



Original Article

Individual signatures outweigh social group identity in contact calls of a communally nesting parrot

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Despite longstanding interest in the evolutionary origins and maintenance of vocal learning, we know relatively little about how social dynamics influence vocal learning processes in natural populations. The “signaling group membership” hypothesis proposes that socially learned calls evolved and are maintained as signals of group membership. However, in fission–fusion societies, individuals can interact in social groups across various social scales. For learned calls to signal group membership over multiple social scales, they must contain information about group membership over each of these scales, a concept termed “hierarchical mapping.” Monk parakeets (*Myiopsitta monachus*), small parrots native to South America, exhibit vocal mimicry in captivity and fission–fusion social dynamics in the wild. We examined patterns of contact call acoustic similarity in Uruguay to test the hierarchical mapping assumption of the signaling group membership hypothesis. We also asked whether geographic variation patterns matched regional dialects or geographic clines that have been documented in other vocal learning species. We used visual inspection, spectrographic cross-correlation and random forests, a machine learning approach, to evaluate contact call similarity. We compared acoustic similarity across social scales and geographic distance using Mantel tests and spatial autocorrelation. We found high similarity within individuals, and low, albeit significant, similarity within groups at the pair, flock and site social scales. Patterns of acoustic similarity over geographic distance did not match mosaic or graded patterns expected in dialectal or clinal variation. Our findings suggest that monk parakeet social interactions rely more heavily upon individual recognition than group membership at higher social scales.

Key words: contact call, group membership, hierarchical mapping, individual signatures, machine learning, monk parakeet, *Myiopsitta monachus*, vocal learning.

INTRODUCTION

Vocal learning has arisen independently multiple times over the course of evolutionary history, stimulating great interest in the origins and maintenance of this complex cognitive trait (Sewall et al. 2016). Among vocal learning taxa, which include humans, bats, cetaceans, songbirds, parrots, and hummingbirds, vocal learning in natural populations can often be detected as patterns of geographic variation in vocalizations (Podos and Warren 2007; Wright and Dahlin 2018). These patterns may manifest as mosaic patterns, as in dialectal variation or, alternatively, as graded patterns characteristic of clinal variation (Podos and Warren 2007; Wright and Dahlin 2018). Despite documentation of geographic patterns attributed to vocal learning, we still face a dearth of knowledge about

processes underlying the evolution and maintenance of this trait. A growing literature points to complex social dynamics as potential drivers of the evolution and maintenance of vocal learning (Bradbury and Balsby 2016; Sewall et al. 2016; Wright and Dahlin 2018). Namely, the “signaling group membership” hypothesis proposes that socially learned calls provide fitness benefits to individuals by signaling group membership or familiarity in dynamic societies (Sewall et al. 2016; Wright and Dahlin 2018).

Much of what we know about the influence of social dynamics on vocal learning comes from passerines, a primary focus of vocal learning research for decades (Podos and Warren 2007). In passerines, song is typically used for territory defense and mate attraction (Searcy and Andersson 1986), mediating interactions over limited geographic and social scales (e.g., a territorial male interacting with a male neighbor or intruder, or singing to a nearby female audience). On the other hand, vocal learning species that exhibit

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fission–fusion social dynamics and use learned calls during social interactions may provide novel insight into the social dynamics that underlie vocal learning (Sewall et al. 2016). Social interactions in fission–fusion societies are more likely to encompass higher social scales and broader geographic areas. Species with such fission–fusion dynamics might exhibit distinct processes of vocal learning, leading to complex patterns of shared call structure over geographic areas. Therefore, in fission–fusion societies, a fundamental assumption of the signaling group membership hypothesis is that individuals can encode complex social group membership in acoustic structure to signal social affiliations across multiple social scales, a phenomenon known as “hierarchical mapping” (Bradbury and Vehrencamp 1998). If social affiliations are encoded by hierarchical mapping, socially learned calls will show greater acoustic similarity within groups over multiple social scales, driven by learned convergence across social scales such as pairs, families, larger social groups, or regional populations.

Parrots are particularly compelling models for testing these ideas, as many species are thought to form complex fission–fusion societies with multiple levels of social structure (Hobson et al. 2014) and use socially learned contact calls to mediate social interactions (Bradbury and Balsby 2016; Sewall et al. 2016; Wright and Dahlin 2018). Monk parakeets (*Myiopsitta monachus*) are small parrots native to South America that have been repeatedly and independently introduced across the world through the global pet trade (Russello et al. 2008). These parrots build stick nests that range in size from a single to multiple chambers (Figure 1A). In addition to breeding, monk parakeets use these nests for roosting throughout the year (Eberhard 1998). Nests are clustered in geographic space, often in the same or neighboring trees. In the native range, this spatial clustering of nests often reflects the extent and abundance of introduced eucalyptus trees (genus *Eucalyptus*), which are native parakeets’ preferred nesting substrate (Bucher and Aramburu 2014). Monk parakeets likely interact with individuals beyond their nesting sites during foraging trips or natal dispersal. Although our knowledge of dispersal behavior is limited (Martin and Bucher 1993; Goncalves da Silva et al. 2010), monk parakeet socioecology is characterized by complex fission–fusion social dynamics (Hobson et al. 2013; Hobson et al. 2014; Hobson et al. 2015), posing opportunities for interactions across multiple social scales. Pairs, and less often, trios, are the fundamental unit of monk parakeet social structure (Hobson et al. 2014).

Like many parrot species, monk parakeets exhibit extensive vocal learning abilities in captivity, imitating acoustic signals by conspecifics and heterospecifics (Forshaw 1977). Under natural conditions, monk parakeets likely use socially learned calls to mediate social interactions over multiple social scales, such as flocks or roosting sites. Social learning of contact calls has been reported in the invasive range, in which mosaic patterns of acoustic similarity among neighboring nesting sites in the United States indicated that invasive monk parakeets learn calls from their local social group (Buhrman-Deever et al. 2007). It remains unclear whether these patterns in the invasive range reflect patterns of social learning in monk parakeets’ native range, and are therefore a general characteristic of the species, or if vocal learning processes have been altered through introduction to new habitats.

Here, we recorded native populations of monk parakeets in Uruguay to test the hierarchical mapping assumption of the signaling group membership hypothesis, and to determine whether native range monk parakeets exhibited dialectal or clinal patterns of acoustic similarity in contact calls. We tested the hierarchical

mapping assumption by evaluating patterns of acoustic similarity over multiple social scales. We predicted that acoustic similarity would be highest within groups across social scales (e.g., convergence on shared calls within groups), including the individual scale. As Hobson et al. (2014) identified pairs as the fundamental unit of social structure, we expected to identify the strongest acoustic convergence within pairs. Given what is known about monk parakeet socioecology, we expected to find either dialectal or clinal patterns of geographic variation in contact calls. We reasoned that fission–fusion social dynamics in the native range could be limited to nesting sites, such that birds would only learn contact calls from conspecifics at the same nesting site. If so, then we expected to find highly similar calls within sites, coupled with a sharp decline in acoustic similarity between sites, as in dialectal variation (Podos and Warren 2007; Wright and Dahlin 2018). However, native parakeets often form large flocks while foraging on crops within several kilometers of nesting sites (Forshaw 1977, Smith-Vidaurre, personal observation). It was plausible, therefore, that fission–fusion and vocal learning could occur over broader geographic areas, gradually declining over increasing distance. If so, then we expected acoustic similarity would decrease linearly over increasing geographic distance, as in clinal variation (Podos and Warren 2007; Wright and Dahlin 2018).

METHODS

Sampling locations

We recorded contact calls of native monk parakeets across a 513 km transect in southern Uruguay from Piedra de los Indios (PIED) in the department of Colonia in the west (latitude -34.41 , longitude -57.84) to Ojos de Agua (OJOS) in the department of Rocha in the east (latitude -33.80 , longitude -53.50). Recording was performed intensively on the western end of the transect to obtain finer-grained sampling (Figure 1B,C). We also recorded at one site in northern Uruguay in the department of Salto (ARAP: latitude -30.94 , longitude -57.51). Recording was performed over 7 months (early May to late November 2017) at 42 sites across 7 departments. We retained 39 sites with sufficient sampling depth for final analyses (Figure 1B, Supplementary Table 1). Most recording sessions were conducted near groups of nests located in eucalyptus tree patches, either in semirural areas surrounded by intensive agriculture, or in the city of Montevideo.

Hierarchical social scales

The individual scale was the fundamental social scale of this study, with pair, flock and site considered “higher” social scales. We repeatedly sampled individuals at three sites for the individual scale. We defined pairs as two birds flying together, and flocks as three or more birds flying together. Sites were defined as unique recording locations, which generally represented visibly separate clusters of nests. The individual, pair and flock scales were nested within the site scale.

Marking individuals for repeated sampling at the individual scale

Individuals were marked while trapping near nests in Colonia June–July 2017 to facilitate tracking and recording repeated contact calls from known individuals. We marked individuals with a collar holding an anodized aluminum tag carved with a unique three-character code (Senar et al. 2012). Parakeets were trapped using

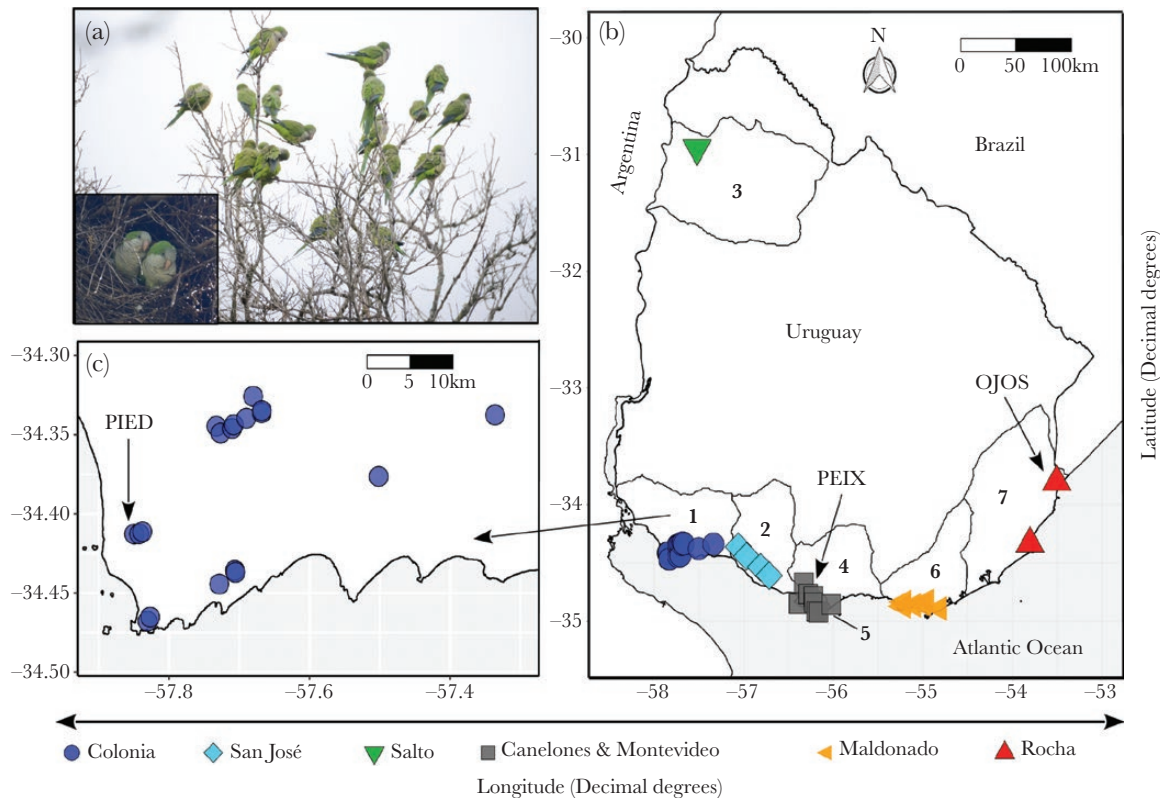


Figure 1

Sampling map of recording sites. (A) Parakeets staging in a small social group. Inset photo: Pair roosting in one chamber of a multichambered nest. Photo credit to Tania Molina Medrano. (B) Map of Uruguay demonstrating recording sites across a 407 km straight-line transect (PIED to OJOS), with one site sampled further north in Salto. Departments are outlined and numbered (1 = Colonia, 2 = San José, 3 = Salto, 4 = Canelones, 5 = Montevideo, 6 = Maldonado, 7 = Rocha). Sites within departments are encoded with corresponding symbols and colors. (C) Inset map of sites in the Colonia department. The three labeled sites (PIED, PEIX, OJOS) in panels A and B are used in Figure 3 and Supplementary Figure 2.

baited raptor bow nets (BN 5ft diameter manual, Mike's Falconry Supplies) during the day, or mist-nets or a hoop-net to capture individuals at nests in the dark.

Recording contact calls across social scales

Contact calls were recorded with Marantz PMD661 MKII and PMD660 solid state recorders, set to mono channel and equipped with Sennheiser ME67 long shot-gun microphones and foam windcreens. Recordings were digitized with 44100 Hz sampling frequency and 16 bit sampling depth. We recorded calls within 5–30 m of parakeets leaving or returning to nests, from 6:00 to 10:00 and 15:00 to 18:00. These times roughly corresponded to the main periods of foraging trips. We recorded in the middle of the day (10:00–15:00) at sites with limited access to the public. Recording sessions of 0.5–2 h were performed over a single day per site to obtain calls at higher social scales (pairs, flocks, sites) from birds flying to and from nesting sites. Recording sessions were repeated when conditions were poor and a single session per site with the highest quality calls was retained. At sites where we marked individuals, we targeted these marked birds over several days to obtain repeated contact calls per individual. Repeated contact calls were also recorded from five unmarked birds roosting in isolation, such that our dataset of repeatedly sampled individuals was composed of calls from both marked and unmarked birds. It was rarely possible to isolate more than

one contact call from the same individual over higher social scales, as parakeets called infrequently. Therefore, we focused on obtaining a single high-quality contact call per individual when sampling higher social scales. We recorded group size to identify pairs and flocks. As in many parrot species, monk parakeet pairs maintain close proximity while flying, such that pairs are readily apparent within the context of larger social groups (Forshaw 1977).

Contact call selection and quality control processing

Contact calls were selected from original recordings using Raven version 1.5 (Bioacoustics Research Program 2014, Cornell Laboratory of Ornithology). We recorded metadata while selecting calls, including group size and identity at higher social scales. Quality control processing was performed in the R environment (R Core Team 2018) using Rraven version 1.0.4 (Araya-Salas 2017) and warbleR version 1.1.15 (Araya-Salas and Smith-Vidaurre 2017). We removed contact calls that overlapped with other acoustic signals. High-quality calls were retained by implementing a quality threshold based on visual inspection and measurements of signal-to-noise ratio. We addressed potential repeated sampling of individuals at higher social scales by removing calls that may have arisen from repeated sampling of individuals (Supplementary Methods 1.1).

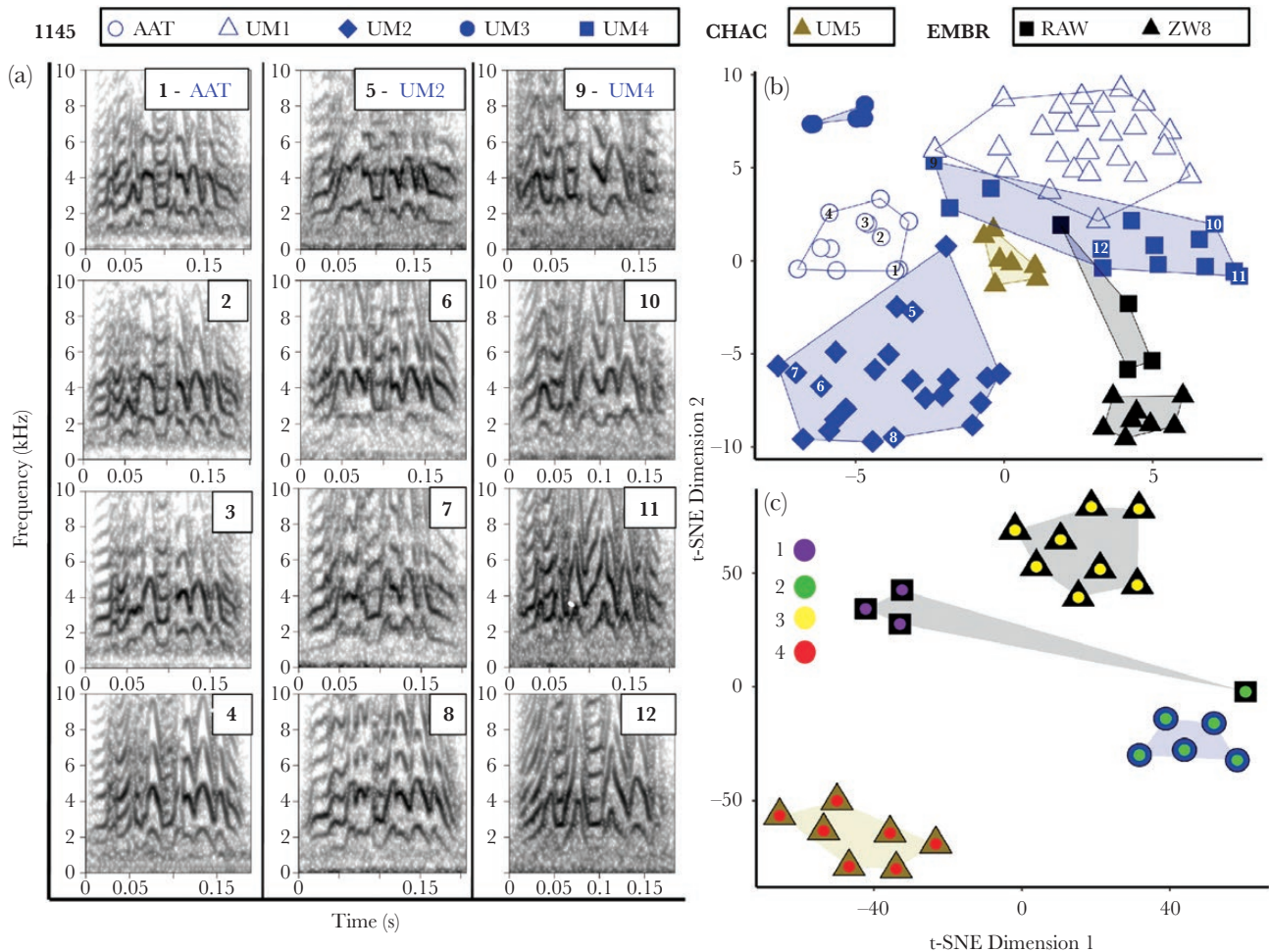


Figure 2

High acoustic convergence in contact calls at the individual scale. (A) Example catalog with spectrograms of four randomly selected calls for three repeatedly sampled individuals from site 1145, demonstrating visible patterns of individual consistency and distinctiveness. The legend at the top of the figure indicates site and individual identity. (B) Distribution of contact calls in SPCC acoustic space for all repeatedly sampled individuals. (C) Distribution of calls of four repeatedly sampled individuals (UM3, UM5, RAW, ZW8) in random forests acoustic space from model validation. Dimensionality of similarity matrices was reduced using t-Distributed Stochastic Neighbor Embedding (t-SNE). Shape symbols indicate the individual that produced a given call, while colored circles inside symbols indicate assignment to one of four clusters yielded by model-based clustering (23/24 calls correctly classified, 95.8% clustering accuracy). Convex hull polygons in B and C delineate the acoustic space encompassed by each individual's set of calls.

General approach to measuring acoustic similarity

Monk parakeet contact calls are broadband signals characterized by complex frequency modulation, and multiple overtones (Supplementary Figure 2A), similar to acoustic signals of some other parrot and songbird species (Fee et al. 1998; Bradbury et al. 2001; Bradbury and Vehrencamp 2014). We used three complementary methods to assess similarity of these complex signals: visual inspection of call catalogs, spectrographic cross-correlation (SPCC) (Clark et al. 1987), and supervised random forests, a machine learning algorithm (Breiman 2001). Visual inspection and SPCC have traditionally been used to assess similarity of learned acoustic signals (Nowicki and Nelson 1990; Farabaugh et al. 1992; Wright 1996; Guerra et al. 2008). Random forests has been used less frequently to measure acoustic similarity (Keen et al. 2014; Humphries et al. 2018) and has not yet been reported as a method to measure similarity of parrot acoustic signals. We assessed patterns of acoustic similarity across the individual, pair, flock, and site social scales, as well as local and regional geographic distance.

Assessing contact call similarity by visual inspection

Categorization based on visual similarity of spectrograms is commonly employed in studies of avian acoustic signals and has been shown to be repeatable across observers (Saunders 1983; Nowicki and Nelson 1990; Farabaugh et al. 1992). We generated spectrograms in R using a Hanning window, window length of 378, overlap of 90, minimum color level of -53 , bandpass filter of 0.5–9 kHz, and amplitude threshold of 15 (Supplementary Methods 1.1). We visually inspected call spectrogram catalogs to perform a preliminary assessment of similarity patterns at the individual and site scales during quality control processing (see Methods: *Contact Call Selection and Quality Control Processing*). Our preliminary results indicated relatively high similarity at the individual scale, but high variability within sites. We used these preliminary results to inform our random forests approach (described below).

We also conducted a more rigorous visual classification study in which we asked multiple observers to categorize monk parakeet contact calls. We created a web application using Shiny, a

framework for designing dynamic and interactive visualizations in the R environment, to collect classifications across 12 observers (Chang et al. 2018). Of these observers, two were experienced with monk parakeet calls, five were familiar with calls from other parrot species, and five were naive to spectrograms. Our Shiny app was designed to present a four-class problem per each of the four social scales (individual, pair, flock, and site) to observers. Observers were presented with blinded, randomly sorted spectrograms at each social scale and prompted to place calls into classes based on visible patterns of acoustic similarity. Visual inspection results were used to assess classification accuracy at the individual scale across observers, and also used to generate visual similarity matrices for a direct comparison with our SPCC and random forests approaches. See Methods: *Validation of our Analytical Approach and Findings* below, as well as *Supplementary Methods 1.1–1.2* for further information.

Measuring acoustic similarity by SPCC

SPCC has often been used to characterize acoustic similarity of parrot contact calls (Wright 1996; Cortopassi and Bradbury 2000; Bradbury et al. 2001; Buhman-Deever et al. 2007; Guerra et al. 2008; Wright et al. 2008; Salinas-Melgoza and Wright 2012). We used SPCC to measure similarity of monk parakeet contact calls across social scales and geographic distance (*Supplementary Methods 1.3*).

Employing random forests to measure acoustic similarity

Supervised random forests is an ensemble machine learning method used to predict categorical labels in a classification approach or continuous values in a regression approach (Valletta et al. 2017). We used random forests to measure acoustic similarity while accounting for the complex structure of monk parakeet contact calls. Models were built from a set of hundreds of acoustic and spectrogram image features that characterized contact call acoustic structure (described in detail in *Supplementary Methods 1.5–1.6*). As our preliminary results indicated relatively high similarity at the individual scale, we trained models by classifying calls from half of the repeatedly sampled individuals. Classification accuracy was validated with the second half of repeatedly sampled individuals. We selected a final model to predict acoustic similarity for calls at the higher social scales. The final output for subsequent analyses was a pairwise matrix of proximity values, as used in another study with avian acoustic signals (Keen et al. 2014). See *Supplementary Figure 1* for a general workflow of this analytical approach and *Supplementary Methods 1.4–1.15* for more details on implementation and validation.

Evaluating patterns of acoustic similarity across social scales and geographic distance

We used Mantel tests to ask if calls were more similar within groups compared to among groups at each social scale, and if acoustic similarity decreased over increasing geographic distance. We encoded pairwise group identity within each social scale as binary matrices, in which 1 represented 2 calls in the same group and 0 represented 2 calls in different groups. Mantel tests were implemented with 9999 permutations, using geographic distance at the local (sites in the department of Colonia) and regional (all sites) geographic scales. Partial Mantel tests were implemented to account for site identity at nested social scales. We further investigated patterns of acoustic similarity over geographic distance using Mantel-based

spatial autocorrelation. This analysis performs Mantel tests of calls within discrete bins of geographic distance, and implements a permutation approach to calculate *P*-values. The resulting correlogram was used to evaluate whether acoustic similarity decreased linearly with increasing geographic distance (*Supplementary Methods 2*).

Validation of our analytical approach and findings

We validated our analytical approach using SPCC and random forests to measure acoustic similarity of monk parakeet contact calls. We compared patterns of SPCC and random forests acoustic similarity in monk parakeets to yellow-naped amazons (*Amazona auropalliata*), a species with well-documented hierarchical mapping and regional dialects (Wright, 1996, *Supplementary Methods 3.1.1–3.1.13*). Interobserver reliability of visual classification at the individual scale was calculated to validate preliminary findings by visual inspection (*Supplementary Methods 3.2*). We further validated our approach and findings by comparing our three methods of evaluating contact call similarity. Classification accuracy was obtained across social scales by each similarity method (*Supplementary Methods 3.3*). We designed a permutation test to ask whether differences in sampling between the individual scale (repeatedly sampled individuals were often recorded while perched in isolation) and higher social scales (individuals were often recorded while flying with social partners) could have skewed our results (*Supplementary Methods 3.4*). The strength of this effect of sampling was assessed by comparing the effect sizes of acoustic convergence at the individual and higher social scales (*Supplementary Methods 3.4, Supplementary Tables 4 and 5*). Finally, we asked whether motivational differences within sampling windows could have affected similarity measurements at the individual scale by assessing the degree to which the temporal separation of calls from the same individual affected the similarity of these calls (*Supplementary Methods 3.5, Supplementary Table 6*).

RESULTS

Sample size after quality control processing

At the individual scale, we used calls from three marked and five unmarked birds recorded at three sites in Colonia ($n_{\text{Individuals}} = 8$, $n_{\text{Calls}} = 97$, $n_{\text{Sites}} = 3$, *Supplementary Table 1*). The mean number of calls per individual was 12.12, with a range of 4–25 calls per bird. We had originally marked 25 birds across 4 sites. However, due to difficulties in locating marked individuals within large fission–fusion flocks, and with birds removing neck collars, we obtained high-quality repeated contact calls from only three marked individuals. Our temporal resolution at this social scale was a single day (as for calls at higher social scales).

We used the following sample sizes across higher social scales: pair scale ($n_{\text{Pairs}} = 44$, $n_{\text{Calls}} = 88$, $n_{\text{Sites}} = 21$), flock scale ($n_{\text{Flocks}} = 29$, $n_{\text{Calls}} = 77$, $n_{\text{Sites}} = 22$), and site scale ($n_{\text{Sites}} = 39$, $n_{\text{Calls}} = 605$). The pair and flock scales represented 14.5% and 12.7% of the calls used for higher social scales, respectively. Mean flock size was 5.27 birds, with a range of 3–20. The site social scale encompassed a mean of 15.51 calls per site (range of 5–34 calls). The subset of 18 sites in Colonia encompassed 275 calls, with a mean of 15.28 calls per site (range of 6–34 calls). Only 19 calls were removed that potentially could be attributed to repeated sampling of individuals at higher social scales (*Supplementary Methods 1.1*).

Higher acoustic convergence at the individual scale

Visual inspection of repeatedly sampled individual's call catalogs (see examples in Figure 2A) demonstrated that individuals produced visibly consistent and distinctive calls, pointing to high acoustic similarity at this social scale. We found high agreement across 12 observers in visual classification of calls to individuals, with $71.82\% \pm 15.94\%$ (mean \pm SD) classification accuracy. These findings confirmed our preliminary finding of relatively high individual consistency and distinctiveness (Supplementary Methods 3.2). Indeed, calls at the individual scale grouped strongly by individual identity in SPCC acoustic space (Figure 2B). Notably, different individuals at the same site were as over-dispersed in acoustic space as individuals from different sites (Figure 2B). The Mantel test using SPCC measurements further confirmed a significant and high degree of acoustic similarity within individuals (Mantel $r = 0.43$, Table 1).

Low acoustic convergence at the pair, flock, and site social scales

Visual inspection of call catalogs by site demonstrated no obvious patterns of acoustic similarity within sites (Supplementary Figure 2A). In fact, the call variability visible within sites was nearly as high as variability among sites (Supplementary Figure 2A). This pattern remained evident when we visualized calls for all sites or three representative sites distributed across the geographic transect in SPCC and random forests acoustic space (Figure 3). Calls across the geographic transect presented no visibly clear regional clustering patterns in SPCC and random forests acoustic space (Figure 3A,B). Calls for three sites distributed across the transect (western end: PIED, middle: PEIX, and eastern end: OJOS, Supplementary Table 1) likewise demonstrated no clear clustering patterns by site identity, but instead showed high overdispersion within sites, as seen with repeatedly sampled individuals (Figure 2B). These three distant sites (each > 100 km apart) almost completely overlapped in acoustic space using both acoustic similarity methods (Figure 3C,D and Supplementary Figure 2B,C).

Our comparison of similarity methods further supported these findings. Classification accuracy of calls across all three similarity methods generally decreased as the social scale became higher, with generally lower convergence at all social scales higher than the individual scale (Supplementary Figure 6). Mantel tests did identify statistically significant acoustic convergence at most social scales and across acoustic similarity methods, with the exception of flock membership using SPCC acoustic similarity (Table 1). Mantel tests at the flock and site social scales identified stronger acoustic convergence with random forests similarity compared to SPCC (Table 1, Mantel r statistics for random forests were at least three times greater than SPCC at these social scales). However, these relationships between acoustic convergence and group identity were relatively weak, as demonstrated by the fact that the Mantel statistic for the individual scale was an order of magnitude larger than Mantel statistics for the higher social scales (Table 1).

Nonlinear patterns of acoustic similarity over geographic distance

The mean pairwise geographic distance across our longitudinal geographic transect was 132.58 km, with a range of 0.15–407.24 km. When adding in site ARAP (department of Salto), the mean pairwise distance in the full data set was 143.85 km, with a range of 0.15–513.59 km. For the subset of 18 sites in Colonia, the

mean pairwise distance among sites was 14.31 km, with a range of 0.15–48.16 km. We found no visible evidence of the mosaic patterns of geographic variation that are typical of vocal dialects. There was no visible grouping by region nor site identity when we examined the distribution of calls at higher social scales across the geographic transect in both SPCC (Figure 3A,C) and random forests acoustic space (Figure 3B,D). Instead, calls from distant geographic areas were often close neighbors in acoustic space (Figure 3).

We observed a slight effect of geographic distance using random forests acoustic similarity. Calls from the western end of the transect (Colonia department calls in Figure 3B or site PIED in Figure 3D) were slightly differentiated from calls on the eastern end of the transect (Rocha department calls in Figure 3B or site OJOS in Figure 3D) in random forests acoustic space. Mantel tests identified a statistically significant decrease in random forests acoustic similarity with increasing geographic distance. However, Mantel correlation values were low, indicative of a relatively weak relationship between random forests acoustic similarity and geographic distance (Table 1). We identified a nonlinear pattern of local and regional geographic variation using Mantel-based spatial autocorrelation. At the local geographic scale, SPCC and random forests identified significantly higher acoustic similarity than expected from 0 to 2 km (e.g., within sites or among neighboring sites, Figure 4). SPCC and random forests both identified a significant drop in acoustic similarity, albeit at different distances: 2–4 km and 4–6 km, respectively (Figure 4). Random forests subsequently identified two peaks of greater acoustic similarity than expected over greater distances (8–10 km and 16–18 km, Figure 4). We identified a similar nonlinear pattern at the regional scale. Acoustic similarity was highest over close geographic distances by both SPCC and random forests, then dropped by both methods (SPCC: 60–80 km, random forests: 60–110 km) (Figure 4).

Our validation results with calls from the yellow-naped amazon demonstrated that random forests reconstructed the mosaic patterns characteristic of previously documented regional dialects in this species, which were first identified using SPCC acoustic similarity (Supplementary Methods 3.1, Supplementary Figures 3 and 4, Wright 1996). This validation of our analytical approach points to the robustness of the findings we present here with monk parakeets.

DISCUSSION

Vocal learning is a social process, and yet we know relatively little about how social dynamics influence vocal learning processes. The signaling group membership hypothesis proposes that individuals gain fitness benefits from signaling social group membership with socially learned calls (Sewall et al. 2016). Vocal learning species that exhibit complex fission–fusion dynamics can interact over various social scales, such as pairs or flocks of varying sizes. Under the signaling group membership hypothesis, vocal learning species in fission–fusion societies should signal group membership over various social scales, also termed “hierarchical mapping” (Bradbury and Vehrencamp 1998). We tested this assumption of hierarchical mapping with monk parakeets, a parrot species with complex fission–fusion social dynamics (Hobson et al. 2014). We assessed whether contact call structure reflected group membership by asking whether calls were more similar within than among groups over multiple social scales, then asked how patterns of acoustic similarity manifested over geographic space.

Table 1
Mantel Test Results Across Social Scales and Geographic Distance

	Scale	Sample Sizes	SPCC		Random Forests	
			Mantel r	Mantel p	Mantel r	Mantel p
Social Scales	*Individual	$n_{\text{Individuals}} = 8$ $n_{\text{Sites}} = 3$ $n_{\text{Calls}} = 97$	0.43	0.0001	-	-
	*Pair	$n_{\text{Pairs}} = 44$ $n_{\text{Sites}} = 21$ $n_{\text{Calls}} = 88$	0.05	0.0001	0.08	0.0001
	*Flock	$n_{\text{Flocks}} = 29$ $n_{\text{Sites}} = 22$ $n_{\text{Calls}} = 77$	0	0.5403	0.06	0.0011
	Site	$n_{\text{Sites}} = 39$ $n_{\text{Calls}} = 605$	0.04	0.0001	0.13	0.0001
	Site (Colonia)	$n_{\text{Sites}} = 18$ $n_{\text{Calls}} = 275$	0.05	0.0001	0.16	0.0001
Geographic Distance	Local (Colonia)	$n_{\text{Sites}} = 18$ $n_{\text{Calls}} = 275$	0.02	0.3167	0.07	0.0004
	Regional (all sites)	$n_{\text{Sites}} = 39$ $n_{\text{Calls}} = 605$	-0.05	0.9946	0.1	0.0001

Asterisks refer to partial Mantel tests performed to control for site identity at nested social scales. P-values in bold were significant after a Bonferroni correction (alpha of 0.05 adjusted to 0.00385).

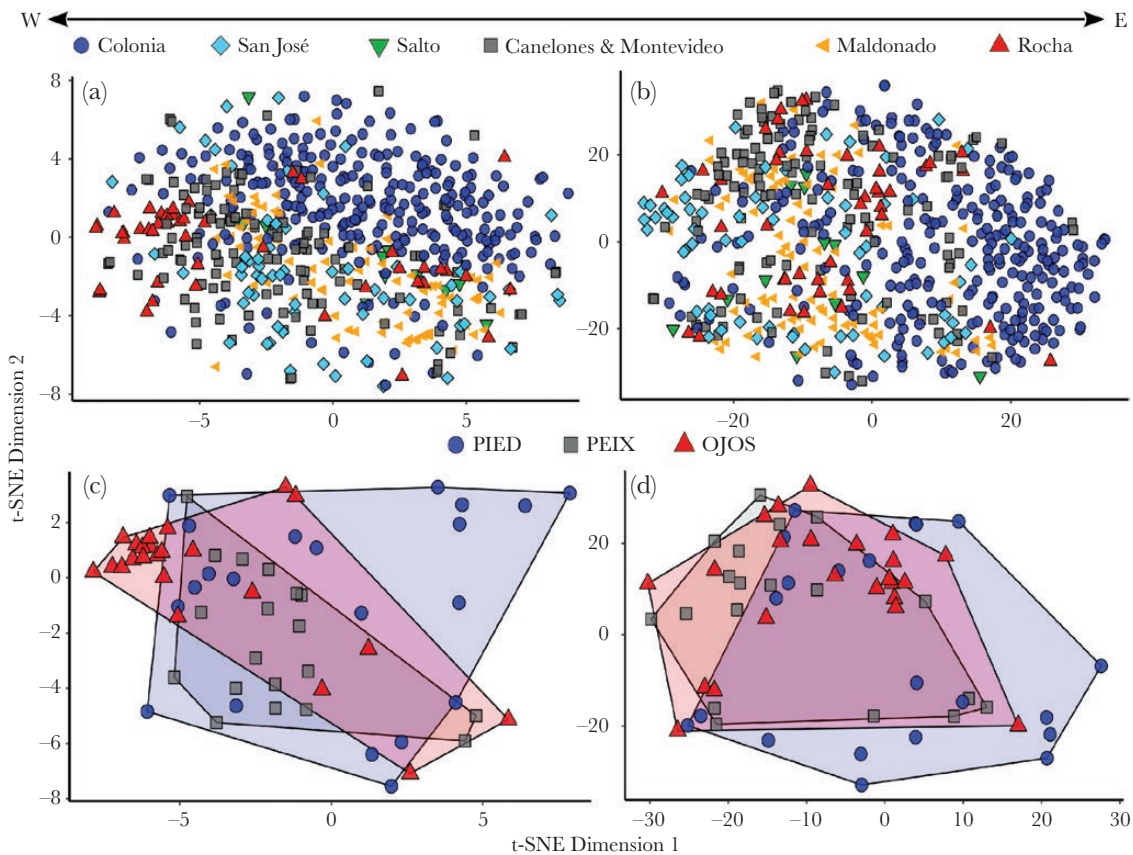


Figure 3
Distribution of contact calls across the geographic transect ($n_{\text{Calls}} = 605$) in SPCC (A, C) and random forests (B, D) acoustic space. Dimensionality of similarity matrices was reduced with t-SNE. Colors and symbols correspond to departments across the geographic transect. (A) All calls distributed in SPCC acoustic space. (B) All calls distributed in random forests acoustic space. (C) Calls for three sites from the western end (PIED), middle (PEIX) and eastern end (OJOS) of the geographic transect in SPCC acoustic space. (D) Calls for three sites in random forests acoustic space. Convex hull polygons in C and D demonstrate the area encompassed by each site's calls in acoustic space.

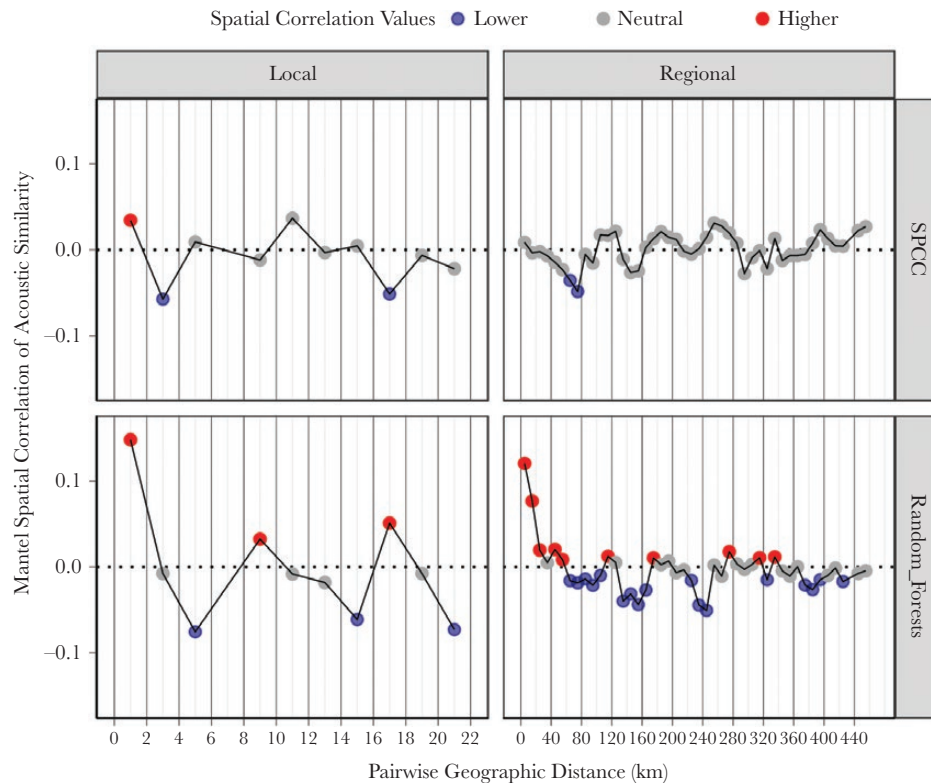


Figure 4

Mantel-based correlogram of SPCC or random forests acoustic similarity values over local and regional geographic scales. Two-kilometer intervals were used for the local geographic scale and 10 km intervals for the regional scale. Spatial autocorrelation values significantly lower than expected (using Holm's P -value correction for multiple testing and alpha of 0.05) are shown in blue, while those significantly higher than expected are shown in red. Nonsignificant values ("Neutral") are shown in light gray.

Statistically significant acoustic convergence was identified across all social scales in this study. This acoustic convergence was, however, strikingly low at all social scales except the individual scale. We also found no evidence of dialectal nor clinal geographic variation, an interesting contrast to most other parrot species studied to date (Wright and Dahlin 2018). These patterns were identified using three different approaches, confirming their robustness. Below we discuss these findings in more detail, and their implications for hierarchical mapping and the signaling group membership hypothesis.

Higher acoustic convergence at the individual scale than all other social scales

The assumption of hierarchical mapping in the contact calls of native monk parakeets was supported by the statistical significance of higher acoustic similarity within groups versus among groups at each social scale. However, the hierarchical mapping we identified was characterized by stronger individual signatures than group membership at higher social scales, suggesting that individual identity is the most important social information that native range monk parakeets encode in contact calls.

Native range monk parakeets may therefore rely on individual signatures to recognize social group members, as documented in free-ranging mated pairs of green-rumped parrotlets (*Forpus passerinus*) (Berg et al. 2011) and short-billed white-tailed black cockatoos (*Calyptorhynchus funerem latirostris*) (Saunders 1983), free-ranging parent-offspring interactions in rose-breasted galahs (*Eolophus roseicapilla*) (Rowley 1980), captive groups of budgerigars

(*Melopsittacus undulatus*) (Brown et al. 1988) and spectacled parrotlets (*Forpus conspicillatus*) (Wanker et al. 1998), and wild-caught brown-throated conures (*Eupsittula pertinax*) held in short-term captivity (Buhrman-Deever et al. 2008). An emphasis on signaling individual identity may arise from monk parakeets' socioecology, which includes communal and colonial nesting behavior (Eberhard 1998), complex fission-fusion social dynamics (Hobson et al. 2014), and potential nest territoriality. Nest territoriality is not well understood in monk parakeets, but the amount of time devoted to harvesting sticks and nest-building, as well as occasional stealing of sticks (Eberhard 1998) and fights over nests (Smith-Vidaurre, personal observation), indicate that nests are structures of sufficient value to merit defense. Colonial and communal nesting, complex social dynamics and territoriality are all factors considered to select for individual recognition systems in animal signals (Tibbetts and Dale 2007). An important limitation of our study is that we performed sampling for the individual scale over a limited time frame (a single day). If signaling individual identity is indeed as important as our present results indicate, then individual signatures in contact calls may remain relatively stable over time. The temporal stability of such individual signatures will be important to address in future work.

The strong relationship we identified between acoustic similarity and individual identity, relative to higher social scales, contrasts with findings from the invasive range in the United States. Contact calls in a local geographic area in the state of Connecticut showed relatively strong acoustic convergence at the site social scale, a pattern

consistent with vocal dialects (Buhrman-Deever et al. 2007). It is unclear whether this difference between native and invasive populations is a result of changes in social structure and signaling systems during invasion, or simply a difference in the sampling or analysis approaches between the two studies; a more direct comparison using the same analytical approaches is ongoing.

Our study does not rule out the possibility that the low degree of acoustic convergence we identified over higher social scales could be used by native parakeets to discriminate among social group members and nonmembers. Previous research demonstrates that captive monk parakeet responses to contact call playbacks were significantly associated with affiliative dyadic relationships (Hobson et al. 2015). These findings indicate that monk parakeets can discriminate frequent, affiliative social partners by contact call structure (Hobson et al. 2015), although more work is needed to determine whether monk parakeets use individual signatures or shared call structure within groups (or perhaps both) to identify social partners.

Geographic patterns of acoustic similarity were neither dialectal nor clinal

Our initial predictions were that monk parakeets would display either the dialectal or clinal patterns of geographic variation that have been attributed to vocal learning in other species (Podos and Warren 2007; Wright and Dahlin 2018). We found no obvious grouping of contact calls in acoustic space by regions or sites (Figure 3), as would be found in a mosaic dialectal pattern (e.g., yellow-naped amazons; Wright 1996). We explored the possibility of a geographic cline. Clinal geographic variation can be attributed to fission–fusion social dynamics, in which individuals learn from others as they move among local flocks, resulting in a visibly striking pattern of linearly decreasing acoustic similarity over increasing geographic distance (Bradbury et al. 2001). However, we detected a nonlinear relationship between acoustic similarity and geographic distance (Figure 4). Both SPCC and random forests agreed on significant patterns of lower acoustic similarity than expected over short geographic distances (within 2–6 km) (Figure 4), suggesting there is a slight tendency for birds at neighboring sites to avoid overlapping in acoustic space. Random forests identified slightly higher acoustic similarity than expected at greater geographic distances (>250 km) (Figure 4), indicating that the pressure to avoid overlapping in acoustic space may be reduced at distances over which individuals are less likely to interact. These patterns of geographic variation did not reflect our initial predictions. We conclude that the nonlinear, unstructured patterns of geographic variation we identified in native range monk parakeet contact calls do not match dialectal nor clinal variation as recognized in the vocal learning literature (Bradbury et al. 2001; Podos and Warren 2007; Wright and Dahlin 2018). Future efforts to track monk parakeet dispersal could shed light on how social interactions manifest over social and geographic scales in natural populations.

Validation of our analytical approach and findings

We validated our analytical approach measuring acoustic similarity of monk parakeet calls with SPCC and supervised random forests, a machine learning method. Both SPCC and random forests reconstructed previously documented patterns of acoustic similarity in yellow-naped amazons (Wright 1996, Supplementary Figures 3 and

4), demonstrating that the results we present here with monk parakeets are not artifacts of our analytical approach. The robustness of our findings is further supported by the fact that classification accuracy of calls back to social groups generally decreased over higher social scales by all methods we used to evaluate similarity of these acoustic signals (Supplementary Figure 6).

We identified the strongest pattern of acoustic convergence at a social scale with the lowest sample size. Given the probabilistic nature of observing behaviors under wild conditions, a small sample size should have biased our results towards failing to identify patterns of acoustic convergence at the individual scale. The fact that we did identify strong individual signatures with a small sample size additionally points to the robustness of this finding, and is likely due to the depth of sampling we were able to obtain per individual. Sampling for the individual scale was often performed in a different social context (individuals perched alone) than higher social scales (individuals were often sampled while flying in groups). However, we found that the difference in acoustic structure attributable to social context was small and unlikely to bias the results we present here (Supplementary Tables 4 and 5). We also found that motivational differences over narrow sampling windows did not significantly influence the results we present here for the individual scale (Supplementary Table 6).

Future research on the evolution and maintenance of vocal learning

Direct testing of hypotheses addressing the evolution and maintenance of vocal learning, such as the signaling group membership hypothesis, is necessary to broaden our understanding of this complex and compelling trait. Much of the vocal learning literature has focused on species that exhibit clear patterns of acoustic convergence over social scales and geographic space, such as vocal dialects or geographic clines (Podos and Warren 2007). Novel insights on the evolution and maintenance of vocal learning could arise from studying species that do not exhibit such classic patterns of acoustic convergence attributed to vocal learning, such as monk parakeets.

Although we did not identify strong acoustic convergence within social groups over higher social scales in monk parakeet contact calls, nor regional dialects or clines, this general lack of acoustic convergence need not signify a lack of vocal learning in this species. Monk parakeets' vocal learning abilities are striking in captivity, and we have no reason to expect that this species' propensity for vocal learning in captivity should not extend to natural conditions. Further research with monk parakeet acoustic signals would shed additional light on vocal learning processes in this species.

We propose several additional hypotheses that could be tested in future research with monk parakeets and other species with similar patterns of vocal variation. First, it is possible that individuals rely on contact call acoustic convergence to discriminate among social group members and nonmembers over multiple social scales. Although we detected low levels of acoustic convergence over higher social scales in this study, these may be functionally relevant to native range parakeets. This hypothesis could be tested in playback experiments with short-term captives using calls recorded from captives' nesting sites, as well as neighboring and distant sites (Vehrencamp et al. 2003). It could also be tested by experimentally altering social group stability in captivity, and recording contact calls and social network connections over time. Alternatively, if monk parakeets rely on individual signatures to discriminate among

group members, then individuals should not converge upon similar calls within social groups in an experimental context, but rather use learning to alter their calls to be acoustically distinct from others around them. Finally, acoustic convergence by vocal learning could be more pronounced in other call types in the vocal repertoire, which could be evaluated using playback or predator stimuli experiments with short-term captives to reliably elicit other call types (Martella and Bucher 1990).

CONCLUSIONS

We found strong individual signatures in native range monk parakeet contact calls, coupled with low acoustic convergence across the pair, flock and site social scales. We found unstructured patterns of geographic variation that did not match our expectations for dialectal or clinal geographic variation. Our findings suggest that native range monk parakeets use individual signatures in contact calls to navigate social interactions, underscoring an intriguing relationship between vocal learning processes and social dynamics that could be evaluated in future research. Monk parakeets are a vocal learning species that has been repeatedly and independently introduced around the world, presenting unparalleled opportunities to ask how the process of introduction impacts social structure and in turn, the vocal learning processes that underlie variability in acoustic signals.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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The authors declare no conflicts of interest associated with their authorship nor the publication of this article.

AUTHOR CONTRIBUTIONS

G.S.V. helped design the study, performed fieldwork, curated and analyzed data, and was the primary author of the manuscript. M.A.S. contributed to data analysis and reviewed the manuscript. T.F.W. helped design the study, and contributed to fieldwork, data analysis, and writing the manuscript.

ETHICAL NOTE

This research was conducted under an approved Institutional Animal Care and Use protocol (IACUC no. 2017-006, New Mexico State University, USA) and an animal care and use protocol approved by la Comisión de Ética en el Uso de Animales (CEUA no. 240011-002512-17, la Universidad de la República, Uruguay).

Data accessibility: Analyses reported in this article can be reproduced using the data and code provided by Smith-Vidaurre et al. (2019). Code is also available on GitHub: <https://github.com/gsvidaurre/strong-individual-signatures>.

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