazon contact calls could be 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 spectrographic cross-correlation, 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, and evaluated the robustness of the conclusions using data simulating either clinal or dialectal variation.

2 Materials and methods

2.1 Data collection

We recorded the contact calls of unmarked and unsexed yellow-naped amazons occurring in and around the same roost sites at which population sizes were surveyed by Dupin *et al.* (2020). Contact calls are the most frequently emitted acoustic signal in this species, particularly in and around the roost (Wright, 1996). We recorded calls during the morning as individuals left night roosts or in the morning as they arrived. We recorded calls from both flying and perched birds 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 shotgun microphone and a Marantz PMD660 solid state digital recorder at a frequency of 22.05 kHz, with an amplitude resolution of 16 bits. Individuals were differentiated in recordings via detailed dictation by the recordist. This project was approved by New Mexico State University's Institutional Animal Care and Use Committee (IACUC protocols 2016-023 and 2018-009).

2.2 Sampling sites

We recorded contact calls from yellow-naped amazons during June and July of 2016, 2018, and 2019; both months that fall just after the species' breeding season (Matuzak and Brightsmith, 2007). Sites were determined based on previous survey history, local anecdotes, local organizations working with yellow-naped amazons, and eBird reports. We attempted to record contact calls at as many locations as logistically possible where yellow-naped amazon populations were known to exist at the time of sampling, or were historically present (Dahlin et al., 2018). In 2016, we recorded calls at 22 sites in Costa Rica and 9 in Nicaragua, in 2018 and 2019 we recorded at 10 sites in southern Mexico, as well as 2 sites in Guatemala during 2019, and 4 sites in the Bay Islands, Honduras in 2019; one site in the Bay Islands was a private location which remains undisclosed at the owner's request. In total, we recorded contact calls at 47 sites across the yellow-naped amazon range (Figure 1). We were unable to record calls from 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 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 types. 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, calls across the range were identified as contact calls when they fit these patterns. After all contact calls within each file were identified, the highest quality calls were selected by manually annotating the start and end times on the spectrograms using Raven.

2.4 Visual assessment of call types

Annotations from Raven were imported into R for further analysis using the function `imp_raven` from the package `Raven` (Araya-Salas, 2020). We visually assessed variation in call structure by creating a spectrogram catalogue of all calls using the `catalog` function from the `warbleR` package (Araya-Salas & Smith-Vidaurre, 2017) (see Data Availability). To do this, 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 limits to filter out low and high frequency background noise such as traffic, insects, and other bird species.

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. Call selections that included noise even after the bandpass filtering were examined individually to determine whether that noise would interfere with the analysis. If noise did not overlap substantially with the call, it was retained for further analysis.

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) (see Data Availability). Each call was then categorized based on its acoustic structure; calls with noticeably different acoustic structures were categorized as a distinct call type. This method is subjective but has proven to be useful as a tool to assess the overall degree of difference between call types, 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 used spectrographic cross-correlation (SPCC) to estimate pairwise dissimilarity across all calls 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 were set at 0.5kHz and 2.5 kHz, respectively. Pairwise cross-correlation values were converted into vectors representing variation in acoustic structure using classic metric multidimensional scaling (hereafter, MDS) and Kruskal non-metric MDS plots. Kernel plots were then produced to show 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. 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.* (2021) (see Data Availability).

We used principal component analysis on spectrographic features as an alternative approach to measure similarity between call types across the range. We accomplished this by first using the `spectro_analysis` function from the `warbleR` package in R (Araya-Salas & Smith-Vidaurre, 2021) to measure 26 acoustic parameters on each call, and then the `prcomp` function from the R stats package (R Core Team, 2021) to apply principal component analysis (PCA) to reduce dimensionality. We plotted the first 2 principal components for each region to compare to the MDS bidimensional plots (above). We used the function `leveneTest()` from the `car` package (Fox and Weisberg, 2019) to assess for equal variances, and the function `shapiro.test()` from the package `MASS` (Venables and Ripley, 2002) to evaluate the normality of our dataset. We performed Welch's ANOVA using `oneway.test()` from the R stats package (R Core Team, 2021) on principle components 1 and 2 from our PCA output to evaluate for differences among call types. To determine which call type 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, 2023).

We explored the relationship between geographic distance and acoustic similarity of contact calls using a custom routine based on the Mantel correlogram with the function `mantel.correlog` from the package `vegan` (version 2.5-7) (Oksanen *et al.*, 2020). Mantel correlograms show the change in dissimilarity (in this case acoustic dissimilarity) as a function of spatial distance. Hence, they can be useful to assess patterns of variation in yellow-naped amazon calls across the species' geographic range. Dissimilarity typically measures a fixed set of even spatial distances across a specified geographic range, but results can vary markedly for different spatial resolutions. Therefore, we calculated several Mantel correlograms with different spatial resolutions (6 distances from 25 to 250 km) and estimated the mean and standard deviations across the correlograms for each distance value after interpolation.

We used a multiple regression model for distance matrices (Lichstein, 2007) in the function `MRM` from the R package `ecodist` (Goslee and Urban, 2007) to statistically evaluate whether distance or dialect assignment had a significant effect on call structure in yellow-naped amazons. This method uses a permutation approach to estimate statistical significance of the regression coefficients to account for the lack of independency of observations. A dissimilarity matrix based on the pairwise cross-correlation matrix (1 - spcc matrix) was used as a response variable while a

pairwise distance matrix and a dialect membership binary matrix, were used as a predictor. The latter, created with the function `binary_triangular_matrix` in the R package `PhenotypeSpace` (Araya-Salas and Odom 2022), uses 0s and 1s to represent whether two calls belong to the same dialect (0) or not (1), and therefore can be used to assess the variation in call structure explained by dialects.

Finally, we use simulations to evaluate whether our statistical approach could tease apart dialectal from clinal variation in call acoustic structure. For this, we created synthetic data sets with the same number of locations and calls per location as in the actual data set. Locations were equally spaced across the x axis (separated by one unit) in a bidimensional space. The position of each observation within each location was set randomly by adding random variation from a normal distribution (centered at 0 with standard deviation of 0.1) on both the x and y axis. For each pattern of acoustic variation we simulated a vector representing a hypothetical acoustic feature. The clinal geographic pattern was simulated by simply adding random variation (from a normal distribution centered at 0 with standard deviation of 0.2) to the x axis value of each observation. The dialectal geographic pattern was simulated by randomly assigning an integer number to each location (i.e. the same value to all observations within a location) and then adding random variation to each observation (from a normal distribution centered at 0 with standard deviation of 0.2). We also simulated a random variation pattern in which the acoustic feature value was assigned randomly regardless of locality of geographic distance to other observations. The three continuous simulated vector (clinal, dialectal and random variation) as well as the geographic positions were converted into pairwise distance matrices using the function `dist` in R (R Core Team, 2021). Distances were zero-centered and transformed to unit variance to enable effect size comparisons between different models. As with the real data set, dialect membership was represented by a binary matrix that uses 0s and 1s to represent whether two calls belong to the same dialect (0) or not (1), created by the function `binary_triangular_matrix` from the package `PhenotypeSpace` (Araya-Salas and Odom 2022). Multiple regression for distance matrices (Lichstein, 2007) were also used to evaluate the association between geographic distance and dialect membership (predictors) and the three acoustic feature variables (responses). Single response models were run for each acoustic feature variable. The simulation was replicated 100 times and the results were averaged across replicates.

3 Results

3.1 Contact calls and quality assessment

We surveyed for yellow-naped amazons at 72 locations in Mesoamerica where they are known to exist 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 recorded contact calls at 22 locations in Costa Rica and 9 in Nicaragua. We recorded calls at 10 sites in Mexico between 2018 and 2019. In 2019 we recorded contact 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. 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 types across the range

Our visual classification of yellow-naped amazon contact calls yielded 14 different call types across the species range (Figure 2). We identified 4 types in Mexico and 2 types in Guatemala. In the Bay Islands Honduras, we recorded 2 distinct types. Previously, Wright *et al.* reported 3 call types in Costa Rica during a 1994 survey and the same 3 types and a new sub-type 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 indicated that birds in Costa Rica give 2 different call types, both of which were reported in the previous surveys. The third call type previously reported on the norther border of Costa Rica in 1994 and 2005 was not recorded there in 2016 but was seen in populations in the south of Nicaragua, along with 3 other call types. Sixteen percent of the 243 birds in our dataset exhibited bilingualism. Overall, these observations were infrequent, and only 19 bilingual birds were retained in our dataset for analyses. These individuals were primarily concentrated in Costa Rica ($N = 16$), although bilingual birds were also recorded in Mexico ($N = 2$) and Guatemala ($N = 1$). It should be noted that we did observe and record bilingual birds in Nicaragua; however, none of those birds were preserved in our dataset due to low quality recordings or an insufficient number of recordings. Our visual assessment suggested that the mosaic patterns of vocal variation consistent with dialects was present throughout the range, rather than a clinal variation of call types. Dialect types in this species appear to result from discreet modifications to a basic call structure (Figure 3) that result in superficially similar call types 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 types identified across the range (Figure 4). When all identified types from across the range were plotted in acoustic space, it was difficult to detect separate distributions as many overlapped to a significant extent. When we examined acoustic overlap on a country-level basis, we noticed that the types sampled in the northern portion of the range showed more acoustic separation amongst themselves than did call types 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 types. 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 call types in each country generally reflected the patterns exhibited in the corresponding SPCC plots. When we created a PC plot for all call types identified across the range, there was little visual separation among call types. An ANOVA on PC1 and PC2 did indicate significant differences between call types for both PC1 ($F = 294.3$, $df = 299.41$, $p = < 2.2 \cdot 10^{-16}$) and PC2 ($F = 53.292$, $df = 300.36$, $p = < 2.2 \cdot 10^{-16}$).

3.5 Spatial patterns of acoustic similarity

The Mantel-based spatial autocorrelogram illustrated 2 distinct patterns in our data. First, within 250 km yellow-naped amazon contact calls generally exhibit high similarity (Figure 5). After this distance acoustic similarity decreases markedly and remains at a low level for the remaining geographic distance range.

The multiple regression of distance matrices revealed a significant association between acoustic dissimilarity and dialect membership ($p \leq 0.0001$) but no association to geographic distance ($p = 0.281$). Call dissimilarity was higher between calls from different dialects relative to calls from the same dialect. The effect size of dialect membership (0.65) was three orders of magnitude higher than the absolute effect size of geographic distance (-0.003).

The simulated data revealed that our statistical approach is capable of discerning between the two hypothesized patterns of geographic variation. When modeling acoustic similarity in clinal variation, the effect of geographic distance on acoustic similarity was consistently higher (effect size mean = 1.000; sd = 0.001) than that of dialect membership (effect size mean = -0.024; sd = 0.005). The opposite pattern was observed when predicting acoustic similarity in data simulating dialectal variation: the effect size of dialect membership was consistently higher (mean = 1.440; sd = 0.257) than that of geographic distance (mean = 0.020; sd = 0.178). In both simulations 95% of the replicates produced significant effects for both predictors. Finally, for the random variation simulation, geographic distance and dialect membership both produce equally low effect sizes (mean = -0.001; sd = 0.009 and mean = 0.001; sd = 0.016; respectively). Effects were significant in less than 95% of these replicated models.

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 14 different call types observed across the species' range confirm that this pattern is present throughout the Mesoamerican range of this species. Currently wild yellow-naped amazons in many parts of their range are isolated into discreet regional populations due to loss of habitat and declining populations (Dupin et al., 2020). In each region we sampled, we were able to visually detect more than one acoustically discreet call type with a distinct geographic distribution. Our SPCC and PCA analyses validated many, but not all, of our visually identified acoustic types. Importantly, multiple regressions of distance matrices from our data gave stronger support for dialect variation than clinal variation, with effect sizes of similar

magnitude to the same analysis run on data simulating dialect variation. In general, our data indicate that conditions which lead to dialect formation are intrinsic to the social structure and communication system of yellow-naped amazons, which appears to depend heavily on vocal learning.

4.1 Global patterns of vocal variation

In 1996, Wright identified 3 distinct contact call types in Costa Rican populations (Wright, 1996), and later confirmed the geographic and temporal stability of those same call types (Wright et al., 2005). Our visual assessment of over 2000 contact calls recorded from 47 sites across the range of the yellow-naped amazon revealed the presence of 14 distinct call types, including those identified in the initial description of dialects in Costa Rica. Results from our SPCC analyses and PCA support many of our visual classifications; however, they also indicate that several call types 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 several previous studies of acoustic variation in parrots (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 types 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 somewhat robust to noise, field recordings may contain considerable acoustic interference from insects, other birds, vehicles, and farm animals. We implemented a bandpass filter to remove high and low frequency noise and discarded those recordings with substantial overlapping noise within the frequency range as the calls themselves but retained calls with lower levels of masking noise.

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; Smith-Vidaurre et al., 2021). There is little understanding as to why parrot species exhibit vocal dialects, but several hypotheses have been formed to explain their function (Wright and Dahlin, 2018). 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 (2001) reported no genetic correlation with yellow-naped amazon contact calls, stating instead that individuals exhibited high dispersal across dialect boundaries. 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 types 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 types have a common origin, and that variation is a result of imperfect learning and cultural drift. 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 types 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 (Buhrman-Deever *et al.*, 2007).

Several birds in our dataset exhibited more than one call type. In most cases of bilingualism there appeared a dominant call type used with high frequency by an individual, and a secondary type that a bird would emit infrequently. Wright reported the occasional 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 seems more likely that call types predate this isolation, as some of the earliest recordings from this area show distinct regional call types (see Wright and Wilkinson 2001). These regional call types may be maintained by a tendency towards philopatry and selection towards matching regional types to enhance group identification, as suggested by playback responses of dialect variants of another vocalization type, pair duets (Wright and Dorin, 2001). In southern Nicaragua and Costa Rica, where yellow-naped amazon populations are more contiguous, many call types are restricted to a certain geographic area, while others are currently more widespread. In the northern-most country of Mexico, yellow-naped amazons are much more patchily distributed, which may explain why call types exhibit almost no acoustic overlap (Sewall *et al.*, 2016).

Though we were able to sample populations across the yellow-naped amazons' range, there are several regions we were unable to survey due to 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 call types across the range, including those unsampled populations.

4.3 Summary and future directions

Our cultural atlas of vocal variation in contact calls across the range of the yellow naped amazon supports the hypothesis that vocal dialects are present across the range of this species. Contact call types exhibited separation by geographic region with only rare cases of bilingual birds, a trend seen in original studies on Costa Rican populations. These results suggest 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. 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.

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 (né Dupin) 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 planned the study, collected data, supervised the research and data analysis, and assisted in writing the paper.

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. Many parrot species are known to be open-ended vocal learners and can acquire new vocalizations well into adulthood. Our study on the yellow-naped amazon calls across its range illustrate that the mosaic pattern of discrete call types (e.g., vocal dialects) previously described in one part of the range, are characteristic of all surveyed populations. This suggests that the processes that give rise to these dialects are a general characteristic of the species. Additionally, our analyses show that the call types we identified across the range share a basic structure that has likely been modified in different populations via learning errors and cultural drift. More generally, wild parrots have abundant potential to reveal more about vocal learning processes and how this form of behavioral plasticity contributes to communication and social interactions.

10 References

- Araya-Salas, M., & K. Odom. 2022. PhenotypeSpace: an R package to quantify and compare phenotypic trait spaces. R package version 0.1.0.
- Araya-Salas, M., and Smith-Vidaurre, G. (2017). warbleR: an R package to streamline analysis of animal acoustic signals. *Methods Ecol Evol.* 8:2. 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. *Proc R Soc B.* 286:1903. doi: 10.1098/rspb.2019.0666.
- Baker, M. C. (2000). Cultural diversification in the flight call of the Ringneck Parrot in Western Australia. *Condor.* 102:4. 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.* 103:3. doi: 10.1071/MU02035.
- Beecher, M. D., and Brenowitz, E. A. (2005). Functional aspects of song learning in songbirds. *Trends Ecol Evol.* 20:3. 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.* 55:6. 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.* 70:3. doi: 10.1007/s00265-016-2068-4.
- 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.* 109:2. 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.* 285:1892. 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.* 76:2. 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*. 11:2. doi: 10.1080/09524622.2000.9753454.
- Dahlin, C. R., Blake, C., Rising, J., and Wright, T. F. (2018). Long-term monitoring of Yellow-naped Amazons (*Amazona auropalliata*) in Costa Rica: breeding biology, duetting, and the negative impact of poaching. *J Field Ornithol*. 89:1. doi: 10.1111/jof.12240.
- 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*. 60:5. 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*. 12:10. doi: 10.3390/d12100377.
- Fox, J., Weisberg, S. (2019). *An R Companion to Applied Regression*, Third edition. Thousand Oaks, CA: Sage.
- Goslee, S. C., and Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *J Stat Softw*. 22. doi: 10.18637/jss.v022.i07.
- Herrera, N., Lara, K., and Funes, C. (2020). Estado poblacional de la Lora Nuca Amarilla (*Amazona auropalliata*) en El Salvador. *Zeledonia*. 24:1. Retrieved from <https://www.zeledonia.com>
- 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*. 26:1. doi: 10.1080/09524622.2016.1201778.
- Kroodsma, D. E., Byers, B. E., Halkin, S. L., Hill, C., Minis, D., Bolsinger, J. R., Dawson, J. A., Donelan, E., Farrington, J., Gill, F. B. and Houlihan, P. (1999). Geographic variation in black-capped chickadee songs and singing behavior. *Auk*. 116:2. doi: 10.2307/4089373
- Lee, J. H., Podos, J., and Sung, H. C. (2019). Distinct patterns of geographic variation for different song components in Daurian Redstarts *Phoenicurus aureus*. *Bird Study*. 66:1. doi: 10.1080/00063657.2019.1614144.
- Lichstein, J. W. (2007). Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecol*. 188. doi: 10.1007/s11258-006-9126-3.
- 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. *Can J Exp Psychol*. 63:1. 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*. 189. doi: 10.1007/s00359-003-0441-z.
- Martins, B. A., Rodrigues, G. S. R., and de Araújo, C. B. (2018). Vocal dialects and their implications for bird reintroductions. *Perspect Ecol Conserv*. 16:2. 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*. 78:2. 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. R package version 2.5-7. <https://CRAN.R-project.org/package=vegan>
- Peters, G.-J., and Verboon, P. (2023). Rosetta: Parallel use of statistical packages in teaching. R package version 0.3.6. <https://r-packages.gitlab.io/rosetta/>
- 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*. 41:2. doi: 10.1111/ecog.02779.
- Podos, J., and Warren, P. S. (2007). The evolution of geographic variation in birdsong. *Adv Stud Behav*. 37. doi: 10.1016/S0065-3454(07)37009-5.
- R Core Team, R. (2021). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- 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. *J Caribbean Ornithol*. 23:1. Retrieved from <https://jco.birdscaribbean.org/index.php/jco>
- 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*. 7:11. 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*. 13:2. 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*. 148:4. 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. *Behav Ecol*. 31:2. doi: 10.1093/BEHECO/ARZ202.
- Tyack, P. L. (2020). A taxonomy for vocal learning. *Philos Trans R Soc B*. 375:1789. doi: 10.1098/rstb.2018.0406.
- Venables, W. N., and Ripley, B. D. (2002). *Modern Applied Statistics with S*, Fourth edition. New York: Springer.
- West, M. J., and King, A. P. (1985). Studying dialects in songbirds: Finding the common ground. *Behav Brain Sci*. 8:1. doi: 10.1017/S0140525X0001997X.
- Whitehead, H. (2010). Conserving and managing animals that learn socially and share cultures. *Learn Behav*. 38:3. doi: 10.3758/LB.38.3.329.
- Whiten, A. (2019). Cultural Evolution in Animals. *Annu Rev Ecol Evol S*. 50. doi: 10.1146/annurev-ecolsys-110218-025040.
- Wiley, R. H. (1971). Song Groups in a Singing Assembly of Little Hermits. *Condor*. 73:1. 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*. 28:3. 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*. 26:1, 7-9.
- Wright, T. F. (1996). Regional dialects in the contact call of a parrot. *Proc R Soc B*. 263:1372. doi: 10.1098/rspb.1996.0128.

- Wright, T. F., and Dahlin, C. R. (2018). Vocal dialects in parrots: Patterns and processes of cultural evolution. *Emu*. 118:1. 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*. 76:3. doi: 10.1016/j.anbehav.2008.03.025.
- Wright, T. F., and Dorin, M. (2001). Pair duets in the yellow-naped amazon (Psittaciformes: *Amazona auropalliata*): responses to playbacks of different dialects. *Ethology*. 107:2. doi: 10.1046/j.1439-0310.2001.00632.x.
- 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*. 29:2. 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*. 14:4. 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. *Proc R Soc B*. 268:1467. doi: 10.1098/rspb.2000.1403.

10 Data Availability Statement

The original contributions presented in the study are publicly available. All relevant code for analyses can be found at the following GitHub repository: <https://github.com/mgenes/cultural-atlas-of-vocal-variation>. Data for analyses can be found at <https://doi.org/10.5061/dryad.9cnp5hqq7>.

11 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 type with the country of origin listed above and the call type 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. Grey shading indicates the 95% confidence interval around the estimated correlation coefficient.