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## Moderate evidence for heritability in the duet contributions of a South American primate

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### Abstract

Acoustic signals are ubiquitous across mammalian taxa. They serve a myriad of functions related to the formation and maintenance of social bonds, and can provide conspecific information about caller condition, motivation, and identity. Disentangling the relative importance of evolutionary mechanisms that shape vocal variation is difficult, and little is known about heritability of mammalian vocalizations. Duetting—coordinated vocalizations within male and female pairs—arose independently at least four times across the Primate Order. Primate duets contain individual- or pair-level signatures, but the mechanisms that shape this variation remain unclear. Here, we test for evidence of heritability in two call types (pulses and chirps) from the duets of captive coppery titi monkeys (*Plecturocebus cupreus*). We extracted four features—note rate, duration, minimum and maximum fundamental frequency—from spectrograms of pulses and chirps, and estimated heritability of the features. We also tested whether features varied with sex or body weight. We found evidence for moderate heritability in only one of the features examined (chirp note rate), whereas inter-individual variance was the most important source of variance for the rest of the features. We did not find evidence for sex differences in any of the features, but we did find that body weight and fundamental frequency of chirp elements covaried. Kin recognition

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Conflict of interest

The authors declare no conflict of interest.

has been invoked as a possible explanation for heritability or kin signatures in mammalian vocalizations. Although the function of primate duets remains a topic of debate, the presence of moderate heritability in titi monkey chirp elements indicates that chirps may serve a kin recognition function.

### Keywords

vocal variation; kinship; duetting; *Plecturocebus cupreus*

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### Introduction

A fundamental goal in evolutionary biology is to understand the various evolutionary processes which lead to observed patterns of variation. Acoustic signals, like any phenotypic trait, are subject to a combination of neutral (Kimura 1983) and adaptive (Morton 1975) evolutionary processes. Understanding evolutionary pressures on acoustic signals is of particular interest, as inter- and intra-specific variation in acoustic signals has important implications for mate choice and recognition, as well as speciation (Wilkins et al. 2012). The importance of both genetic and environmental influences on the development of behaviors is well-recognized, but disentangling the relative influences of each remains a challenge (Mundinger and Lahti 2014) and is likely to be taxa-specific.

Quantifying the genetic basis of variation in vocalizations has important implications for understanding the evolutionary processes that shape vocal diversity, but relatively little is known about the heritability of mammalian calls (Blumstein et al. 2013), particularly in respect to the heritability of individually distinct call features. In bats (*Nycticeius humeralis*), there is evidence for heritability of individual signatures in pup isolation calls (Scherrer and Wilkinson 1993). In Belding's ground squirrel (*Spermophilus beldingi*), individuals within a particular site were more similar to each other than individuals from a different site, and the authors attribute individual acoustic variation to genetic influences (McCowan and Hooper 2002). In yellow-bellied marmots (*Marmota flaviventris*), there was evidence for heritability of call features in yearlings and adults, whereas variation in juvenile calls was better explained by maternal effects (effects on offspring phenotype which are shared by offspring with the same mother; Blumstein et al. 2013).

Despite the prevalence of kin signatures across taxa and signal modalities, relatively little is known about how kin signatures develop (Sharp et al. 2005). Kin signatures may be genetically determined or acquired (Sherman et al. 1997), and the mechanisms appear to vary across taxa. For example, in bell miners (*Manorina melanophrys*), vocal similarity correlates with genetic relatedness, which has important implications for understanding kin recognition in this system (McDonald and Wright 2011). Bell miners live in large colonies of hundreds of individuals, which are organized into breeding pairs that are assisted by helpers. Helpers tend to be closely related to the breeding pairs, and helpers also have calls that are more similar to the breeding male than non-helpers. Importantly, in this system young interact with related and unrelated group members, which makes the possibility for learning less likely (although it has not been ruled out empirically; Leedale et al. 2020).

Whereas in red-backed fairy-wrens (*Malurus melanocephalus*) there is evidence that kin signatures are learned in the egg, as female songs are similar to their mothers' in-nest calls (that they heard only as embryos; Dowling et al. 2016). This is also the case in long-tailed tits (*Aegithalos caudatus*), where it was shown experimentally that nestlings learn calls from provisioning parents during the nestling period (Sharp et al. 2005).

Nonhuman primates (hereafter primates) have a limited capacity for vocal learning relative to other taxa (Fedurek and Slocombe 2011). However, in contrast to early views that primate calls are innate and genetically fixed (Brockelman and Schilling 1984; Owren et al. 1993), there is growing evidence for phenotypic plasticity in primate vocalizations across taxa (Clink, Lau, et al. 2019; Clink, Tasirin, et al. 2019; Crockford et al. 2004; Tanaka et al. 2006; Terleph et al. 2018). In duetting primates, there is evidence that species-specific acoustic structure is genetically fixed (Brockelman and Schilling 1984). However, in gibbons, there is evidence that male juveniles sing female-specific duet contributions (Koda et al. 2014), and juvenile females track their mothers and are more well-synchronized with their mothers as they reach more advanced stages of social independence (Koda et al. 2013). In addition, convergence in titi monkey (Clink, Lau, et al. 2019) and tarsier (Clink, Tasirin, et al. 2019) duetting partners indicates that duets exhibit some degree of vocal plasticity.

A few studies of primate vocalizations have aimed to quantify the influence of genetics on acoustic structure. For example, the ability to distinguish between kin and non-kin based on acoustic signals (and the adaptive advantages it confers) has been invoked as an explanation for acoustic similarity among closely related mandrill individuals (*Mandrillus sphinx*; Levréro et al. 2015). In indris, male (but not female) song features had a strong relationship with genetic distance, providing evidence that male songs may contain information about relatedness (Torti et al. 2017); this was also the case with mouse lemur (*Microcebus murinus*) advertisement calls which contained acoustic patrilineal signatures (Kessler et al. 2012). In captive chimpanzees (*Pan troglodytes*), within-group vocal convergence in pant hoots could not be linked to genetics, as males were from diverse origins, and convergence was attributed to vocal learning (Marshall et al. 1999). This was also the case in Campbell's monkeys (*Cercopithecus campbelli*), as acoustic similarity was related to social bond strength but not genetic relatedness (Lemasson et al. 2011). Male kin signatures in mouse lemur advertisement calls were invoked as a mechanism for inbreeding avoidance (Kessler et al. 2012), whereas male signatures in indri vocalizations were attributed to reduced potential for inbreeding in extra-pair copulations, or as a way to mediate aggression among related males (Torti et al. 2017).

Across a diverse range of taxa and vocalization types, there is evidence for inter-individual differences in call features (Darden et al. 2003; Delgado et al. 2013; Favaro et al. 2016; Ji et al. 2013; Kershenbaum et al. 2013; Kirschel et al. 2011; Terry et al. 2005; Trimble and Charrier 2011). Inter-individual differences in call features may be adaptive, as identity signaling may confer advantages to the signaler, such as decreased harassment by neighbors and increased stability in reciprocal interactions (Tibbetts and Dale 2007). Variation in call features may be the result of neutral evolution wherein a unique combination of ontogenetic, environmental, and genetic factors lead to observed patterns of variation (Podos and Warren 2007); neutral and adaptive explanations are not mutually exclusive. Individual differences

may also be the result of phenotypic plasticity wherein individuals actively differentiate from their neighbors, similar to what is seen in the territorial drumming of kangaroo rats (Randall 1995). For taxa that exhibit vocal learning, inter-individual differences can arise through imperfect copying or novel variants (Wilkins et al. 2012), and in some cases, learned traits could have higher heritability than genetic traits (Danchin et al. 2004). Substantial inter-individual variation has been found in a variety of primate taxa, including loud calls of orangutans (*Pongo pygmaeus* (Spillmann et al. 2017), duet contributions of male (*Hylobates funereus* (Lau et al. 2018); *H. lar* (Terleph et al. 2018)) and female gibbons (*H. funereus* (Clink et al. 2017); *H. lar* (Terleph et al. 2015)) male and female titi monkeys (*Plecturocebus cupreus* (Lau et al. 2020)) female tarsiers (*Tarsius spectrumgurskyae* (Clink, Tasirin, et al. 2019)) and indris (*Indri indri* (Torti et al. 2018)), but the processes that lead to this variation remain poorly understood.

Inter-individual differences can occur in both temporal and spectral parameters of the vocalizations. Fundamental frequency of vocalizations is determined by the rate of the opening and closing of the vocal folds of the larynx, and fundamental frequency has been shown to vary substantially across call types, individuals, sex, and species (Taylor and Reby 2010). The vocal folds can develop independently of skeletal structures, which means there does not necessarily need to be a correlation between fundamental frequency and body size (e.g. in humans (Künzel 1989)). It has also been argued that because fundamental frequency can be actively modulated by the calling animal that it may not be a reliable predictor of body size (Fitch 1997). But, when comparing across age and sex classes within a species, a relationship between body size and fundamental frequency is often observed (e.g. hamadryas baboons *Papio hamadryas* (Pfefferle and Fischer 2006); baboons *Papio cynocephalus ursinus* (Fischer et al. 2002)). Inter-individual differences in fundamental frequency can also arise via variation in hormone levels, as male white-handed gibbons with higher androgen levels were shown to have higher fundamental frequency vocalizations than males with lower androgen levels (Barelli et al. 2013). The mechanisms that lead to inter-individual differences in temporal structure are not well understood.

Here, we aim to investigate the influence of genetic relatedness on acoustic structure of coppery titi monkey (*Plecturocebus cupreus*) duets. Previous work has shown that the duet contributions of titi monkeys are individually distinct (Lau et al. 2020) and that duets exhibit a degree of vocal plasticity, as duetting individuals converge with their partner in rate of note output (Clink, Lau, et al. 2019). The function(s) of duetting in titi monkeys and other nonhuman primates remains a topic of debate (Singletary and Tecot 2020), although a recent playback study in black-fronted titi monkeys (*Callicebus nigrifrons*) provided evidence that titi monkey duets serve a joint territorial defense function (Caselli et al. 2015). Titi monkey duets are species-specific (Adret et al. 2018), providing evidence for genetic influence in species-specific duet structure, but relatively little is known about individual-level genetic influences. We analyzed the duet contributions recorded in a captive colony of titi monkeys with known relatedness to test the hypothesis that titi monkey duet features are heritable. We used Bayesian multilevel models to estimate heritability of four features—note rate (notes per sec), duration (sec), minimum and maximum fundamental frequency (Hz)—estimated from spectrograms of pulse and chirp duet contributions. We also tested whether duet features vary by sex or weight of the calling individual, as variation in duet features may

arise due to sex-differences or differences in body weight. We predicted that: 1) there would be evidence for heritability in all duet features examined; 2) spectral features (*e.g.* minimum and maximum fundamental frequency) would vary with body size; and 3) there would not be substantial differences between male and female duet contributions.

## Methods

### Study subjects

Titi monkeys are pair-living South American primates that regularly engage in species-specific duets (Adret et al. 2018). There is little evidence for sex-specificity in duet contributions, but there is a high degree of synchrony as duetting partners alternate consistently between the high- and low-frequency components of the duet (Müller and Anzenberger 2002; Robinson 1979). The present study focused on a captive colony of coppery titi monkeys (*Plecturocebus cupreus*; hereafter titi monkeys) at the California National Primate Research Center (CNPRC), Davis, CA, USA. Subjects at the CNPRC are housed in male-female pairs along with their offspring and are in acoustic contact (and very little visual contact) with other members of the colony. Detailed descriptions of housing conditions can be found in Tardif et al. (2006).

### Acoustic data collection

Data were collected opportunistically in the morning hours (between 06:00 and 07:30) from March 2017 to March 2019 using a Marantz PMD 660 flash recorder and a Marantz Professional Audio Scope SG-5B directional condenser microphone. We recorded at a sampling rate of 44.1 kHz, 16-bit resolution, and saved as Waveform (.wav) audio files. All recordings were taken less than 3 meters from the calling animals. Titi monkey duets have a substantial amount of overlap in male and female duet contributions and a lack of sex-specificity, which makes isolating the individual contributions difficult. Therefore, to identify the calling individual we video-recorded the duetting animals using a Canon Vixia HF R200 camera and paired the acoustic recordings with the video. For acoustic analysis, we only used high-quality recordings during which one pair was vocalizing, and in the case where we had multiple high-quality duet recordings from the same pair, we chose the highest quality duet for analysis. See Lau et al. (2020) for more details on acoustic data collection.

### Acoustic analysis

Our analysis focused on two components of titi monkey duets: pulses (Clink, Lau, et al. 2019) and chirps (Lau et al. 2020); see Figure 1 for a representative spectrogram of a titi monkey duet. We created spectrograms of duets in Raven Pro 1.5 Sound Analysis Software (K. Lisa Yang Center for Conservation Bioacoustics, Ithaca, NY, USA) using the following settings: a 512-point (11.6 ms) Hann window (3 dB bandwidth =124 Hz), 75% overlap, and a 1024-point DFT, yielding time and frequency measurement precision of 2.9 ms and 43.1 Hz. One observer (ARL) isolated the pulse and chirp elements from the duets and saved each element as a .wav file. For each duet element (pulse and chirp) we created selection tables in Raven Pro 1.5. We used robust measurements for feature extraction, which are less susceptible to inter- and intra-observer variability in note selection (Charif et al. 2010).

For each pulse and chirp element, we estimated the following features: duration of the entire element (seconds), number of notes, minimum 5% and maximum 95% fundamental frequency in the element and rate of note repetition (number of notes over total duration). The correlation between number of notes and duration of the elements was 0.96 for chirps and 0.93 for pulses, so we used only duration in our analyses. See Table 1 for a summary of features used in the analyses and Figure 2 for a spectrogram highlighting how notes were identified from pulses and chirps.

### Pedigree analysis

The CNPRC maintains records of each animals' parentage, sex, birth, and death, which allowed us to calculate kinship for each dyad in the colony. The program PEDSYS (Dyke 1999) was used to calculate a multigenerational pedigree for the entire colony; see Kanthaswamy and Bales (2018) for details on pedigree construction. We calculated the kinship coefficient ( $k$ ) for each pair of individuals in the colony based on the pedigree. The kinship coefficient is the probability that two alleles, taken at random from two individuals, are identical by descent (Crow et al. 1970); in practice the kinship coefficient provides a measure of genetic similarity of two individuals (Ballou et al. 2010). The median kinship coefficients for the colony was  $0.15 \pm 0.12$  SD, and values ranged from zero (not related) to 1 (self). See Table 2 for a summary of the number of pairs of individuals in three kinship categories ( $k \leq 0.1$ ,  $0.1 < k < 0.25$ ,  $k \geq 0.25$ ) by sex and call type.

### Statistical analyses

We aimed to test the hypothesis that titi monkey duets contain kin signatures. We were also interested to see if call features varied with the sex or weight of the animal. To test our hypotheses we used Bayesian multilevel models implemented in the R package 'brms' (Bürkner 2018), which serves as an interface to STAN (Stan Development Team 2017). We created separate models for each pulse and chirp feature, resulting in eight unique models with the relevant call feature as the outcome and two predictors: body weight (kg) and sex (categorical). Each model also included a genetic covariance matrix and a random effect for individual identity. The genetic covariance matrix was based on the pedigree analysis described above. For all features we specified a Gaussian distribution, and we log-transformed low and high frequency features to address skew. Following Bürkner (2021) we specified weakly informative normal priors for the slope and intercept parameters, and weakly informative half-t priors for the variance components. We simulated 2000 samples from four chains after a warm-up of 2000 samples, for a total of 8000 samples for inference. We inspected trace plots to ensure proper mixing and converging; trace plots for each model are available in Electronic Supplementary Material (ESM 1).

Heritability is defined as the proportion of genetic variance relative to the total variance for the trait(s) of interest (Lynch et al. 1998). We used intra-class correlation coefficients (ICCs) to estimate the amount of variance in each call feature that could be attributed to three levels in our dataset: genetic, inter-individual, and intra-individual. ICCs measure the relative contribution of each level to the total variance and ICC values range between 0 and 1, with an ICC value close to 1 indicating that level is an important source of variation (Merlo et al. 2005). We considered the ICC values for the genetic-level variance to



represent heritability of the call feature. The values we report can be considered corrected heritability as the models include body weight and sex as predictors. There is a debate in the literature about whether to include fixed effects in models of heritability (De Villemereuil et al. 2018; Wilson 2008), so for completeness we also include a summary of all models without the fixed effects for each of the features as Electronic Supplementary Material (ESM 2). These estimates were calculated the same way as described above, except in this case the models did not contain body weight or sex as predictors. Following the Bayesian analysis reporting guidelines (Kruschke 2021) we describe the posterior distributions of parameters using quantiles, and report the median along with 95% equal-tailed credible interval calculated using the 'posterior\_summary' function in the 'brms' package (Bürkner 2018). We used the 'bayes\_R2' function in the 'brms' package to calculate an  $R^2$  value for Bayesian regression models;  $R^2$  values provide information regarding model fit (Gelman et al. 2019). All analyses were conducted in the R programming environment version 3.6.2 (R Core Team 2019). Figures were made using either the 'ggpubr' or 'ggplot2' packages (Kassambara 2018; Wickham 2016, p. 2).

### Data availability

All R code and data needed to recreate analyses are available on Dryad (<https://doi.org/10.5061/dryad.0vt4b8h15>).

### Results

We report the results of the analysis of 302 pulses (N=30 males; N=29 females) and 244 chirps (N=22 males; N=19 females; Table 1). Violin plots showing the distributions of the pulse and chirp features are presented in Figure 3. We used ICCs to estimate the relative contribution of three levels in our dataset (Genetic, inter-individual and intra-individual) to the total variance for each call feature. We found that genetic variance was an important source of variance for only one of the call features: chirp note rate [ICC median= 0.40; 95% posterior credible interval (0.09, 0.58)]. For the majority of call features, inter-individual variance was the most important source of variance (Figure 4; Table 3). We did not find any sex differences in call features, but we did find body weight was a reliable negative predictor of low frequency and high frequency of the chirp elements. We also found a positive relationship between body weight and duration of the pulse element (Table 3; Figure 5).  $R^2$  values for each model are also shown in Table 3.

### Discussion

We found moderate evidence for heritability of in a single feature of titi monkey duets. Out of eight features examined, only note rate of chirp elements had moderate heritability (ICC= 0.40), whereas the rest of the features had low heritability. The presence of heritability in animal vocalizations has been attributed to possible selection for the ability to discriminate between kin and non-kin (Scherrer and Wilkinson 1993). Therefore, given moderate heritability in one of the chirp features examined, it is possible that titi monkey chirp elements provide kin recognition cues. The fact that we found low to moderate evidence for heritability in titi monkeys but male indri vocalizations varied consistently with genetic relatedness (Torti et al. 2017), is particularly interesting given the shared natural history



traits (pair living, territoriality and duetting; Adret et al. 2018; Torti et al. 2013) between indris and titi monkeys. For most features in our analysis, inter-individual variance was the most important source of variance; this was particularly pronounced for the chirp features. In addition, we found a negative relationship between body size and minimum and maximum fundamental frequency of the chirp elements, and that there was a positive relationship between body weight and duration of the pulse elements. Our finding that titi monkey duet features vary by individual is consistent with previous work on this species (Lau et al. 2020).

As with most bioacoustics studies, we had to make choices about which feature(s) we estimated from spectrograms of the duet elements and used for our subsequent analysis. We chose a small subset of relatively uncorrelated spectral and temporal features based on previous work done in other species (Blumstein et al. 2013; Levréro et al. 2015; Torti et al. 2017). And although we did not find strong evidence for heritability in the majority of these features, it is possible that other aspects of the duets provide evidence of genetic relatedness to listening animals. Future work that incorporates playbacks of closely and distantly related titi monkey individuals will be informative. Another potential limitation of our study is that our data come from a captive colony wherein animals are housed at an artificially high density relative to what would occur in the wild. Little is known about the degree of vocal learning in titi monkeys, but it is possible that captive titi monkeys are able to hear so many vocal ‘models’ that their duets sound less like their parents’ than they would in the wild. Both male (Koda et al. 2014) and female (Koda et al. 2013) gibbon juveniles track their mother’s duet, and older females have duets that are more synchronized with their mothers. In our colony, juveniles appear to track their same-sex parent (Lau, unpublished data), but the moderate evidence for kin signatures in duet features indicates that inter-individual variation in duet features is probably not influenced by the parent.

Our finding of moderate heritability in chirp note rate is particularly interesting in light of the fact that lemur (Macedonia and Taylor 1985) and gibbon (Geissmann 1984) hybrids differ from parental species in terms of the rhythmic structure of their vocalizations. A correlation between temporal patterns and genetic relatedness was also found in indris (Torti et al. 2017). It is unclear why we found a genetic signature in chirp note rate but not in pulses, but these findings indicate that the two call types may serve different functions. In addition, the fact that we found a strong relationship between minimum and maximum fundamental frequency of chirp elements and body size indicates that chirp elements may provide the listener with information about the size of the calling animal (Taylor and Reby 2010). Previous work on pulse elements in this species showed that pulse rate declined with age (Clink, Lau, et al. 2019). Combined, these results indicate that titi monkey duets contain information about body size and genetic relatedness (this study), age (Clink, Lau, et al. 2019), and individual identity (Lau et al. 2020) of the calling animals. Whether listening animals are able to interpret and use this information in meaningful way remains to be seen.

The ability to distinguish between kin and non-kin is important for many social animals, particularly if correct identification of kin leads to reduced aggression or inbreeding avoidance in closely related animals. Playback experiments have been particularly useful for testing the ability for animals to recognize kin versus non-kin based on acoustic cues. For example, cooperatively breeding long-tailed tits (*Aegithalos caudatus*) responded differently

to playbacks of calls of kin and non-kin, providing evidence that they can differentiate based on acoustic cues alone (Sharp et al. 2005). In a similar experiment, adult female rhesus macaques (*Macaca mulatta*) were able to discriminate between kin and non-kin (Rendall et al. 1996). This was also the case for female baboons (*Papio hamadryas ursinus*) which showed an ability to attribute both kinship and dominance information to the calls of individuals (Bergman et al. 2003). In female mouse lemurs, individuals looked towards the speaker faster, approached the speaker sooner, and spent more time near the speaker when it broadcast advertisement of unrelated males compared to related males (Kessler et al. 2012). To our knowledge there have not been experimental tests of the ability of duetting primates to distinguish between duets of kin and non-kin, and future playback studies will be informative to help elucidate whether or not primate duets can serve a kin recognition function.

The high-levels of inter-individual variation shown in this study and previous work demonstrating pair convergence in acoustic features (Clink, Lau, et al. 2019) add to the growing body of literature indicating that rather than being inflexible and innate, primate vocalizations exhibit a high degree of plasticity (Hedwig et al. 2015; Lemasson et al. 2005; Snowdon 2009). Although the function of primate duets remains a topic of debate, it is clear that these long-distance vocalizations transmit information about the calling individual or pair to neighboring conspecifics. The occurrence of strong kin signatures in indri duets but relatively weak signatures in titi monkey duets raises more questions about the potential differences in function of long-distance calls between the two primate groups. In addition, it is unclear whether the different duet components (pulse and chirp) of titi monkey duets serve different functions, or if titi monkey listeners can discern between the different duet components or different calling individuals. Further tests using playbacks will help further our understanding of what types of information titi monkeys glean from their duetting neighbors, and whether titi monkey duets are used for kin recognition. And importantly, further tests in other duetting primate species that investigate both the potential for kin signatures and kin recognition will provide important insight into the function and evolution of duetting across the Order Primates.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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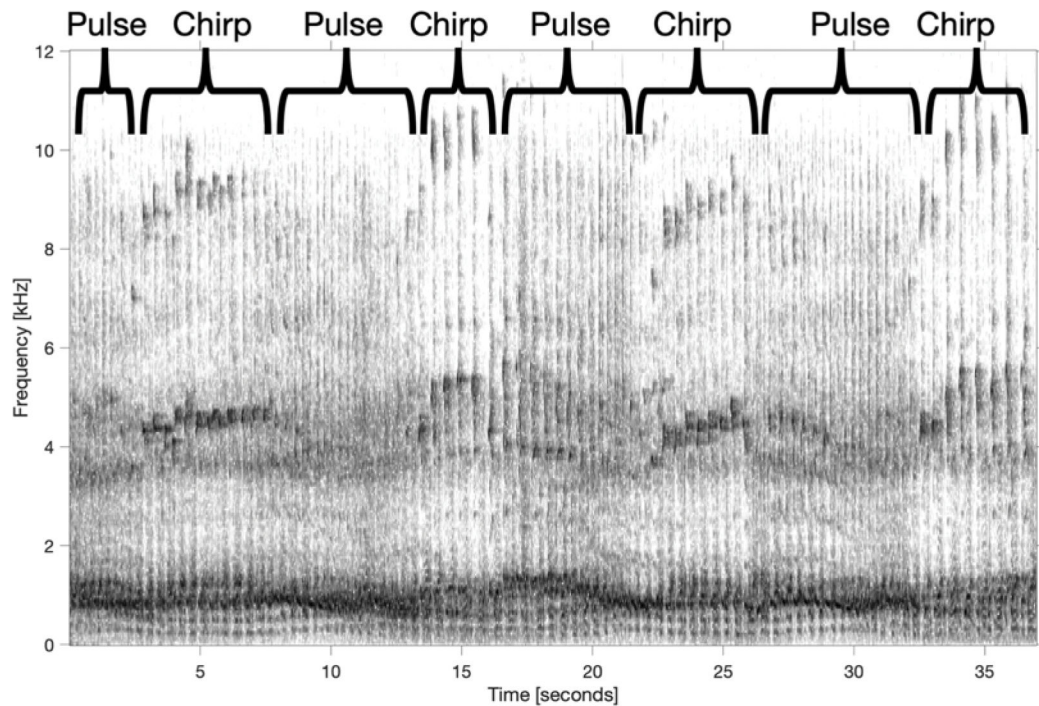
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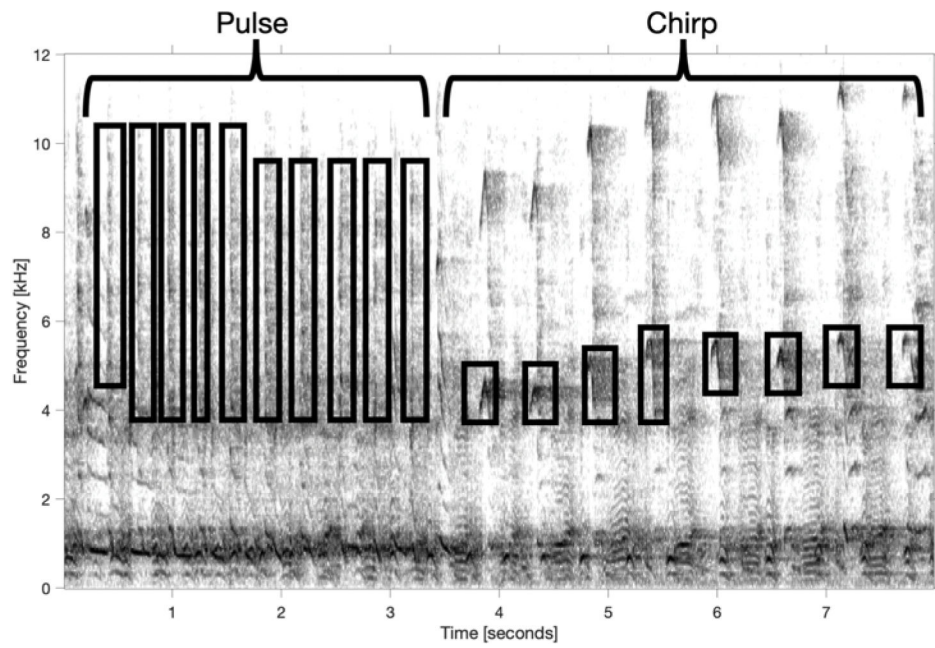




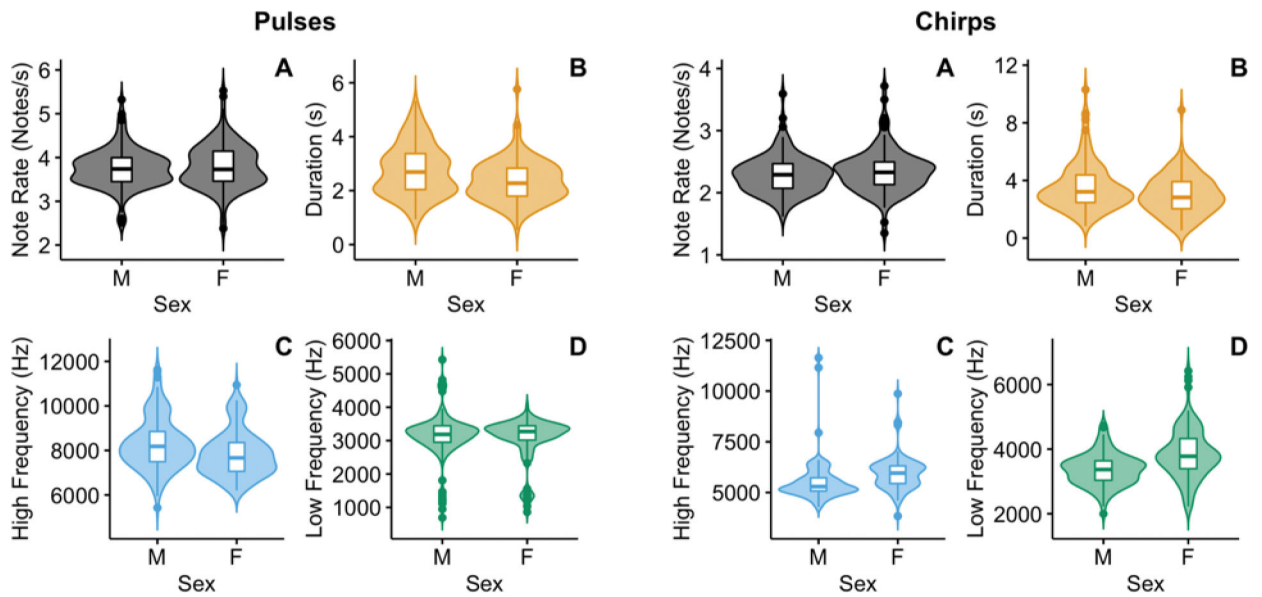
**Figure 1. Representative spectrogram of a duet sequence from a pair of coppery titi monkeys at the CNPRC.**

Duetting individuals alternate duet contributions and the first ‘pulse-chirp’ in this spectrogram was emitted by the male of the pair, and the second ‘pulse-chirp’ was emitted by the female. This alternating pattern was continued throughout the duet, but only a portion of the duet is shown for visual clarity. Spectrograms were made in the Matlab-based program Triton (Wiggins 2003) using 1000-point (22.7 ms) Hann window with 85% overlap.



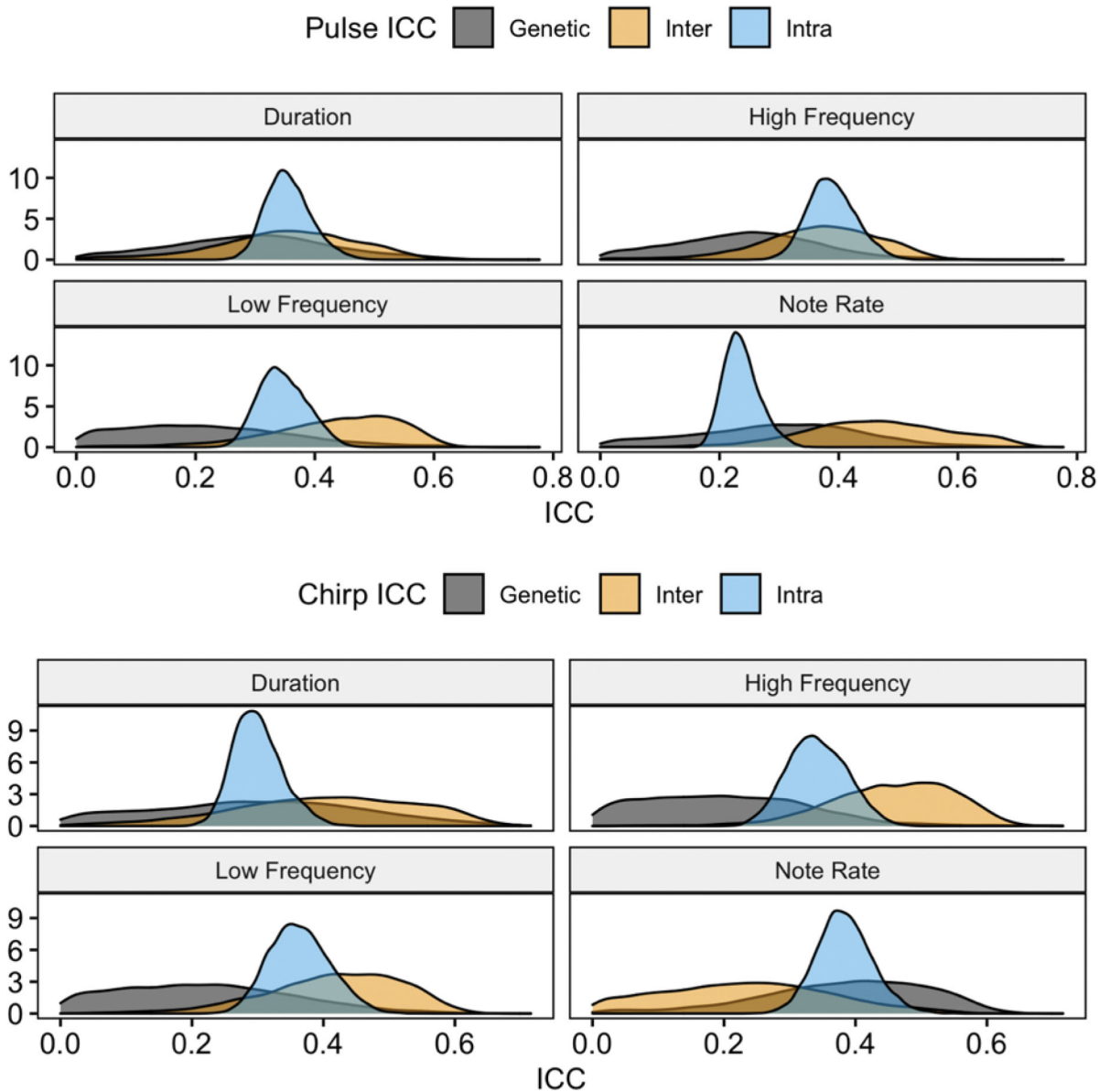


**Figure 2. Representative spectrogram of a single ‘pulse-chirp’ duet contribution.** The black boxes indicate how individual notes were identified. Spectrograms were made in the Matlab based program Triton (Wiggins 2003) using 1000-point (22.7 ms) Hann window with 85% overlap.



**Figure 3. Violin plots showing the distribution of pulse and chirp features used in the present analysis.**

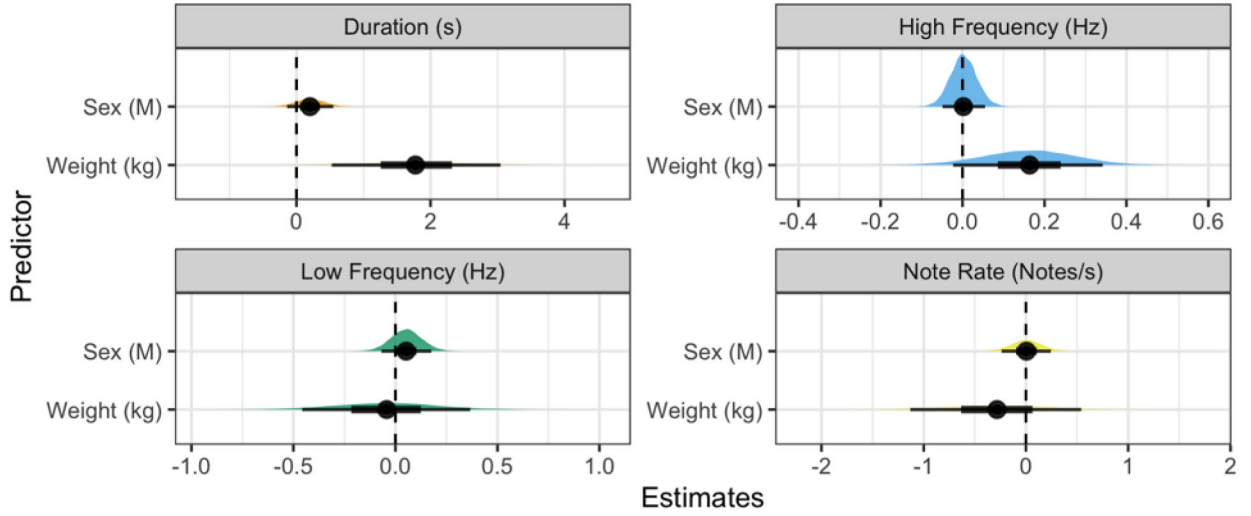
Violin plots show the kernel probability density at different values, and the box plots indicate the median value as a horizontal line, and the interquartile range as the borders of the box plot. The x-axis indicates whether the call came from a male or female, and the y-axis indicates the value of that particular feature (see Table 1 for a full description of the features).



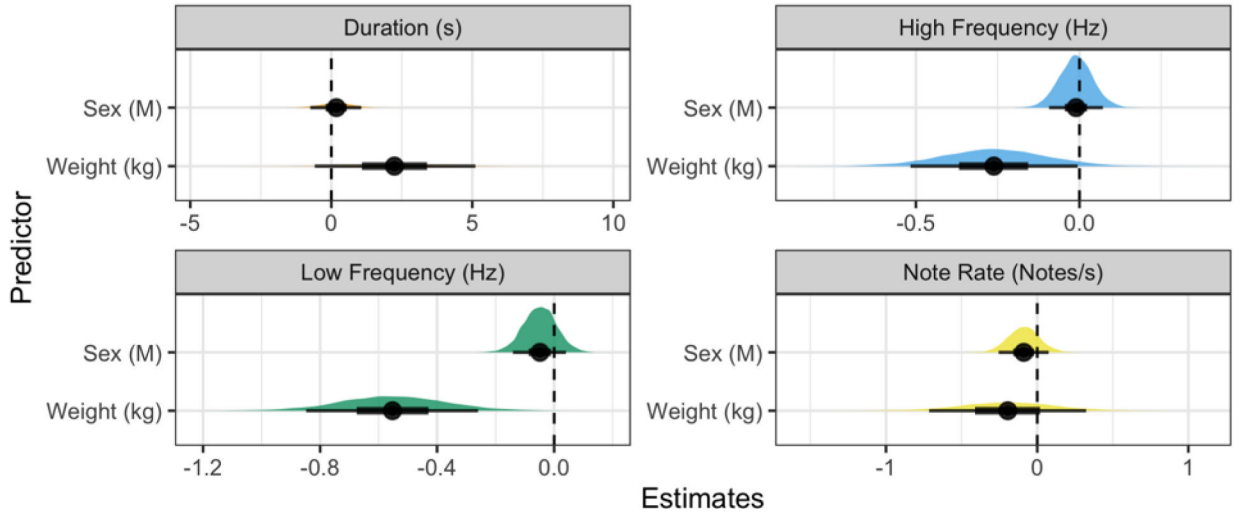
**Figure 4. Posterior densities of the intraclass correlation coefficients (ICCs) for three levels in our dataset (Genetic, inter-individual and intra-individual) for four features estimated from spectrograms of titi monkey pulse and chirp duet elements.**

We found that genetic relatedness was the most important source of variance for only one feature (note rate for chirp elements). For the rest of the call features, inter-individual variance was the most important source of variance. For each of the figures the y-axis refers to “density” and only the relative densities between classes matter.

### A. Pulse coefficients



### B. Chirp coefficients



**Figure 5. Coefficient plots from models of four features estimated from spectrograms of titi monkey pulse (A) and chirp (B) duet elements.**

Each model contained sex and body weight of the calling individual as predictors. We found that body weight was a reliably positive predictor of pulse duration, whereas there was a negative relationship between body weight and minimum and maximum frequency of chirp elements. In the plots above, each point indicates the median posterior density credible interval value, the inner black bars represent the 50% credible interval, and the outer black bars represent the 95% credible intervals. The colored distribution plots indicate the associated uncertainty in the point estimates.

**Table 1.**

Summary of outcome and predictor variables used in the present analysis.

<i>Outcome</i>	<i>Description</i>	<i>Call Type</i>	<i>Sex</i>	<i>N</i>	<i>Mean ± SD</i>	<i>Range</i>		
Note rate (notes over total duration)	<i>Number of notes divided by total duration</i>	Chirp	F	119	2.35 ± 0.35	1.35–3.72		
			M	125	2.29 ± 0.31	1.61–3.59		
		Pulse	F	140	3.8 ± 0.51	2.38–5.53		
			M	162	3.75 ± 0.44	2.51–5.32		
Duration (s)	<i>Total duration of the duet element in seconds</i>	Chirp	F	119	2.98 ± 1.36	0.54–8.89		
			M	125	3.57 ± 1.65	0.83–10.30		
		Pulse	F	140	2.34 ± 0.77	0.54–5.76		
			M	162	2.76 ± 0.95	0.94–5.32		
		Low frequency (Hz)	<i>Minimum fundamental frequency of the duet element</i>	Chirp	F	119	3864.09 ± 784.24	2227.30–6418.50
					M	125	3372.01 ± 499.77	1999.00–4726.40
Pulse	F			140	3042.32 ± 658.83	861.30–4048.20		
	M			162	3145.96 ± 693.27	689.10–5426.40		
High frequency (Hz)	<i>Maximum fundamental frequency of the duet element</i>	Chirp	F	119	5949.46 ± 826.30	3839.6–9869.20		
			M	125	5521.28 ± 953.66	4285.90–11641.80		
		Pulse	F	140	7831.32 ± 1019.45	6201.60–10938.90		
			M	162	8299.59 ± 1161.45	5426.40–11627.90		
		<i>Predictor</i>	<i>Description</i>	<i>Call Type</i>	<i>Sex</i>	<i>N</i>	<i>Mean ± SD</i>	<i>Range</i>
		Weight (kg)	<i>Body weight (kg) of the individual</i>	Chirp	F	119	1.09 ± 0.12	0.88–1.32
M	125				1.29 ± 0.14	0.89–1.52		
Pulse	F			140	1.11 ± 0.12	0.88–1.47		
	M			162	1.28 ± 0.13	0.89–1.52		
Sex	<i>Categorical variable (male or female)</i>	Chirp	F	119	~	~		
			M	119	~	~		
		Pulse	F	161	~	~		
			M	175	~	~		

Each model included one duet feature as the outcome, and features were estimated for both pulse (N=30 males; N=29 females) and chirp (N=22 males; N=19 females) elements. Sex of the calling animal and body weight (kg) were used as predictors in all models.

**Table 2.**

Summary of the number of pairs of individuals (dyads) in three kinship ( $k$ ) categories ( $k \leq 0.1$ ,  $0.1 < k < 0.25$ ,  $k \geq 0.25$ ) by sex and call type.

Call Type	$k \leq 0.1$	$0.1 < k < 0.25$	$k \geq 0.25$	N dyads	N Individuals	N calls	Mean calls per individual	Range per individual
Chirp (F)	46	88	37	171	19	119	6.3	3–16
Chirp (M)	59	139	33	231	22	125	5.7	2–14
Pulse (F)	119	216	71	406	29	140	4.8	1–15
Pulse (M)	100	276	59	435	30	162	5.4	2–15

Our dataset consisted of 244 chirps (N=22 males; N=19 females) and 302 pulses (N=30 males; N=29 females). The  $k \geq 0.25$  category does not include pairs of animals wherein  $k=1$  (self). See main text for description of how we calculated the kinship coefficient.

**Table 3.**

Median, lower and upper 95% equal-tailed credible interval of the posterior distributions for parameter estimates from full models of the four features estimated from spectrograms of pulse and chirp titi monkey duet contributions.

Call Type	Model	Parameter	Median	Q2.5 (Lower bound)	Q97.5 (Upper bound)		
Pulse	Note rate	Intercept	4.09	2.83	5.34		
		Weight (kg)*	-0.30	-1.35	0.73		
		Sex (M)*	0.01	-0.30	0.30		
		Genetic random effect	0.28	0.02	0.60		
		Individual random effect	0.45	0.23	0.60		
		Residual variance	0.22	0.20	0.24		
		Genetic (ICC; corrected)	0.29	0.03	0.56		
		Inter-individual (ICC)	0.47	0.23	0.69		
		Intra-individual (ICC)	0.24	0.19	0.30		
		R-squared	0.78	0.75	0.80		
		Pulse	Duration (s)	Intercept	0.39	-1.46	2.18
				Weight (kg)*	1.74	0.23	3.30
				Sex (M)*	0.20	-0.22	0.62
Genetic random effect	0.46			0.05	0.92		
Individual random effect	0.55			0.13	0.80		
Residual variance	0.54			0.50	0.60		
Genetic (ICC; corrected)	0.30			0.04	0.56		
Inter-individual (ICC)	0.36			0.08	0.55		
Intra-individual (ICC)	0.35			0.29	0.44		
R-squared	0.63			0.57	0.67		
Pulse	High frequency (Hz)			Intercept	8.79	8.52	9.05
				Weight (kg)*	0.16	-0.06	0.38
				Sex (M)*	0.00	-0.06	0.07
		Genetic random effect	0.06	0.00	0.12		
		Individual random effect	0.09	0.03	0.12		
		Residual variance	0.09	0.08	0.10		
		Genetic (ICC; corrected)	0.25	0.02	0.48		
		Inter-individual (ICC)	0.37	0.14	0.54		
		Intra-individual (ICC)	0.38	0.32	0.48		
		R-squared	0.57	0.50	0.62		
		Pulse	Low frequency (Hz)	Intercept	8.03	7.41	8.62
				Weight (kg)*	-0.05	-0.56	0.46



Call Type	Model	Parameter	Median	Q2.5 (Lower bound)	Q97.5 (Upper bound)
		Sex (M) <sup>*</sup>	0.05	-0.10	0.20
		Genetic random effect	0.11	0.01	0.29
		Individual random effect	0.22	0.10	0.29
		Residual variance	0.17	0.16	0.19
		Genetic (ICC; corrected)	0.21	0.01	0.51
		Inter-individual (ICC)	0.45	0.19	0.60
		Intra-individual (ICC)	0.34	0.27	0.43
		R-squared	0.67	0.62	0.71
Chirp	Note rate	Intercept	2.62	1.87	3.36
		Weight (kg) <sup>*</sup>	-0.20	-0.85	0.45
		Sex (M) <sup>*</sup>	-0.09	-0.30	0.11
		Genetic random effect	0.24	0.04	0.38
		Individual random effect	0.14	0.01	0.29
		Residual variance	0.23	0.21	0.26
		Genetic (ICC; corrected)	0.39	0.07	0.58
		Inter-individual (ICC)	0.23	0.02	0.50
		Intra-individual (ICC)	0.38	0.31	0.47
		R-squared	0.52	0.44	0.58
Chirp	Duration (s)	Intercept	0.58	-3.40	4.59
		Weight (kg) <sup>*</sup>	2.24	-1.27	5.67
		Sex (M) <sup>*</sup>	0.16	-1.00	1.29
		Genetic random effect	0.87	0.05	1.87
		Individual random effect	1.19	0.31	1.73
		Residual variance	0.85	0.77	0.94
		Genetic (ICC; corrected)	0.30	0.02	0.61
		Inter-individual (ICC)	0.41	0.10	0.63
		Intra-individual (ICC)	0.30	0.24	0.38
		R-squared	0.70	0.65	0.74
Chirp	High frequency (Hz)	Intercept	8.95	8.60	9.31
		Weight (kg) <sup>*</sup>	-0.25	-0.58	0.06
		Sex (M) <sup>*</sup>	-0.01	-0.11	0.09
		Genetic random effect	0.04	0.00	0.13
		Individual random effect	0.11	0.07	0.15
		Residual variance	0.08	0.08	0.09
		Genetic (ICC; corrected)	0.18	0.01	0.44
		Inter-individual (ICC)	0.48	0.27	0.61
		Intra-individual (ICC)	0.34	0.26	0.44

Call Type	Model	Parameter	Median	Q2.5 (Lower bound)	Q97.5 (Upper bound)
		R-squared	0.66	0.60	0.70
Chirp	Low frequency (Hz)	Intercept	8.85	8.46	9.26
		Weight (kg) *	-0.55	-0.91	-0.19
		Sex (M) *	-0.05	-0.16	0.06
		Genetic random effect	0.07	0.00	0.17
		Individual random effect	0.12	0.06	0.17
		Residual variance	0.11	0.10	0.12
		Genetic (ICC; corrected)	0.22	0.02	0.49
		Inter-individual (ICC)	0.42	0.18	0.58
		Intra-individual (ICC)	0.36	0.28	0.46
		R-squared	0.69	0.64	0.73

We report the variance of both genetic -and individual-level random effects, along with the residual variance, for each model. We also report the calculated intraclass correlation coefficients (ICC) for the three levels in our dataset. The fixed effects or predictors included in our models are denoted using an asterisk (\*). For each model we also report the  $R^2$  values (see main text for details).