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Individuality in the vocalizations of infant and adult coppery titi monkeys (*Plecturocebus cupreus*)

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Abstract

As social animals, many primates use acoustic communication to maintain relationships. Vocal individuality has been documented in a diverse range of primate species and call types, many of which have presumably different functions. Auditory recognition of one's neighbors may confer a selective advantage if identifying conspecifics decreases the need to participate in costly territorial behaviors. Alternatively, vocal individuality may be nonadaptive and the result of a unique combination of genetics and environment. Pair-bonded primates, in particular, often participate in coordinated vocal duets that can be heard over long distances by neighboring conspecifics. In contrast to adult calls, infant vocalizations are short-range and used for intragroup communication. Here, we provide two separate but complementary analyses of vocal individuality in distinct call types of coppery titi monkeys (*Plecturocebus cupreus*) to test whether individuality occurs in call types from animals of different age classes with presumably different functions. We analyzed 600 trill vocalizations from 30 infants and 169 pulse-chirp duet vocalizations from 30 adult titi monkeys. We predicted that duet contributions would exhibit a higher degree of individuality than infant trills, given their assumed function for long-distance, intergroup communication. We estimated 7 features from infant trills and 16 features from spectrograms of adult pulse-chirps, then used discriminant function analysis with leave-one-out cross-validation to classify individuals. We correctly classified infants with 48% accuracy and adults with 83% accuracy. To further investigate variance in call features, we used a multivariate variance components model to estimate variance partitioning in features across two levels: within- and between-individuals. Between-individual variance was the most important source of variance for all features in adults, and three of four features in infants. We show that pulse-chirps of adult titi monkey duets are individually distinct, and infant trills are less individually distinct, which may be due to the different functions of the vocalizations.

KEYWORDS

discriminant function analysis, pair bonding, vocal duetting, vocalization individuality

1 | INTRODUCTION

Acoustic communication is ubiquitous in both marine and terrestrial animals and is important for a wide range of behaviors including resource acquisition and defense, mating, and conspecific recognition (Wilkins, Seddon, & Safran, 2013). Acoustic signals can provide pertinent social information about caller quality, status, or identity (Bradbury & Vehrencamp, 1998, pp. 658–665). Vocal individuality, the characteristic of being vocally discriminable from other individuals (Pollard & Blumstein, 2011), can arise in various ways. For instance, vocal individuality can be the result of evolution by natural selection. Recognition of familiar conspecifics may be especially adaptive, as the correct identification of caller identity may have impacts on perceiver fitness depending on the context (Tibbetts & Dale, 2007). For example, predation (Blumstein, Verneyre, & Daniel, 2004), mate choice (Zelano & Edwards, 2002), and kin selection (Zelano & Edwards, 2002) are all contexts under which incorrect identification of another animal can be hugely detrimental to an individual's fitness. However, vocal individuality could alternatively occur through neutral evolution, wherein idiosyncratic aspects of an individual's experience including ontogeny (Lapshina et al., 2012) and genetics (Geissmann, 1984) lead to individually distinct phenotypes in the absence of selection.

Vocal individuality has been documented in many mammalian species, across call types and age classes. Vocal individuality has been shown in juvenile gazelles (Lapshina et al., 2012) and seal pups (Collins, Terhune, Rogers, Wheatley, & Harcourt, 2006; Phillips & Stirling, 2000; Van Opzeeland & Van Parijs, 2004) and allows parents to recognize their offspring. By 2 weeks of age, Weddell seal pups are individually distinct enough that mothers can differentiate their offspring from unrelated pups (Collins et al., 2006). In chacma baboons, mothers are able to discriminate their infant from familiar, unrelated infants based on contact calls, but not distress calls (Rendall, Notman, & Owren, 2009). However, in some species, all age classes have individually distinct vocal elements (South American sea lions [Ndez-Juricic, Enriquez, Campagna, & Ortiz, 1999]). In adult mammals, vocal individuality can be used to maintain cohesion with group members during foraging bouts in which individuals are out of sight (ring-tailed lemurs [Macedonia, 1986], giant otters [Mumm, Urrutia, & Knörnschild, 2014]). Alarm calls in squirrels are individually identifiable, and this individuality is stable over time (Matrosova, Volodin, & Volodina, 2009). Thus, we see a pervasive pattern of vocal individuality in mammalian species across age classes and call types, and in some cases, there is evidence that it is adaptive.

Many primate species rely on vocal communication to maintain social relationships (McComb & Semple, 2005). In nonhuman primates, vocal communication can provide honest signals about caller status or conditions that are constrained by physiology (Fitch & Hauser, 1995). Vocal communication is highly linked to primates' unique neurobiology (Egnor & Hauser, 2004), can be a learned behavior (Snowdon, Elowson, & Roush, 1997), and is heavily reinforced during infancy as parents respond to infant calls, and infants adjust accordingly (Takahashi et al., 2015). Individually distinct vocalizations have been noted in the loud calls of a variety of primate species such

as chimpanzees (Mitani, Gros-Louis, & Macedonia, 1996), orangutans (Delgado, 2007), gray mouse lemurs (Zimmermann, Vorobieva, Wrogemann, & Hafen, 2000), and rufous mouse lemurs (Zimmermann et al., 2000). Further, most studies that have investigated vocal individuality in primates provide evidence that it exists and is potentially adaptive, as the results of previous playback studies could not be explained otherwise. For example, vervet monkeys move away from or approach grunt vocalization playbacks from different individuals, suggesting calls contain cues about individual status (Cheney & Seyfarth, 1982). Further, when exposed to playbacks of familiar and unfamiliar individuals, chimpanzees responded aggressively to unfamiliar individuals, but not to familiar individuals (Herbinger, Papworth, Boesch, & Zuberbühler, 2009).

Monogamous, pair-bonding primates often engage in duets or coordinated, stereotyped vocalizations between the male and female pair mates. Duets presumably serve a territorial function (Marshall & Marshall, 1976), although the function of duets remains a topic of debate (Marshall-Ball, Mann, & Slater, 2006). Duetting has evolved independently multiple times across the order Primates. In many duetting primate species, duet contributions have been shown to be individually distinct (gibbons [Barelli, Mundry, Heistermann, & Hammerschmidt, 2013; Clink, Bernard, Crofoot, & Marshall, 2017; Feng, Cui, Ma, Fei, & Fan, 2014; Lau, Clink, Crofoot, & Marshall, 2018; Terleph, Malaivijitnond, & Reichard, 2015], tarsiers [Clink, Tasirin, & Klinck, 2019], and indris [Gamba et al., 2016]). As territorial animals, the duetting primates likely benefit from individual recognition, as the ability to identify conspecifics aurally may decrease the need for costly territorial defense behaviors. Titi monkeys are one such taxa in which males and females duet periodically each morning, with each adult titi vocalizing back and forth in coordination (Adret et al., 2018; Müller & Anzenberger, 2002; Robinson, 1979). There is little sex specificity in the organization of these duet vocalizations, as both sexes have an identical, overlapping vocal repertoire (Müller & Anzenberger, 2002; Robinson, 1979). Vocal individuality has not yet been studied in any titi monkey species, presumably due in part to the overlapping contributions of male and female duetting partners, which make acoustic analysis impossible without the use of combined video and acoustic recordings.

Previous studies assessing vocal individuality in territorial primates (Barelli et al., 2013; Clink et al., 2017; Clink, Tasirin et al., 2019; Feng et al., 2014; Gamba et al., 2016; Lau et al., 2018; Terleph et al., 2015) focused on the vocalizations of adult individuals. In humans, infant cries are individually distinct to listening adults (Gustafson, Green, & Cleland, 1994); in squirrel monkeys, mothers are able to recognize infants based on call playbacks (Symmes & Biben, 1985); and in marmosets, infant calls slowly develop into adult vocalizations (Pistorio, Vintch, & Wang, 2006). Infant calls are typically used when in distress or to communicate need to their attachment figure (Symmes & Biben, 1985). However, common marmoset fathers do not respond differentially to familiar versus unfamiliar infants, suggesting that infant vocal individuality may not be meaningful in all species (Zahed, Prudom, Snowdon, & Ziegler, 2008). No studies to date have characterized or analyzed the spectral properties of infant titi monkey vocalizations and

investigating variation in infant vocalizations can provide insights into call function. For instance, more individualized vocalizations may aid infants in soliciting care from or being recognized by parents.

Here, we investigate vocal individuality in two distinct age classes of the pair-bonding coppery titi monkeys (*Plecturocebus cupreus*, previously *Callicebus cupreus*) at the California National Primate Research Center (CNPRC; Bales et al., 2017). The adults in this population reliably vocalize each morning and present a unique opportunity: Caller identity is known, all recordings are collected from a standardized distance with identical recorder settings, and the pairing of audio and video recordings allows for individual identification in an otherwise unreadable spectrogram. The duets of this species consist of pulse-chirp vocalizations in which one individual emits quickly repeated broadband notes (pulses) followed by high-frequency notes (chirps). This pulse-chirp vocalization element is spectrally distinct from lower frequency vocalizations in the duet and is sung by both sexes multiple times throughout the morning duet. Further, the pulse element of this population's duet has been shown to vary based on individual age and pairing length (Clink, Lau, & Bales, 2019). In this population, infant titi monkeys emit trill vocalizations when distressed (Hoffman, Mendoza, Hennessy, & Mason, 1995) or when separated from the family group (Larke, Toubiana, Lindsay, Mendoza, & Bales, 2017). Thus, these infant trills function as intragroup communication, in contrast to adult titi monkeys' intergroup duet calls. Presumably, intragroup communication in titi monkeys occurs within visual contact of family groups that are composed of only a few members. Thus, individuals communicating within their group may not benefit from being individually distinct, as other cues such as an individual's location, can inform family members of caller identity. In contrast, intergroup communication likely occurs when animals are not in visual contact, leaving acoustic cues as the only means with which to communicate identity. This data set presents an opportunity to assess vocal individuality in two different age groups, potentially providing insight into the evolution of individually distinct signaling. We predicted that adult calls would be more individually distinct than infant calls, given the assumed differences in call function.

2 | METHODS

2.1 | Ethical note

No animals were handled in this study. We collected all vocalizations noninvasively and opportunistically from outside each animals' cage. This project was approved by the Institutional Animal Care and Use Committee of the University of California, Davis, and complied with the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

2.2 | Study location and subjects

All recordings of coppery titi monkey (*P. cupreus*) duets were collected at the CNPRC. All study subjects were captive-born at this

facility. The titi monkeys were housed indoors in enclosures measuring $1.2 \times 1.2 \times 2.1$ m. The room was maintained at 21°C on a 12-hr light cycle with lights on from 06:00 to 18:00. Subjects were fed a diet of monkey chow, carrots, bananas, apples, and rice cereal twice a day. Water was available ad libitum and additional oat foraging enrichment was provided twice a day. Subjects were housed in male–female pairs with up to three offspring. All groups were in acoustic contact with other titi monkey pairs but had minimal visual contact with animals outside their own housing. This housing situation is the same as described in previous studies of this colony (Mendoza & Mason, 1986; Tardif et al., 2006).

2.3 | Data collection

Adult titi monkey ($N = 30$; 15 females, 15 males) duets were recorded opportunistically each morning between 06:00 and 07:30 for 2 years (March 2017 to March 2019). We used a Marantz PMD 660 flash recorder and a Marantz Professional Audio Scope SG-5B directional condenser microphone. Recordings were made with a sampling rate of 44.1 Hz and 16-bit resolution and saved as waveform (.wav) audio files. Subjects were recorded duetting with their pair mate (Figure 1). We collected all recordings noninvasively from outside each pair's cage and <3 m from the calling animals. The gain setting was constant for all recordings.

Infant titi monkey ($N = 30$; 15 females, 15 males) trills were recorded between 07:00 and 08:00 during an infant open field test when subjects were 4 months old. Recordings from our subjects span 4 years (February 2015 to January 2019) of testing in this colony. For more information about this specific test paradigm, see Larke et al. (2017) and Savidge and Bales (2020). Audio taken during video recording of each test (.mp4) was converted to waveform (.wav) audio files for analysis. We collected all recordings 1 m from the infant.

2.4 | Acoustic analysis

All adult audio recordings were compared with videos of the corresponding duet bout to identify the calling individual. Previous authors have referred to this particular call sequence as a “pump” and “chirrup” (Robinson, 1979), but we will refer to these as “pulse-chirps” (Clink, Lau et al., 2019) to better reflect the spectral characteristics of the notes and to keep consistency with terms used in the frog (Martínez-Rivera & Gerhardt, 2008), bird (Laiolo, Tella, Carrete, Serrano, & López, 2004), and marine mammal (Mathevon, Casey, Reichmuth, & Charrier, 2017) literature. We only included pulse-chirps with a high signal-to-noise ratio (>10 dB) where it was clear there was only one individual emitting the pulse-chirp call sequence. We used all pulse-chirp calls ($N = 157$ total; mean = 5.73 calls \pm 3.50 standard deviation [SD] per individual; range = 2–14) from a single duet bout for each individual ($N = 30$).

Infant trills ($N = 600$ total; 20 per infant) were selected directly from the corresponding spectrograms without the need for video

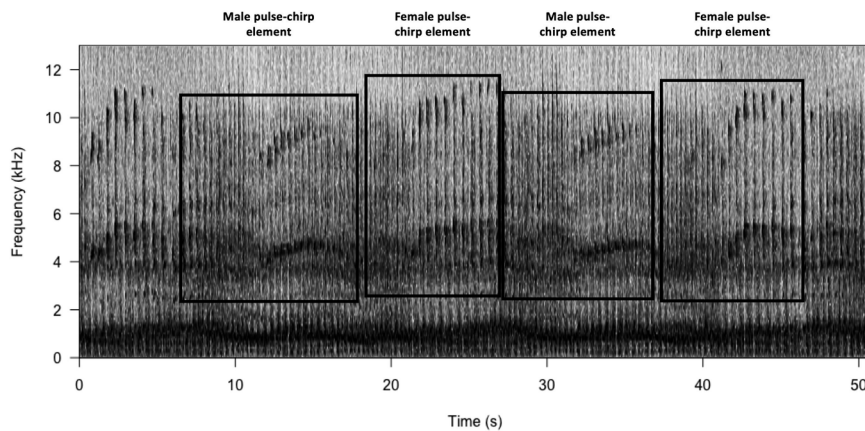


FIGURE 1 Representative spectrogram of a coppery titi monkey (*Plecturocebus cupreus*) morning duet vocalization. The alternating male and female pulse-chirp contributions are highlighted

comparison, as no other infants were present during the infant open field test and thus identity was certain. We truncated our analysis to 20 randomly chosen trills per infant and only included trills with a high signal-to-noise ratio (>10 db). All trills were recorded in the same context; see Larke et al. (2017) for details of study design. During this condition, infants are free to roam an unfamiliar open field arena while an empty transportation box is placed in front of the viewing window.

We created spectrograms using Raven Pro 1.5 Sound Analysis Software (Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Ithaca, NY). We generated spectrograms with a 512-point (11.6 ms) Hann window (3 dB bandwidth = 124 Hz), with 75% overlap, and a 1,024-point discrete Fourier transform, yielding time and frequency measurement precision of 2.9 ms and 43.1 Hz. We did not down-sample the original sound files. One observer (A. R. L.) isolated each of the pulse-chirp sequences from the duet sequence and saved them as individual .wav files (Figure 2a). Seven trained observers manually selected all adult pulse-chirp notes and one observer manually selected all infant trills using the selection table feature in Raven Pro, after confirming that inter- and intra-observer reliability was $>95\%$.

For each adult pulse-chirp element we estimated the following features using Raven Pro selection tables; for pulses ($N = 5$ features): number of pulse notes, mean interquartile range bandwidth (the average interquartile bandwidth for all pulses), mean center frequency, duration of the entire pulse element, and pulse rate; for chirp notes ($N = 11$ features): mean note bandwidth, mean note highest frequency, mean note lowest frequency, duration of the chirp element, duration of time vocalizing, number of chirp notes, minimum bandwidth, maximum bandwidth, highest frequency of all chirp notes, highest frequency of the first chirp note, and highest frequency of the last chirp note (Table 1 and Figure 2b). We conducted earlier experiments to test for the influence of reverberation, recording location, and variation in cage configuration on spectral feature estimates using two omnidirectional microphones placed at two different distances, 5 and 8 m from the vocalizing animals. We compared frequency measures (bandwidth and maximum frequency) from two channels to confirm that there was no difference in acoustic feature estimation based on

recording location. For each infant trill vocalization (Figure 3a), we estimated the following spectral and temporal features using Raven Pro: lowest frequency, highest frequency, duration, bandwidth, center frequency, trill count, and trill rate (Table 2 and Figure 3b).

2.5 | Linear discriminant function analysis (DFA)

To assess adult individuality, we compared all titi monkey pulse-chirp duet vocalizations using DFA based on the 16 features estimated from each vocalization. DFA is a supervised analysis that uses input features to estimate the maximum difference between calls from each individual (Venables & Ripley, 2013, pp. 331–337). Although we had multiple duet recordings from different pairs, we only used the pulse-chirp vocalizations from one duet recording per pair to conform to the assumptions of DFA. We chose the highest quality, longest duet recording from each pair for use in this analysis.

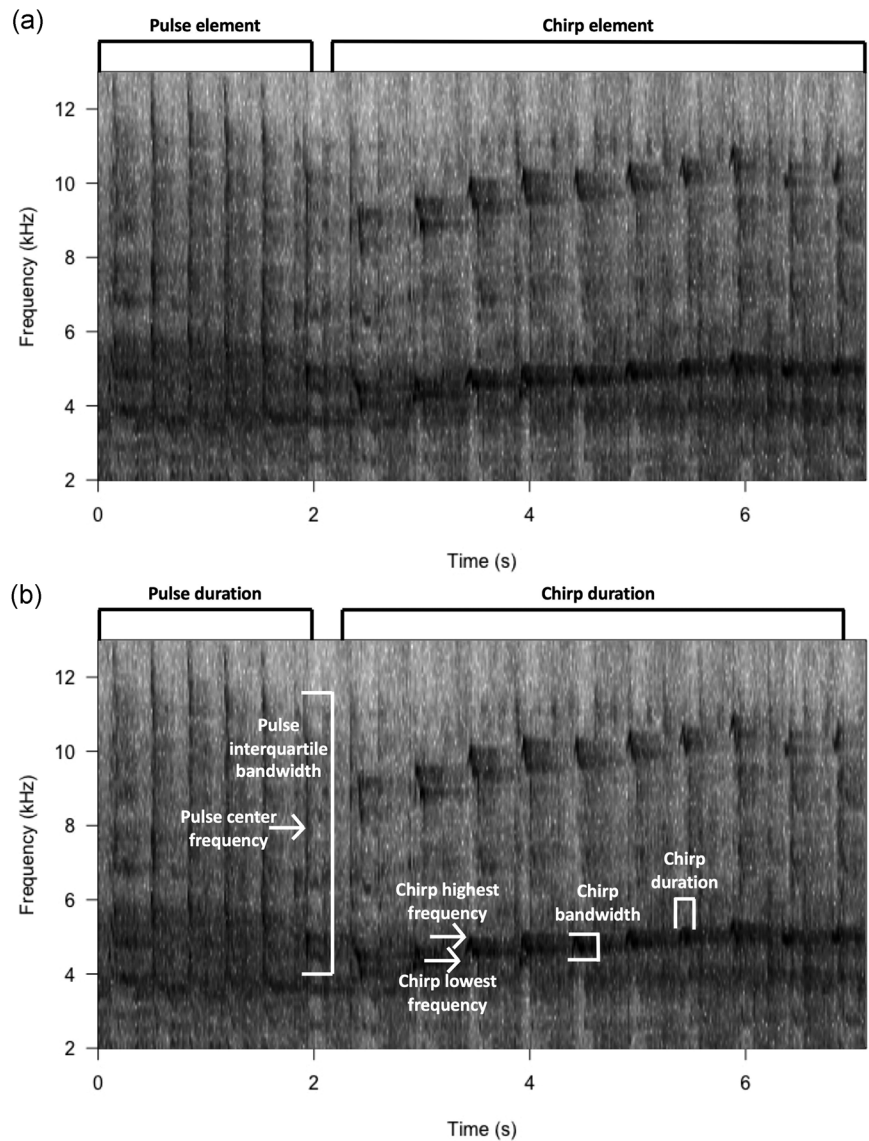
To assess infant individuality, we compared all infant titi monkey trill vocalizations using DFA based on the seven features estimated from each vocalization. All 20 trills for each individual were taken from one recording sessions to conform to the assumptions of DFA.

We used leave-one-out cross-validation (LOOCV) to assess the results of the DFA for both infant and adult individuals. LOOCV removes one vocalization from the sample, returns DFA with all other vocalizations, and classifies the excluded vocalization. All analyses were conducted in R language and programming environment (R Development Core Team, 2017) using the MASS package (Ripley et al., 2013).

2.6 | Multivariate variance components model

We used a multivariate variance components model (Clink, Grote, Crofoot, & Marshall, 2018; Lau et al., 2018) that was implemented using the rstan package (Guo et al., 2016), to assess the proportion of variance attributable to our two levels, individual (capturing inter-individual variance) and vocalization (capturing intraindividual variance). For both adults and infants, we utilized the same model. We

FIGURE 2 (a) Representative coppery titi monkey (*Plecturocebus cupreus*) pulse-chirp element spectrogram. The pulse and chirp elements are highlighted individually. (b) Representative coppery titi monkey (*P. cupreus*) pulse-chirp element spectrogram. Features estimated from the pulse and chirp elements are highlighted



defined our model for individual monkey m and vocalization/call c , where y is the log-transformed feature vector, a is the individual-specific random intercept, and e is the vocalization-specific error term (Clink et al., 2018; Lau et al., 2018).

$$y_{m,c} = a_c + e_{m,c}.$$

Variance/covariance matrices were used at each level to assess the variability of each spectral or temporal acoustic parameter in addition to the covariance between different features. The matrices for a and e are defined as Σ_a and Σ_e . See Lau et al. (2018) and Clink et al. (2018) for more details on model development and specifications.

We generated 1,500 warm-up samples, followed by 1,500 parameter samples from each of two Markov chains, for a total of 3,000 samples for posterior inference. Computing took ca. 20 min using a MacBook Air with 1.3 GHz Intel Core; both the adult and

infant analysis took around 10 min to run and were not run simultaneously.

We calculated intraclass correlation coefficients (ICCs) that measure the relative contributions of interindividual variance and intraindividual variance, to the overall variance (Merlo et al., 2006). We calculated ICC at the level l for each acoustic feature from posterior samples of Σ_a and Σ_e as:

$$ICC_l = \frac{\text{Variance of feature at level } l}{\text{Total variance of feature}}.$$

ICC values range from 0 to 1. An ICC near 1 indicates that the level (individual or vocalization) is contributing a large amount of variance to total variance (Merlo et al., 2006).

Not all call features were used in the model as some features were highly correlated and were excluded based on visual inspection of scatter plot matrices of all features. For the adult pulse-chirp vocalization analysis, we excluded number of pulses (which was

TABLE 1 Definitions of the 16 spectral and temporal features estimated from spectrograms of coppery titi monkey (*Plecturocebus cupreus*) pulse-chirp vocalizations

Element	Parameter	Definition
Pulse element	Number of pulses	Number of pulse notes in the pulse element
	Mean interquartile bandwidth (kHz)	Mean frequency difference between the first and third quartile of all pulse notes
	Mean center frequency (kHz)	Mean center frequency of all pulse notes
	Duration of pulse element (s)	Duration of the pulse element
	Pulse rate	Rate of pulse note repetition
Chirp Notes	Mean note bandwidth (kHz)	The mean difference between the frequency 5% and frequency 95% of all chirp notes
	Mean note highest frequency (kHz)	Mean highest frequency of all chirp notes
	Mean note lowest frequency (kHz)	Mean lowest frequency of all chirp notes
	Duration of chirps (s)	Duration between start of the first chirp note and end of the last chirp note
	Duration of time vocalizing (s)	Sum of all chirp note durations
	Number of chirps	Number of notes in the chirp element
	Minimum bandwidth (kHz)	Bandwidth of the chirp note with the lowest bandwidth (difference between the frequency 5% and frequency 95%)
	Maximum bandwidth (kHz)	Bandwidth of the chirp note with the highest bandwidth (difference between the frequency 5% and frequency 95%)
	Highest frequency of all chirps (kHz)	Highest frequency across all chirp notes
	Highest frequency first note (kHz)	Highest frequency of the first chirp note
	Highest frequency last note (kHz)	Highest frequency of the last chirp note

correlated with pulse duration); mean note lowest frequency, highest frequency of all chirps, highest frequency first note, and highest frequency last note (all of which were correlated with mean note highest frequency); number of chirps (which was correlated with chirp duration); and minimum bandwidth and maximum bandwidth (which were correlated with mean note bandwidth). For the infant trills, we excluded lowest frequency and center frequency (both of which were correlated with highest frequency). We checked the goodness of fit of our model using a Q-Q plot of posterior mean distances between observations and their predicted values, as compared with a suitable *F* distribution. R programming language and environment was used for all analyses in this study (R Development Core Team, 2017).

3 | RESULTS

3.1 | Vocalization individuality

We analyzed 157 morning duet pulse-chirp vocalizations from 30 adult titi monkeys (range = 2–14) and were able to identify individual animals with 83% accuracy using LOOCV (Figure 4). Our classification accuracy was significantly higher than random chance (3.33%). We found that there was substantial interindividual variation in all spectral and temporal features measured (Table 3).

We were able to classify 600 infant trill vocalizations from 30 titi monkeys (*N* = 20 trills per subject) with a 48% accuracy (Figure 5). The 48% accuracy of our LOOCV is higher than the accuracy of random chance (3.33%). There was substantial variation in all spectral and temporal features that were measured (Table 4).

3.2 | Sources of variance in titi monkey duets

Based on our multivariate variance components model for adults, between-individual variance explained more of the total variance for all features included in the model (pulse mean interquartile bandwidth, pulse mean center frequency, pulse duration, pulse rate, chirp mean note bandwidth, chirp mean note highest frequency, chirp duration of time vocalizing, and chirp duration) than within-individual variance (Figure 6). The posterior density estimates of ICCs for interindividual-level variance for all features (pulse mean interquartile bandwidth [ICC posterior density mean = 0.68; 95% credibility interval [CI] = 0.52, 0.81], pulse mean center frequency [mean = 0.79; 95% CI = 0.66, 0.89], pulse duration [mean = 0.54; 95% CI = 0.36, 0.71], pulse rate [mean = 0.83; 95% CI = 0.72, 0.91], chirp mean bandwidth [mean = 0.59; 95% CI = 0.42, 0.74], chirp mean high frequency [mean = 0.78; 95% CI = 0.65, 0.88], chirp time vocalizing [mean = 0.77; 95% CI = 0.63, 0.86], and chirp duration [mean = 0.67; 95% CI = 0.51, 0.80]) were higher than the posterior density estimates of ICCs for intraindividual-level variance. The posterior density estimates of ICCs for intraindividual-level variance are equivalent to one minus the posterior density estimates of ICCs for interindividual-level variance. Our goodness of fit test showed that the agreement between the observed and theoretical quantiles was good for all observations (Figure S1).

3.3 | Sources of variance in titi monkey infant trills

For infants, the variance between individuals explained more of the total variance for three of the four features included in the model (bandwidth,

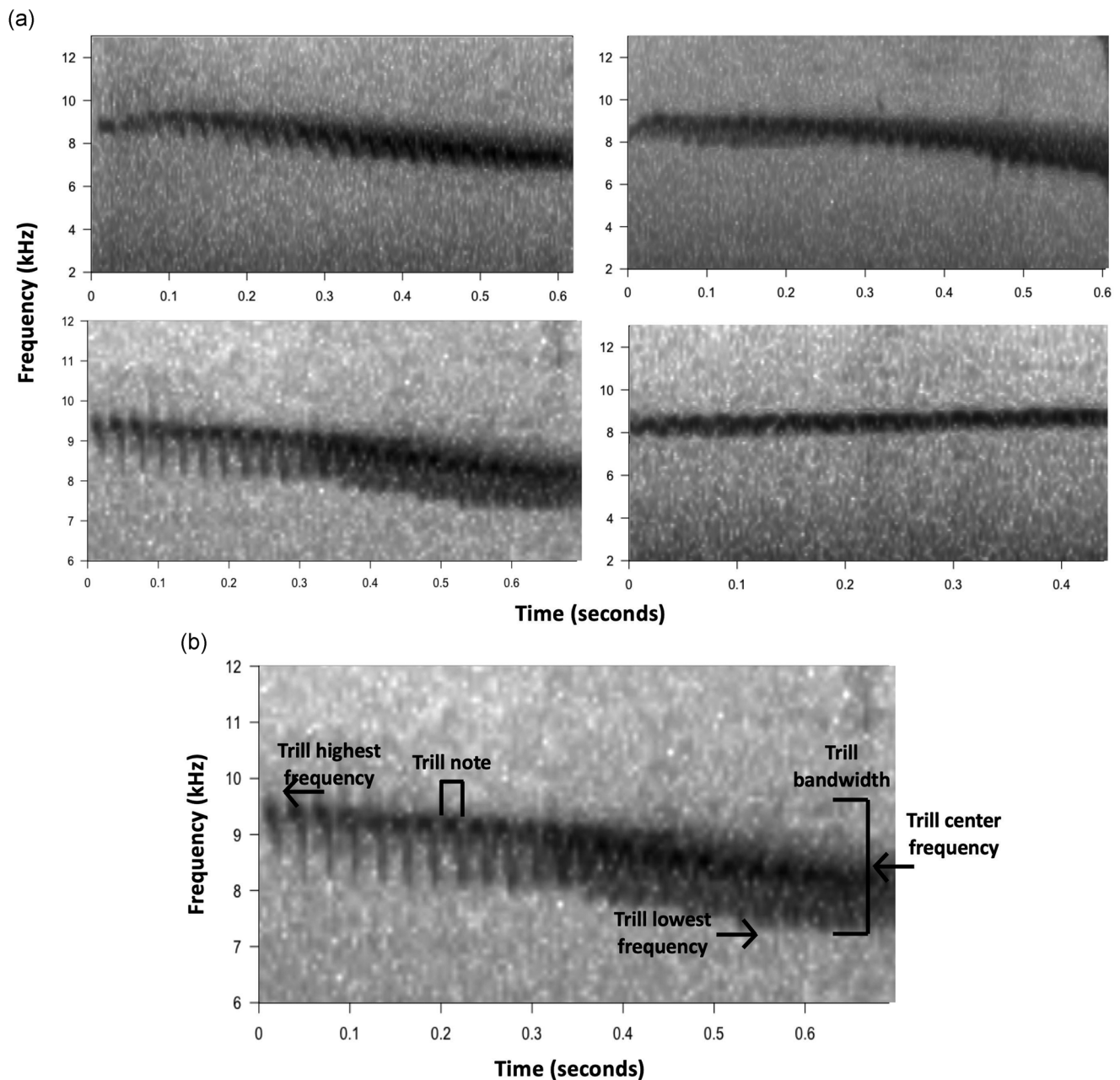


FIGURE 3 (a) Representative spectrograms of infant titi monkey (*Plecturocebus cupreus*) trills. (b) Representative spectrogram of infant titi monkey (*P. cupreus*) trills. Features estimated from the spectrogram are highlighted

highest frequency, and trill rate) than the variance in the vocalizations of any one individual (Figure 7). The posterior density estimates of ICCs for interindividual-level variance for bandwidth (ICC posterior density mean = 0.60; 95% CI = 0.46, 0.75), highest frequency (mean = 0.80; 95% CI = 0.69, 0.88), and trill rate (mean = 0.71; 95% CI = 0.58, 0.83) were higher than the posterior density estimates of ICCs for intraindividual-level variance. Trill duration was the only parameter included in the model for which variance within individuals explains more of the total variance than variance between individuals. The posterior density estimate of the ICC for interindividual-level for duration (mean = 0.57; 95% CI = 0.41, 0.71) was higher than the posterior density estimate for

interindividual-level variance. Similarly, for infants, our goodness of fit test showed that the agreement between the observed and theoretical quantiles is good for all observations (Figure S2).

4 | DISCUSSION

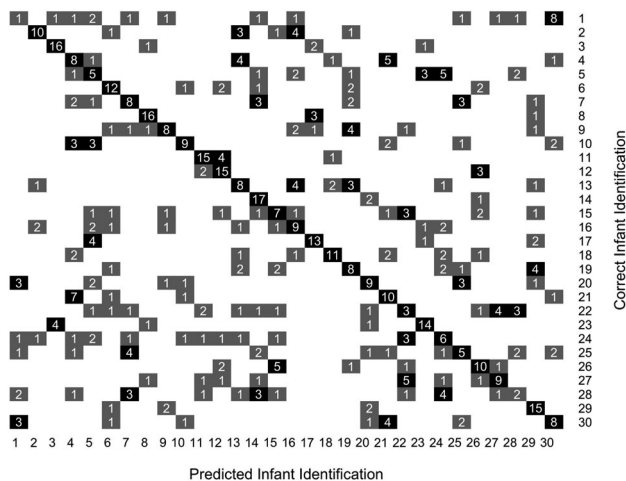
4.1 | Adult vocal individuality

We provide some of the first evidence of vocal individuality in titi monkeys (*Plecturocebus* spp.). Based on the pulse-chirp morning

TABLE 3 Means and standard deviations for all 16 spectral and temporal features estimated from spectrograms of 169 coppery titi monkey (*Plecturocebus cupreus*) pulse-chirp vocalizations from 30 individuals

Element	Parameter	Mean \pm SD	Range
Pulse element	Number of pulses	8.9 \pm 2.9	4–19
	Mean interquartile bandwidth (Hz)	1,014.8 \pm 499.4	107.7–2,340.0
	Mean center frequency (Hz)	4,598.6 \pm 679.6	2,091.8–6,770.1
	Duration of pulse element (s)	2.3 \pm 0.8	1.0–4.8
	Pulse rate (number of notes/pulse duration)	0.26 \pm 0.03	0.19–0.42
Chirp notes	Mean note bandwidth (Hz)	423.3 \pm 137.1	201.0–861.3
	Mean note highest frequency (Hz)	5,036.0 \pm 514.5	3,722.9–6,664.0
	Mean note lowest frequency (Hz)	4,135.3 \pm 491.8	3,072.4–5,741.4
	Duration of chirps (s)	3.2 \pm 1.4	0.6–10.3
	Duration of time vocalizing (s)	0.8 \pm 0.5	0.1–3.1
	Number of chirps	7.1 \pm 2.7	2–18
	Minimum bandwidth (Hz)	257.9 \pm 112.2	86.1–775.2
	Maximum bandwidth (Hz)	641.2 \pm 197.8	258.4–1,378.1
	Highest frequency of all chirps (Hz)	5,456.9 \pm 553.2	3,839.6–6,756.4
	Highest frequency first note (Hz)	4,490.1 \pm 601.8	3,103.6–6,617.8
	Highest frequency last note (kHz)	5,302.3 \pm 646.7	3,545.3–6,756.4

Abbreviation: SD, standard deviation.

**FIGURE 5** Confusion matrix for the discriminant function classification of 600 trill vocalizations from 30 infant coppery titi monkeys (*Plecturocebus cupreus*). The total number of correct classifications are along the diagonal

4.4 | Future directions

While the present study adds titi monkeys to the rich literature of individually distinct, vocal primate species, there is much more to be studied in these highly vocal animals. Future studies should first assess whether or not these individualized pulse-chirp morning duet vocalizations are stable over time and across changes in group composition. Previously, Clink, Lau et al. (2019) found that titi monkey pair mates converge in the pulse rate of their duets,

TABLE 4 Means and standard deviations for the seven spectral and temporal features estimated from spectrograms of 600 infant coppery titi monkey (*Plecturocebus cupreus*) trill vocalizations from 30 individuals

Parameter	Mean \pm SD	Range
Lowest frequency (Hz)	7,271.1 \pm 667.9	5,250.0–8,906.2
Highest frequency (Hz)	8,097.0 \pm 654.6	600.0–10,125.0
Duration (s)	0.5 \pm 0.1	0.2–0.9
Bandwidth (Hz)	825.9 \pm 408.9	187.5–2,906.2
Center frequency (Hz)	7,719.7 \pm 640.5	5,812.5–9,375.0
Trill count	20.3 \pm 5.5	6–36
Trill rate (number of notes/trill duration)	0.026 \pm 0.003	0.018–0.040

Abbreviation: SD, standard deviation.

providing evidence for vocal plasticity, and future longitudinal studies will be informative for understanding the development, ontogeny, and plasticity of vocalizations in this species. These future studies will provide valuable insight into the temporal stability of these vocalizations and may elucidate whether individually distinct call features are stable over a longer or shorter time period. Other species of titi monkeys should be studied in the wild to assess whether this pattern of individuality exists in species with different vocal repertoires and social behavior (Adret et al., 2018). Further, playback studies should be conducted to assess whether the individuality detected by these analyses are perceptible by titi monkeys.

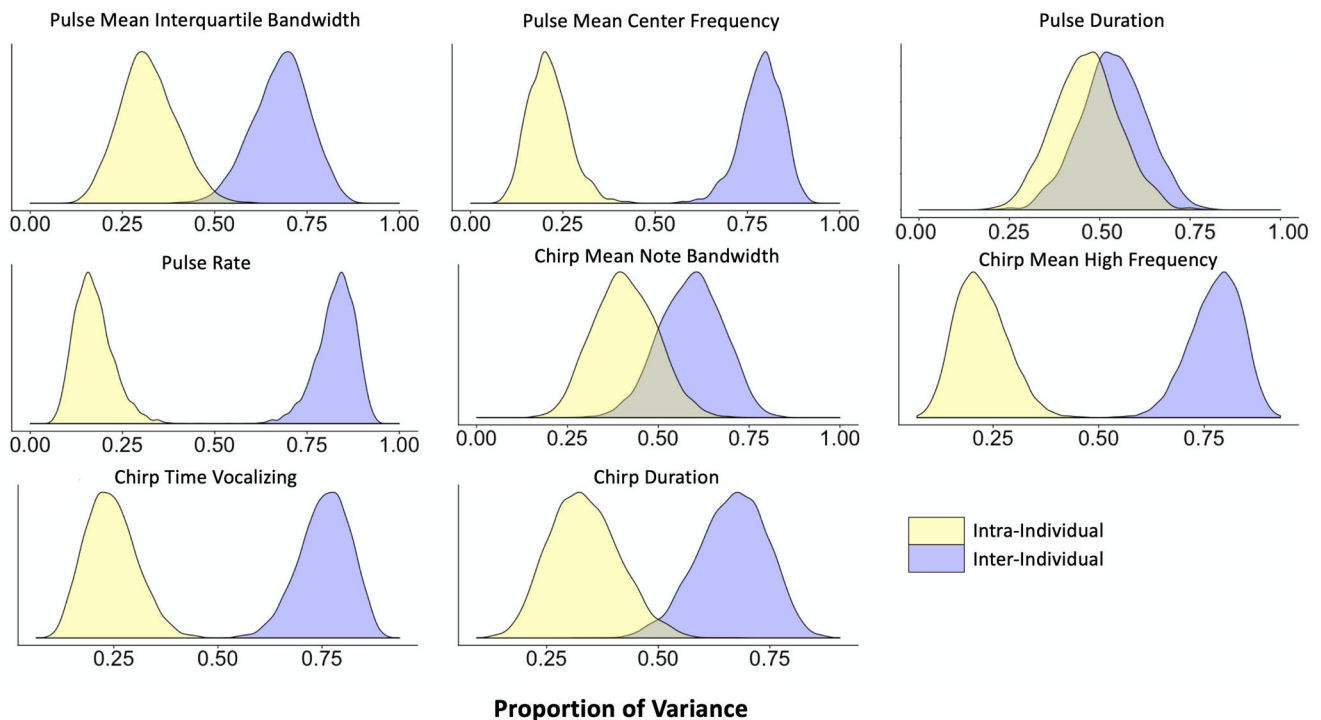


FIGURE 6 Posterior densities of intraclass correlation coefficients for eight spectral and temporal features of 169 pulse-chirp duet vocalizations from 30 adult coppery titi monkeys (*Plecturocebus cupreus*). In each plot, density is represented on the y axis and is not labeled. Densities are comparable only within each parameter's plot, and the relative densities between each level (intraindividual and interindividual) are important

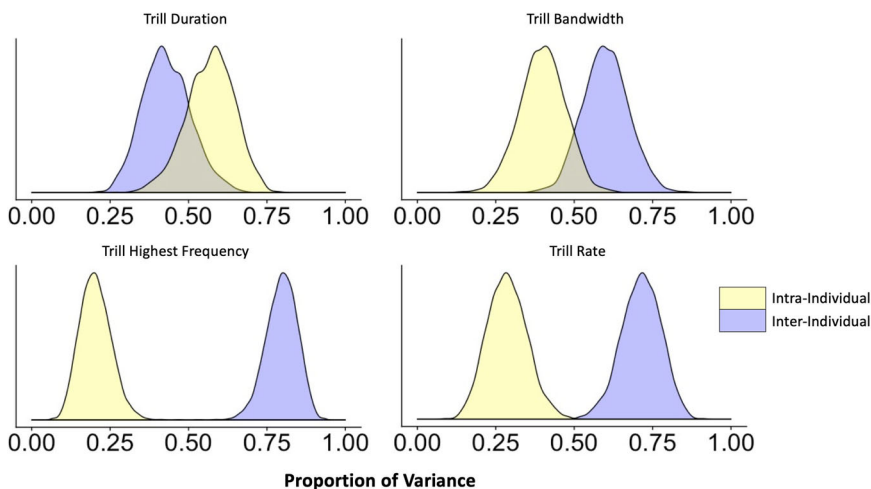


FIGURE 7 Posterior densities of intraclass correlation coefficients for four spectral and temporal features of 600 trills from 30 infant coppery titi monkeys (*Plecturocebus cupreus*). In each plot, density is represented on the y axis and is not labeled. Densities are comparable only within each parameter's plot, and the relative densities between each level (intraindividual and interindividual) are important

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The data set analyzed in the present study is available as electronic Supporting Information Material (Online Resource 1, Online Resource 2), as well as the accompanying R script (Online Resource 3).

Sound files are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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