



# Evidence for High Variability in Temporal Features of the Male Coda in Müller's Bornean Gibbons (*Hylobates muelleri*)

Allison R. Lau, et al. [full author details at the end of the article]

Received: 27 November 2017 / Accepted: 17 July 2018 / Published online: 8 September 2018  
© Springer Science+Business Media, LLC, part of Springer Nature 2018

## Abstract

Most pair-living primate species engage in duets, wherein males and females produce coordinated vocalizations. Previous analyses of male gibbon contributions to the duet have shown that calls are individually distinct. Here we investigate variation in the temporal and spectral parameters in the male contribution to the duet, also known as the coda, of wild, nonhabituated male Müller's Bornean gibbons (*Hylobates muelleri*), recorded both opportunistically and as a response to playbacks at the Stability of Altered Forest Ecosystems site in Sabah, Malaysia. We used linear discriminant function analysis to estimate the intra- and interindividual variation in 13 spectral and temporal parameters of the vocalizations ( $N=337$ ) of 31 male gibbons. To further understand how call features vary within and between individuals we used a multivariate, variance components model to investigate how variance in features was partitioned at these two levels. We could identify males with a 66% accuracy using leave-one-out cross-validation, a relatively low score compared to female Müller's Bornean gibbons and males of other species. We found that for some features (such as maximum frequency of the notes) most of the variance occurred between males, but for others (specifically total duration of the call and duration of rest in between notes) most of the variance occurred within a single male. Overall, male Müller's Bornean gibbon coda vocalizations showed greater variability relative to their female counterparts, raising questions about potential differences in the function of the male and female contributions to the duet in Müller's Bornean gibbons and the gibbon taxon as a whole.

**Keywords** Discriminant function analysis · Individuality · Multivariate variance components model · Stability of altered Forest ecosystems site · Vocalization

---

Handling Editor: Joanna M. Setchell

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s10764-018-0061-7>) contains supplementary material, which is available to authorized users.

## Introduction

Duets, or the coordinated vocalizations of male and female individuals, occur in a broad range of taxa, including insects (Bailey 2003), frogs (Tobias *et al.* 1998), birds (Langmore 1998; Sonnenschein and Reyer 1983), and primates (Geissmann 2002; Geissmann and Orgeldinger 2000; Mitani 1985a). The function of vocal duets is the topic of much debate, with the major explanatory hypotheses being 1) maintenance of contact between mated pairs in dense forest (the acoustic contact hypothesis: Thorpe 1963); 2) joint territory defense and maintenance of intergroup spacing (Mitani 1985a); 3) strengthening of the pair bond (Geissmann 1999; Geissmann and Orgeldinger 2000); 4) mate guarding (Sonnenschein and Reyer 1983); and 5) advertisement of the pair-bond (Cowlshaw 1992). With such a broad range of species displaying duetting behavior, it is likely that duetting serves different functions. However, the repeated, independent evolution of coordinated singing between males and females in a variety of taxa suggests strong selection for duets over solo singing (Marshall-Ball *et al.* 2006).

Gibbons are pair-living apes that regularly engage in species-specific duets (Geissmann 2002; Marshall and Marshall 1976). Gibbons typically live in small groups composed of a male and female in addition to one or more juvenile offspring (Cowlshaw 1992). In duetting gibbon species, the duet comprises a repeated set of stereotyped vocalizations (Marshall and Marshall 1976). These components are typically sex specific and must be sung in a specific order to convey the full message of the territorial signal. For example, when they are played back in a different order than they are usually sung, the duet elicits a weaker vocal response from nearby groups than an intact duet (Mitani and Marler 1989). Some species of gibbons include male coda vocalizations in their duets, which are species specific in terms of spectral characteristics and note organization, but always occur directly following the female great call (Marshall and Marshall 1976). The male coda vocalization changes in complexity over the course of the duet (Terleph *et al.* 2017). Although males do vocalize during other portions of the duet, the male coda is particularly important because males change the onset of their coda to match when females vocalize (Terleph *et al.* 2017).

Male and female gibbons make individually distinct contributions to the duet (Marshall and Marshall 1976). Most studies of individuality in gibbon vocalizations focus on females (white-handed gibbon [*Hylobates lar*: Terleph *et al.* 2015], Müller's Bornean gibbon [*H. muelleri*: Clink *et al.* 2017], silvery gibbon [*H. moloch*: Dallmann and Geissmann 2009], agile gibbon [*H. agilis*: Haimoff and Gittins 1985]), probably because of the elaborate nature of their calls. The duet vocalizations of male gibbons are generally thought to be more variable than those of females (Cowlshaw 1992), but there is still evidence that they are individually identifiable. The duet vocalizations of male black-crested gibbons (*Nomascus concolor*) and the duet vocalizations of Cao-vit gibbons (*N. nasutus*) show strong song stability: each call can be accurately connected to a single individual (1 yr. of stability documented for *N. concolor* [Fan *et al.* 2011], 2–6 yr. of stability documented for *N. nasutus* [Feng *et al.* 2014]). For male Bornean white-bearded gibbons (*H. albibarbis*), individuality of duet vocalizations has been documented within notes, phrases, and song bouts (Wanelik *et al.* 2012).

Müller's Bornean gibbons (*Hylobates muelleri*) live in the northeast portion of Borneo in Sabah, Malaysia. This pair-living species elicits species-typical vocal duets with sex-specific vocalizations, similar to the rest of their genera. The *H. muelleri* duet

begins with the adult female's "wa" vocalizations, followed by a vocalization by the adult male (Mitani 1985c). After this introduction, the female utters her first great call, which is often followed by the male coda. Throughout the duet, the female continues to produce great call vocalizations while the male follows with codas. The male tends to perform a brachiating display following his coda. Interspersed between repetitions of the great call and coda are vocalizations in which the male and female overlap (Mitani 1985c). The male coda is shorter and less complex than the female great call. *H. muelleri* use vocal territory defense as a mechanism of reinforcing monogamy (Mitani 1984); groups define home ranges based on broadcasted vocalizations (Mitani 1985a); groups respond differently to playbacks broadcasted in, on the edge of, and outside the group's territory (Mitani 1985b); gibbons do not respond differently to playbacks of self, neighbor, or stranger groups (Mitani 1985c); and female great call duet vocalizations are individually identifiable (Clink *et al.* 2017), but individuality in male coda vocalizations has not yet been investigated in this species.

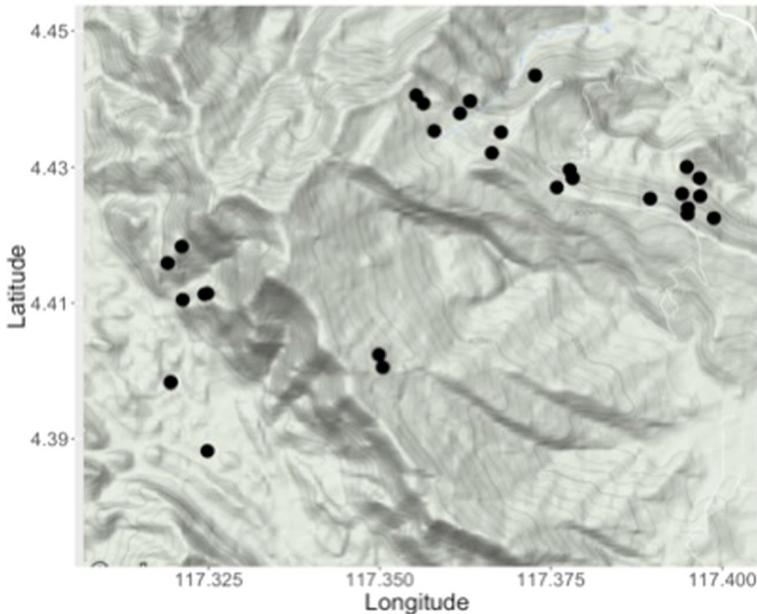
Based on findings that other male gibbon vocalizations are individualized (Fan *et al.* 2011; Feng *et al.* 2014; Wanelik *et al.* 2012), we hypothesized that there is a similar pattern of individuality in male *Hylobates muelleri* codas. If this is the case, we predicted that male *H. muelleri* will be identifiable based on temporal and spectral characteristics of their calls.

## Methods

### Data Collection

We recorded gibbons at the Stability of Altered Forest Ecosystems (SAFE) site in Sabah, Malaysia (Ewers *et al.* 2011) from 2013 to 2015 (Fig. 1). We collected recordings using a Marantz PMD 660 solid-state digital flash recorder and a RODE NTG-2 directional condenser microphone at a sampling rate of 44.1 kHz and 16-bit resolution.

We recorded gibbons opportunistically during spontaneous duets ( $N=12$ ) and in response to playback recordings used to attract and elicit vocal responses from focal gibbon groups ( $N=19$ ). A previous analysis of female gibbons from the site showed that there were no differences between recordings taken during different field seasons or with playback vs. non-playback methods (Clink *et al.* 2017) and we tested for this in the male codas. We collected recordings between 05:30 h and 10:00 h. All playbacks used the same recording, and were transmitted via a Roland CUBE Street EX 4-Channel 50-W Battery Powered Amplifier. We used a playback vocalization of a gibbon group of the same species recorded ca. 90 km from SAFE at another field site, Maliau Basin Conservation Center, and was equally foreign to all gibbon groups (Brockelman *et al.* 1998) in SAFE. We chose the playback vocalization for the high signal-to-noise ratio, and inclusion of the female great call, male coda, and portions of the duet where both the male and female overlap. We conducted one 15-min playback (five repetitions of a 3-min duet recording taken from the beginning of the duet) at each recording location. The playback vocalization contained 10 female great calls, 3 male codas, and other typical coordinated male and female vocalizations. We aimed to reduce exposure of groups to playbacks by playing them for the minimum amount of



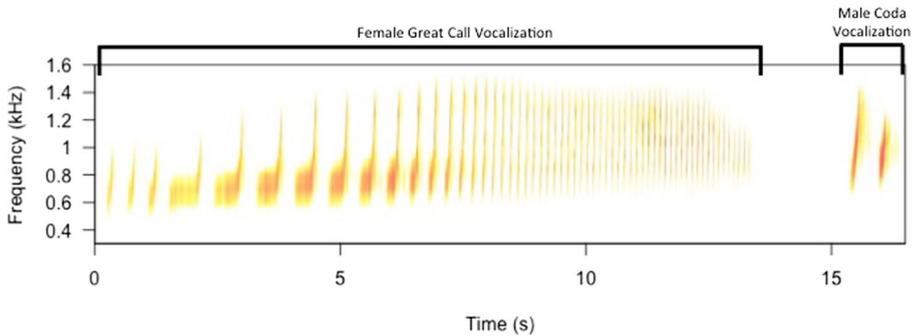
**Fig. 1** Map of 31 recording locations of male *Hylobates muelleri* vocalizations recorded from 2013 to 2015 at the Stability of Altered Forest Ecosystems site in Sabah, Malaysia.

time possible. On hearing a vocal response from a gibbon group, we cut off the playback to record the elicited duet. If 15 min passed with no response from a gibbon group, we abandoned the site and no further playback attempts were made. We found that most groups, if they were going to respond, generally responded in <3 min.

We considered groups recorded >500 m away from each other as separate groups (Brockelman *et al.* 1998). We conducted playbacks along established trail systems at our site ca. every 300 m, or every 500 m if a group responded to the playback, as this is the documented width of gibbon territories (Brockelman and Srikosamatara 1993). We aimed to reduce the exposure of groups to playbacks by conducting playbacks only once at each point, although it is possible that neighboring groups heard the playback on the edge of their territories before we moved to the presumed center. We randomly selected one recording for analysis in the event two recordings were taken within 500 m of each other. We collected recordings during five field seasons.

### Acoustic Analysis

Our analysis focuses on the male coda of the duet, which we define as calls that begin within the 5 s of the end of the female great call (Fig. 2). If we recorded a male gibbon during more than one recording session, we chose the recording in which the male gibbon vocalized the greatest number of times to accumulate the largest sample size. We did not use other recordings to minimize the risk of incorrectly identifying groups between recording sessions and to adhere to the assumptions of linear discriminant analysis. The calls analyzed here are distinct from male solo vocalizations, which occur early in the morning before the duet begins and in which only male gibbons sing. We



**Fig. 2** Spectrogram of male and female duet vocalizations of *Hylobates muelleri* recorded between 2013 and 2015 at the Stability of Altered Forest Ecosystems site in Sabah, Malaysia.

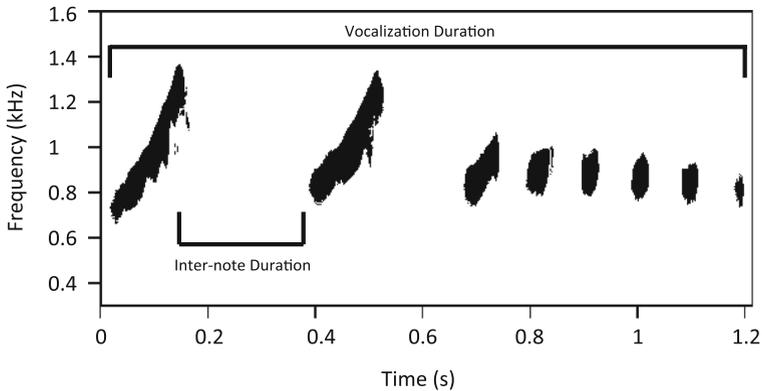
did not use recordings in which more than one male sang simultaneously or a female consistently overlapped with the male coda.

We created spectrograms using Raven Pro 1.5 Sound Analysis Software (Bioacoustics Research Program 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 manually selected all notes, thus eliminating the risk for interobserver error, and a selection table automatically extracted 13 spectral and temporal parameters of interest. We used spectral parameters from each of the first two notes including 95% frequency, start frequency, end frequency, note duration, and bandwidth (Table I). We extracted temporal parameters from each vocalization: number of notes per vocalization, internote duration (duration of rest between the first two notes), and total duration of the vocalization (Table I; Fig. 3).

**Table I** Table of spectral and temporal parameters extracted from male *Hylobates muelleri* codas recorded between 2013 and 2015 at the Stability of Altered Forest Ecosystems site in Sabah, Malaysia

Spectral and temporal parameters	Definition
95% Frequency (Hz)	Highest frequency achieved during the 95% percentile of the selection, similar to maximum frequency
Start frequency (Hz)	Frequency at the beginning of the note, calculated from the first five values from peak frequency contour
End frequency (Hz)	Frequency at the end of the note, calculated from the last five values from peak frequency contour
Note duration (s)	Duration of the note
Bandwidth (Hz)	The difference between the frequency 5% and frequency 95% of the note
Number of notes	Number of notes in the male coda
Internote interval (s)	Interval between first two notes of the male coda
Vocalization duration (s)	Duration of the entire coda

We measured the first 5 parameters individually for the first 2 notes of each male coda; we measured the last 3 parameters once for the entire coda for a total of 13 parameters



**Fig. 3** Spectrogram of a male Müller's Bornean coda recorded at the Stability of Altered Forest Ecosystems site in Sabah, Malaysia between 2013 and 2015. Internote interval and vocalization duration temporal parameters are shown.

To assess individuality, we used discriminant function analysis (DFA), a supervised analysis that uses the extracted parameters to maximize differences between vocalizations of each individual. Male codas varied widely in number of notes ( $N = 2$  to  $N = 10$ ) and duration (Fig. 4). DFA requires that each call vector must be the same length and must have the same features (Venables and Ripley 2002), so we used only the first two notes of each vocalization for this analysis. We used number of notes in the vocalization and duration of entire vocalization to capture variability in codas longer than two notes (Clink *et al.* 2017; Wanelik *et al.* 2012).

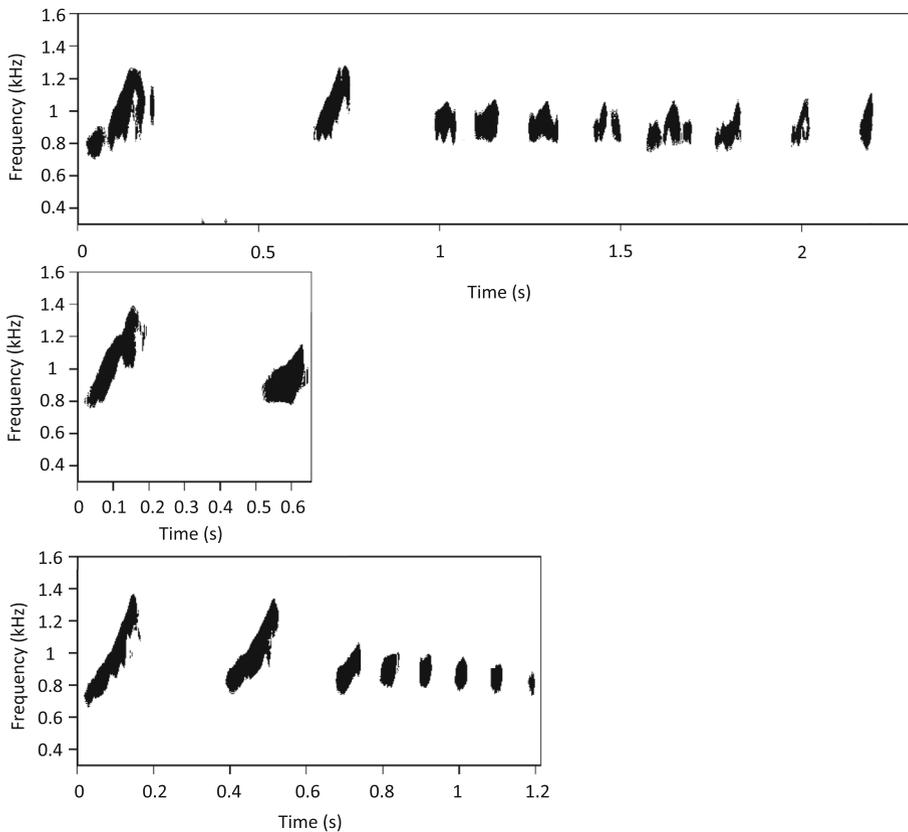
### Linear Discriminant Function Analysis

We compared the male codas using DFA of each vocalization based on the 10 temporal and 3 spectral parameters estimated for each call (Venables and Ripley 2002). We used leave-one-out cross validation (LOOCV) to assess the results of the DFA. LOOCV takes one vocalization out of the sample, runs the DFA with all other vocalizations, and then attempts to assign the excluded vocalization to the correct individual. We reran this analysis using our complete dataset, then again separately using spontaneous vocalizations and vocalizations elicited by playbacks to compare the results between playback-elicited and spontaneous duetting. We used a chi-square test of independence to test for significant differences in DFA with LOOCV between these three methods (playback-elicited, spontaneous, and all).

### Multivariate Variance Components

We used a multivariate, variance components model created using the rstan package (Guo *et al.* 2016) to assess the proportion of variance attributed to each of our two levels, call and male. We defined our model for call (individual vocalization)  $c$ , and male  $m$ , as

$$y_{m,c} = a_m + e_{m,c}$$



**Fig. 4** Spectrograms of three different male *Hylobates muelleri* codas recorded between 2013 and 2015 at the Stability of Altered Forest Ecosystems Site in Sabah, Malaysia.

where  $y$  is the log-transformed feature vector,  $a$  is a male-specific random intercept, and  $e$  is a call-specific error term (Clink *et al.* 2018). At both levels, variance/covariance matrices measure the variability of each acoustic feature in addition to the covariance between different features. The matrices for  $a$  and  $e$  are defined as  $\Sigma_a$  and  $\Sigma_e$ .

We used a multivariate  $t$  distribution for the two additive terms, which allows for probability far from the mean of the observations (Roth 2013). We used the formulas  $\Sigma_a = \nu_a \Phi_a / (\nu_a - 2)$  and  $\Sigma_e = \nu_e \Phi_e / (\nu_e - 2)$ , where  $\nu_a$  and  $\nu_e$  are degrees of freedom parameters and  $\Phi_a$  and  $\Phi_e$  are scale matrices, to derive the variance/covariance matrices  $\Sigma_a$  and  $\Sigma_e$ . We further decomposed the scale matrices as  $\Phi_a = D_a \Omega_a D_a$ , where  $D_a$  is a diagonal matrix and  $\Omega_a$  is a correlation matrix (Stan Development Team 2016). We used a half-Cauchy prior for the elements of  $D_a$ , and used scale parameter = 5. We used an LKJ prior for  $\Omega_a$ , and used parameter 1.5 (Stan Development Team 2016).  $\Phi_e$  was parameterized following the same methods. We used a gamma prior with shape = 2 and rate = 0.1 for  $\nu_i$  truncated on the left at the value 2 to prevent singularities in expressions like  $\Sigma_a = \nu_a \Phi_a / (\nu_a - 2)$ .

We first generated 2500 warm-up samples, then followed with 500 parameter samples from both of two Markov chains, for a total of 1000 samples for posterior inference. Computing took ca. 25 min using a MacBook Air with 1.3 GHz Intel Core.

We calculated intraclass correlation coefficients (ICCs) that measure the relative contributions of male-to-male variation, and call-to-call variation, to the overall variance (Merlo *et al.* 2005). We calculated the ICC at level  $l$  for each feature from posterior samples of  $\Sigma_a$  and  $\Sigma_e$  as

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

ICC values range from 0 to 1, as the diagonals of  $\Sigma_a$  and  $\Sigma_e$  can only be positive. An ICC near 1 suggests that the level (male or vocalization) is contributing a large amount of variance (Merlo *et al.* 2005).

We checked the goodness of fit of our model using a Q–Q plot of posterior mean distances between observations and their predicted values, vs. an appropriate  $F$  distribution (Clink *et al.* 2018). We used packages and functions of the R programming language for all analyses in this study (R Core Team 2015). We ran the analysis using our full dataset, and then reran the analysis separately for spontaneous vocalizations and vocalizations elicited by playbacks to compare the results between our two methods of vocalization collection.

**Ethical Note** No animals were handled in this study. We collected all recordings noninvasively. We conducted all fieldwork under the permission of the Sabah Biodiversity Centre JKM/MBS 1000–2/2(90). This study follows all applicable laws in Malaysia and the United States of America.

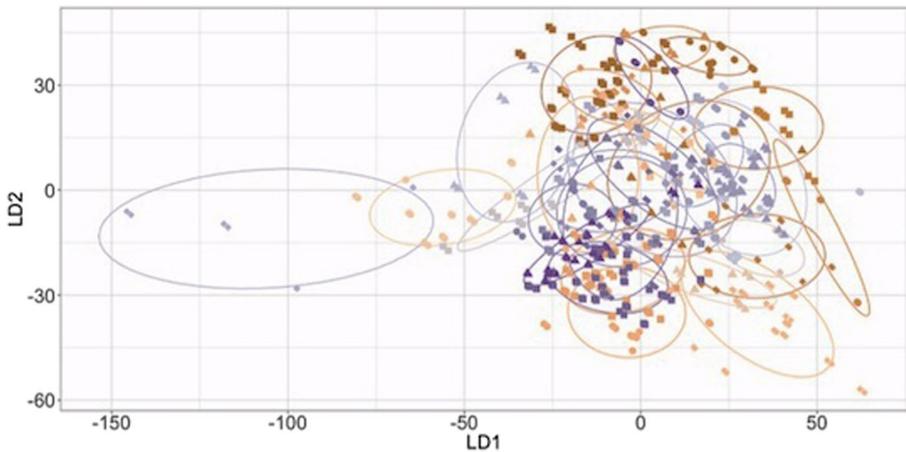
The authors declare that they have no conflict of interest.

**Data Availability** The datasets analyzed (Online Resource 1) during the current study are available as electronic supplementary material along with the corresponding R script (Online Resource 2). The raw wav files are available from the corresponding author on reasonable request.

## Results

### Evidence of Reduced Vocal Individuality

Our analysis of 337 codas by 31 male gibbons could identify individual males with 66% accuracy (Fig. 5). The overlap in the DFA plot does not fully describe the amount of variation seen in male gibbon duet vocalizations as the plot represents 13 dimensions of analysis on a 2-dimensional plane (Table II). Our analysis of spontaneously recorded vocalizations ( $N = 12$  gibbons,  $N = 131$  vocalizations) could identify male gibbons with 77% accuracy, while our analysis of playback-elicited vocalizations ( $N = 19$  gibbons,



**Fig. 5** Scatterplot of the first two linear discriminants for male gibbon *Hylobates muelleri* ( $N=31$ ) coda vocalizations ( $N=337$ ) recorded between 2013 and 2015 at the Stability of Altered Forest Ecosystems site in Sabah, Malaysia. Each point represents a single vocalization. Ellipses represent the 90% confidence interval for each gibbon.

$N=206$  vocalizations) could identify male gibbons with 71% accuracy. Our chi-squared test revealed a significant difference between the accuracy of DFA with LOOCV for spontaneous vocalizations, playback-elicited vocalizations, and all vocalizations together,  $\chi^2(2, N=3) = 2.97, P = 0.23$ .

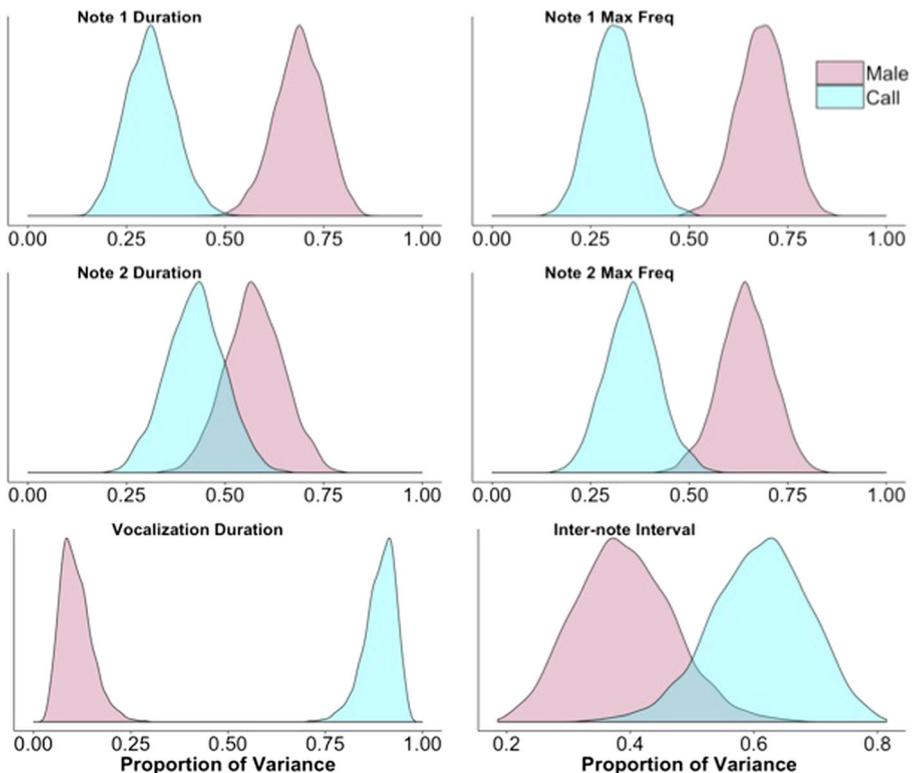
### Sources of Variance in Male Gibbon Vocalizations

Based on our multivariate, variance components model, variance between individuals explained more of the total variance for our note-specific features (note 1 duration, note

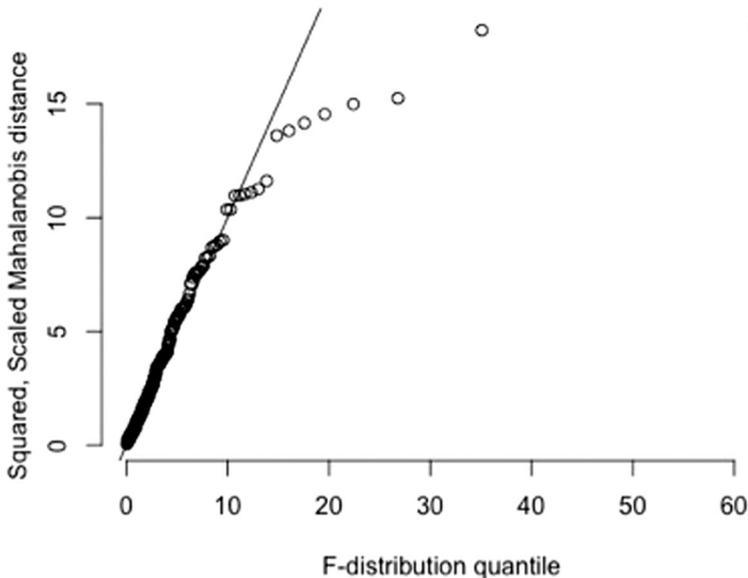
**Table II** Spectral and temporal parameters for male *Hylobates muelleri* codas recorded between 2013 and 2015 at the Stability of Altered Forest Ecosystems site in Sabah, Malaysia

Parameter	Note	Mean $\pm$ SD	Range
95% Frequency (Hz)	1	1084.8 $\pm$ 136.3	732.1–1421.2
	2	1044.2 $\pm$ 123.3	732.1–1378.1
Start frequency (Hz)	1	759.2 $\pm$ 71.6	611.5–1042.2
	2	785.1 $\pm$ 62.6	628.8–975.0
End frequency (Hz)	1	1055.6 $\pm$ 139.3	712.5–1369.5
	2	1006.6 $\pm$ 126.6	697.7–1395.4
Duration (s)	1	0.14 $\pm$ 0.04	0.05–0.33
	2	0.14 $\pm$ 0.06	0.06–0.54
Bandwidth (Hz)	1	315.0 $\pm$ 108.0	86.1–602.9
	1	255.6 $\pm$ 95.2	86.1–559.9
Number of notes	n/a	3.8 $\pm$ 1.5	2–10
Internote interval (s)	n/a	0.36 $\pm$ 0.21	0.04–1.92
Vocalization duration (s)	n/a	1.28 $\pm$ 0.47	0.32–2.74

1 maximum frequency, note 2 duration, and note 2 maximum frequency) than variance in the vocalizations of one individual (Fig. 6). For example, the posterior density estimates of ICCs for individual-level variance in note 1 duration (ICC posterior mean = 0.69; 95% credibility interval = (0.56, 0.80)) and note 1 maximum frequency (mean = 0.69; CI = (0.56, 0.80)) were higher than the posterior density estimates of ICCs for vocalization-level variance. Note 2 had a similar pattern (Fig. 6). For two features, vocalization duration (mean = 0.89; CI = 0.80, 0.95) and internote interval (mean = 0.61; CI = 0.45, 0.75), vocalization-level variance explained more of the total variance than individual-level variance. This shows that while the first two notes of the male coda are consistent within one male's vocalizations, the duration of the coda vocalization and number of notes varies across vocalizations of one male. Our goodness of fit test showed that the agreement between the empirical and theoretical quantiles is good for all observations (Fig. 7). When we analyzed spontaneous and playback vocalizations separately, there were no major differences in our results; the relative proportion of variance for each parameter did not change when we ran the data separately.



**Fig. 6** Posterior densities of intraclass correlation coefficients for six spectral and temporal parameters of the codas ( $N=337$ ) of 31 Müller's Bornean male gibbons (*Hylobates muelleri*) from recordings taken between 2013 and 2015 at the Stability of Altered Forest Ecosystems site in Sabah, Malaysia. In each graph, the  $y$ -axis refers to density and is not labeled. Densities are comparable only within each parameter's graph, and the relative densities between each class (variation in one individual male's vocalizations versus variation between all 31 males) matter.



**Fig. 7** Posterior mean Mahalanobis distances, squared and scaled by the number of features, vs.  $F$  distribution quantiles to test goodness of fit to the theoretical expectation of the model for the codas ( $N=337$ ) of 31 Müller's Bornean male gibbons (*Hylobates muelleri*) from recordings taken between 2013 and 2015 at the Stability of Altered Forest Ecosystems site in Sabah, Malaysia.

## Discussion

We found evidence for low individuality in male *Hylobates muelleri* coda vocalizations through linear discriminant analysis, with only a 66% accuracy in leave-one-out cross-validation. We then showed that there was substantial interindividual variation in temporal and spectral features of notes 1 and 2, but substantial intraindividual variation in the total duration of the coda and duration of rest between notes. We reran all analyses separately for spontaneously recorded vocalizations and playback elicited vocalizations, and found significant differences in the accuracy of LOOCV. However, this is confounded by the fact that as we run analyses on subsets of our data, our sample size decreases, thus boosting the LOOCV value. The ability of leave-one-out cross-validation to identify male *H. muelleri* individuals (66% correct) is noticeably less than the 100 and 74.6% accuracy for males of other gibbon species (*Nomascus nasutus*: Feng *et al.* 2014; *Hylobates lar*: Barelli *et al.* 2013), or the 95.7% accuracy in female gibbons of the same species (*H. muelleri*: Clink *et al.* 2017) based on the parameters chosen in our analysis.

As more parameters are added to linear discriminant function analysis, the ability of leave-one-out cross-validation to accurately classify individuals increases (Venables and Ripley 2002). Comparatively, female gibbon duet vocalizations analyses used a greater number of parameters (female:  $N=23$ , compared to male:  $N=13$ ) for a similar number of vocalizations (female:  $N=376$ , male:  $N=337$ ) and individuals (female:  $N=33$ , male:  $N=31$ ). This larger number of parameters may have led to a higher percentage of correct classifications during leave-one-out cross-validation. However, based on previous studies, the number of parameters used in our study is justified, as

adding any more parameters would not aid in capturing additional information ( $N = 14$  parameters in *H. albibarbis*; Wanelik *et al.* 2012).

A potential problem with our analysis is that we excluded spectral parameters for notes after the first two notes of each vocalization because of the requirements of DFA. All individuals' vocalizations contained two or more notes, so we had to truncate our feature extraction to only two notes. The spectral and temporal parameters of notes three and onwards may contain important information about individuality, and thus our results may exaggerate or underreport the level of individuality in male *Hylobates muelleri* gibbon codas. However, the parameters vocalization duration and number of notes serve to capture some of the variation we see visually in vocalization structure beyond the first two notes.

At least three possible explanations exist for the relatively low individuality we see in male *Hylobates muelleri* vocalizations. First, previous studies of male gibbons vocalizations analyzed either the early morning male gibbon solo (Feng *et al.* 2014) or duets (Fan *et al.* 2011; Wanelik *et al.* 2012). Here, we only analyzed recordings of male vocalizations taken during duets. Duet codas and male solo vocalizations differ in structure (Marshall and Marshall 1976). The high levels of individuality seen in males of other gibbon species (Feng *et al.* 2014) may thus reflect the differences in the type of vocalization used. To our knowledge, no study to date has compared the levels of intra- and interindividual variation in both male solos and male duet vocalizations in a particular species. However, our results support a general trend observed in male silvery gibbons (*Hylobates moloch*), whose solo vocalizations are quite variable temporally both within and between male gibbons (Geissmann *et al.* 2005). Our results are also consistent with the flexibility in white-handed (*Hylobates lar*) male coda vocalizations (Terleph *et al.* 2017). The high variability we see within each male's codas may reflect their flexibility in timing their vocalizations with their females' great calls. Our findings indicate the need for further exploration into the differences between the male solo vocalizations and male codas within species.

A second explanation for the low individuality we observed in male vocalizations may be that the female contribution to the duet is more important in the territorial display than the male contribution. Vocalizations are physically taxing and require substantial energy (Cramer 2013; Drăgănoiu *et al.* 2002). While the female great call, a long and potentially costly vocalization, carries information about individual identity (Clink *et al.* 2017), the male coda may exist only to support and coordinate with the female's contribution. During the duet, as the female sings her great call, male gibbons often shake branches and swing from tree to tree (Mitani 1985a). Visual displays are quite common in territorial species, and make the pair appear larger and stronger (birds: Armstrong 1942; Malacarne *et al.* 1991; Peek 1972; frogs: Hödl and Amézquita 2001; Wogel *et al.* 2004). In some species, the male's main contribution to the pair's territorial display is a visual display (Armstrong 1942). This would explain why the male gibbon spends less time vocalizing in duets and why male codas exhibit reduced individuality: perhaps the male allocates energy toward a dramatic visual display.

A third possible explanation for the high variability we found in male codas may be related to the high levels of anthropogenic disturbance at our site (Ewers *et al.* 2011). In rufous-collared sparrow (*Zonotrichia capensis*) vocalizations, the terminal trills vary quite widely in frequency and duration across various habitat types (Handford and Lougheed 1991). Our study population comes from the SAFE site, in which various

logging practices have altered the forest in which our *Hylobates muelleri* groups reside (Ewers *et al.* 2011). Vocalizations travel differently in various habitat types: low-frequency vocalizations with a slow repetition rate travel farther in densely forested environments and vice versa (Podos *et al.* 2004). It is possible that structural changes in the forest at SAFE have influenced the amount of variability we recorded in male gibbon duet vocalizations.

Our results indicate male gibbon vocalization individuality is not a universal pattern across the gibbon taxon, and patterns of individuality are species specific. We encourage future exploration into the differences between male solo and coda vocalizations to determine which portion (if either) of the male gibbon *Hylobates muelleri* vocal repertoire contains information about identity. We also suggest further investigation into the sources of variance in gibbon duet vocalizations on a larger scale across the gibbon taxon.

**Acknowledgements** We gratefully acknowledge Dr. Mark Grote for his statistical guidance in developing the model for this project. We thank Dr. Henry Bernard for serving as our local collaborator. Endless gratitude goes to the UC Davis Provost Undergraduate Fellowship and the Explorer's Club Youth Activity Fund for supporting A. R. Lau. We also express our immense thanks for the Fulbright Student Researcher Scholarship, the American Society of Primatologists Conservation Grant, UC Davis Summer Research Fellowship, the Cleveland Metroparks Zoo Grant, and the Primate Conservation Inc. Research Grant for providing financial support for D. J. Clink. Thank you to C. T. Lau for comments on early drafts of this article and support throughout the entirety of this project. A huge thank you goes to Dr. Joanna Setchell and two anonymous reviewers for incredibly helpful revisions of this article.

## References

- Armstrong, E. A. (1942). *Bird display*. Cambridge University Press Archive.
- Bailey, W. J. (2003). Insect duets: Underlying mechanisms and their evolution. *Physiological Entomology*, 28(3), 157–174.
- Barelli, C., Mundry, R., Heistermann, M., & Hammerschmidt, K. (2013). Cues to androgens and quality in male gibbon songs. *PLoS One*, 8(12), e82748. <https://doi.org/10.1371/journal.pone.0082748>.
- Bioacoustics Research Program. (2014). Raven Pro: Interactive sound analysis software (version 1.5). Ithaca: The Cornell Lab of Ornithology. Available from <http://www.birds.cornell.edu/raven>.
- Brockelman, W., & Srikosamatara, S. (1993). Estimation of density of gibbon groups by use of loud songs. *American Journal of Primatology*, 29(2), 93–108.
- Brockelman, W. Y., Reichard, U., Treesucon, U., & Raemaekers, J. J. (1998). Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behavioral Ecology and Sociobiology*, 42(5), 329–339.
- Clink, D. J., Bernard, H., Crofoot, M. C., & Marshall, A. J. (2017). Investigating individual vocal signatures and small-scale patterns of geographic variation in Bornean gibbon (*Hylobates muelleri*) female great calls. *International Journal of Primatology*, 38, 656–671.
- Clink, D. J., Grote, M. N., Crofoot, M. C., Marshall, A. J., (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.
- Cowlshaw, G. (1992). Song function in gibbons. *Behaviour*, 121(1), 131–153.
- Cramer, E. R. (2013). Physically challenging song traits, male quality, and reproductive success in house wrens. *PLoS One*, 8(3), e59208.
- Dallmann, R., & Geissmann, T. (2009). Individual and geographical variability in the songs of wild silvery gibbons (*Hylobates moloch*) on java, Indonesia. *The gibbons*, 91–110.
- Drăgănoiu, T. I., Nagle, L., & Kreutzer, M. (2002). Directional female preference for an exaggerated male trait in canary (*Serinus canaria*) song. *Proceedings of the Royal Society of London B: Biological Sciences*, 269(1509), 2525–2531.
- Ewers, R. M., Didham, R. K., Fahrig, L., Ferraz, G., Hector, A., Holt, R. D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J. L., & Turner, E. C. (2011). A large-scale forest fragmentation experiment: The stability of

- altered Forest ecosystems project. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 366(1582), 3292–3302.
- Fan, P. F., Xiao, W., Feng, J. J., & Scott, M. B. (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.
- Feng, J.-J., Cui, L.-W., Ma, C.-Y., Fei, H.-L., & Fan, P.-F. (2014). Individuality and stability in male songs of Cao Vit gibbons (*Nomascus nasutus*) with potential to monitor population dynamics. *PLoS One*, 9(5): e96317.
- Geissmann, T. (1999). Duet songs of the Siamang, *Hylobates Syndactylus*: II. Testing the pair-bonding hypothesis during a partner exchange. *Behaviour*, 136(8), 1005–1039.
- Geissmann, T. (2002). Duet-splitting and the evolution of gibbon songs. *Biological Reviews*, 77(1), 57–76.
- Geissmann, T., & Orgeldinger, M. (2000). The relationship between duet songs and pair bonds in siamangs, *Hylobates syndactylus*. *Animal Behaviour*, 60(6), 805–809.
- Geissmann, T., Bohlen-Eyring, S., & Heu, A. (2005). The male song of the Javan silvery gibbon (*Hylobates moloch*). *Contributions to Zoology*, 74(1/2), 1–25.
- Guo, J., Lee, D., Sakrejda, K., Gabry, J., Goodrich, B., et al (2016). Rstan: R interface to Stan. *R package version*, 2, 0–3.
- Haimoff, E. H., & Gittins, S. P. (1985). Individuality in the songs of wild agile gibbons (*Hylobates agilis*) of peninsular Malaysia. *American Journal of Primatology*, 8(3), 239–247.
- Handford, P., & Lougheed, S. C. (1991). Variation in duration and frequency characters in the song of the rufous-collared sparrow, *Zonotrichia capensis*, with respect to habitat, trill dialects and body size. *Condor*, 93(3), 644–658.
- Hödl, W., & Amézquita, A. (2001). Visual signaling in anuran amphibians. *Anuran Communication*, 121–141.
- Langmore, N. E. (1998). Functions of duet and solo songs of female birds. *Trends in Ecology & Evolution*, 13(4), 136–140.
- Malacame, G., Cucco, M., & Camanni, S. (1991). Coordinated visual displays and vocal duetting in different ecological situations among western Palearctic non-passerine birds. *Ethology Ecology and Evolution*, 3(3), 207–219.
- Marshall, J. T., & Marshall, E. R. (1976). Gibbons and their territorial songs. *Science*, 193(4249), 235–237.
- Marshall-Ball, L., Mann, N., & Slater, P. J. B. (2006). Multiple functions to duet singing: Hidden conflicts and apparent cooperation. *Animal Behaviour*, 71(4), 823–831.
- Merlo, J., Chaix, B., Yang, M., Lynch, J., & Råstam, L. (2005). A brief conceptual tutorial of multilevel analysis in social epidemiology: Linking the statistical concept of clustering to the idea of contextual phenomenon. *Journal of Epidemiology & Community Health*, 59(6), 443–449.
- Mitani, J. C. (1984). The behavioral regulation of monogamy in gibbons (*Hylobates muelleri*). *Behavioral Ecology and Sociobiology*, 5, 225–229.
- Mitani, J. C. (1985a). Gibbon song duets and intergroup spacing. *Behaviour*, 92, 59–96.
- Mitani, J. C. (1985b). Location-specific responses of gibbons (*Hylobates muelleri*) to male songs. *Zeitschrift für Tierpsychologie*, 70, 219–224.
- Mitani, J. C. (1985c). Responses of gibbons (*Hylobates muelleri*) to self, neighbor, and stranger song duets. *International Journal of Primatology*, 6, 193–200.
- Mitani, J. C., & Marler, P. (1989). A phonological analysis of male gibbon singing behavior. *Behaviour*, 109, 20–45.
- Peek, F. W. (1972). An experimental study of the territorial function of vocal and visual display in the male red-winged blackbird (*Agelaius phoeniceus*). *Animal Behaviour*, 20(1), 112–118.
- Podos, J., Huber, S. K., & Taft, B. (2004). Bird song: The interface of evolution and mechanism. *Annual Review of Ecology, Evolution, and Systematics*, 35, 55–87.
- R Core Team (2015). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Roth, M. (2012). On the multivariate t distribution. Linköping University Electronic Press.
- Sonnenschein, E., & Reyer, H. U. (1983). Mate-guarding and other functions of antiphonal duets in the slate-coloured boubou (*Laniarius funebris*). *Ethology*, 63(2–3), 112–140.
- Stan Development Team. (2016). Stan modeling language: User's guide and reference manual.
- Terleph, T. A., Malaivijitnond, S., & Reichard, U. (2015). Lar gibbon (*Hylobates lar*) great call reveals individual caller identity. *American Journal of Primatology*, 77(7), 811–821.
- Terleph, T. A., Malaivijitnond, S., & Reichard, U. H. (2017). Male white-handed gibbons flexibly time duet contributions. *Behavioral Ecology and Sociobiology*, 72(1), 16.
- Thorpe, W. H. (1963). Antiphonal singing in birds as evidence for avian auditory reaction time. *Nature*, 197(4869), 774–776.

- Tobias, M. L., Viswanathan, S. S., & Kelley, D. B. (1998). Rapping, a female receptive call, initiates male-female duets in the south African clawed frog. *Proceedings of the National Academy of Sciences of the USA*, 95(4), 1870–1875.
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). New York: Springer Science+Business Media.
- Wanelik, K. M., Azis, A., & Cheyne, S. M. (2012). Note-, phrase- and song-specific acoustic variables contributing to the individuality of male duet song in the Bornean southern gibbon (*Hylobates albibarbis*). *Primates*, 54(2), 159–170.
- Wogel, H., Abrunhosa, P. A., & Weber, L. N. (2004). The tadpole, vocalizations and visual displays of *Hylodes nasus* (Anura: *Leptodactylidae*). *Amphibia-Reptilia*, 25(2), 219–226.

## Affiliations

Allison R. Lau<sup>1,2,3</sup> · Dena J. Clink<sup>1</sup> · Margaret C. Crofoot<sup>1,4</sup> · Andrew J. Marshall<sup>5</sup>

✉ Allison R. Lau  
alljones@ucdavis.edu

<sup>1</sup> Department of Anthropology, University of California, Davis, Davis, CA 95616, USA

<sup>2</sup> California National Primate Research Center, University of California, Davis, Davis, CA 95616, USA

<sup>3</sup> Department of Psychiatry and Behavioral Sciences, University of California, Davis, Sacramento, CA 95817, USA

<sup>4</sup> Smithsonian Tropical Research Institute, Balboa, Ancon, Panama, Republic of Panama

<sup>5</sup> Department of Anthropology, Program in the Environment, Department of Ecology and Evolutionary Biology, and School for Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109, USA