Limited Evidence for Individual Signatures or Site-Level Patterns of Variation in Male Northern Gray Gibbon (*Hylobates funereus*) Duet Codas

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Abstract

Many animals rely on acoustic signals to mediate social interactions with conspecifics. Duets—the alternating vocal exchange between two animals—are of particular interest given the presumed intra- and intergroup communicative functions. Importantly, when there are sex-specific differences in duet contributions, the contribution of each sex may serve different function(s). We investigated variation in male Northern gray gibbon codas from seven sites on Malaysian Borneo using three complementary approaches. First, we used supervised classification to see how well we could classify male gibbon codas to the respective male. Second, we investigated the relative contribution of intramale, intermale, and intersite variance to total variance using a Bayesian multivariate, variance components model. Lastly, we investigated small-scale patterns of variation (<10 km) in male codas from a single site to test two mutually exclusive hypotheses related to small-scale patterns of variation. First, if call features are transmitted from father to offspring, we predicted neighboring males would have codas that were more similar to each other than males at further distances. Alternatively, if males actively differentiate from their neighbors, we predicted to see the opposite pattern. We

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did not find high levels of vocal individuality in male codas, as individual classification accuracy was relatively low (<63%) and there were no site-level differences in codas. We did not find support for either of our hypotheses regarding small-scale patterns of variation. Taken together, our findings indicate high levels of intraindividual variation in male codas. Future work that explores both the function(s) of the male and female contribution to the duets, along with investigations of heritability of duet features will be informative.

Introduction

Quantifying patterns of variation in acoustic signals has important implications for understanding the selective pressures that shape them, and can provide insight into their function(s) (Wilkins *et al.,* 2012). For example, site-level differences in acoustic signals that vary with certain ecological variables (e.g., forest structure) are consistent with the acoustic adaptation hypothesis (Morton, 1975), whereas strong individual signatures indicate that the signal may be used for recognition of conspecifics (Taylor *et al.,* 2016). Although there has been mixed support for the acoustic adaptation hypothesis in birds (Boncoraglio & Saino, 2007; Irwin *et al.,* 2008; Kirschel *et al.,* 2011; Wiley, 1991) and mammals (Campbell *et al.,* 2010; Hedwig *et al.,* 2015; Sun *et al.,* 2013), geographic variation in acoustic signals has been documented across diverse taxonomic groups including insects (Duijm, 1989), anurans (Jang *et al.,* 2011), birds (Irwin *et al.,* 2008; Searcy *et al.,* 2002), marine mammals [harbor seals (*Phoca vitulina*: Bjørgesæter *et al.,* 2004); fin whales (*Balaenoptera physalus*: Delarue *et al.,* 2009); dolphins *Tursiops truncatus* (Jones & Sayigh, 2002)], and terrestrial mammals [singing mice (*Scotinomys* spp.: Campbell *et al.,* 2010); nonhuman primates (Burton & Nietsch, 2010; Clink, Grote, *et al.,* 2018b; de la Torre & Snowdon, 2009; Delgado, 2007; Mitani *et al.,* 1999; Wich *et al.,* 2008)].

In addition to site- or population-level patterns of variation, acoustic signals can also vary at the level of the individual [e.g., contain individual signatures (Terry *et al.,* 2005)]. Variation at the individual level does not preclude variation at the site or population level (Tibbetts & Dale, 2007). Variation in acoustic signals can arise through a combination of mechanisms including evolution by natural selection (Morton, 1975), neutral evolutionary processes [e.g., drift; (Yurk *et al.,* 2002)], and imperfect copying during vocal learning (Podos & Warren, 2007). There is limited evidence for vocal learning in nonhuman primates relative to humans and songbirds (Janik & Slater, 1997), although there are a few documented cases (e.g., Lemasson *et al.,* 2011; Watson *et al.,* 2015). Therefore, neutral and adaptive evolutionary mechanisms presumably play a stronger role than vocal learning in shaping primate acoustic signals.

Duets are the coordinated, alternating vocal exchanges that occur between two individuals (Langmore, 2002). Duets are of particular interest to evolutionary biologists, as the evolution of complex signals such as these indicates that they were shaped by strong selection pressures and confer an adaptive advantage over solo singing (Hall, 2004). In the Order Primates duetting evolved independently at least four times in the

indris (Indriidae), tarsiers (Tarsiidae), titi monkeys (Callicebinae), and gibbons [Hylobatidae (Geissmann, 2002)]. Duetting primates tend to be pair living and territorial, with one of the presumed function of the duets being defense of the territory against conspecifics (Haimoff, 1986). Primate duets generally have sex- and species-specific structure, but there is evidence from white-handed gibbons (*Hylobates lar*) that duets vary slightly based on the context in which they are emitted [e.g., in the presence of predators or during an intergroup interaction (Andrieu *et al.,* 2020)]. The structure of indri (*Indri indri*) song has also been shown to vary with context (Torti *et al.,* 2013).

Most male gibbons in the genus *Hylobates* have two types of long-distance vocalizations: male solos and male duet contributions (Geissmann, 2002). There are two exceptions—Javan gibbons (*H. moloch*) and Kloss's gibbons (*H. klossii*)—that do not duet (Geissmann *et al.,* 2005; Tenaza, 1976). Many studies have focused on male gibbon solos, investigating evidence for individual signatures (Feng *et al.,* 2014; Sun *et al.,* 2011), adherence to linguistic laws (Clink *et al.,* 2020a; Clink & Lau, 2020; Huang *et al.,* 2020) and the influence of environmental variables on singing behavior (Clink *et al.,* 2020b). Previous work on white-handed gibbons found that males flexibly time their duet contribution (termed the coda) based on the timing of the female contribution [known as a great call (Terleph *et al.,* 2018a)], and that there were interindividual differences in male codas (Terleph *et al.,* 2018b). In contrast, previous work on Northern gray gibbons (*H. funereus*) from a single site in Malaysian Borneo indicated that there was relatively low levels of individuality in the male codas (Lau *et al.,* 2018). There are distinct structural differences between the male codas in white-handed and Northern gray gibbon duets, and it is unclear if the discrepancies in results are related to differences in structure of the codas or different methodological approaches. The function of the male gibbon coda is still unclear, with some of the proposed functions including the emphasis of sexual identity and advertisement of male quality; as the coda is part of the duet it also presumably serves some of the same functions as the duet (Terleph *et al.,* 2018b).

Relatively little is known about the ontogeny of male codas and heritability of duet features in both males and females. There is evidence that mother–daughter vocal interactions are important for white-handed gibbon female development, as subadult daughters at a more advanced stage of social independence had calls that were more well synchronized with their mothers than younger females (Koda *et al.,* 2013). Immature male agile and white-handed gibbons were shown to produce female-specific duet contributions, and the authors posit that male production of female calls may change over the course of development and be mediated by changes in androgen levels (Koda *et al.,* 2014). The role of the father in vocal development of male gibbons remains unclear. It is possible that features of male codas may be passed from father to offspring [either through genetics (Blumstein *et al.,* 2013) or learning (Lemasson *et al.,* 2011)]. Given the relatively short documented dispersal distance of males into adjacent groups (Matsudaira *et al.,* 2018), this would result in a pattern wherein male gibbons from neighboring territories have calls that are more similar than males from territories that are further away. Alternatively, there is evidence that some animals actively differentiate their acoustic signals from their neighbors [e.g., kangaroo rats (*Dipodomys spectabilis*: Randall, 1995)], which would result in the opposite pattern wherein males from neighboring territories have calls that are highly dissimilar.

Here we investigate individual- and site-level variation in Northern gray gibbon (*Hylobates funereus*; hereafter gibbons) male codas recorded from seven different sites on Malaysian Borneo. Both adaptive and evolutionary mechanisms may shape individual- and site-level patterns of variation in male gibbon codas, and understanding intraspecific patterns of variation in these acoustic signals is a crucial first step for testing hypotheses related to the evolution of acoustic diversity (Wilkins *et al.,* 2012). We took three distinct but complementary approaches to investigate variation in gibbon codas. First, we used a supervised classification technique (support vector machines) to see how well we could classify male gibbon codas to the respective individual and site. Given the conflicting reports regarding individual signatures in male gibbon codas (Lau *et al.,* 2018; Terleph *et al.,* 2018b) we aimed to include a larger sample size than previous studies and compare two different feature extraction methods (see details in the text that follows), as the choice of features may substantially influence classification results (Clink, Crofoot, & Marshall, 2018a). Second, we used a Bayesian multivariate, variance components model to investigate how variance in a subset of uncorrelated spectral and temporal features estimated from the spectrograms of codas was partitioned across three levels (intramale, intermale, and intersite).

Lastly, we investigated small-scale patterns of geographic variation (*ca.* 10 km) within one of our sites that had the largest sample size of male individuals ($N = 16$ males). We aimed to test two mutually exclusive hypotheses related to small-scale patterns of variation. First, if call features are transmitted from father to offspring, then we predicted a positive relationship between geographic distance (e.g., distance between male gibbon territories) and call dissimilarity, because male gibbons tend to disperse into adjacent groups (Matsudaira *et al.,* 2018). Alternatively, if animals actively differentiate from their neighbors then we predict that calls from neighboring gibbons will be very dissimilar.

Methods

Data Collection

We recorded the duet vocalizations from pairs of gibbons at seven different sites in Sabah, Malaysia during multiple field seasons from January 2013 to September 2016 (see Fig. 1 for a map of the sites). The forests of north Borneo are considered aseasonal (Walsh & Newbery, 1999), so we do not expect seasonal variation in calling or environmental conditions to substantially impact our results. Male gibbons of this species engage in early morning solos around dawn, whereas duets tend to start slightly later; the majority of solos and duets occur between 05:00–11:00 h local time (Clink *et al.,* 2020b). Rain has been shown to reduce overall calling activity so we did not collect data on mornings when there was rain (Brockelman & Srikosamatara, 1993; Clink *et al.,* 2020b). To record duets, we used a Marantz PMD 660 recorder (Marantz, Kawasaki, Kanagawa Prefecture, Japan) equipped with a Røde NTG-2 directional condenser microphone (Røde Microphones, Sydney, Australia). We recorded all duets using a sampling rate of 44.1 kHz, 16-bit size, and we saved each file as Waveform audio files (.wav). To augment data collection, we broadcast a previously recorded duet (recorded in Maliau Basin Conservation Area, Sabah, Malaysia) into the presumed
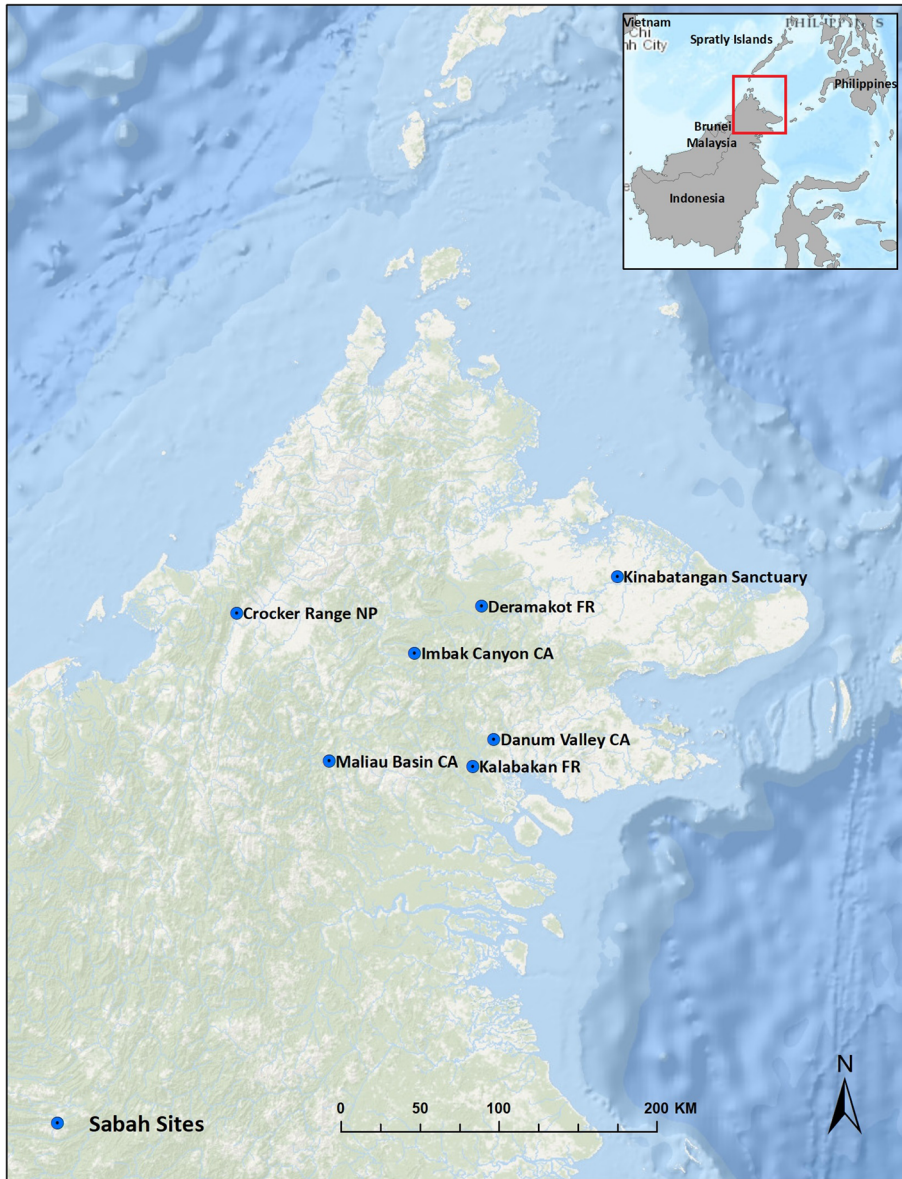
Fig. 1 Map of recording locations in Sabah, Malaysia. The map was created using ArcGIS® software by Esri.

territories of gibbon pairs using Roland CUBE Street EX 4-Channel 50-W Battery Powered Amplifier (Roland Corporation, Osaka Prefecture, Japan).

Recording distances to the animals varied from directly under the tree to *ca.* 100 m from the observer. Variation in recording distance can have an influence on frequency and bandwidth estimates (Zollinger *et al.,* 2012). In an attempt to avoid some of the confounding issues with variable recording distance and the potential impacts on frequency and bandwidth we focused our analyses only on calls with relatively high signal-to-noise ratio (SNR) (≥10 dB). A high SNR value can be used as a proxy for

recording distance, with recordings obtained at a closer distance from the animals having a higher SNR. We distinguished between calling pairs of gibbons based on a combination of recording location and group composition. Following Brockelman and Srikosamatara (1993), we considered pairs that were recorded >500 m apart to be separate. In certain instances where we recorded at the same recording location on different days, we analyzed recordings from only a single day.

Acoustic Analysis

We created spectrograms using the Raven Pro 1.6 Sound Analysis Software (Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Ithaca, NY, USA) with a 2400-point (54.4 ms) Hann window (3 dB bandwidth = 26.4 Hz), with 50% overlap, and a 4096-point Discrete Fourier Transform, yielding time and frequency measurement precision of 27.2 ms and 10.8 Hz. Following Terleph et al. (2018b), we defined codas as the male contribution to the duet that occurred within 5 s of the female great call (Fig. 2). Using Raven selection tables, we estimated the following features from spectrograms of each note in the coda: start and stop time(s), duration(s), bandwidth (Hz), minimum frequency (Hz), and maximum frequency (Hz). All estimates we report were taken from the fundamental frequency of the notes. See Fig. 3 for a summary of the features extracted from male codas. The features we estimated in Raven are robust features, which are calculated based on the energy of the selection and are less sensitive to intra- and interobserver variation in selections (Rice et al., 2014). Two observers (DJC and MZ) annotated all codas after ensuring that intra- and interobserver reliability was >90%.
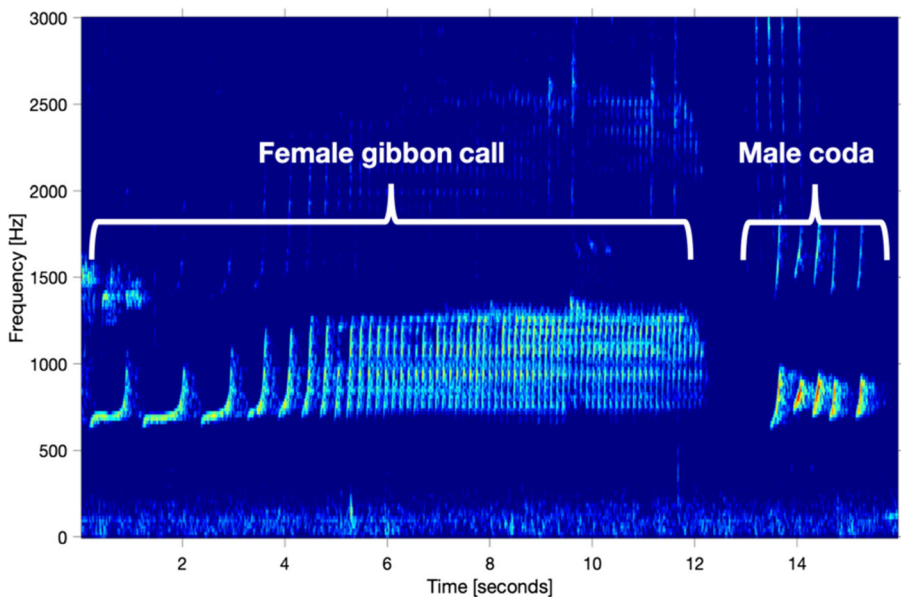
Fig. 2 Representative spectrogram of the duet contributions of a female and male gibbon. The spectrogram was made in the MATLAB®-based program Triton (Wiggins, 2003) with a 1600-point Hann window and 95% overlap. Spectrogram settings differ slightly from what was used for analysis (see text for details) and were used to optimize visualization of the spectrogram for publication.
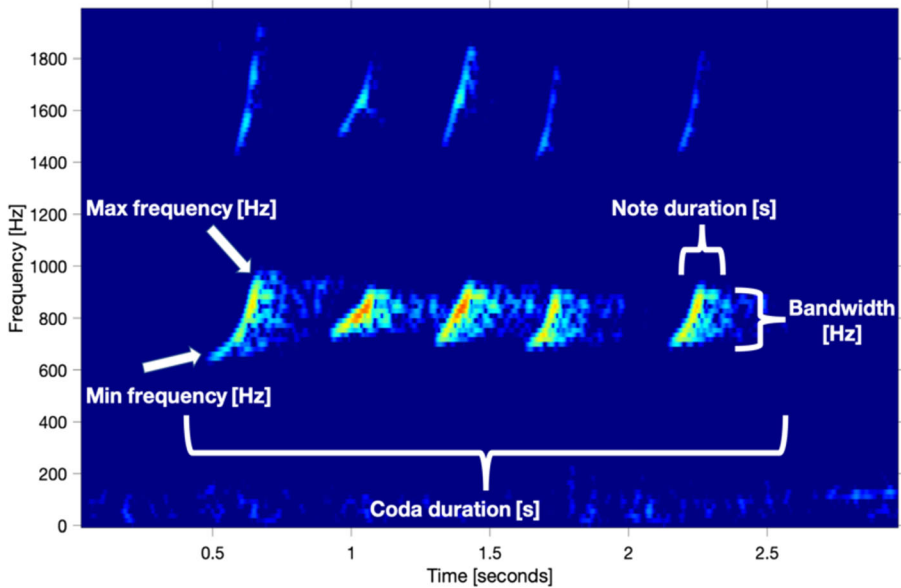
Fig. 3 Representative spectrogram of the male gibbon coda indicating how features were estimated. The spectrogram was made in the MATLAB®-based program Triton (Wiggins, 2003) with a 1600-point Hann window and 95% overlap. Spectrogram settings differ slightly from what was used for analysis (see text for details) and were used to optimize visualization of the spectrogram for publication.

We used R version 3.6.2 (R Core Team, 2020) to calculate 20 features for each coda using the Raven selection tables: coda duration, number of notes, the minimum, mean, and maximum values for 5% frequency, 95% frequency and bandwidth, note rate (number of notes/duration of coda) along with the duration, minimum, and maximum frequency for the first and second notes in the coda (Table I). As the choice of features is often subjective and can influence classification ability, we calculated a second set of features—Mel-frequency cepstral coefficients (MFCCs)—for each male coda. MFCCs were originally developed for human speech applications (Han *et al.,* 2006), and previous work has shown that MFCCs are highly effective features for discriminating between female gibbons of this species (Clink, Crofoot, & Marshall, 2018a; Clink & Klinck, 2020). Unlike feature extraction from the spectrogram, MFCCs are calculated over the entire signal and do not require researchers to make *a priori* decisions about which features to estimate.

To calculate MFCCs we used the R package tuneR (Ligges *et al.,* 2016). For the majority of classification problems each observation (in our case each male coda) must have a feature vector of equal length. Male codas in our dataset varied in duration from 0.42 s to 4.46 s, so to account for differences in duration we calculated MFCCs over a standardized number of time windows (8), which resulted in the same number of MFCCs for each coda regardless of duration. For each time window we calculated 12 MFCCs between 500 and 1500 Hz, which corresponds to the fundamental frequency range of the male coda. MFCCs do not provide information about how the signal changes over time, so to account for this we also included delta-cepstral coefficients that can provide information about temporal dynamics of a signal (Kumar *et al.* 2011).

Table I Description of features estimated for each male coda along with the mean, standard error, and range of values

Feature	Mean ± SEM	Range
Coda duration(s)	1.47 ± 0.11	0.34–4.46
Number of notes	3.3 ± 0.25	2–9
Minimum low frequency (Hz)	710.08 ± 15.6	506.03–925.93
Minimum high frequency (Hz)	925.79 ± 32.55	602.93–1345.83
Minimum bandwidth (Hz)	194 ± 22.44	32.3–527.56
Maximum bandwidth (Hz)	335.52 ± 27.12	53.83–689.06
Mean minimum frequency (Hz)	750.01 ± 14.06	516.8–960.38
Mean maximum frequency (Hz)	1011.2 ± 30.52	675.6–1399.66
Maximum low frequency (Hz)	789.95 ± 14.45	527.56–1087.43
Maximum high frequency (Hz)	1096.49 ± 34.23	710.6–1550.39
Mean bandwidth (Hz)	261.2 ± 22	50.24–565.25
Minimum note duration(s)	0.12 ± 0.01	0.03–0.35
Maximum note duration(s)	0.21 ± 0.02	0.05–0.63
Note rate (number of notes/duration)	2.31 ± 0.13	0.81–5.92
Note 1 duration(s)	0.14 ± 0.01	0.03–0.44
Note 1 minimum frequency (Hz)	744.6 ± 16.08	506.03–979.76
Note 1 maximum frequency (Hz)	1053.29 ± 37.88	602.93–1550.39
Note 2 duration(s)	0.16 ± 0.02	0.03–0.63
Note 2 minimum frequency (Hz)	772.38 ± 15.86	527.56–1087.43
Note 2 maximum frequency (Hz)	1021.58 ± 32.44	624.46–1496.56

We omitted the first MFCC for each time window, as this corresponds to the loudness of the signal (Muda *et al.*, 2010) and is not appropriate for signals recorded from unhabituated animals at various recording distances. This resulted in a vector for each coda that included 11 MFCCs and 11 delta cepstral coefficients for 8 time windows, and we also included the coda duration, which resulted in a vector with a length of 177 features.

Supervised Classification of Individuals

We used a support vector machine (SVM) supervised classification algorithm to test if we could effectively classify codas to the respective individual or site. A high classification accuracy at the individual or site level would indicate that coda features vary consistently between individuals or sites. As our data were two-factorial and contained multiple codas from multiple males from different sites, the use of linear discriminant function analysis (a commonly used supervised classification approach) was not appropriate (Mundry & Sommer, 2007). We implemented SVMs in the R package e1071 (Meyer *et al.*, 2020) using a radial basis kernel type and calculated the classification accuracy using leave-one-out cross-validation. We compared classification accuracy using the 20 features extracted from the spectrogram and classification accuracy using MFCCs.

Supervised Classification of Codas Emitted Under Different Contexts

The majority of pairs included in our study (49 out of 57 pairs; 836 out of 911 codas) were recorded in response to simulated territorial intrusions or playbacks. All the pairs that we recorded duetting spontaneously were from a single site (Kalabakan Forest Reserve). To test for differences in codas emitted spontaneously and under playback conditions we used SVMs as described above for all codas recorded at Kalabakan Forest Reserve, but in this case we tested for the ability to classify codas to two categories: playback or spontaneous duetting.

Reduced Dataset

Our original dataset consisted of 911 codas from 57 males from seven different sites. To avoid the potentially confounding influence of including codas emitted under different contexts, we removed the 75 codas emitted under spontaneous duetting conditions from our dataset. In addition, 29 of the codas in our original dataset contained just a single note. As many of the features we estimated from spectrograms required the codas to contain at least two notes we necessarily had to omit these codas from our dataset. Therefore, our reduced dataset—which we used for all subsequent analyses—consisted of 841 codas from 50 males from seven sites (Table II).

Multivariate, Variance Components Model

Supervised classification allows us to test for discriminability of codas but provides little insight into which specific call features vary. Therefore, to investigate which male coda features varied across individuals and sites we used a multivariate, variance

Table II Recording locations of Northern gray gibbons in Sabah, Malaysia along with number of males and codas

Site	Latitude	Longitude	Number of males	Number of codas (range per male)
Crocker Range National Park	5.2934	116.01360	2	19 (6–13)
Deramakot Forest Reserve	5.3322	117.40666	9	145 (6–38)
Danum Valley Conservation Area	4.5752	117.47651	5	125 (9–41)
Imbak Canyon Conservation Area	5.0662	117.02557	10	201 (6–53)
Lower Kinabatangan Wildlife Sanctuary	5.4978	118.17861	3	27 (8–10)
Maliau Basin Conservation Area	4.4528	116.53899	5	87 (7–25)
Kalabakan Forest Reserve	4.4224	117.35560	16	237 (4–37)
		Total	50	841

components model to investigate how variance was partitioned across the three levels in our dataset: intramale, intermale, and intersite. For this modeling approach, we focused only on the features estimated from the spectrogram, as these types of features are more appropriate for hypothesis testing and interpretation than MFCCs (Clink, Grote, *et al.,* 2018b). For example, it is difficult to interpret in a biologically meaningful way if there is a difference between males or sites in the second MFCC of the first time window, whereas a difference in duration of the first note of the male coda is much easier to interpret. In addition, due to the intensive computational costs and assumptions regarding a lack of multicollinearity among features we had to reduce the number of features we included in our model. We chose six coda features from our original dataset that were relatively uncorrelated (<0.4) for this modeling approach: coda duration(s), note 1 duration(s), note 1 maximum frequency (Hz), note 2 duration(s), note 2 maximum frequency (Hz), and note rate (number of notes over total duration).

We defined the model for investigating sources of variance in male codas as follows for coda c, male m, site s:

$$\mathbf{y}_{s,m,c} = \mathbf{a}_s + \mathbf{b}_m + \mathbf{e}_{s,m,c} \tag{1}$$

where $\mathbf{y}$ is the feature vector (log-transformed), $\mathbf{a}$ is the site-level random intercept, $\mathbf{b}$ is the male-specific random intercept, and $\mathbf{e}$ is the coda-specific error term. The terms $\mathbf{a}$, $\mathbf{b}$, and $\mathbf{e}$ correspond to intersite, intermale, and intramale sources of variance respectively, and the variance/covariance matrices are defined as $\Sigma_\mathbf{a}$, $\Sigma_\mathbf{b,}$ and $\Sigma_\mathbf{e}$. Further details about model development can be found in (Clink, Grote, *et al.,* 2018b; Lau *et al.,* 2018).

To measure the relative contribution of the three levels in our dataset to the total variance, we calculated intraclass correlation coefficients (ICCs). For each of the six features in our reduced dataset, we calculated ICC at each level l from the posterior samples of $\Sigma_\mathbf{a}$, $\Sigma_\mathbf{b}$, and $\Sigma_\mathbf{e}$ as follows:

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

ICC values range from 0 to 1, and an ICC value close to 1 indicates that the particular level is an important source of variation (Merlo *et al.,* 2005). To fit the model we used the R package rstan (Stan Development Team, 2020). We ran two separate Markov chains for a total of 3000 iterations with a warmup of 1500 iterations. Inspection of trace plots of model parameters and convergence diagnostics indicated that mixing of chains was sufficient for inference.

Acoustic Dissimilarity as a Function of Distance

To investigate small-scale patterns of geographic variation in male codas, we focused our analysis on a subset of males that came from a single site that had the largest sample size (Kalabakan Forest Reserve; $N = 16$ males). For this analysis we used the 20 features extracted from the spectrogram and calculated the Euclidean distance between all features for each pair of male codas. This resulted in an acoustic dissimilarity measure for each pair of codas, with a value of zero indicating no dissimilarity (i.e., the codas were exactly the same) and large

values indicating that the codas are substantially different. We also calculated the geographic distance between recording locations using the GPS points of the recording locations. We removed pairs of codas with a geographic distance of zero (e.g., codas recorded from the same male) as including these observations would have biased our results to show that males recorded closer together have calls that are more similar. We used a smoothing spline to fit a smooth curve to the pairs of observations using a smoothing parameter of 1. To obtain a 95% confidence band, we resampled the observed pairs (with replacement) 1000 times, fit the spline as outlined in the preceding text to each bootstrapped sample, and calculated quantiles from the aggregated curves (Clink *et al.,* 2017).

Data Visualization

We used a uniform manifold learning technique (UMAP) to visualize clustering of male codas at the individual level. UMAP is a dimensionality reduction technique that has been successfully used to visualize differences in distinct taxonomic groups of birds (Parra-Hernández *et al.,* 2020), forest soundscapes (Sethi *et al.,* 2020), and female gibbon vocalizations (Clink & Klinck, 2020). We implemented UMAP using both features extracted from the spectrogram and MFCCs using the R package umap (Konopka, 2020) and plotted the results using the ggplot2 package (Wickham, 2016).

Ethical Note

Approval for the collected data was granted by the Sabah Biodiversity Council [access license number: JKM/MBS 1000-2/2 JLD.3 (42)] and data were collected in accordance with the University of California, Davis, Institutional Animal Care and Use Committee (IACUC) Protocol 29-30. The authors declare there are no conflicts of interest.

Data Availability and R Code

All data and R code needed to recreate our analyses are openly available on GitHub: https://github.com/DenaJGibbon/Variation-in-male-gibbon-codas.

Results

Supervised Classification of Codas Emitted Under Different Contexts

We found that we could assign male codas from Kalabakan Forest Reserve to the correct recording condition—spontaneous duet (N = 75) or duet produced under a simulated territorial intrusion (N = 253)—with 90.2% accuracy.

Supervised Classification of Individuals and UMAP Projections

We were able to assign codas to their respective male using SVM and leave-one-out cross validation with a 51.4% accuracy using features from the spectrogram and a
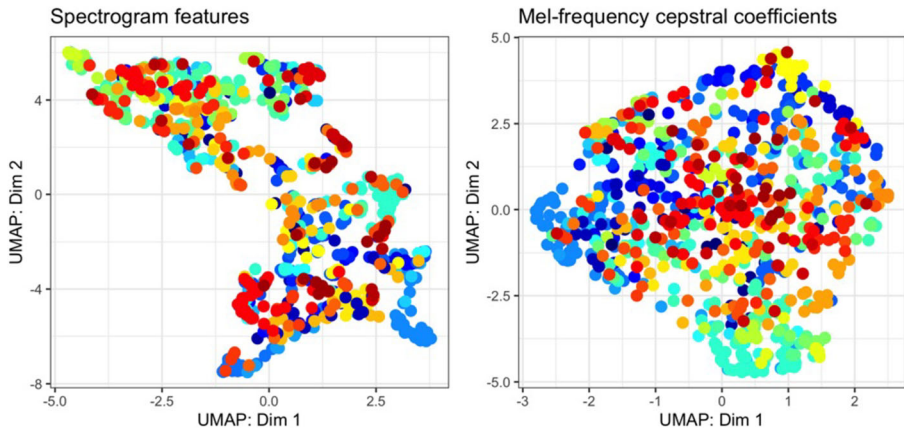
Fig. 4 UMAP projections for 841 codas from 50 Northern gray gibbon males in Sabah, Malaysia from January 2013 to September 2016. Each point represents a two-dimensional embedding of a single male coda. The plot on the left was made using features extracted from the spectrogram and the plot on the right was made using MFCCs (see Methods for details). The color of the points indicates codas from an individual male.

62.3% accuracy using MFCCs. We were able to classify male codas to the correct site with a 62.8% accuracy using features extracted from the spectrogram and 73.6% using MFCCs. UMAP projections of spectrogram features and MFCCs estimated from male codas did not show clear evidence of clustering by individual male (Fig. 4).

Sources of Variance

We did not find that site-level variance was an important source of variance for any of the features, as the ICC values were all close to zero (Fig. 5). For two of the features (note 1 and note 2 maximum frequency) intermale variance was the most important source of variance. For the rest of the features (note 1 and note 2 duration, coda
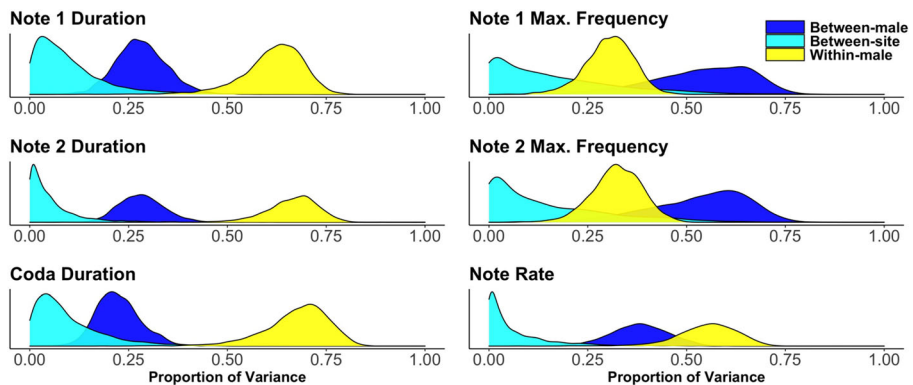
Fig. 5 Posterior densities of intraclass correlation coefficients for six features estimated from Northern gray gibbon male codas recorded in Sabah, Malaysia from January 2013 to September 2016. For the majority of the features intramale variance was the most important source of variance, but for two features (note 1 and note 2 maximum frequency) intermale variance was the most important source of variance. For each plot the *y*-axis refers to density and values are not shown, as only relative densities matter.

duration, and note rate) intramale variance was the most important source of variance, indicating that these features vary substantially within a single duet bout.

Acoustic Dissimilarity as a Function of Distance

There was no evidence for small-scale patterns of geographic variation, as there was neither a positive or negative relationship between call similarity and geographic distance (Fig. 6). This means that males were equally likely to have codas that were similar or dissimilar regardless of the location of their territories. The confidence band is very narrow for these data, indicating relatively high levels of certainty.

Discussion

Unlike the calls of many primates (Clink *et al.,* 2017, 2019; Fedurek *et al.,* 2016; Leliveld *et al.,* 2011; Spillmann *et al.,* 2017) we did not find substantial evidence for individual signatures in male gibbon codas, as our classification ability was relatively low (<63%). These findings were further supported by our second approach wherein we quantified sources of variance in a subset of coda features. We found that intermale variance was the most important source of variance for only two of the six features (the maximum frequency of the first and second notes of the coda), whereas intramale variance was the most important for the other features. In contrast to many previous studies—including one on the female contribution to the duet in this gibbon species (Clink, Grote, *et al.,* 2018b)—we did not find evidence for site-level patterns of variation in any of the male coda features we examined. Lastly, when we investigated spatial patterns of variation across a single site, we did not find that males that had territories closer together were more or less likely to have dissimilar codas. Our findings that show substantial intraindividual variation in coda features is in line with
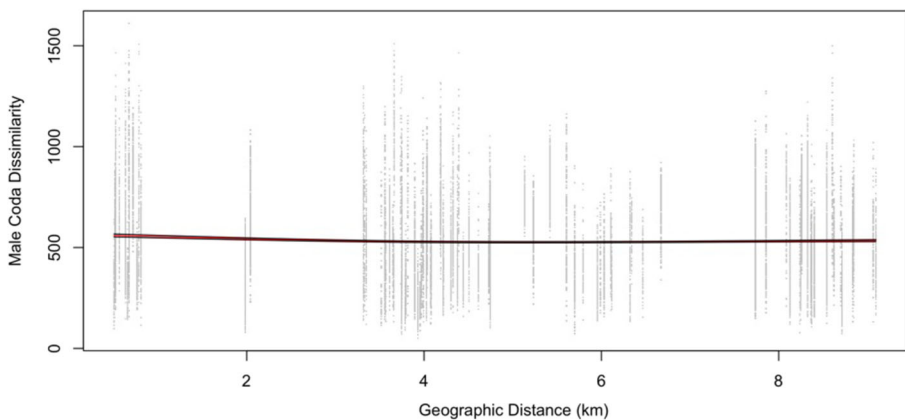
Fig. 6 Acoustic dissimilarity of male gibbon codas as a function of distance recorded in the Kalabakan Forest Reserve, Sabah, Malaysia from January 2013 to September 2016. Individual points represent pairwise distance between pairs of male codas (dissimilarity) and recording locations (geographic distance). The curve is a smoothing spline with 95% bootstrap confidence band.

previous work on white-handed gibbons that showed male codas change substantially over the course of a duet bout (Terleph *et al.,* 2018b).

Relative to many studies of primate vocalizations that obtain recordings from habituated animals, we were able to record a relatively large sample size of duetting males because we focused on recording unhabituated animals. But there are some potential limitations to our methods. First, although we distinguished between pairs based on a combination of recording location and group demography, it is possible that we recorded the same pair on two different days and classified it as two separate pairs. In this case, our classification accuracy would be reduced. The fact that we were able to distinguish between the female duet contribution from the same recordings used in the present study with a relatively high accuracy [>90% accuracy for 53 females (Clink & Klinck, 2020)] indicates that our lower classification accuracy for male codas is not due to misclassification of males, but rather a reflection of the reduced individuality of male codas. Second, the majority of our recordings were taken in response to simulated intrusions or playbacks. We did this to augment data collection, and our sample size would have been substantially smaller if we did not use playbacks to elicit a vocal response. We found that we could classify male codas from a single site to the correct context (playback or spontaneous duet) with *ca.* 90% accuracy. We interpreted this result to mean that there were potentially important differences between codas emitted under these two contexts. As only a small portion of our original dataset (*ca.* 8% of calls) were recorded under spontaneous conditions we opted to remove these codas for subsequent analyses to avoid any potentially confounding factors. There is evidence that birds modify vocal output under simulated territorial intrusions (Hall, 2000; Hall & Peters, 2008; Illes & Yunes-Jimenez, 2009), and future systematic studies that compare duets and codas emitted under spontaneous and simulated territorial intrusion scenarios will be highly informative.

The lack of individual signatures in male codas may provide some insight into the (potential) function of this call type. Our classification accuracy of 51.4% accuracy (spectrogram features) or 62.8% accuracy (MFCCs) was substantially higher than chance (*ca.* 2.0%) but was much lower than that of female gibbons of this species [>90% for 53 females (Clink & Klinck, 2020)]. As the choice of spectrogram features can often be subjective, we aimed to capture more of the variation in the codas by using MFCCs as features. Although our classification accuracy improved substantially when using MFCCs, it was still lower than the classification accuracy of male solo phrases of this species [*ca.* 85% accuracy for 13 males (Clink *et al.,* 2020a)], but similar to that of white-handed-gibbon male coda classification [*ca.* 50% accuracy for 12 males; (Terleph *et al.,* 2018b)]. Individual signatures in animal vocalizations can arise through a combination of neutral and adaptive evolutionary forces, and in cases in which there is a strong individual signature, it is generally presumed that one of the functions of the call is to confer information about the individual (e.g., caller location) to conspecifics (Tibbetts & Dale, 2007). In the case of gibbon duets, it appears that the female contribution to the duet—likely used in combination with calling location given the territorial nature of gibbons—provides cues to individual (or pair) identity, whereas the male coda serves a different function.

Our analysis of intra- and intermale variance revealed that intermale variance was the most important source of variance for two features: the maximum frequency of the first and second notes. These findings are in line with previous work showing that the frequency of male gibbon solos is correlated with androgen levels, which vary across

individuals (Barelli *et al.,* 2013). Therefore, it seems likely that variation in the maximum frequency of the notes in male codes in our dataset is also related to varying androgen levels. Although little is known about how (and if) call features are heritable, there is evidence that overall structure of gibbon duets is determined by genetics, as shown by hybrid studies (Geissmann, 1984; Tenaza, 1985). This is in stark contrast to many songbirds that learn their songs during development (Kroodsma & Baylis, 1982). In taxa that exhibit vocal learning, microgeographic variation in vocalizations may arise through song sharing or vocal copying errors (Podos & Warren, 2007). Whereas variation in calls that are innate (e.g., not learned) is generally predicted to covary with genetic relatedness or distance (Wright *et al.,* 2001). The genetic structure of Northern gray gibbons across their range has not yet been investigated, and further studies that investigate genetic structure and patterns of variation in different call types will be informative and help elucidate why there are site-level patterns of variation in the female, but not male, contribution to the duet in this species.

In addition to investigating large-scale patterns of geographic variation (on a scale of 100–200 km) we were also interested in small-scale patterns of variation at a single site (*ca.* 10 km). The fact that we did not find patterns consistent with either of our predictions (e.g., neighboring groups would be more or less similar to their neighbors) warrants further research into the mechanism(s) in which call features develop and are maintained across individuals. Future longitudinal studies that determine similarity of call features among parent and offspring will be particularly useful for improving our understanding of the mechanisms that shape patterns of vocal variation in gibbon vocalizations.

In conclusion, patterns of variation in Northern gray gibbon male codas showed high levels of intraindividual variability. This may be due in part to the fact that gibbon codas have been shown to increase in complexity over the course of the duet (Terleph *et al.,* 2018b), which would lead to substantial variability of codas within a single duet bout. This is consistent with our findings of substantial intramale variance and a lower classification accuracy relative to other call types in this species (Clink *et al.,* 2020a). Importantly, the results we report are based on codas that were emitted under a simulated territorial intrusion context, and further work that investigates differences between codas emitted spontaneously and under playback conditions will help improve our understanding of the functions of the male coda, along with the generalizability of our results. There is still much to be learned about the male and female contribution to the duets of Northern gray gibbons and other species of gibbon. In particular, future studies that can tease apart the relative importance of genetic versus learning in shaping call features will help improve understanding of how variation in gibbon vocalizations arises. In addition, a better understanding of the function(s) of the duet, along with the male and female contributions, can be obtained through carefully designed playback studies, and future studies elucidating the different functions of duets and the distinct call types will be highly informative.

Ethical Note The authors declare there are no conflicts of interest.

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