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RESEARCH ARTICLE

Individuality in Male Songs of Wild Black Crested Gibbons (*Nomascus concolor*)

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This is the first study of vocal individuality in male songs of black crested gibbons. The sound recordings were carried out at two field sites, Pinghe, Ailao Mountains, and Dazhaizi, Wuliang Mountains, both located in Yunnan province, China. A total of 127 coda phrases of 38 male songs bouts of eight individual male gibbons were analyzed. Stepwise discriminant function analysis was used to examine the acoustic individuality of the males. We found that individuality among neighbors was very pronounced. Moreover, individuality within a site (i.e. among neighbors) is higher than among individuals between sites. Our finding suggests that black crested gibbons may actively increase their degree of vocal individuality against that of their immediate neighbors by vocal adjustment. Am. J. Primatol. 73:431–438, 2011. © 2010 Wiley-Liss, Inc.

Key words: *Nomascus concolor*; male song; individuality; individual identification; vocal adjustment

INTRODUCTION

The gibbons or small apes usually live in monogamous territorial family groups typically consisting of an adult pair and one to three immature offspring [Chivers, 1977, 2001; Leighton, 1987]. All gibbon species produce elaborate, loud, long, and stereotyped patterns of vocalization often referred to as songs [Geissmann, 1993, 1995, 2002; Haimoff, 1984; Marshall & Marshall, 1976]. Gibbon songs are species-specific [Geissmann, 1995, 2002] and are usually produced early in the morning. Individuals of *Hylobates klossii* [Tenaza, 1976] and *Hylobates moloch* [Kappeler, 1984] produce solo songs; however, all mated pairs of other gibbon species combine their song contributions to produce complex, but relatively stereotyped vocal interactions known as duets. In all gibbon species except hoolock gibbons (*Hoolock hoolock*) [Marler & Tenaza, 1977; Marshall & Marshall, 1976], male and female song contributions are sex-specific [e.g. Geissmann, 1993]. The song types of mated gibbons differ among species. Crested gibbon (genus *Nomascus*) songs are notable in several respects: (1) Mated pairs produce duet song bouts, whereas only nonmated individuals appear to produce solo songs; (2) duet song bouts are male-dominated; (3) male song phrases are highly stereotyped; and (4) song contributions of adults are highly sex-specific with typically no overlap between the sexes in either note repertoire or phrase repertoire [Geissmann, 2002; Geissmann et al., 2000]. Gibbon song characters are largely genetically determined [Geissmann, 1995]; however, they also display an impressive degree of situational variability, or flexibility, within the parameters of species-typical patterns [Haraway & Maples, 1998]. For example, field playback experiments confirmed that kloss's gibbons and moloch gibbons sing longer bouts when chorusing with a same sexed neighbor than when singing alone [Kappeler, 1984; Tenaza, 1976].

Many functions have been attributed to gibbon songs. Most authors mention spacing among groups, defense of resources (such as territories, food sources or mates), mate attraction, and strengthening and/or advertisement of the pair bond [Cowlishaw, 1992; Geissmann, 1999; Geissmann & Orgeldinger, 2000; Geissmann et al., 2005; Leighton, 1987; Mitani, 1984, 1985a,b, 1987; Raemaekers & Raemaekers, 1985a,b]. Several studies demonstrated that gibbon songs are also individual-specific [Dallmann & Geissmann, 2001a,b, 2009; Haimoff & Gittins, 1985; Haimoff & Tilson, 1985; Oyakawa et al., 2007]. The individuality in gibbon songs was suggested to allow singing individuals to more efficiently and effectively locate and identify neighboring nonmate conspecifics

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[Haimoff & Gittins, 1985]. Statistical analysis of female songs of agile gibbons (*Hylobates agilis*), Kloss's gibbons (*H. klossii*) and silvery gibbons (*H. moloch*) revealed that individuality occurs throughout the entire song [Dallmann & Geissmann, 2001b; Haimoff & Gittins, 1985; Haimoff & Tilson, 1985; Oyakawa et al., 2007]. All previous studies of individuality in gibbon songs have focused on the so-called dwarf gibbons of the genus *Hylobates*, whereas vocal individuality in other gibbon genera, including the crested gibbons of the genus *Nomascus*, has apparently not been documented quantitatively.

Animals may modify their vocalization in response to specific social factors. The banner-tailed kangaroo rats (*Dipodomys spectabilis*) are highly territorial. In this species, individuals adjust their footdrumming signals to differ from those of their new neighbors when they move into a new area [Randall, 1995]. Wild chimpanzees (*Pan troglodytes*) living in a fission–fusion social system, male individuals living together in a group may develop community-specific pant hoots through the ability to match the call characteristics of the group [Crockford et al., 2004; Marshall et al., 1999; Mitani & Gros-Louis, 1998]. The authors interpret this as evidence for vocal learning in chimpanzees. Janik and Slater [1997] have argued that vocal learning can only be demonstrated if an animal can learn novel vocalizations, not by merely adjusting its call structure to be distinct from others (or similar to others). Therefore, we use the more general term vocal adjustment rather than vocal learning in this context. In contrast to the chimpanzees mentioned above, gibbons live in small territorial family groups, somewhat like kangaroo rats. But there was no reason given in previous studies about the individuality of gibbon songs. It is unknown whether any form of vocal adjustment contributes to the individuality among neighboring gibbons, and what the ecological effect of vocal adjustment may be.

In order to address this gap in knowledge, we analyzed the individuality of male song in several groups of the black crested gibbon (*Nomascus concolor*) and compared vocal individuality among neighbors within two study sites and also between the sites.

METHODS

Field Sites

The two largest remaining populations of black crested gibbons (*Nomascus concolor*) in China occur in the Ailao Mountains and in the Wuliang Mountains in central Yunnan province [Jiang et al., 2006]. We have conducted successive field studies on the gibbons of both populations at two sites: in Dazhaizi, Wuliang Mountains (2003–present), and in Pinghe, Ailao Mountains (2006–2009). The localities and compositions of the gibbon groups around our two field stations are well established. Each group in Pinghe includes only one adult male and one adult female, but in Dazhaizi, it includes one adult male and two adult females.

There are four groups of gibbons in Dazhaizi. They are separated from other gibbon groups by a large area of unsuitable habitat, and only three of the groups (named D1, D2, and D3) can hear each other (Fig. 1). We focused on these three groups. The habitat in Pinghe is less disturbed, with no gaps among the gibbon groups or around them. We focused on five groups (named P1, P2, P3, P4, and P5) near our field station; these five groups are neighbors and can hear each other's songs.

Our two field sites are 58 km apart from each other. The habitat at the two sites differs in several respects: gibbons in the Wuliang Mountains occur in semi-humid evergreen broad-leaved forests and mid-montane humid evergreen broad-leaved forests at elevations of 1,900–2,700 m, whereas gibbons in the Ailao Mountains are found in mid-montane humid evergreen broad-leaved forests at elevations of 2,600–2,760 m. At our study sites, the gibbons range at elevations of 1,900–2,700 m in Dazhaizi, Wuliang Mountains, and of 2,600–2,760 m in Pinghe, Ailao Mountains. The climate is similar at our two study sites, but the smaller altitudinal range at Pinghe results in a reduced diversity of tree species and in lower canopy height [Sun et al., 2007; Tian et al., 2007].

Data Collection

All fieldwork was conducted in the period from 2008 to 2010. During this period, three researchers and six assistants were doing gibbon field research at the two field sites. The sound recordings of gibbon songs were carried out in the morning hours between 0600 and 1200 hr. One researcher and two assistants identified the caller of each recorded song while the focus group was singing.

All sound recordings were made with a Marantz PMD 660 flash recorder equipped with a RODE NTG-2 directional condenser microphone. The recording parameters included a 48-kHz sampling rate and 16-bit sampling. Sonograms and measurements of vocalizations were carried out using Cool Edit Pro 2.1 software (Syntrillium Software Corporation, Phoenix, Arizona).

Sound recordings of a total of 38 song bouts of eight gibbon groups were recorded and analyzed. In order to compare the vocal individuality within and between our study sites, we selected the coda phrase. The coda is the most characteristic phrase in song bouts of male crested gibbons, produced as a response to, and at or near the end of, a female's great-call [Haimoff, 1984]. The coda has a more complex structure and isat the same time more stereotyped than other male song phrases [Geissmann, 1993, 1995]. The coda phrase has also been found particularly useful for studying relationships between

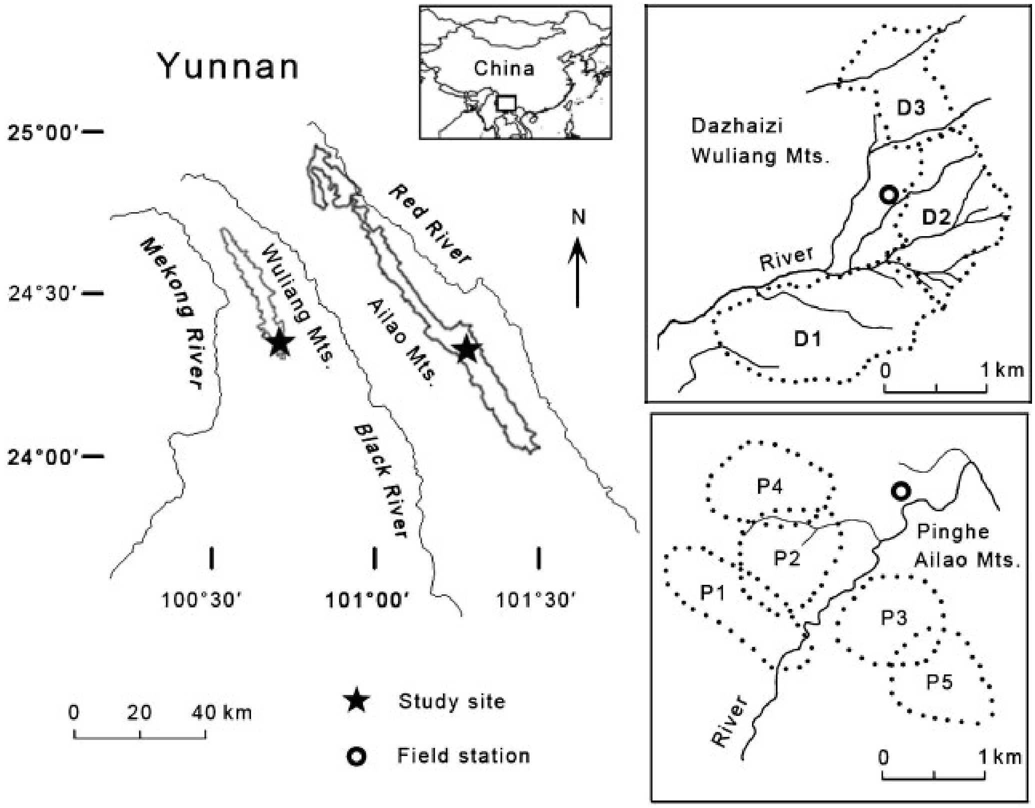

Fig. 1. Map showing the location of the two study sites in Yunnan province (left), and the distribution of the study groups at each site (right). The contour lines of two mountain ranges in the left map correspond to the boundaries of the Wuliang Mountain National Nature Reserve and the Ailao Mountain National Nature Reserve, respectively.

TABLE I. Number of Song Bouts and Coda Phrases Recorded and Analyzed in This Study

		Coordinates of home range center		Sound recordings	
Field site	Gibbon group	N	E	Song bouts	Coda phrase
Pinghe	P1	24°19.9′	101°16.4′	2	7
	P2	24°20.1′	101°16.7′	4	18
	P3	24°19.7′	101°17.3′	5	19
	P4	24°20.2′	101°16.6′	4	5
	P5	24°19.4′	101°17.4′	4	14
Dazhaizi	D1	24°20.5′	100°42.1′	9	20
	D2	24°21′	100°42.5′	8	36
	D3	24°21.7′	100°42.3′	2	8

groups and populations of crested gibbons [Konrad & Geissmann, 2006]. We analyzed only the first four notes of each coda phrase by the adult males. To avoid empty cells in the data matrix, we ignored coda phrases consisting of less than four notes. Thus, a total of 127 coda phrases were found suitable for analysis. The numbers of song bouts and coda phrases recorded and analyzed for each individual are listed in Table I. All aspects of the current research adhered to the American Society of Primatolgists' principles for the ethical treatment of nonhuman primates.

Statistical Analysis

A total of 26 variables of coda phrases were defined and measured. The description of these variables is listed in Table II, and an example sonogram is presented in Figure 2.

Coda phrases of all eight male gibbons in both sites were selected to evaluate individuality in songs. We used stepwise discriminant function analysis (DFA) to identify differences in vocalization among individuals. We chose Wilks' λ as the criterion for variable selection. To test the significance of change

TABLE II. Descriptions and Kruskal–Wallis Test of the Song Variables of Male Black Crested Gibbons From Pinghe and Dazhaizi

			H value	
No.	Variable name	Description	Pinghe	Dazhaizi
1	codu	Duration from the start of first note to the end of the last one in a coda phrase (s)	7.60	2.66
2	conotes	Number of notes in a coda phrase	11.87*	10.14*
3	co1bfr	Frequency at the beginning point of the first note (Hz)	42.78**	32.74**
4	co1efr	Frequency at the end point of first note (Hz)	6.12	6.14*
5	co1mfr	Frequency at the middle point of the first note (Hz)	30.48**	25.07**
6	co1du	Duration of the first note (s)	48.26**	48.60**
7	coit1	Time interval between the end of first note and the start of the second one (s)	35.03**	48.39**
8	co2bfr	Frequency at the beginning point of the second note (Hz)	52.68**	40.88**
9	co2efr	Frequency at the end point of second note (Hz)	5.86	2.66
10	co2lf1	Frequency at the first wave trough of the second note (Hz)	35.58**	21.80**
11	co2lf2	Frequency at the second wave trough of the second note (Hz)	23.51**	22.59**
12	co2lt	Duration from the beginning of second note to the first wave trough (s)	18.61**	7.92*
13	co2ht	Duration from the beginning of second note to its highest frequency point (s)	18.96**	40.36**
14	co2du	Duration of the second note (s)	19.14**	41.15**
15	coit2	Time interval between the end of second note and the start of third one (s)	39.77**	35.57**
16	co3bfr	Frequency at the beginning point of the third note (Hz)	34.57**	20.69**
17	co3efr	Frequency at the end point of the third note (Hz)	38.83**	32.72**
18	co3lfr	The lowest frequency of the third note (Hz)	26.56**	33.66**
19	co3lt	Duration from beginning of third note to its wave trough (s)	16.67*	8.38*
20	co3du	Duration of the third note (s)	29.23**	3.55
21	co3it	Time interval between the end of third note and the start of fourth one (s)	20.05**	3.45
22	co4bfr	Frequency at the beginning point of the fourth note (Hz)	4.19	17.03**
23	co4efr	Frequency at the end point of the fourth note (Hz)	47.41**	48.14**
24	co4lfr	The lowest frequency of the fourth note (Hz)	26.57**	15.52**
25	co4lt	Duration from beginning of fourth note to its wave trough (s)	5.14	7.35*
26	co4du	Duration of the fourth note (s)	16.18*	22.24**

*$P<0.05$; **$P<0.001$.

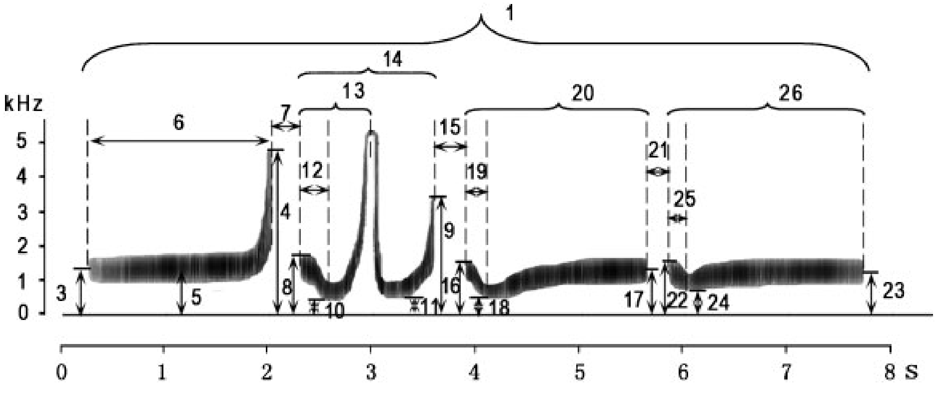

Fig. 2. Sonogram (only fundamental frequencies shown) of a coda phrase showing some of the variables measured during this study (See Table II for number codes.).

in the selection criterion when we entered or removed a variable from the model, we used the probability of F and applied P-to-enter = 0.05 and P-to-remove = 0.1 as significance levels [Konrad & Geissmann, 2006]. Results were cross-validated by the ''leave-one-out'' method, where each case of the analysis was classified by the functions derived from all cases other than that case. We applied the Kruskal–Wallis test in each site to confirm variables contributing to the individuality of songs.

In order to examine the vocal individuality among neighbors, we analyzed the data from each study site separately. In order to compare individuality between the two study sites, we then combined the two data sets and examined whether and how this changed the classification accuracy.

All statistical analyses were conducted using the SPSS 16.0.0 statistical software package (IBM Corporation, Somers, New York).

RESULTS

Individuality Among Neighbors

Coda phrases of the five males in Pinghe and the three males in Dazhaizi were subjected to a stepwise DFA separately. The two-dimensional plot of DFA confirmed strong acoustic individuality in the male songs at each site (Fig. 3). All (100%) original and cross-validated grouped cases were correctly classified in Pinghe; all original and 98.4% of the cross-validated grouped cases were correctly classified in Dazhaizi. Only one case (D3 in Dazhaizi) was incorrectly classified to D1 of the same site (see also Table III).

Thirteen and nine variables were selected separately by stepwise discriminant analysis on Pinghe and Dazhaizi, respectively; only four variables were selected by both of them: frequency at the middle point of the first note (co1mfr), time interval between the end of the first note and the start of the second one (coit1), frequency at the beginning point of the second note (co2bfr), and frequency at the end point of the fourth note (co4efr). The results of the Kruskal–Wallis test are shown in Table II. Most variables (21 of 26 variables in Pinghe, 22 of 26 variables in Dazhaizi) show a significant degree of individuality in *Nomascus concolor* in each site.

Individuality Among All Individuals of Two Sites

All coda phrases of all eight individuals from the sites Pinghe and Dazhaizi were merged in a stepwise DFA, and the cross-validated classification accuracy is shown in Table III. The classification accuracy in each site remains the same as for the previous site-specific analyses: only one phrase was classified incorrectly within the same site. However, ten phrases were incorrectly classified to the wrong site. The cross-validated classification accuracy of P4, D1, and D2 was reduced to 60, 85, and 88.9%, respectively, from 100%; D3 was reduced to 75% from 87.5%.

The wrongly classified phrases are not randomly distributed among the cells of Table III. Ten of 11 misplacements occur *between* sites, more than expected by chance. The difference is statistically significant (χ^2-test, $\chi^2 = 12.94$, $df = 1$, $P < 0.001$). This suggests that the coda phrases are more variable between neighboring groups than between study sites.

TABLE III. Cross-Validated Classification Accuracy of Stepwise DFA of All Coda Phrases of Eight Gibbons From the Pinghe (P1-5) and the Dazhaizi (D1-3) Study Sites

		Predicted group membership								
	Group	P1	P2	P3	P4	P5	D1	D2	D3	Total
Count	P1	7	0	0	0	0	0	0	0	7
	P2	0	18	0	0	0	0	0	0	18
	P3	0	0	19	0	0	0	0	0	19
	P4	0	0	0	3	0	2	0	0	5
	P5	0	0	0	0	14	0	0	0	14
	D1	0	0	0	3	0	17	0	0	20
	D2	0	0	0	0	4	0	32	0	36
	D3	0	0	0	1	0	1	0	6	8

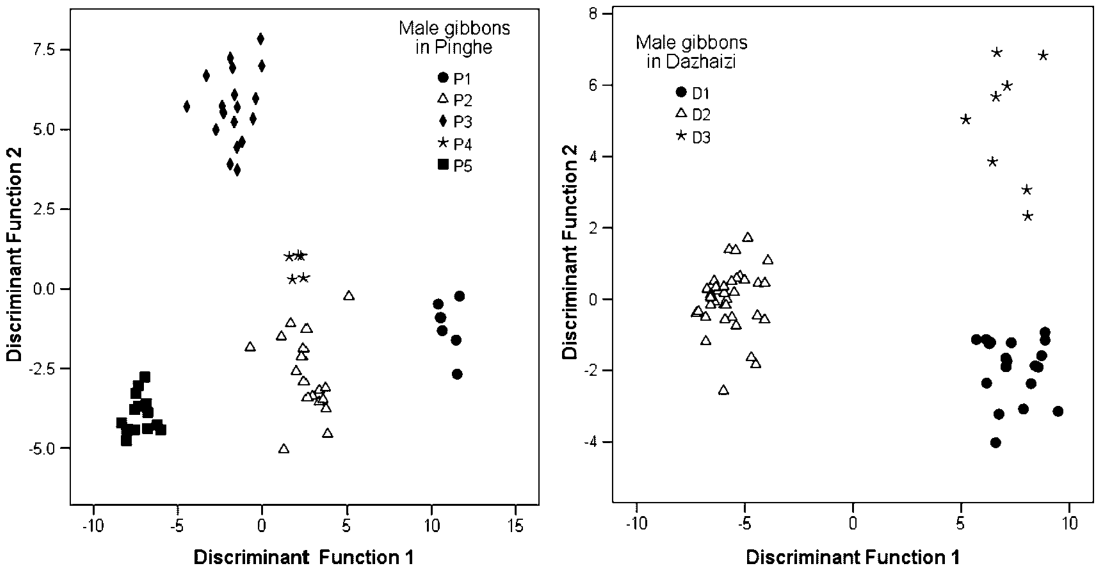

Fig. 3. Discriminant scores of male song individuality in Pinghe (left) and Dazhaizi (right).

DISCUSSION

We find strong acoustic individuality among neighboring male gibbons both in Pinghe and Dazhaizi. All individuals can be identified by DFA within each site; only one of the 127 phrases was classified incorrectly, with most measurements contributing to the individuality. In these respects, our results on vocal individuality of crested gibbons (genus *Nomascus*) correspond to those of earlier studies on dwarf gibbons (genus *Hylobates*). It appears that gibbon song vocalizations can be used as a vocal fingerprint to identify individuals. Whether gibbons use these differences to discriminate among songs of neighbors and non-neighbors has not yet been demonstrated. Individuals of several bird and primate species, however, discriminate between familiar and unfamiliar songs by responding to them differentially [e.g. Catchpole & Slater, 2008; Falls, 1982; Wich et al., 2002]. The ability to discriminate between neighbors and strangers may provide several advantages. For instance, neighbors are residents in their own territory who are unlikely to pose a serious threat to established territory boundaries. Responding to established neighbors therefore requires less time and energy than responding to song from strangers. Strangers represent a bigger threat to a resident and its territory; therefore, the resident should invest in a stronger response to repel them.

In contrast to the high classification accuracy among individuals in the same site, we found lower classification accuracy when data from both sites were combined. Of course, more mistakes can be expected when the number of individuals increases. However, in the combined analysis, ten of 11 misplacements occurred between sites. This significant result could only occur if individuality within a site (i.e. among neighbors) is more pronounced than between sites. Two possible reasons may be proposed to account for this phenomenon: (1) variability in male songs may be a response to the great-call of their mates; since, generally, only the mated pair within a gibbon group produces duet songs, adult males may adapt their songs to those of their partners as part of the social bonding process; (2) like the drumming patterns in kangaroo rats, vocal individuality among neighboring male black crested gibbons is actively maintained at a higher level than among randomly selected gibbons of different sites. However, in Dazhaizi, the three studied gibbon groups are all polygynous, each adult male pairs with two adult females. It may be difficult for males to adapt their songs to two singing partners. The latter explanation appears more plausible than the first one, since the individuality in gibbon songs among neighbors makes it possible for individuals to discriminate between neighbors and strangers, and benefit from this ability as discussed above, even though there has been only limited evidence of vocal adjustment in gibbons [Geissmann, 1999]. The marked vocal individuality among neighboring black crested gibbons conceivably increases the reliability of vocal identification.

Somewhat similar findings to ours have been reported for wild chimpanzees and kangaroo rats. As mentioned earlier, male chimpanzees develop community-specific pant hoots through the ability to match the call characteristics. In contrast to chimpanzees living in the same community, gibbon families and individuals of kangaroo rats are both highly territorial, and both exhibit marked acoustic individuality. Similar to kangaroo rats, the gibbons in our study do not appear use vocal adjustment to match calls of conspecifics, but to distinguish themselves from their neighbors.

Our two study sites are 58 km apart from each other. They are separated by the Black River (Heishui He), which may promote genetic isolation between the two populations. In fact, some authors suggested that the populations in Ailao and Wuliang are distinct enough to deserve taxonomical recognition on the subspecies level as *N. c. concolor* and *N. c. jingdongensis*, respectively [Ma & Wang, 1986; Su et al., 1996], although this distinction has been questioned more recently [Geissmann, 1995; Geissmann et al., 2000; Monda et al., 2007; Thinh et al., 2010]. Furthermore, the habitats and altitudes differ between the two sites (see Methods: Field Sites). Each of these factors (i.e. geographical, topographical, and ecological separation) could potentially lead to vocal differences between the populations. As a result, we expected calls between our two study sites to differ more than calls within each site. Finding the opposite lends some support to view that the gibbons at each site are taxonomically identical.

More importantly, however, finding something that runs against all expectations also adds strength to our interpretation. Greater vocal individuality within than between sites leads us to postulate a mechanism that enhances vocal individuality among neighboring gibbon males. This conclusion would be plausible already if our study sites were identical in all respects and geographically and topographically contiguous. However, given that our finding is contrary to what should be expected based on knowledge about the diversity of animal calls in general and gibbon songs in particular, our proposed explanation receives further support.

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