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Investigating Individual Vocal Signatures and Small-Scale Patterns of Geographic Variation in Female Bornean Gibbon (*Hylobates muelleri*) Great Calls

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Abstract Quantifying patterns of variation in primate vocalizations has important implications for understanding the evolutionary processes that lead to variation in phenotypic traits more broadly. Here, we investigated individuality and patterns of geographic variation across a small geographic scale (*ca.* 10 km) in female Bornean gibbon (*Hylobates muelleri*) great calls. We analyzed calls recorded from wild, unhabituated gibbon groups at the Stability of Altered Forest Ecosystems site in Sabah, Malaysia. We estimated 23 acoustic features in 376 great calls from 33 different females. We used linear discriminant function analysis to investigate intra- and interindividual variation in great calls. To examine small-scale patterns of geographic variation great calls we investigated measures of acoustic dissimilarity as a function of distance. We found that temporal features (such as the duration of the notes and the duration of rest between notes) contributed substantially to individuality. We were able to identify females based on their calls with 95.7% accuracy using leave-one-out cross-validation. We found no discernible patterns of geographic variation at our site; females with

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neighboring territories were just as likely to have similar calls as females with more distant territories. It is possible that we did not sample across a large enough geographic range, or that substantial interindividual variation effectively swamped across-site patterns of variation. Our findings add to the growing body of evidence for individual vocal signatures in primates and mammals, but further research is needed to understand the evolutionary mechanisms that contribute to individuality in gibbon calls.

Keywords Discriminant function analysis · Individual variation · Stability of altered forest ecosystems site · Vocal fingerprinting

Introduction

Individuality of animal vocalizations can arise through variation of the spectral and/or temporal parameters of calls (Bradbury and Vehrencamp 1998), and understanding how these parameters contribute to individual vocal signatures can provide important insights into the evolution and maintenance of acoustic diversity. For example, differences in the spectral characteristics of calls may be due to differences in body size or morphology. A classic example of such patterns is from red deer (*Cervus elaphus*), in which the minimum resonance frequencies (formants) of stag roars decreased with body size and age (Reby and McComb 2003). Interindividual variation in resonance frequencies can also influence deer reproductive success, as female deer show preference for males roars with lower minimum resonance frequencies (Charlton *et al*. 2007). Animals may alter the spectral characteristics of their calls based on behavioral state (Morton 1977), but in some cases the spectral characteristics of vocalizations are limited by anatomical constraints, i.e., formant spacing, and are likely to reflect morphological differences between individuals (Fitch and Hauser 2002; Reby and McComb 2003).

Copying errors, or the introduction of novel variants, during song learning may lead to accelerated acoustic divergence (Lachlan and Servedio 2004; Wilkins *et al*. 2012). It is also possible that copying errors may lead to variation in temporal parameters of vocalizations. For example, in agile gibbons (*Hylobates agilis*), daughters at a more advanced stage of social independence exhibited calls that matched their mothers' with a higher degree of temporal precision than younger females (Koda *et al*. 2013). Individuality may also arise when vocal animals actively differentiate their calls (either spectrally or temporally) from those of neighboring groups, as seen in highly territorial banner tailed kangaroo rats (*Dipodomys spectabilis*). In this species, individuals alter their foot drumming signals when they move into a new area so that they are distinct from their neighbors (Randall 1995). Active vocal adjustment was also a proposed explanation for a high degree of vocal individuality in male black crested gibbons (*Nomascus concolor*) within a single site compared to variation between sites (Sun *et al*. 2011). As with other phenotypic traits, individual vocal signatures most likely arise through a combination of ecological and evolutionary mechanisms (Podos *et al*. 2004).

Gibbons provide a useful model for investigating patterns of vocal individuality as they regularly engage in duets, wherein males and females engage in alternating, sex-specific phrases (Haimoff 1984; Marshall and Marshall 1976). Social pairs of gibbons share specific home ranges or territories that they defend against intrusion by other conspecifics, and it has been hypothesized that their morning duets serve the function of mediating intergroup spacing, wherein duets advertise occupancy of an area to conspecifics (Mitani 1985a). Other proposed functions of gibbon duets include strengthening or maintaining pair bonds (Geissmann and Orgeldinger 2000) and active territorial defense (Cowlishaw 1992); these hypotheses are not mutually exclusive. Unlike many birds (Kroodsma and Baylis 1982; Marler 1990), gibbons do not learn their songs by copying models; instead, the vocal repertoires of gibbons appear to be genetically determined (Tenaza 1985). Studies have shown that the songs of gibbon hybrids exhibit sex-specific characteristics of both parental species, even if such individuals hear the song of only one of the parental species (Geissmann 1984; Tenaza 1985).

Although a strong genetic component results in species-specific, stereotyped great calls (Brockelman and Schilling 1984), substantial individuality remains. Individuality has been documented in great calls from females of many gibbon species, including agile gibbons (*Hylobates agilis*) in Peninsular Malaysia (Haimoff and Gittins 1985), Borneo, and Sumatra (Heller *et al.* 2010); white-handed gibbons in Khao Yai National Park, Thailand (*H. lar*; Terleph *et al.* 2015); and silvery gibbons (*H. moloch*) on Java, Indonesia (Dallmann and Geissmann 2009). It is likely that individuality in gibbon great calls encodes information regarding individual identity (Tenaza 1976), and that gibbons use this information to locate and identify conspecifics (Haimoff and Gittins 1985).

In this study we aimed to 1) identify the acoustic parameters that contribute to individuality in the great calls of Bornean gibbon (*Hylobates muelleri*) females; and 2) examine the patterns of variation in gibbon great calls over a small geographic scale (*ca.* 10 km) at the Stability of Altered Forest Ecosystems Site, Sabah, Malaysia. We tested two, mutually exclusive hypotheses regarding patterns of geographic variation to provide insight into the mechanisms that contribute to vocal individuality. For example, if mothers pass on certain call characteristics to their daughters, and daughters form territories close to their mothers, then we predict that females in close geographic proximity will have calls that are more similar than will females that are farther away from each other. In populations in which dispersal has been studied, gibbons tend to disperse into neighboring territories, with relatively short dispersal distances, e.g., *ca.* 700 m (Brockelman *et al.* 1998; Tenaza 1975), so this is a reasonable prediction. Alternatively, gibbons may actively engage in vocal adjustment, so that their calls are distinct from those of their neighbors. Gibbon calls be heard from 1 to 2 km away, depending on the terrain and weather conditions (Brockelman and Ali 1987; Brockelman and Srikosamatara 1993). Therefore, if gibbons actively differentiate their calls from their neighbors', we predict that gibbon females with territories in close proximity (<2 km) will have calls that are highly distinct.

Methods

Data Collection

We carried out fieldwork at the Stability of Altered Forest Ecosystems site (Ewers *et al.* 2011) in the Kalabakan Forest Reserve (N04°422,367′, E117°3559′), Sabah, Malaysia. The area lacks distinct wet and dry seasons, and consists mainly of lowland tropical rainforest dominated by species in the family Dipterocarpaceae (Döbert *et al.* 2015).

We collected recordings of gibbon duets in January 2013, July–August 2013, December 2015, August 2015, and September 2016 using a Marantz PMD 660 flash recorder equipped with a RODE NTG-2 directional condenser microphone. We recorded signals at a sample rate of 44.1 kHz and a sample size of 16 bits. The study site exhibits an aseasonal climate, so there were no *a priori* reasons to predict that different recording seasons would lead to differences in call parameters. We present results based on analyses on the full data set, but we also analyzed data from a single field season with the largest sample size (August 2015; *N* = 17 gibbon females) separately to ascertain whether including multiple field seasons had a substantial influence on our results.

To augment data collection, we used a Roland CUBE Street EX 4-Channel 50-W Battery Powered Amplifier to broadcast a recorded duet in assumed territories of gibbon groups. We broadcast the same duet (recorded by D. J. Clink at the Maliau Basin Conservation Area, Sabah, Malaysia) for all playbacks to control for the potentially confounding influence of differences in caller identity and the quality of the playback recording. We played a 3-min unaltered clip that contained male and female portions of the duet up to five times, with a 30-s pause in between each playback to observe for evidence of group response. Once the group responded, either vocally or by approaching the speaker, we stopped the playback. There is some evidence that birds alter spectral or temporal aspects of their calls in response to such simulated territorial intrusions (Benedict *et al.* 2012; Leedale *et al.* 2015). Determining if gibbon females do the same is beyond the scope of this article, but to ensure that the inclusion of calls collected during playbacks did not alter our results, we ran our analyses only on the calls collected during playbacks (*N* = 17 females), and again on all calls.

Distinguishing among Females

Gibbons occupy relatively small home ranges that range in size from 14 to 50 ha (Asensio *et al.* 2014; Savini *et al.* 2008; Suwanvecho and Brockelman 2012), although this can vary substantially between populations and species (Fan and Jiang 2008), and home range locations tend to be highly stable across years (Bartlett *et al.* 2016; Mitani 1985a; Savini *et al.* 2008). The average natal dispersal distance is *ca.* 700 m (Brockelman *et al.* 1998), which means that offspring generally move into territories close to their parents. We followed the general rule of thumb for conducting acoustic surveys and considered groups that mapped >500 m apart as separate groups, as this is the approximate width of a gibbon territory (Brockelman and Ali 1987) and is a commonly used metric to distinguish between separate groups during fixed-point count surveys (Brockelman and Srikosamatara 1993; Cheyne *et al.* 2008; Phoonjampa *et al.* 2011).

We collected data over 3 yr. during five field seasons. During each field season we focused our sampling in different areas of the field site (*ca.* 1.5 km apart), in an attempt to mitigate the potential for rerecording females that had dispersed from their original territories. For recordings collected during the same field season, we considered females that were recorded >500 m apart to be unique females. During recordings we attempted to make visual contact with the group, and documented group composition, along with other distinguishing group characteristics, such as the presence of co-singing daughter(s) or distinct male/female contributions to the duet. We recorded at a distance of *ca*. 150 m or less from the duetting individuals, as recordings taken from farther distances exhibit attenuation and a reduction in the signal-to-noise ratio (Dabelsteen and Larsen 1993) and are not suitable for analysis. Often, more than one group responded to the playback, which allowed us to record two separate groups that mapped <500 m apart with a high degree of certainty. In a few instances, we accessed new recording locations with the opening of logging roads at our site, and some of these groups mapped closely to groups recorded during previous seasons (map of recording locations by season in Fig. 1). To ensure repeat sampling of the same females did not bias our results, we conducted our analyses only on females that mapped ≥800 m from any other groups (N = 9 females), and then again on the pooled data (N = 33 females).

Acoustic Analyses

Our research focused on the female contribution to the duet, known as the great call (Geissmann 2002). Bornean gibbon great calls consist of a combination of long, frequency-modulated notes as well as shorter, broadband trill notes; we defined trills as notes of ≤0.135 s (see Fig. 2), as note repetition rate increases substantially at this point in the call. Calling bouts can last from a few minutes up to a few hours (D. J. Clink, *pers. obs*.), with a mean calling time of *ca*. 15 min (Mitani 1985a). We created spectrograms using the program Raven Pro 1.5 Sound Analysis Software (Cornell Lab of Ornithology Bioacoustics Research Program, Ithaca, NY). We made 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, as computing power was sufficient to create spectrograms using the original sampling rate.

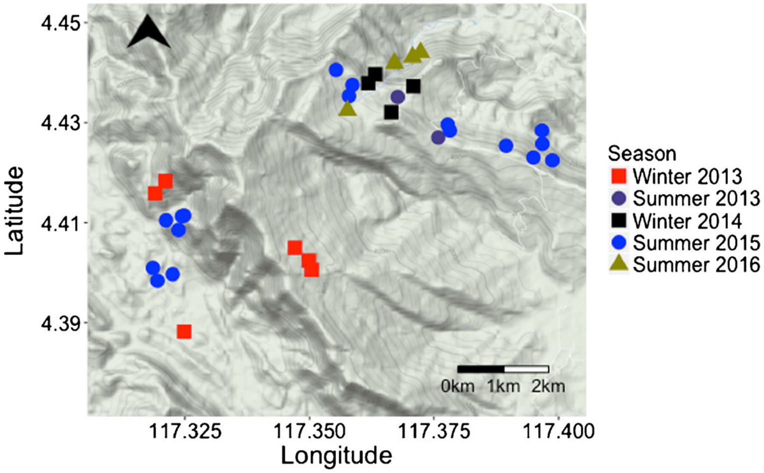

Fig. 1 Recording locations of Bornean gibbon females (N = 33) across the Stability of Altered Forest Ecosystems site, Sabah, Malaysia, taken from January 2013 to September 2016. Each point represents a separate recording location, and different shape and color combinations represent different recording seasons. Contour map was created using the ggmap function in R (Kahle and Wickham 2013).

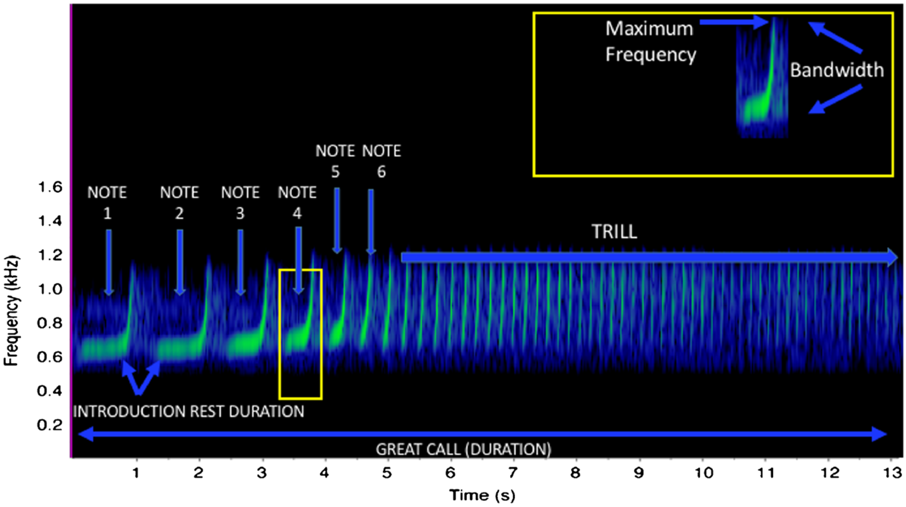

Fig. 2 Representative spectrogram of Bornean gibbon female great call recorded at the Stability of Altered Forest Ecosystems site, Sabah, Malaysia, with features extracted for analysis in this study. **A** description of each of the features is provided in Table I. We adjusted brightness and contrast settings using the Raven spectrogram view to remove background noise from the spectrogram image.

Using the spectrograms created in Raven Pro, we extracted 23 features from each great call (Table I). D. J. Clink conducted all analyses; to minimize intraobserver variability, we used the band-limited energy detector (BLED) in Raven Pro to identify notes from the spectrogram and estimate call parameters (BLED configurations: minimum frequency: 0.40 kHz; maximum frequency: 1.60 kHz; minimum duration: 0.02 s; maximum duration: 1.60 s; minimum separation 0.04 s). In addition to minimizing variability, the use of the BLED also reduces call processing time by automating the note selection process. To further increase intraobserver reliability, we used the robust measurements in Raven Pro. For example, to calculate maximum frequency, the robust measurements divide the selection into two frequency intervals containing 95% and 5% of the energy. Therefore, our frequency estimates are 95% of the maximum frequency (referred to herein as maximum frequency); the actual maximum frequency values of gibbon calls are slightly higher. Unlike selection-based measurements that can be highly influenced by inter- or intrauser variability, robust measurements are calculated based on the energy of the selected call segment (Rice *et al.* 2014), and are therefore less sensitive to observer variability.

Acoustic Dissimilarity as a Function of Distance

To investigate patterns of geographic variation, we calculated an acoustic distance measure between pairs of great calls using the 23 features extracted from each call. We calculated Mahalanobis distances between pairs of vocalizations, which accounts for different feature scalings and variances/covariances between features (Mardia *et al.* 1979). This resulted in an acoustic dissimilarity value for each pair of vocalizations, with a value of 0 indicating no dissimilarity, i.e., calls were exactly the same, and large values indicating that the calls were highly dissimilar. We also calculated the

Table I The 23 features extracted from spectrograms of Bornean gibbon female great calls recorded at the Stability of Altered Forest Ecosystems site, Sabah, Malaysia, from January 2013 to September 2016

	Feature	Description
1	Note 1 duration	Duration (s) of the first note
2	Note 1 bandwidth	Bandwidth of the first note
3	Note 1 max frequency	95% of the maximum frequency of the first note
4	Note 2 duration	Duration (s) of the second note
5	Note 2 bandwidth	Bandwidth of the second note
6	Note 2 max frequency	95% of the maximum frequency of the second note
7	Note 3 duration	Duration (s) of the third note
8	Note 3 bandwidth	Bandwidth of the third note
9	Note 3 max frequency	95% of the maximum frequency of the third note
10	Note 4 duration	Duration (s) of the fourth note
11	Note 4 bandwidth	Bandwidth of the fourth note
12	Note 4 max frequency	95% of the maximum frequency of the fourth note
13	Note 5 duration	Duration (s) of the fifth note
14	Note 5 bandwidth	Bandwidth of the fifth note
15	Note 5 max frequency	95% of the maximum frequency of the fifth note
16	Note 6 duration	Duration (s) of the sixth note
17	Note 6 bandwidth	Bandwidth of the sixth note
18	Note 6 max frequency	95% of the maximum frequency of the sixth note
19	Introduction note duration	Combined duration (s) of the introductory notes
20	Introduction rest duration	Combined duration (s) of the rest between introductory notes
21	Number of notes	Total number of notes in the great call
22	Introduction duration	Duration (s) of the introductory portion of the call with notes >0.135 s
23	Trill duration	Total duration (s) of the portion of the call with notes <0.135 s long

geographic distance between pairs of great calls. We removed pairs with a spatial distance of 0 km from this analysis, as we assumed that these were calls taken from the same female, and calculating an acoustic dissimilarity measure for calls from the same female may have (incorrectly) biased our results to show that females that are close together tend to have calls that are similar. We then used a smoothing spline to fit a smooth curve to our pairs of observations using a smoothing parameter of 1. We obtained an approximate 95% bootstrap confidence band by resampling the observed pairs 1000 times with replacement, fitting the spline to each bootstrap sample and calculating quantiles from the aggregated curves.

Statistical Analyses

To understand how acoustic parameters distinguish great calls of different females, we used a linear discriminant function analysis (DFA). DFA is a multivariate technique that maximizes the separation of class means to intraclass variance (Venables and Ripley 2002); it is a supervised technique wherein groups are defined prior to analysis, in contrast to principal component analysis, which is an unsupervised technique. The use of DFA was appropriate for our study, as the dataset structure consisted of replicate calls within females, resembling a one-way analysis of variance with "individual" as the factor (Mundry and Sommer 2007). For some females, we had recordings from multiple days, but to adhere to the single factorial assumptions of DFA we used only calls taken during a single recording session. We set a uniform prior on call assignment, so that probability of membership was equal across females. We used leave-one-out cross validation (LOOCV) to determine the performance of the DFA. LOOCV excludes one observation, runs the DFA, and then uses the resulting function to classify the excluded observation. To adhere to the requirement of DFA, and to minimize uncertainty about female identification, we excluded 11 recording locations and 146 calls from our analysis because of small sample size (<3 recordings), or uncertainty about group identification (recording location <500 m from another group, and/or inability to make visual contact with the group). Therefore, we reduced our original dataset (45 recording locations and 522 calls) to 33 females and 376 calls. Our full analyses were done on this reduced dataset. Functions of the R programming language were used for all analyses and graphical displays (R Core Team 2015).

Data Availability

Data used for analyses are available from corresponding author upon reasonable request.

Results

Individuality in Bornean Gibbon Female Great Calls

We report the results of an analysis on 376 great calls from 33 Bornean gibbon females (median number of calls: 12; range: 3–43). The first five functions of the DFA explained 88% of the variance, with temporal features contributing most to discrimination between females (Electronic Supplementary Material [ESM] Table SI). There was substantial variation in each of the parameters measured (Table II). Interindividual variation was substantially greater than intraindividual variation (Fig. 3a and b). LOOCV accurately classified 95.7% of the observations to the correct female (range 67–100% correct classification of calls to different females; Fig. 4). Fig. 3a is a 2-dimensional representation of 22-dimensional data, whereas LOOCV uses the full suite of discriminant functions when classifying calls. The substantial overlap of clusters is the result of a relatively large number of classes (females) and the condensing of multidimensional data into a small number of dimensions; it does not preclude the ability of LOOCV to effectively distinguish between females. Temporal variables such as the duration of notes 1, 4, and 5, along with the duration of rest between introductory notes, and the duration of the trill, are the largest contributors to individuality in the great calls of Bornean gibbon female. In Fig. 3b, the first discriminant function tends to place females with long note 5 duration in the negative *x*-plane, whereas females with short note 5 duration would tend to be in the positive *x*-plane. The second function tends to place females with long note 1 duration, long duration of rest between introductory

Table II Summary of the 23 features extracted from Bornean gibbon female great calls recorded at the Stability of Altered Forest Ecosystems site, Sabah, Malaysia, from January 2013 to September 2016

Feature	Mean	Min	Max	SD
Note 1 duration (s)	0.87	0.23	1.53	0.22
Note 1 bandwidth (Hz)	179.67	86.10	452.20	72.88
Note 1 max frequency (Hz)	795.77	624.50	1055.10	82.74
Note 2 duration (s)	0.84	0.37	1.36	0.15
Note 2 bandwidth (Hz)	195.30	86.10	473.70	75.15
Note 2 max frequency (Hz)	818.77	667.50	1098.20	79.80
Note 3 duration (s)	0.67	0.28	1.20	0.16
Note 3 bandwidth (Hz)	221.94	86.10	473.70	79.81
Note 3 max frequency (Hz)	860.81	679.70	1119.70	88.29
Note 4 duration (s)	0.49	0.15	0.99	0.15
Note 4 bandwidth (Hz)	254.85	86.10	559.90	94.66
Note 4 max frequency (Hz)	909.14	689.10	1205.90	107.79
Note 5 duration (s)	0.37	0.13	0.84	0.13
Note 5 bandwidth (Hz)	285.67	86.10	581.40	101.59
Note 5 max frequency (Hz)	955.09	689.10	1248.90	116.85
Note 6 duration (s)	0.28	0.08	0.65	0.11
Note 6 bandwidth (Hz)	327.53	107.70	602.90	104.51
Note 6 max frequency (Hz)	1007.77	710.60	1292.00	120.80
Introduction note duration (s)	2.88	1.88	4.29	0.42
Introduction rest duration (s)	3.63	2.57	4.94	0.44
Number of notes	73.20	42.00	124.00	16.49
Introduction duration (s)	5.87	3.17	15.84	1.86
Trill duration (s)	8.00	3.65	15.69	2.10

notes, and short trill duration in the negative y-plane. Females with the opposite pattern would tend to be in the positive y-plane.

Acoustic Dissimilarity as a Function of Distance

We found no evidence for a relationship between geographic distance and call similarity (Fig. 5). In other words, females at our site were equally likely to have calls that were very similar, or highly dissimilar, regardless of how close their territories were. The very narrow 95% bootstrap confidence band suggests that there was no relationship between acoustic dissimilarity and geographic distance at our site (Fig. 5).

Reanalysis with Subsets of the Data

None of our results changed substantively when we analyzed a subset of 190 calls collected during a single season ($N = 17$ females; median number of calls: 11; range: 3–25; ESM Fig. S1; Table SII). Similarly, our results did not change when we analyzed only the 292 calls produced during playbacks ($N = 25$ females; median number of calls:

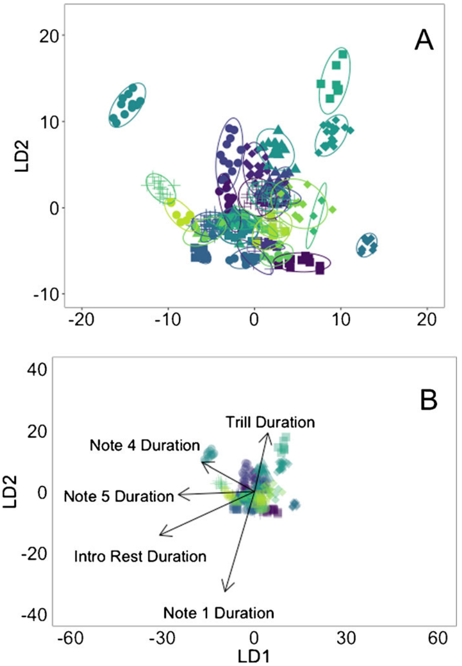

Fig. 3 **(a)** Scatterplot and **(b)** variable loadings of the first two linear discriminant functions for each Bornean gibbon female great call recorded at the Stability of Altered Forest Ecosystems site, Sabah, Malaysia, from January 2013 to September 2016. **(a)** Each point represents a single great call, and different color and shape combinations represent different gibbon females. Ellipses represent 90% confidence intervals for each female. Axes are scaled to maximize visual separation of the points. **(b)** Arrows represent variable loadings of the first and second linear discriminant functions.

11; range: 3–43; ESM Fig. S2; Table SIII). Lastly, our results did not change substantively when we conducted our analysis on 104 calls from females that mapped >800 m apart ($N = 9$ females; median number of calls: 12; range: 6–15; ESM Figs. S3, S4, and S5; Table SIV). The only result that changed was the accuracy of classification using LOOCV, which increased to 96% accuracy. Thus, our decision to include all data in a single analysis did not alter the results presented here.

Discussion

We show that temporal characteristics contribute most to interindividual variation in Bornean gibbon great calls. Using discriminant analysis, we classified 95.7% of individual great calls to the correct female. The plot of the two best separating discriminant functions shows that the calls from most individuals form distinct clusters, but there is also substantial overlap among clusters. We assessed whether there was any link between this overlap, i.e., call similarity, and the location of gibbon territories within our site, but we found no evidence of discernible patterns of geographic variation over a spatial scale of *ca*. 10 km. In other words, calls of females at our site are equally likely to be similar, or different, independent of how close their territories are.

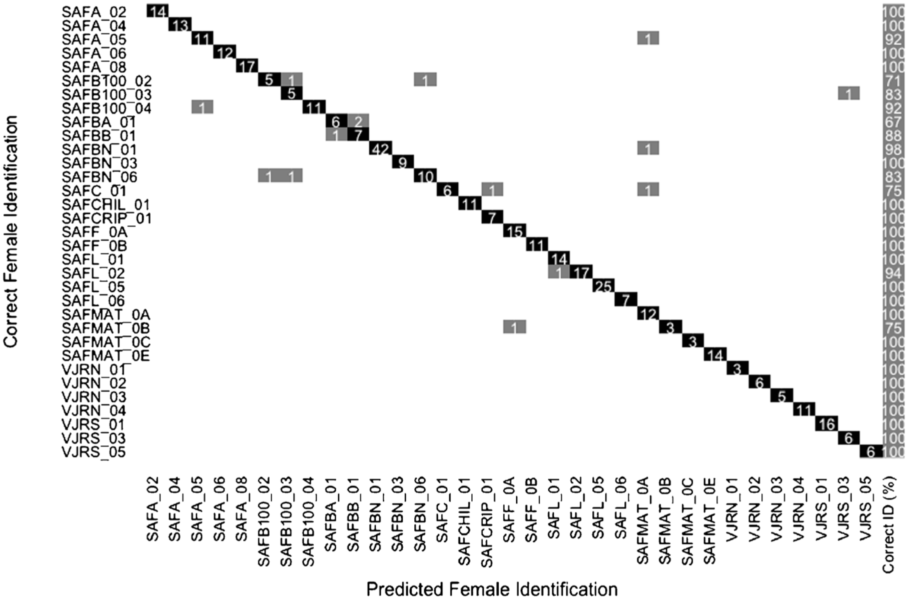

Fig. 4 Confusion matrix for the discriminant function classification of Bornean gibbon females recorded at the Stability of Altered Forest Ecosystems site, Sabah, Malaysia, from January 2013 to September 2016. The total numbers of correct classifications are along the diagonal, and the percentage of correct identifications per female is shown in the far right column

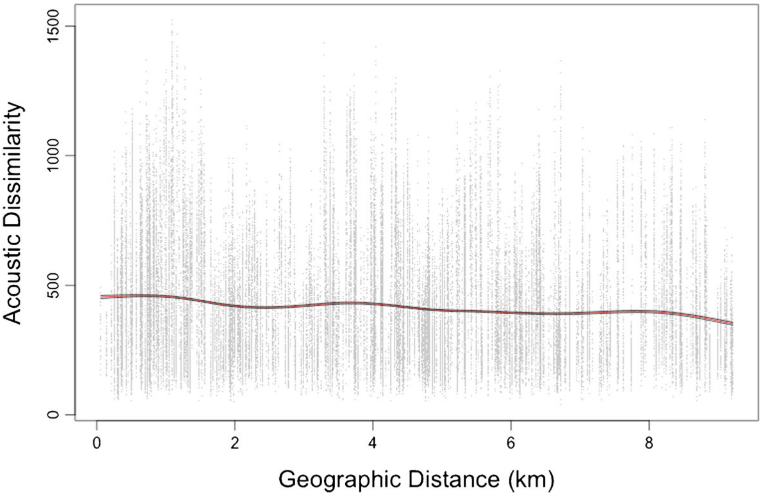

Fig. 5 Acoustic dissimilarity of Bornean gibbon great calls recorded at the Stability of Altered Forest Ecosystems site, Sabah, Malaysia, from January 2013 to September 2016 as a function of geographic distance. Each point represents pairwise distance for a given pair of calls (acoustic distance) and recording locations (geographic distance). For our acoustic dissimilarity measure, a value of 0 indicates identical calls (no dissimilarity) and values much greater than 0 indicate high levels of dissimilarity between call pairs. The curve, with upper and lower bands (which are very narrow for these data), is a smoothing spline with an approximate 95% bootstrap confidence band.

Methodological Considerations

We collected data over 3 yr. on unhabituated gibbons, which means that there was the potential for re-recording females that had dispersed from their original territory. Although we attempted to minimize the potential of rerecording females, the only way we could have been 100% certain about female identity was to collect fecal DNA samples, which is generally not feasible with unhabituated primates. Resampling the same females would have potentially biased our results in the following ways. First, resampling the same female, and considering her as two separate females, would have decreased the accuracy of our leave-one-out cross validation. As our classification accuracy is already quite high, it appears that resampling the same female(s) had a minimal influence on our results. Second, resampling a single female and classifying her as separate females would have biased our geographic variation analysis to indicate that females with neighboring territories have increased levels of call similarity. But we did not find any patterns of geographic variation, either in the pooled data or on the subset of data, which included females that mapped only >800 m apart from each other, which indicates that the possibility of resampling the same females across seasons did not significantly bias our results.

Individuality in Bornean Gibbon Female Great Calls

We found that temporal characteristics contributed substantially to individuality in Bornean gibbon female great calls, whereas spectral characteristics were relatively unimportant. This is in contrast to similar studies of other gibbon species. For example, in agile gibbon females in Sumatra, spectral parameters of the calls contributed more to individuality than temporal parameters (Oyakawa *et al*. 2007), and this was also the case for lar gibbon females (Terleph *et al*. 2015). There is strong evidence that spectral characteristics of gibbon calls are linked to caller quality. For example, in female lar gibbons, younger females produce calls that have higher fundamental frequency and a larger frequency range (Terleph *et al*. 2016). In male lar gibbon calls, there was a significant positive correlation between androgen level and call frequency (Barelli *et al*. 2013). In addition, spectral characteristics of the calls explained more (*ca*. 30%) of the variance in male lar gibbon vocalizations than temporal characteristics (*ca*. 20% of variance explained).

Our finding that temporal features contributed to individuality more than spectral features in Bornean gibbon female calls lacks a clear explanation, although it is likely that temporal features of calls are less limited by physical constraints than the spectral features. It remains to be determined whether gibbons perceive these differences in individual signatures, and if these differences elicit varying behavioral responses. A playback study on Bornean gibbons did not find evidence that gibbons respond differentially to playbacks of self, neighbor, or stranger calls (Mitani 1985b). The author proposed that the selection pressure for individual recognition may have been relaxed in this species, given the low rate of intergroup encounters, or that the playback equipment used may have resulted in the loss of fine-scale frequency or amplitude patterns that gibbons use to discriminate conspecifics. There is convincing evidence that primates (*Cercopithecus aethiops*: Cheney and Seyfarth 1980) and other mammals including dolphins (*Tursiops truncatus*: Sayigh *et al*. 1999), bats (*Tadarida brasiliensis Mexicana*: Balcombe 1990) and fur seals (*Callorhinus ursinus*: Insley 2000) can differentiate conspecifics based on their vocal signatures. Therefore, further investigation to determine if gibbons detect individual differences in vocal signatures of conspecifics is warranted.

Patterns of Geographic Variation

We found no evidence of patterns of geographic variation in female great calls across our site, and did not find support for either of our hypotheses. Although we did not conduct an exhaustive survey of the gibbon population, there were certainly enough groups in close proximity, and relatively far from each other, to detect a pattern if it existed. This is in contrast to many studies that have found evidence of geographic variation in primate vocalizations (Dallmann and Geissmann 2009; Delgado 2007; Mitani *et al.* 1999). It may be that our investigation was not over a large enough spatial scale. Many of the studies investigating patterns of geographic variation in primate vocalizations have compared the intra- and intersite level variation (Burton and Nietsch 2010; Fan *et al.* 2011; Nietsch 1999; Wich *et al.* 2008), but have not looked at variation as a function of distance. Therefore, it is unclear over what spatial scale we should expect to see variation in primate vocalizations. It is also possible that interfemale variation effectively swamped any patterns of geographic variation at our site (Heller *et al.* 2010).

One potentially confounding factor for detecting patterns of geographic variation could be the fact that the Stability of Altered Forest Ecosystems has been extensively logged over the last thirty years (Ewers *et al.* 2011). Despite this, the site still contains the full suite of Bornean felids (Wearn *et al.* 2013) and primates (Bernard *et al.* 2016), although it is unclear if the density of mammals at this site is comparable to that of undisturbed forests. Anthropogenic disturbance may have altered the distribution and dispersal patterns of gibbons at our site, resulting in our inability to detect patterns of vocal variation. In addition, if human disturbance altered gibbon population density, this may have influenced patterns of individuality. For example, eagle owls (*Bubo bubo*) living at high population densities were shown to have reduced levels of vocal individuality (Delgado *et al.* 2013), whereas in South American sea lions (*Otaria flavescens*), higher population density correlated with higher vocal individuality (Trimble and Charrier 2011), but in seven species of passerines that population density did not influence vocal individuality (Blumstein *et al.* 2012). Future studies of patterns of geographic variation in gibbon vocalizations at less disturbed sites will be informative.

Conclusions

We identified individual Bornean gibbon females with a 95.7% accuracy using 23 features extracted from their great calls. Although our results are not surprising, they add to the growing body of evidence for vocal individuality in mammalian vocalizations. We found no discernible pattern of geographic variation of great calls over a small spatial scale. Although we document strong individual signatures in gibbon calls, it remains to be determined if these individual signatures are important for gibbons in individual recognition. It has been proposed that this individuality in gibbon vocalizations can also be used as a "vocal fingerprint," which would allow researchers to track and monitor individuals and populations over time (Sun *et al.* 2011; Wanelik *et al.* 2012). Our results provide further support that the use of vocal fingerprints to monitor gibbon populations will likely be effective.

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Conflict of interest The authors declare that they have no conflict of interest.

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