Published in final edited form as:
Am J Primatol. 2020 June ; 82(6): e23134. doi:10.1002/ajp.23134.

INDIVIDUALITY IN THE VOCALIZATIONS OF INFANT AND ADULT COPPERY TITI MONKEYS (*Plecturocebus cupreus*)

Allison R. Lau[1,2], **Dena J. Clink**[3], **Karen L. Bales**[1,2,4]

[1]Animal Behavior Graduate Group, University of California, Davis, One Shields Avenue, Davis, CA, 95616

[2]California National Primate Research Center, University of California, Davis, Davis, CA, 95616, USA

[3]Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University, Ithaca, NY, 14850

[4]Department of Psychology, University of California, Davis, One Shields Avenue, Davis, CA, 95616, USA

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 non-adaptive 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 calls 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 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 multi-variate 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

---

Corresponding author: Allison Lau, alljones@ucdavis.edu, One Shields Avenue, 135 Young Hall, Davis, CA 95616.

Conflict of Interest Statement
The authors declare there are no conflicts of interest.

individually distinct, and infant trills are less individually distinct, which may be due to the different functions of the vocalizations.

Keywords

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

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 et al., 2013). Acoustic signals can provide pertinent social information about caller quality, status, or identity (Bradbury & Vehrencamp, 1998, p. 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 correct identification of caller identity may have impacts on perceiver fitness depending on the context (Tibbetts and Dale, 2007). For example, predation (Blumstein et al., 2004), mate choice (Zelano and Edwards, 2002) and kin selection (Zelano and 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 (Geissman, 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 (Van Opzeeland and Van Parijs, 2004; Philips and Stirling, 2000; Collins et al., 2006) and allows parents to recognize their offspring. By two 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 et al., 2009). However, in some species, all age classes have individually distinct vocal elements (South American sea lions [Ndez-Juricic et al., 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 et al., 2014]). Alarm calls in squirrels are individually identifiable, and this individuality is stable over time (Matrosova et al., 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 it is adaptative.

Many primate species rely on vocal communication to maintain social relationships (McComb and Semple, 2005). In nonhuman primates, vocal communication can provide honest signals about caller status or condition that are constrained by physiology (Fitch and

Hauser, 1995). Vocal communication is highly linked to primates' unique neurobiology (Egnor and Hauser, 2004), can be a learned behavior (Snowdon et al., 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 et al., 1996), orangutans (Delgado 2007), gray mouse lemurs (Zimmerman et al. 2000), and rufous mouse lemurs (Zimmerman et al. 2000). Further, most studies which 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 et al., 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 et al., 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 [Feng et al., 2014; Barelli et al., 2013; Terleph et al., 2015; Clink et al., 2017; Lau et al., 2018], tarsiers [Clink et al., 2019a], 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 (Robinson, 1979; Adret et al., 2018; Müller & Anzenberger, 2002). There is little sex-specificity in the organization of these duet vocalizations, as both sexes have an identical, overlapping vocal repertoire (Robinson, 1979; Müller and Anzenberger, 2002). 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 (Feng et al., 2014; Barelli et al., 2013; Terleph et al., 2015; Clink et al., 2017; Lau et al., 2018; Clink et al., 2019; Gamba et al., 2016) focused on the vocalizations of adult individuals. In humans, infant cries are individually distinct to listening adults (Gustafson et al., 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 et al., 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 et al., 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 et al., 2019b). In this population, infant titi monkeys emit trill vocalizations when distressed (Hoffman et al., 1995) or when separated from the family group (Larke et al., 2017). Thus, these infant trills function as intra-group communication, in contrast to adult titi monkeys' inter-group duet calls. Presumably, intra-group 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 an individual's location, can inform family members of caller identity. In contrast, inter-group communication likely occurs when animals are not in visual contact, leaving acoustic cues as the only means with which to communicate identity. This dataset 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.

Methods

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 IACUC of the University of California, Davis, and complied with the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Study Location and Subjects

All recordings of coppery titi monkey (*Plecturocebus 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 m x 1.2 m x 2.1 m. The room was maintained at 21° Celsius on a 12-hour 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 and Mason, 1986a; Tardif et al., 2013).

Data Collection

Adult titi monkey (N=30; 15 females, 15 males) duets were recorded opportunistically each morning between 06:00 and 07:30 for two 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 less than 3 meters 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 four months old. Recordings from our subjects span four 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 & 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 meter from the infant.

Acoustic Analysis

All adult audio recordings were compared to videos of the corresponding duet bout in order 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 et al., 2019b) to better reflect the spectral characteristics of the notes and to keep consistent with terms used in the frog (Martínez-Rivera & Gerhardt, 2008), bird (Laiolo et al., 2004), and marine mammal (Mathevon et al., 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 ± 3.50 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 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 2014, Ithaca, NY). We generated spectrograms with a 512-point (11.6 ms) Hann window (3 dB bandwidth = 124 Hz), with 75% overlap, and a 1024-point DFT, 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 (ARL) 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 greater than 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 inter-quartile range bandwidth, 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; 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 meters and 8 meters 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; Figure 3B).

Linear Discriminant Function Analysis

To assess adult individuality, we compared all titi monkey pulse-chirp duet vocalizations using discriminant function analysis (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 and Ripley, 2013, p. 331–337). Although we had multiple duet recordings from different pairs, we only used the pulse-chirp vocalizations from one duet recording per pair in order 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 7 features estimated from each vocalization. All 20 trills for each individual were taken from one recording sessions in order 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).

Multivariate Variance Components Model

We used a multivariate variance components model (Lau et al., 2018; Clink 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 intra-individual variance). For both adults and infants, we utilized the same model. We 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 (Lau et al., 2018; Clink 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 Σa and Σe. See Lau et al. (2018) and Clink et al. (2018) for more details on model development and specifications.

We generated 1500 warm-up samples, followed by 1500 parameter samples from each of two Markov chains, for a total of 3000 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 inter-individual variance and intra-individual variance, to the overall variance (Merlo et al., 2005). We calculated ICC at the level l for each acoustic feature from posterior samples of Σ_a and Σ_e as

$$\mathrm{ICC}_l = \frac{\text{Variance of feature at level } l}{\text{Total variance of feature}}$$

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., 2005).

Not all call features were used in the model as some features were highly correlated and were excluded based on visual inspection of scatterplot matrices of all features. For the adult pulse-chirp vocalization analysis, we excluded number of pulses (which was 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 to a suitable F distribution. R programming language and environment was used for all analyses in this study (R Development Core Team, 2017).

Data Availability

The dataset analyzed in the present study is available as electronic supplementary 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.

Results

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 inter-individual 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).

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 inter-quartile 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 inter-individual-level variance for all features (pulse mean interquartile bandwidth [ICC posterior density mean = 0.68, 95% credibility interval = 0.52, 0.81], pulse mean center frequency [mean = 0.79, CI = 0.66, 0.89], pulse duration [mean = 0.54, CI = 0.36, 0.71], pulse rate [mean = 0.83, CI = 0.72, 0.91], chirp mean bandwidth [mean = 0.59, CI = 0.42, 0.74], chirp mean high frequency [mean = 0.78, CI = 0.65, 0.88], chirp time vocalizing [mean = 0.77, CI = 0.63, 0.86], and chirp duration [mean = 0.67, CI = 0.51, 0.80] were higher than the posterior density estimates of ICCs for intra-individual-level variance. The posterior density estimates of ICCs for intra-individual-level variance are equivalent to one minus the posterior density estimates of ICCs for inter-individual-level variance. Our goodness of fit test showed that the agreement between the observed and theoretical quantiles was good for all observations (Supplementary figure 1).

Sources of variance in titi monkey infant trills

For infants, variance between individuals explained more of the total variance for three of the four features included in the model (bandwidth, highest frequency, and trill rate) than variance in the vocalizations of any one individual (Figure 7). The posterior density estimates of ICCs for inter-individual-level variance for bandwidth (ICC posterior density mean = 0.60, 95% credibility interval = 0.46, 0.75), highest frequency (mean = 0.80, CI = 0.69, 0.88), and trill rate (mean = 0.71, CI = 0.58, 0.83) were higher than the posterior density estimates of ICCs for intra-individual-level variance. Trill duration was the only parameter included in the model for which variance within individuals explains more of the total variance that variance between individuals. The posterior density estimate of the ICC for inter-individual-level for duration (mean = 0.57, CI = 0.41, 0.71) was higher than the posterior density estimate for inter-individual-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 (Supplementary figure 2).

Discussion

Adult Vocal Individuality

We provide some of the first evidence of vocal individuality in titi monkeys (*Plecturocebus* spp.). Based on the pulse-chirp morning duet vocalizations of male and female coppery titi monkeys (*Plecturocebus cupreus*), individuals can be classified with 83% accuracy using LOOCV, which is comparable to individuality studies of similarly vocalizing primates using similar methods (gibbons: 100% accuracy [Feng et al., 2014], 74.6% accuracy [Barelli et al., 2013], 83% accuracy [Terleph et al., 2015], 96% accuracy [Clink et al., 2017], 66% accuracy [Lau et al., 2018]; and tarsiers: females 80% accuracy and males 64% accuracy [Clink et al., 2019a]). Our ability to distinguish between individuals based on the 16 features of interest indicates that titi monkey duet contributions are individually distinct. However, it does not yet provide evidence that the animals calling and listening to these vocalizations can individually distinguish each other.

Infant Vocal Individuality

Based on the trill vocalizations of four-month-old coppery titi monkey infants, infant titi monkeys are individually identifiable by spectral and temporal features with 48% accuracy. This 48% accuracy is noticeably lower than the 83% accuracy for our analogous analyses of adults from the same population as the infants. However, our multivariate-variance components model reveals that inter-individual differences are the most important source of variance for four of the five features included in the model. This indicates that inter-individual differences are still important for this age class but may be a result of individual-level differences in morphology. The fact that infants are less accurately identifiable than adults may be due to the different functions of the two call types. Infant trill vocalizations are used largely in distressing contexts, where the infant is trying to reunite with its parents or gain access to food. The function and utility of the infant trill vocalization is thus usually limited to intra-group communication; and there is usually only one infant in each group. Thus, vocal individuality may not be as important for young titi monkeys’ success as compared to adults. However, it is notable that as more features are added to DFA, the accuracy of LOOCV increases (Venables and Ripley, 2013, p. 331–337). Our adults were analyzed using 16 features, as opposed to 7 features for our infants due to the differences in call structure between the two age classes. This may lead inherently to a lower LOOCV accuracy for our infant analysis, but we were unable to add additional features because infant trills are inherently shorter and less complex than adult duet vocalizations. Our multivariate, variance components model revealed that of the features included in the model, only trill duration varies more within individual infants than between individual infants. This finding is likely due to maturational variables such as lung capacity or breath control (Bruce, 1981).

Implications of Individuality

While it is possible this pattern of vocal individuality is adult duet vocalizations is a non-adaptive by-product of individual differences in development or experience, it may also be an adaptive trait based on titi monkeys' social system. As pair-bonding, territorial primates, individual recognition of familiar conspecifics can be potentially beneficial, as it can reduce the need to engage in territorial behaviors. This pattern of individuality is especially relevant in this species because there is a lack of sex-specificity in both the infant and adult vocal repertoire (Robinson, 1979). Vocal individuality may provide a mechanism by which to discriminate individuals, regardless of sex. In dense tropical forest, titi monkeys often cannot see or smell each other from long distances and must rely on acoustic signaling for conspecific recognition (Robinson, 1981). These individually distinct pulse-chirp vocalizations may allow individuals to respond territorially to unfamiliar intruders and perhaps avoid confrontation with familiar, nearby neighbors.

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 et al. (2019b) found that titi monkey pair mates converge in the pulse rate of their duets, 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.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

This work was supported by the National Institute of Health (grant numbers OD011107, HD092055) and the Good Nature Institute. Equipment for this study was funded by the University of California, Davis Provost Undergraduate Fellowship, awarded to ARL in 2016. We would like to thank Alexander Baxter, Ben Laudermilch, Natalie Lange, Monica Nava, Sascha Recht, YuRim Lee, Dylan Metz, Jaclyn Samra, Joseph Reyelts, and Parker Jarman for their help recording and processing the sound files used in this study. We gratefully acknowledge Jaleh Janatpour, Kevin Theis, and their staff for their excellent care of the titi monkeys in this project.

References

Adret P, Dingess K, Caselli C, Vermeer J, Martínez J, Luna Amancio J, ... & Di Fiore A (2018). Duetting patterns of titi monkeys (Primates, *Pitheciidae: Callicebinae*) and relationships with phylogeny. Animals, 8(10), 178 10.3390/ani8100178

Bales KL, del Razo RA, Conklin QA, Hartman S, Mayer HS, Rogers FD, … & Witczak LR (2017). Focus: comparative medicine: titi monkeys as a novel non-human primate model for the neurobiology of pair bonding. The Yale Journal of Biology and Medicine, 90(3), 373 Retrieved from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5612182/ [PubMed: 28955178]

Barelli C, Mundry R, Heistermann M, & Hammerschmidt K (2013). Cues to androgens and quality in male gibbon songs. PloS One, 8(12), e82748 10.1371/journal.pone.0082748 [PubMed: 24367551]

Bates BC (1970). Territorial behavior in primates: A review of recent field studies. Primates, 11(3), 271–284. 10.1007/bf01793893

Berkson G (1966). Development of an infant in a captive gibbon group. The Journal of Genetic Psychology, 108(2), 311–325. 10.1080/00221325.1966.10532789 [PubMed: 4960212]

Bradbury JW, & Vehrencamp SL (1998). Principles of Animal Communication. Sunderland, Massachusetts: Sinauer Associates, Inc.

Bruce EN (1981). Control of breathing in the newborn. Annals of Biomedical Engineering, 9(5–6), 425–437. 10.1007/bf02364761 [PubMed: 6814308]

Blumstein DT, Verneyre L, & Daniel JC (2004). Reliability and the adaptive utility of discrimination among alarm callers. Proceedings of the Royal Society of London. Series B: Biological Sciences, 271(1550), 1851–1857. 10.1098/rspb.2004.2808 [PubMed: 15315902]

Byrne H, Rylands AB, Carneiro JC, Alfaro JWL, Bertuol F, da Silva, … & Hrbek T (2016). Phylogenetic relationships of the New World titi monkeys (*Callicebus*): first appraisal of taxonomy based on molecular evidence. Frontiers in Zoology, 13(1), 10 10.1186/s12983-016-0142-4 [PubMed: 26937245]

Chau MJ, Stone AI, Mendoza SP, & Bales KL (2008). Is play behavior sexually dimorphic in monogamous species? Ethology, 114(10), 989–998. 10.1111/j.1439-0310.2008.01543.x

Cheney DL, & Seyfarth RM (1982). How vervet monkeys perceive their grunts: field playback experiments. Animal Behaviour, 30(3), 739–751. 10.1016/s0003-3472(82)80146-2

Clink DJ, Tasirin JS, & Klinck H (2019a). Vocal individuality and rhythm in male and female duet contributions of Gursky’s spectral tarsier. Current Zoology. 10.1093/cz/zoz035

Clink DJ, Lau AR, & Bales KL (2019b). Age-related changes and vocal convergence in titi monkey duet pulses. Behaviour, 56(15), 1471–1494. 10.1163/1568539x-00003575

Clink DJ, Grote MN, Crofoot MC, & Marshall AJ (2018). Understanding sources of variance and correlation among features of Bornean gibbon (*Hylobates muelleri*) female calls. The Journal of the Acoustical Society of America, 144(2), 698–708. 10.1121/1.5049578 [PubMed: 30180677]

Clink DJ, Bernard H, Crofoot MC, & Marshall AJ (2017). Investigating individual vocal signatures and small-scale patterns of geographic variation in female Bornean gibbon (Hylobates muelleri) great calls. International Journal of Primatology 38:656–671. 10.1007/s10764-017-9972-y

Collins KT, Terhune JM, Rogers TL, Wheatley KE, & Harcourt RG (2006). Vocal individuality of in-air Weddell seal (*Leptonychotes weddellii*) pup “primary” calls. Marine mammal science, 22(4), 933–951. 10.1111/j.1748-7692.2006.00074.x

Delgado RA (2007). Geographic variation in the long calls of male orangutans (*Pongo spp.*). Ethology, 113: 487–498. 10.1111/j.1439-0310.2007.01345.x

Egnor SR, & Hauser MD (2004). A paradox in the evolution of primate vocal learning. Trends in Neurosciences, 27(11), 649–654. 10.1016/j.tins.2004.08.009 [PubMed: 15474164]

Fan PF, Xiao W, Feng JJ, & Scott MB (2011). Population differences and acoustic stability in male songs of wild western black crested gibbons (*Nomascus concolor*) in Mt. Wuliang, Yunnan. Folia Primatologica, 82:83–93. 10.1159/000329128

Feng JJ, Cui LW, Ma CY, Fei HL, & Fan PF (2014). Individuality and stability in male songs of cao vit gibbons (*Nomascus nasutus*) with potential to monitor population dynamics. PloS One, 9(5), e96317 10.1371/journal.pone.0096317 [PubMed: 24788306]

Fernandez-Duque E, Valeggia CR, & Mason WA (2000). Effects of pair-bond and social context on male–female interactions in captive titi monkeys (*Callicebus moloch*, Primates: *Cebidae*). Ethology, 106(12), 1067–1082. 10.1046/j.1439-0310.2000.00629.x

Fitch WT, & Hauser MD (1995). Vocal production in nonhuman primates: acoustics, physiology, and functional constraints on "honest" advertisement. American Journal of Primatology, 37(3), 191–219. 10.1002/ajp.1350370303 [PubMed: 31936952]

Fox GJ (1972). Some comparisons between siamang and gibbon behaviour. Folia primatologica, 18(1–2), 122–139. 10.1159/000155473

Gamba M, Torti V, Bonadonna G, Randrianarison RM, Friard O, & Giacoma C (2016). Melody in my head, melody in my genes? Acoustic similarity, individuality, and genetic relatedness in the indris of Eastern Madagascar. The Journal of the Acoustical Society of America, 140(4), 3017–3018. 10.1121/1.4969359

Geissmann T (1984). Inheritance of song parameters in the gibbon song, analysed in 2 hybrid gibbons (*Hylobates pileatus × H. lar*). Folia primatologica, 42(3–4), 216–235. 10.1159/000156165

Ghazanfar AA (2013). Multisensory vocal communication in primates and the evolution of rhythmic speech. Behavioral Ecology and Sociobiology, 67(9), 1441–1448. 10.1007/s00265-013-1491-z

Guo J, Lee D, Sakrejda K, Gabry J, Goodrich B, De Guzman J, ... & Fletcher J (2016). rstan: R Interface to Stan. R, 534, 0–3.

Gustafson GE, Green JA, & Cleland JW (1994). Robustness of individual identity in the cries of human infants. Developmental Psychobiology, 27(1), 1–9. 10.1002/dev.420270102 [PubMed: 8112484]

Herbinger I, Papworth S, Boesch C, & Zuberbühler K (2009). Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: a playback study. Animal Behaviour, 78(6), 1389–1396. 10.1016/j.anbehav.2009.09.010

Hoffman KA, Mendoza SP, Hennessy MB, & Mason WA (1995). Responses of infant titi monkeys, *Callicebus moloch*, to removal of one or both parents: evidence for paternal attachment. Developmental Psychobiology, 28(7), 399–407. 10.1002/dev.420280705 [PubMed: 8557176]

Laiolo P, Tella JL, Carrete M, Serrano D, & López G (2004). Distress calls may honestly signal bird quality to predators. Proceedings of the Royal Society of London. Series B: Biological Sciences, 271(suppl_6), S513–S515. 10.1098/rsbl.2004.0239 [PubMed: 15801619]

Larke RH, Toubiana A, Lindsay KA, Mendoza SP, & Bales KL (2017). Infant titi monkey behavior in the open field test and the effect of early adversity. American Journal of Primatology, 79(9), e22678 10.1002/ajp.22678

Lapshina EN, Volodin IA, Volodina EV, Frey R, Efremova KO, & Soldatova NV (2012). The ontogeny of acoustic individuality in the nasal calls of captive goitred gazelles, *Gazella subgutturosa*. Behavioural Processes, 90(3), 323–330. 10.1016/j.beproc.2012.03.011 [PubMed: 22465090]

Lau AR, Clink DJ, Crofoot MC, & Marshall AJ (2018). Evidence for High Variability in Temporal Features of the Male Coda in Müller's Bornean Gibbons (*Hylobates muelleri*). International Journal of Primatology, 39(4), 670–684. 10.1007/s10764-018-0061-7

Lorenz R, & Mason WA (1971). Establishment of a colony of titi monkeys. International Zoo Yearbook, 11(1), 168–174. 10.1111/j.1748-1090.1971.tb01896.x

Macedonia JM (1986). Individuality in a contact call of the ringtailed lemur (*Lemur catta*). American Journal of Primatology, 11(2), 163–179. 10.1002/ajp.1350110208 [PubMed: 31979454]

MacKinnon J, & MacKinnon K (1980). The behavior of wild spectral tarsiers. International Journal of Primatology, 1(4), 361–379. 10.1007/bf02692280

Maples EG Jr, & Haraway MM (1982). Taped vocalization as a reinforcer of vocal behavior in a female agile gibbon (*Hylobates agilis*). Psychological Reports, 51(1), 95–98. 10.2466/pr0.1982.51.1.95

Marshall JT, & Marshall ER (1976). Gibbons and their territorial songs. Science, 193(4249), 235–237. 10.1126/science.193.4249.235 [PubMed: 17796155]

Marshall-Ball L, Mann N, & Slater PJB (2006). Multiple functions to duet singing: hidden conflicts and apparent cooperation. Animal Behaviour, 71(4), 823–831. 10.1016/j.anbehav.2005.05.021

Mathevon N, Casey C, Reichmuth C, & Charrier I (2017). Northern elephant seals memorize the rhythm and timbre of their rivals' voices. Current Biology, 27(15), 2352–2356. 10.1016/j.cub.2017.06.035 [PubMed: 28736171]

Matrosova VA, Volodin IA, & Volodina EV (2009). Short-term and long-term individuality in speckled ground squirrel alarm calls. Journal of Mammalogy, 90(1), 158–166. 10.1644/08-mamm-a-032.1

Martínez-Rivera CC, & Gerhardt HC (2008). Advertisement-call modification, male competition, and female preference in the bird-voiced treefrog *Hyla avivoca*. Behavioral Ecology and Sociobiology, 63(2), 195–208. 10.1007/s00265-008-0650-0 [PubMed: 19789730]

Mason WA (1966). Social Organization of the South American Monkey, *Callicebus moloch*: A Preliminary Report In Tulane Studies in Zoology, *Volume* 13 (pp. 23–28). New Orleans, LA: Tulane University.

Mason WA (1974). Comparative studies of social behavior in *Callicebus* and *Saimiri*: Behavior of male-female pairs. Folia Primatologica, 22(1), 1–8. 10.1159/000155614

Mason WA, & Mendoza SP (1998). Generic aspects of primate attachments: Parents, offspring and mates. Psychoneuroendocrinology, 23(8), 765–778. 10.1016/s0306-4530(98)00054-7 [PubMed: 9924737]

McComb K, & Semple S (2005). Coevolution of vocal communication and sociality in primates. Biology Letters, 1(4), 381–385. 10.1098/rsbl.2005.0366 [PubMed: 17148212]

Mendoza SP, & Mason WA (1986a). Contrasting responses to intruders and to involuntary separation by monogamous and polygynous New World monkeys. Physiology & Behavior, 38(6), 795–801. 10.1016/0031-9384(86)90045-4 [PubMed: 3823197]

Mendoza SP, & Mason WA (1986b). Parental division of labour and differentiation of attachments in a monogamous primate (*Callicebus moloch*). Animal Behaviour, 34(5), 1336–1347. 10.1016/s0003-3472(86)80205-6

Merlo J, Chaix B, Ohlsson H, Beckman A, Johnell K, Hjerpe P, ... & Larsen K (2006). A brief conceptual tutorial of multilevel analysis in social epidemiology: using measures of clustering in multilevel logistic regression to investigate contextual phenomena. Journal of Epidemiology & Community Health, 60(4), 290–297. 10.1136/jech.2004.029454 [PubMed: 16537344]

Mitani JC (1985). Gibbon song duets and intergroup spacing. Behaviour, 59–96. 10.1163/156853985x00389

Mitani JC, Gros-Louis J, & Macedonia JM (1996). Selection for acoustic individuality within the vocal repertoire of wild chimpanzees. International Journal of Primatology, 17(4), 569–583. 10.1007/bf02735192

Müller AE, & Anzenberger G (2002). Duetting in the titi monkey *Callicebus cupreus*: structure, pair specificity and development of duets. Folia Primatologica, 73(2–3), 104–115. 10.1159/000064788

Mumm CA, Urrutia MC, & Knörnschild M (2014). Vocal individuality in cohesion calls of giant otters, *Pteronura brasiliensis*. Animal Behaviour, 88, 243–252. 10.1016/j.anbehav.2013.12.005

Ndez-Juricic EF, Enriquez V, Campagna C, & Ortiz CL (1999). Vocal communication and individual variation in breeding South American sea lions. Behaviour, 136(4), 495–517. 10.1163/156853999501441

Phillips AV, & Stirling I (2000). Vocal individuality in mother and pup South American fur seals, *Arctocephalus australis*. Marine Mammal Science, 16(3), 592–616. 10.1111/j.1748-7692.2000.tb00954.x

Pistorio AL, Vintch B, & Wang X (2006). Acoustic analysis of vocal development in a New World primate, the common marmoset (*Callithrix jacchus*). The Journal of the Acoustical Society of America, 120(3), 1655–1670. 10.1121/1.2225899 [PubMed: 17004487]

Pollard KA, & Blumstein DT (2011). Social group size predicts the evolution of individuality. Current Biology, 21(5), 413–417. 10.1016/j.cub.2011.01.051 [PubMed: 21333537]

Pollock JI (1986). The song of the indris (*Indri indri; Primates: Lemuroidea*): natural history, form, and function. International Journal of Primatology, 7(3), 225–264. 10.1007/bf02736391

R Development Core Team. (2017). R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rendall D, Notman H, & Owren MJ (2009). Asymmetries in the individual distinctiveness and maternal recognition of infant contact calls and distress screams in baboons. The Journal of the Acoustical Society of America, 125(3), 1792–1805. 10.1121/1.3068453 [PubMed: 19275336]

Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D, & Ripley MB (2013). Package ‘mass’. Cran R. 538

Robinson JG (1979). An Analysis of the Organization of Vocal Communication in the Titi Monkey *Callicebus moloch*. Z Tierpsychol 49:381–405. 10.1111/j.1439-0310.1979.tb00300.x [PubMed: 115173]

Robinson JG (1981). Vocal regulation of inter- and intragroup spacing during boundary encounters in the titi monkey, *Callicebus moloch*. Primates 22:161–172. 10.1007/bf02382607

Savidge LE, & Bales KL (2020). An Animal Model for Mammalian Attachment: Infant Titi Monkey (*Plecturocebus cupreus*) Attachment Behavior Is Associated With Their Social Behavior as Adults. Frontiers in Psychology, 11, 25 10.3389/fpsyg.2020.00025 [PubMed: 32047459]

Seyfarth RM, & Cheney DL (1997). Some general features of vocal development in nonhuman primates. Social influences on vocal development, 249 10.1017/cbo9780511758843.013

Snowdon C, Elowson AM, & Roush RS (1997). Social influences on vocal development in New World primates. Social influences on vocal development, 234 10.1017/cbo9780511758843.012

Spence-Aizenberg A, Di Fiore A, & Fernandez-Duque E (2016). Social monogamy, male–female relationships, and biparental care in wild titi monkeys (*Callicebus discolor*). Primates, 57(1), 103–112. 10.1007/s10329-015-0489-8 [PubMed: 26386712]

Stan Development Team. (2016). Stan modeling language users guide and reference manual. Technical report.

Symmes D, & Biben M (1985). Maternal recognition of individual infant squirrel monkeys from isolation call playbacks. American Journal of Primatology, 9(1), 39–46. 10.1002/ajp.1350090105 [PubMed: 31986795]

Takahashi DY, Fenley AR, Teramoto Y, Narayanan DZ, Borjon JI, Holmes P, & Ghazanfar AA (2015). The developmental dynamics of marmoset monkey vocal production. Science, 349(6249), 734–738. 10.1126/science.aab1058 [PubMed: 26273055]

Tardif S, Bales K, Williams L, Moeller EL, Abbott D, Schultz-Darken N, ... & Ruiz J (2006). Preparing New World monkeys for laboratory research. ILAR journal, 47(4), 307–315. 10.1093/ilar.47.4.307 [PubMed: 16963811]

Terleph TA, Malaivijitnond S, & Reichard UH (2015). Lar gibbon (*Hylobates lar*) great call reveals individual caller identity. American Journal of Primatology, 77(7), 811–821. 10.1002/ajp.22406 [PubMed: 25800578]

Tibbetts EA, & Dale J (2007). Individual recognition: it is good to be different. Trends in ecology & evolution, 22(10), 529–537. 10.1016/j.tree.2007.09.001 [PubMed: 17904686]

Van Belle S, Fernandez-Duque E, & Di Fiore A (2016). Demography and life history of wild red titi monkeys (*Callicebus discolor*) and equatorial sakis (*Pithecia aequatorialis*) in Amazonian Ecuador: A 12-year study. American Journal of Primatology, 78(2), 204–215. 10.1002/ajp.22493 [PubMed: 26469781]

Van Roosmalen MG, Van Roosmalen T, & Mittermeier RA (2002). A taxonomic review of the titi monkeys, genus *Callicebus* Thomas, 1903, with the description of two new species, *Callicebus bernhardi* and *Callicebus stephennashi*, from Brazilian Amazonia. Neotropical Primates, 10(supplement), 1–52. Retrived from http://www.primate-sg.org/neotropical_primates

Van Opzeeland IC, & Van Parijs SM (2004). Individuality in harp seal, *Phoca groenlandica*, pup vocalizations. Animal Behaviour, 68(5), 1115–1123. 10.1016/j.anbehav.2004.07.005

Venables WN, & Ripley BD (2013). Modern applied statistics with S-PLUS. Springer Science & Business Media p. 331–337

Wilkins MR, Seddon N, & Safran RJ (2013). Evolutionary divergence in acoustic signals: causes and consequences. Trends in Ecology & Evolution, 28(3), 156–166. 10.1016/j.tree.2012.10.002 [PubMed: 23141110]

Zahed SR, Prudom SL, Snowdon CT, & Ziegler TE (2008). Male parenting and response to infant stimuli in the common marmoset (*Callithrix jacchus*). American Journal of Primatology, 70(1), 84–92. 10.1002/ajp.20460 [PubMed: 17607701]

Zelano B, & Edwards SV (2002). An MHC component to kin recognition and mate choice in birds: predictions, progress, and prospects. The American Naturalist, 160(S6), S225–S237. 10.1086/342897

Zimmermann E, Vorobieva E, Wrogemann D, & Hafen T 2000 Use of vocal fingerprinting for specific discrimination of gray (*Microcebus murinus*) and rufous mouse lemurs (*Microcebus rufus*). International Journal of Primatology, 21(5), 837–852. 10.1023/A:1005594625841

Research highlights:

- Coppery titi monkey (*Plecturocebus cupreus*) adults can be classified with 83% accuracy and infants can be classified with 48% accuracy based on features estimated from spectrograms of adult duets and infant trills.
- Differences in individuality may be due to functional differences in these call types.

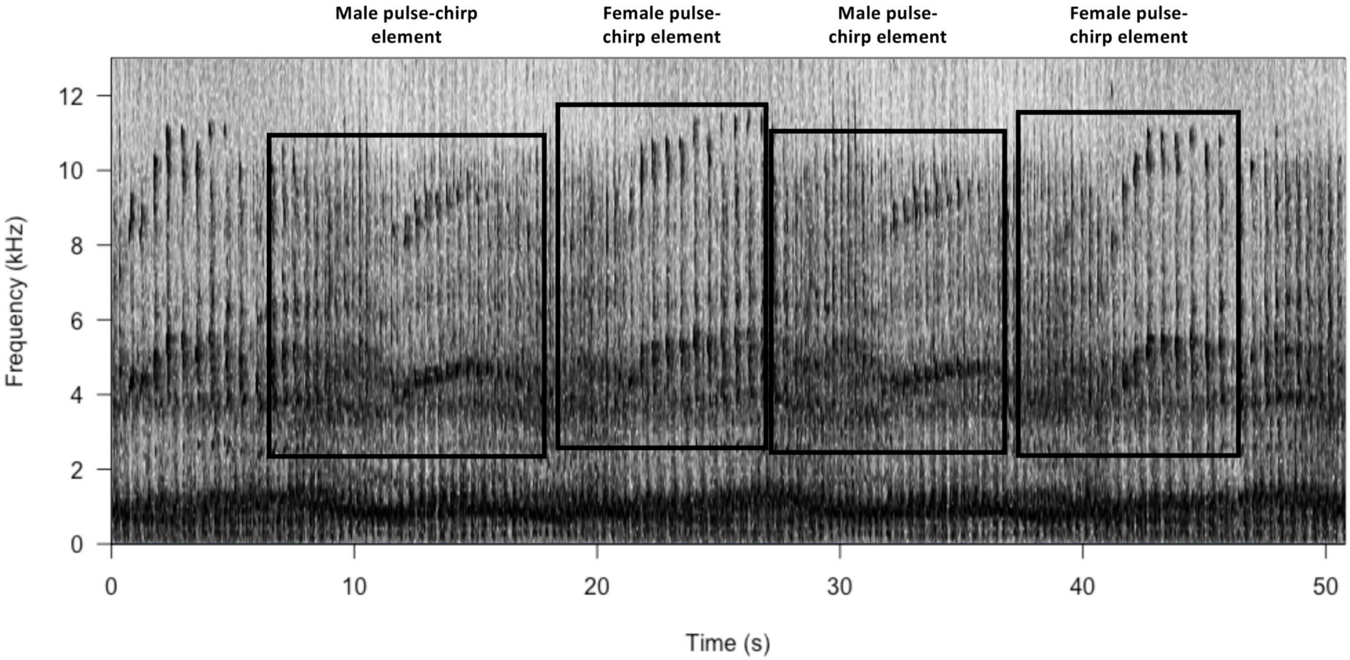
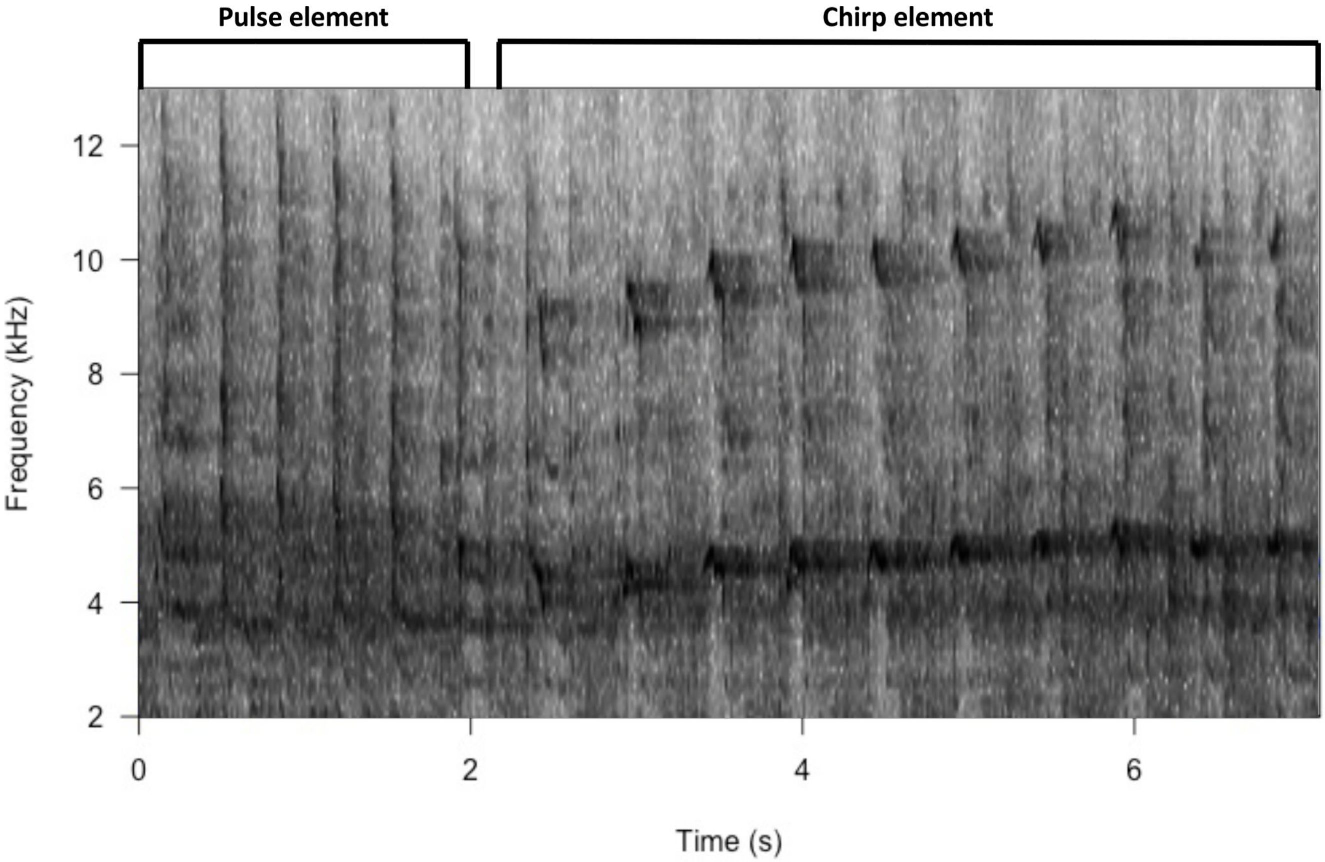


Figure 1.

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


Pulse element
Chirp element
Frequency (kHz)
12
10
8
6
4
2
0
2
4
6
Time (s)

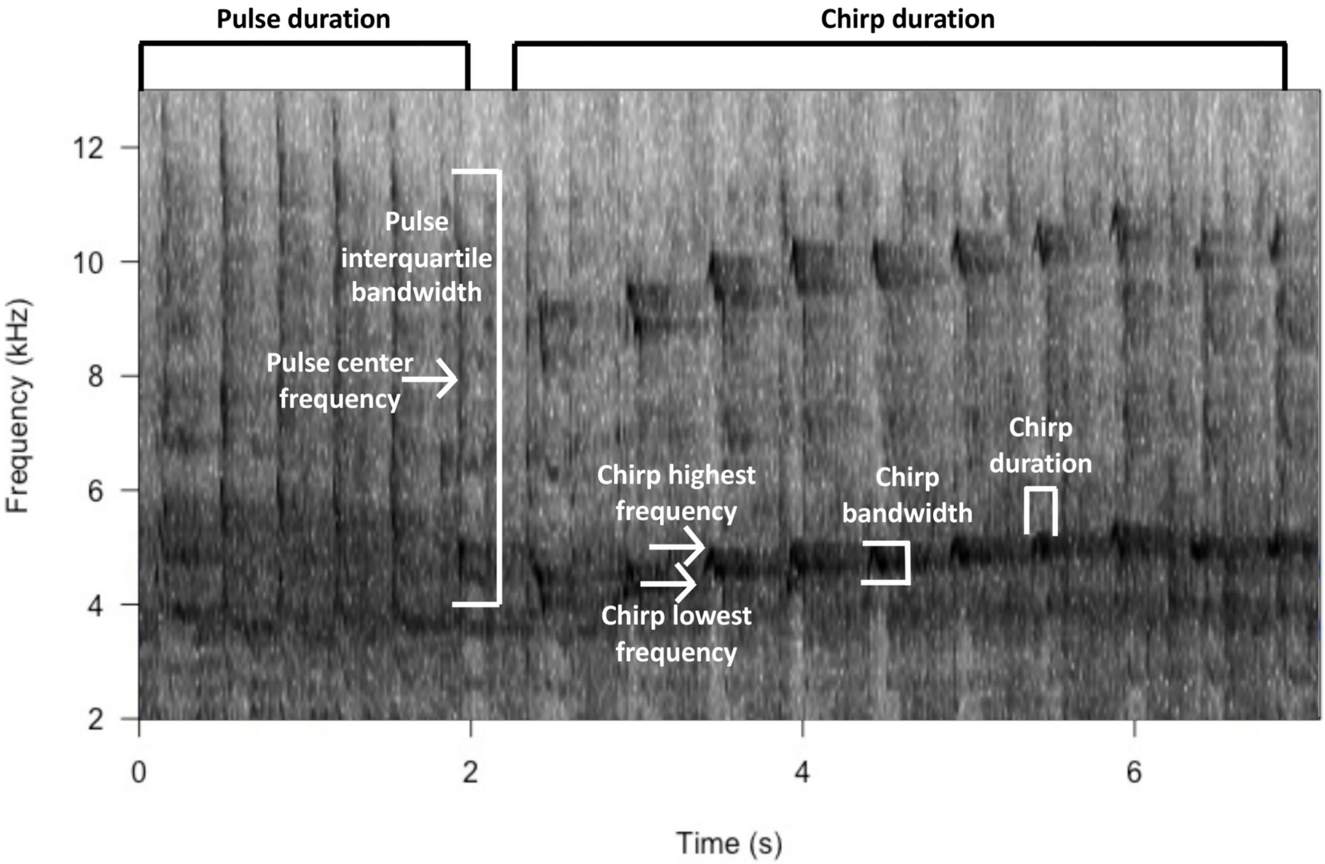


Figure 2.

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

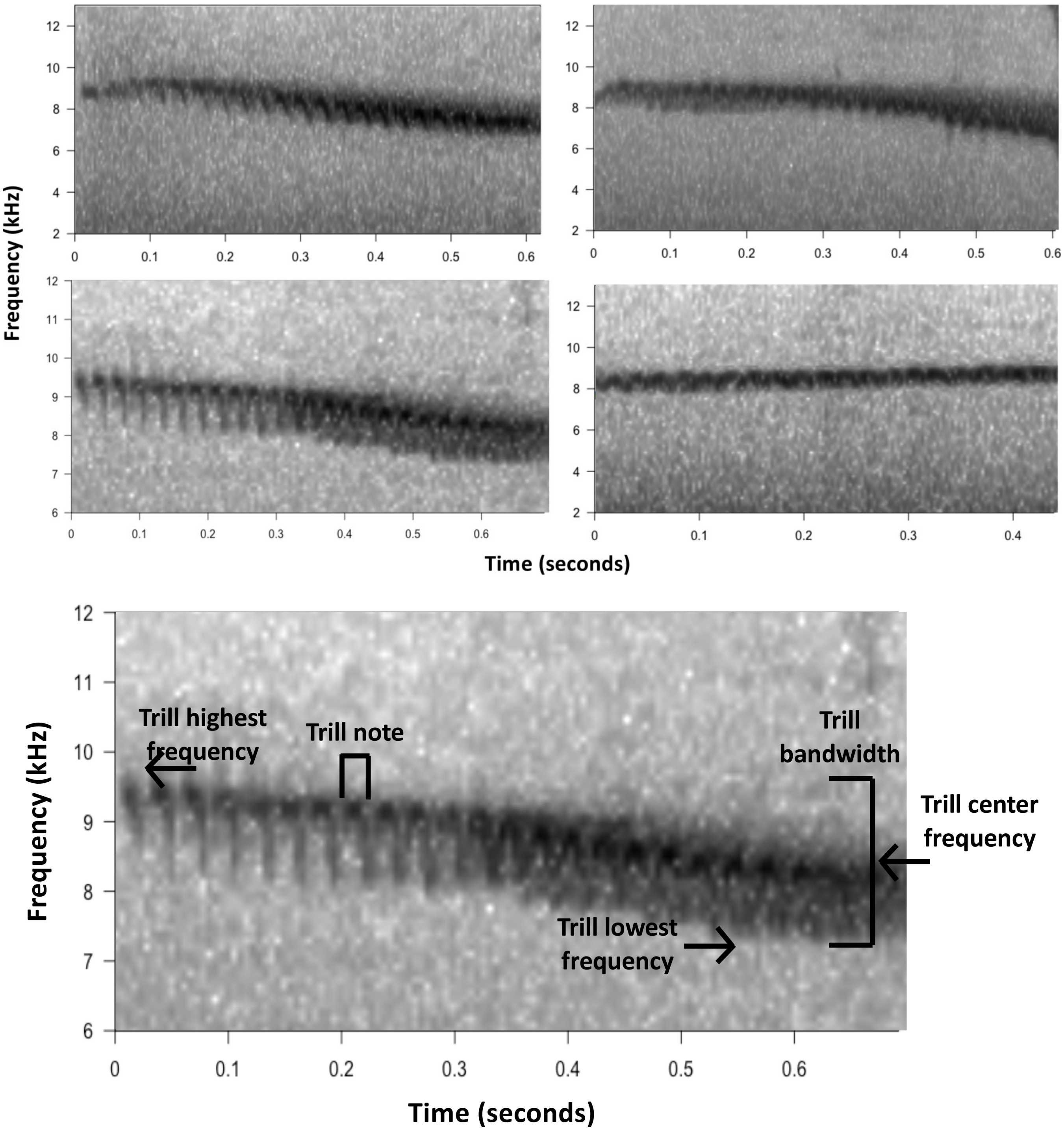
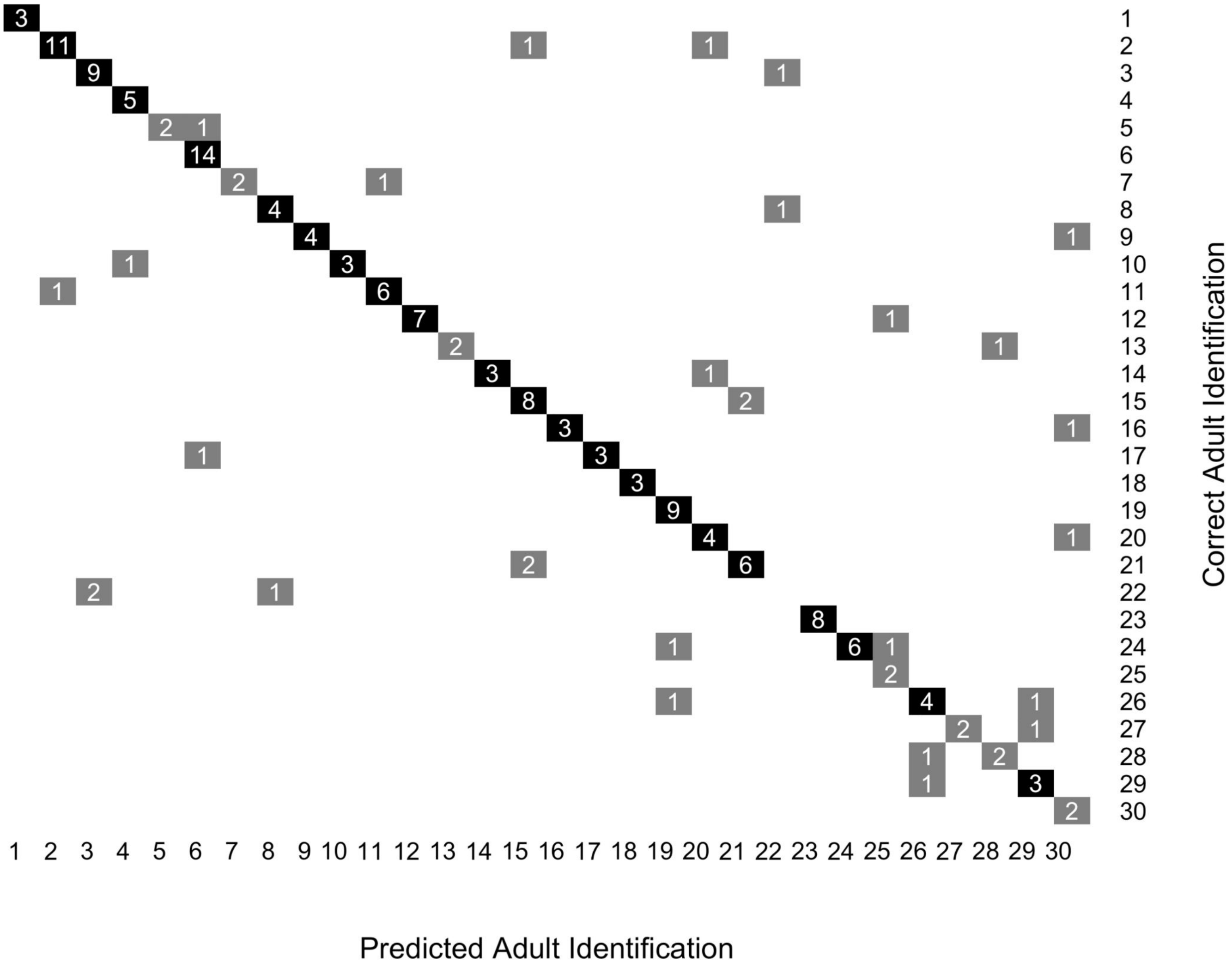


Figure 3.

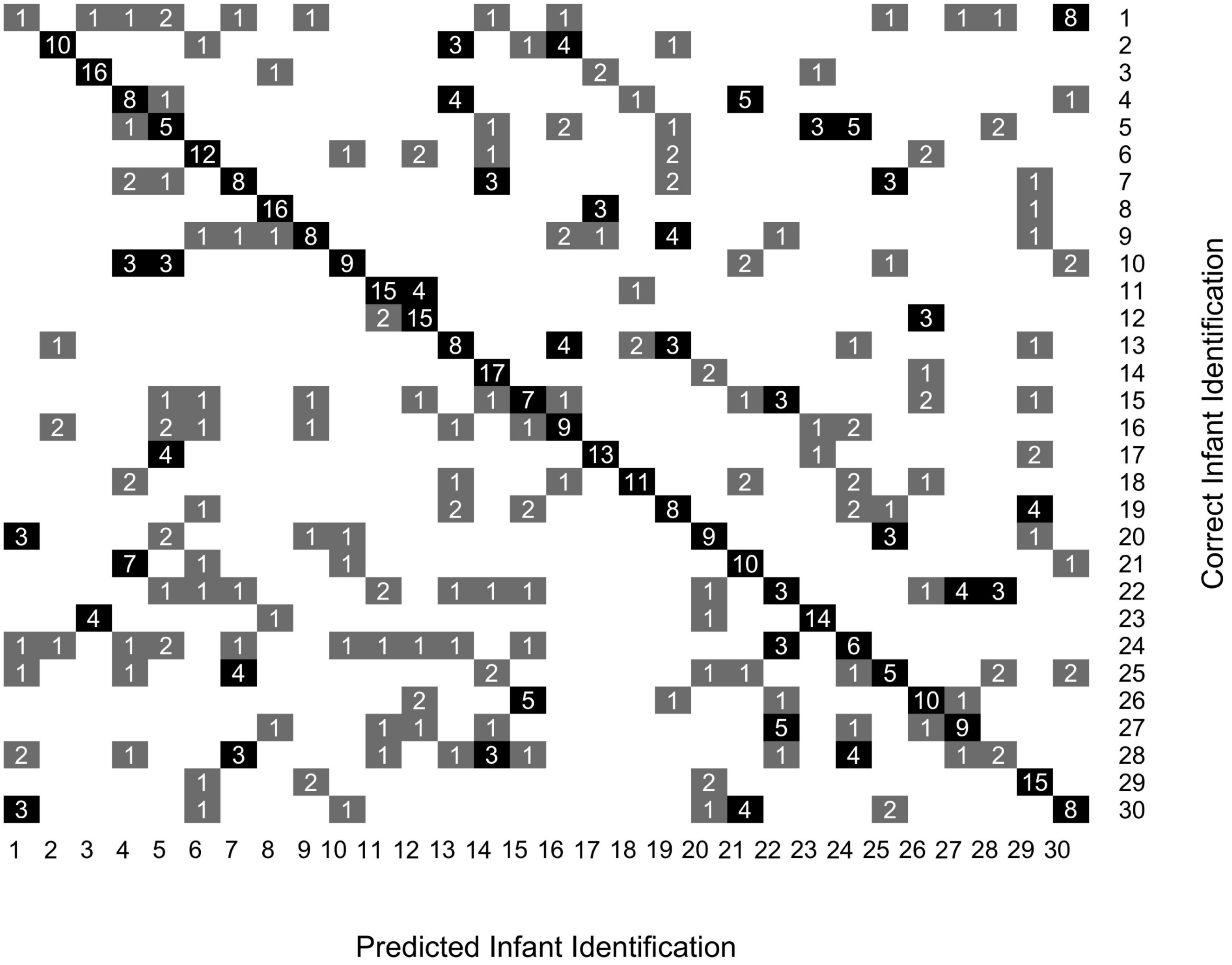
A. Representative spectrograms of infant titi monkey (*Plecturocebus cupreus*) trills. 3B. Representative spectrogram of infant titi monkey (*Plecturocebus cupreus*) trills. Features estimated from the spectrogram are highlighted.



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1	3																													
2		11													1					1										
3			9																			1								
4				5																										
5					2	1																								
6						14																								
7							2				1																			
8								4														1								
9									4																					1
10				1						3																				
11		1									6																			
12												7													1					
13													2															1		
14														3						1										
15															8						2									
16																3														1
17						1											3													
18																		3												
19																			9											
20																				4										1
21															2						6									
22			2					1																						
23																							8							
24																			1					6	1					
25																									2					
26																			1							4			1	
27																											2		1	
28																										1		2		
29																										1			3	
30																														2

Figure 4.

Confusion matrix for the discriminant function classification of 169 pulse-chirp duet vocalizations from 30 adult coppery titi monkeys (*Plecturocebus cupreus*). The total number of correct classifications are along the diagonal.



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1	1		1	1	2		1		1					1		1									1		1	1		8
2		10				1							3		1	4			1											
3			16					1									2						1							
4				8	1								4					1			5									1
5				1	5									1		2			1				3	5				2		
6						12				1		2		1					2							2				
7				2	1		8							3					2						3				1	
8								16									3												1	
9						1	1	1	8							2	1		4			1							1	
10				3	3					9											2				1					2
11											15	4						1												
12											2	15														3				
13		1											8			4		2	3					1					1	
14														17						2						1				
15					1	1			1			1		1	7	1					1	3				2			1	
16		2			2	1			1				1		1	9							1	2						
17					4												13						1						2	
18				2									1			1		11			2			2		1				
19						1							2		2				8					2	1				4	
20	3				2				1	1										9					3				1	
21				7		1				1											10									1
22					1	1	1				2		1	1	1					1		3				1	4	3		
23			4					1												1			14							
24	1	1		1	2		1			1	1	1	1		1							3		6						
25	1			1			4							2						1	1			1	5			2		2
26												2			5				1			1				10	1			
27								1			1	1		1								5		1		1	9			
28	2			1			3				1		1	3	1							1		4			1	2		
29						1			2											2									15	
30	3					1				1										1	4				2					8

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.

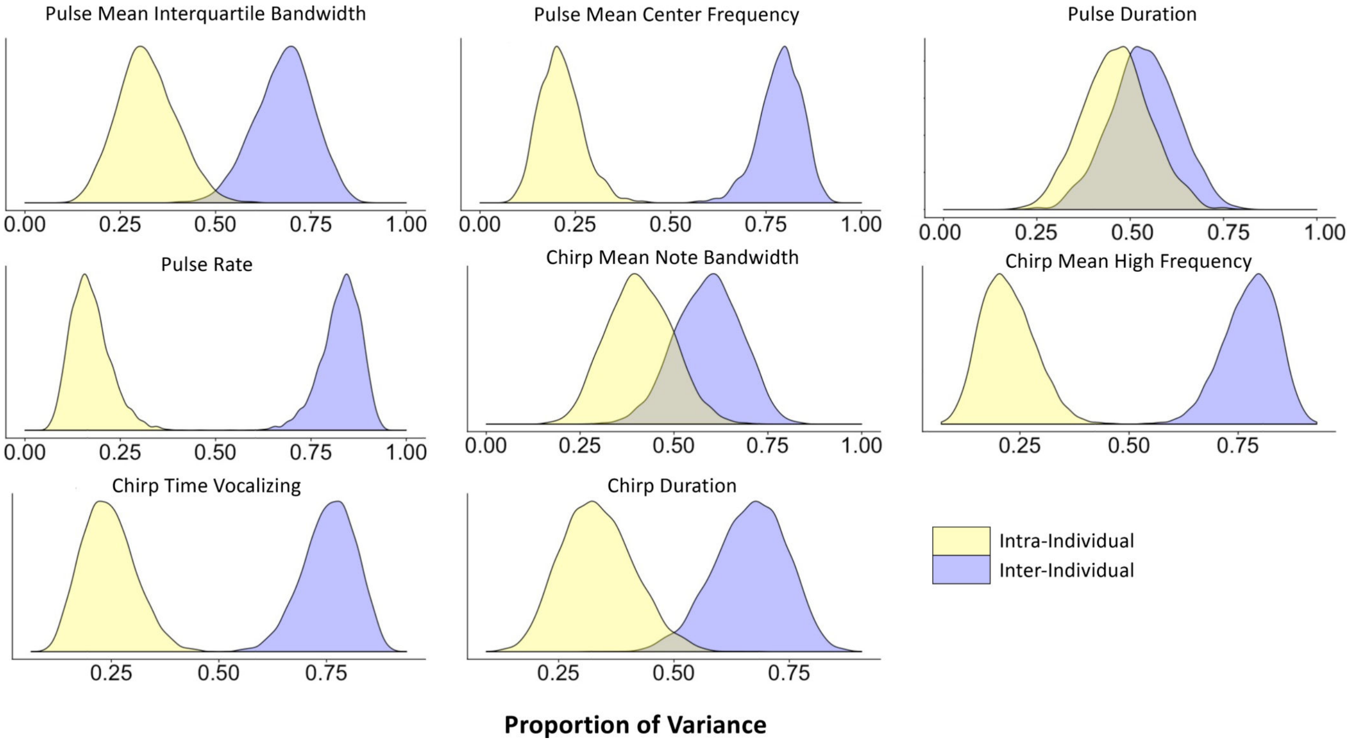


Figure 6.

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 labelled. Densities are comparable only within each parameter's plot, and the relative densities between each level (intra-individual and inter-individual) are important.

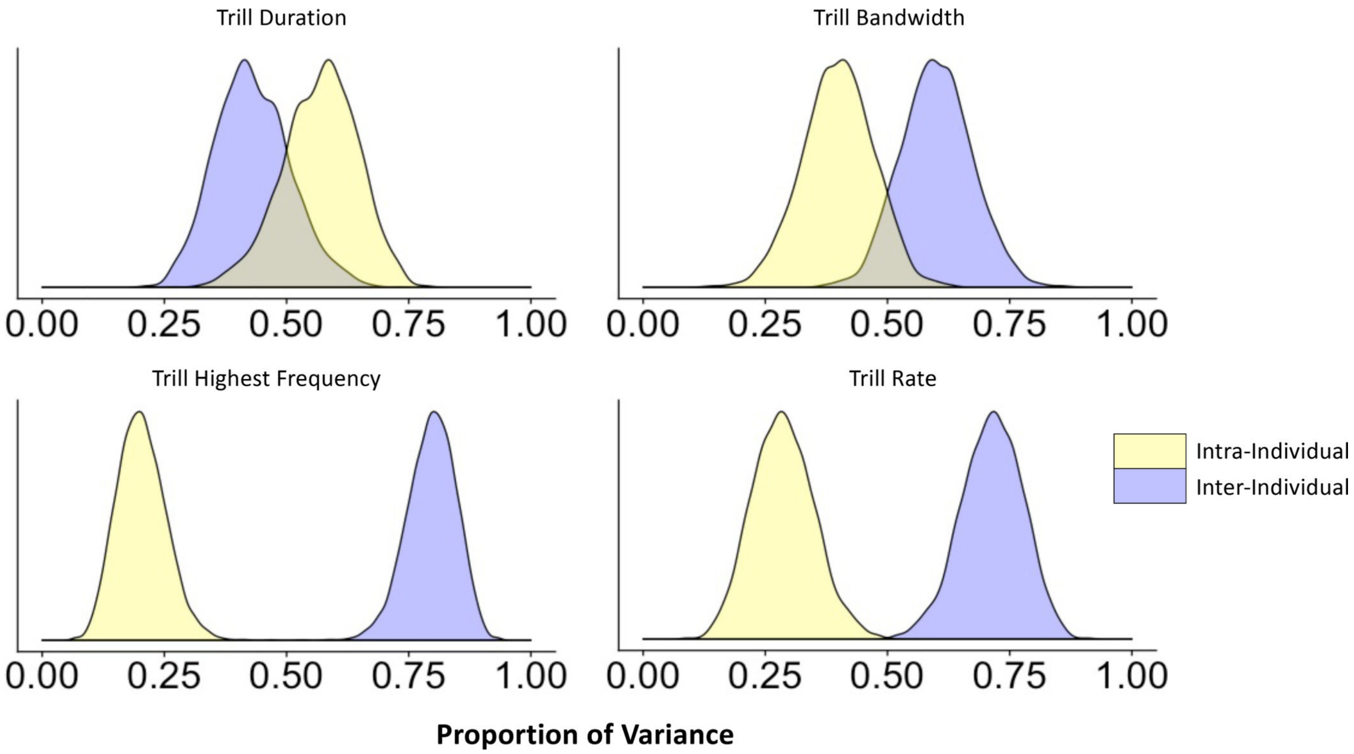


Figure 7.

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 labelled. Densities are comparable only within each parameter's plot, and the relative densities between each level (intra-individual and inter-individual) are important.

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 inter-quartile 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

Table 2:

Definitions of the 7 spectral and temporal features estimated from spectrograms of infant coppery titi monkey (*Plecturocebus cupreus*) trill vocalizations.

Parameter	**Definition**
Lowest Frequency (kHz)	Lowest frequency of the trill vocalization
Highest Frequency (kHz)	Highest frequency of the trill vocalization
Duration (s)	Duration of the trill vocalization
Bandwidth (kHz)	Difference between the lowest and highest frequency of the trill vocalization
Center Frequency (kHz)	Center frequency of the trill vocalization
Trill Count	Number of notes in the trill vocalization
Trill Rate	Number of notes divided by trill duration

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 ± SD	Range
Pulse Element	Number of pulses	8.9 ± 2.9	4 – 19
	Mean inter-quartile bandwidth (kHz)	1014.8 ± 499.4	107.7 – 2340.0
	Mean center frequency (kHz)	4598.6 ± 679.6	2091.8 – 6770.1
	Duration of pulse element (s)	2.3 ± 0.8	1.0 – 4.8
	Pulse rate (# of notes/pulse duration)	0.26 ± 0.03	0.19 – 0.42
Chirp Notes	Mean note bandwidth (kHz)	423.3 ± 137.1	201.0 – 861.3
	Mean note highest frequency (kHz)	5036.0 ± 514.5	3722.9 – 6664.0
	Mean note lowest frequency (kHz)	4135.3 ± 491.8	3072.4 – 5741.4
	Duration of chirps (s)	3.2 ± 1.4	0.6 – 10.3
	Duration of time vocalizing (s)	0.8 ± 0.5	0.1 – 3.1
	Number of chirps	7.1 ± 2.7	2 – 18
	Minimum bandwidth (kHz)	257.9 ± 112.2	86.1 – 775.2
	Maximum bandwidth (kHz)	641.2 ± 197.8	258.4 – 1378.1
	Highest frequency of all chirps (kHz)	5456.9 ± 553.2	3839.6 – 6756.4
	Highest frequency first note (kHz)	4490.1 ± 601.8	3103.6 – 6617.8
	Highest frequency last note (kHz)	5302.3 ± 646.7	3545.3 – 6756.4

Table 4:

Means and standard deviations for the 7 spectral and temporal features estimated from spectrograms of 600 infant coppery titi monkey (*Plecturocebus cupreus*) trill vocalizations from 30 individuals.

Parameter	**Mean ± SD**	**Range**
Lowest Frequency (kHz)	7271.1 ± 667.9	5250.0 – 8906.2
Highest Frequency (kHz)	8097.0 ± 654.6	600.0 – 10125.0
Duration (s)	0.5 ± 0.1	0.2 – 0.9
Bandwidth (kHz)	825.9 ± 408.9	187.5 – 2906.2
Center Frequency (kHz)	7719.7 ± 640.5	5812.5 – 9375.0
Trill Count	20.3 ± 5.5	6 – 36
Trill Rate (# of notes/trill duration)	0.026 ± 0.003	0.018 – 0.040