



Long-Term Vocal Phrase Stability In The White-Handed Gibbon (*Hylobates lar*)

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Abstract – Gibbons are Asian apes that live in stable territories, often for decades. They produce loud, elaborate vocalizations (songs) that include well-coordinated male/female duets that are detectable by immediate neighbors and more distant groups. The female great call, the longest and most conspicuous phrase of the gibbon vocal repertoire, has been hypothesized to serve in territorial defense. Great calls of different individuals are statistically distinguishable, and a structurally stable great call should benefit a caller as it would reliably transmit caller identity over the long-term, to distant animals. The loud climax notes of this vocalization, however, are difficult to produce. We therefore predicted that physical decline with aging should reduce the frequency of high pitch climax notes within the great call. To determine the degree to which great call performance is stable over an extended time frame, we analyzed great calls from a wild population of white-handed gibbons at Khao Yai National Park, Thailand, each summer between 2013 and 2019 (except for 2018). We obtained multiple great calls per year from 9 subjects (5-6 years per animal) and compared calls within each animal between years, using a spectrogram cross-correlation procedure, and by comparing peak fundamental frequencies from call climaxes. We found within-subject stability in the great call and its climax over the 6-year period. This supports the territorial function hypothesis for great calls, as the calls can serve as a reliable indication of caller identity to distant animals. Our data do not support the hypothesis that climax notes change, at least over the time frame analyzed.

Keywords – Gibbons, Bioacoustics, Vocal Communication, Primate vocalizations

Possessing a stable vocal signal is a prerequisite for broadcasting one's identity and, for territorial species, associating oneself with territory occupancy. The ability to defend one's territory, or an individual's resource holding potential (RHP), can be encoded in display behaviors including territorial vocal signals (Fitch & Hauser, 2002; Morton, 1977; Reby & McComb, 2003). Different from border displays, loud territorial vocal signals may be directed at animals further than direct neighbors who share a common border, as the number and strength of distant non-territory holders may be unknown to an individual. Thus, distant individuals may pose as great a threat to one's territory as immediate neighbors. Moreover, it has been shown that territorial animals respond more aggressively towards strangers than neighbors (the "dear enemy" effect) (Temeles, 1994), and thus, to discourage distant individuals from invading, long distance signaling of one's RHP could be part of routine territorial defense. Signaling RHP should be particularly important for species that possess highly stable territories, as such territories have high inherent value to the territory holder and may be a prerequisite for successful reproduction. If territorial invasion can come

from distant individuals who are within earshot, it would be adaptive for a territory holder to regularly broadcast its identity and/or RHP to such animals, with a highly stable signal.

Gibbons are small Asian apes that live in stable territories, often for decades (Mitani, 1984). They produce loud, elaborate vocalizations (songs) that include coordinated male/female duets. The female great call is the longest and most conspicuous phrase of the gibbon vocal repertoire, and it is thought to function in territorial defense and possibly as an advertisement of pair bond status (Chivers & MacKinnon, 1977, Geissmann & Orgeldinger, 2000, Mitani, 1984, 1985). The climax of the white-handed gibbons' (*Hylobates lar*) great call reaches >100 dB SPL (at 2.7 m) (Terleph et al., 2016) and is audible >1 km through dense forest (Raemaekers et al., 1984). This is further than the approximately 400–500 m average diameter of these animals' home ranges (Asensio et al., 2014; Raemaekers et al., 1984; Reichard & Sommer, 1997). Thus, gibbon duets are heard by distant individuals, who are separated from the calling individual by at least one intervening territory. Recent data has confirmed that female great calls, and especially their loud, high-pitched climaxes, are attended to by both directly neighboring individuals and distant groups (Terleph et al., 2022). In Khao Yai National Park, Thailand, where population density is high and available territories are typically occupied, the average natal dispersal distance of white-handed gibbons is between one and two territories away (mean: 710 m) (Brockelman et al., 1998), and thus within the range that great calls carry. The mature offspring of pairs typically disperse to nearby territories where they replace same-sex individuals. They therefore pose the greatest threat to paired territory residents (Brockelman et al., 1998), and they grow up surrounded by the duets of direct and distant neighbors. Therefore, a structurally stable great call should accurately broadcast a territory owner's identity, territorial location, and possible RHP to listeners over the long tenure of territory ownership.

Great calls have been shown to be highly stable over short time periods, and individual animals can be statistically distinguished by their calls alone (Terleph et al., 2015), but prior studies have not evaluated long-term call stability. The loud climax notes of this vocalization are more variable between individuals than the other parts of the call (Terleph et al., 2015) and the most high-pitched climaxes may be difficult to maintain as a caller ages (Terleph et al., 2016). A between-subjects analysis of white-handed gibbon great calls revealed that older animals' (mean age: 29.6 years) call climaxes had a lower fundamental frequency range and lower maximum fundamental frequency than that of younger animals (Mean age: 12.9 years) (Terleph et al., 2016). Because of these observed differences, we predicted an inverse relationship between great call climax fundamental frequency and age. To test if such a trend could be found within subjects over multiple years, we documented the degree to which call stability is maintained over a six-year period, using a within-subjects design that examined the great calls' overall structure and climax note peaks.

Methods

Ethics Statement

Permits were issued by the National Research Council of Thailand (NRCT) and the Department of National Parks, Wildlife and Plant Conservation (DNP) of Thailand, and approved by the Institutional Animal Care and Use Committees of Sacred Heart University and Southern Illinois University Carbondale, USA.

Procedure

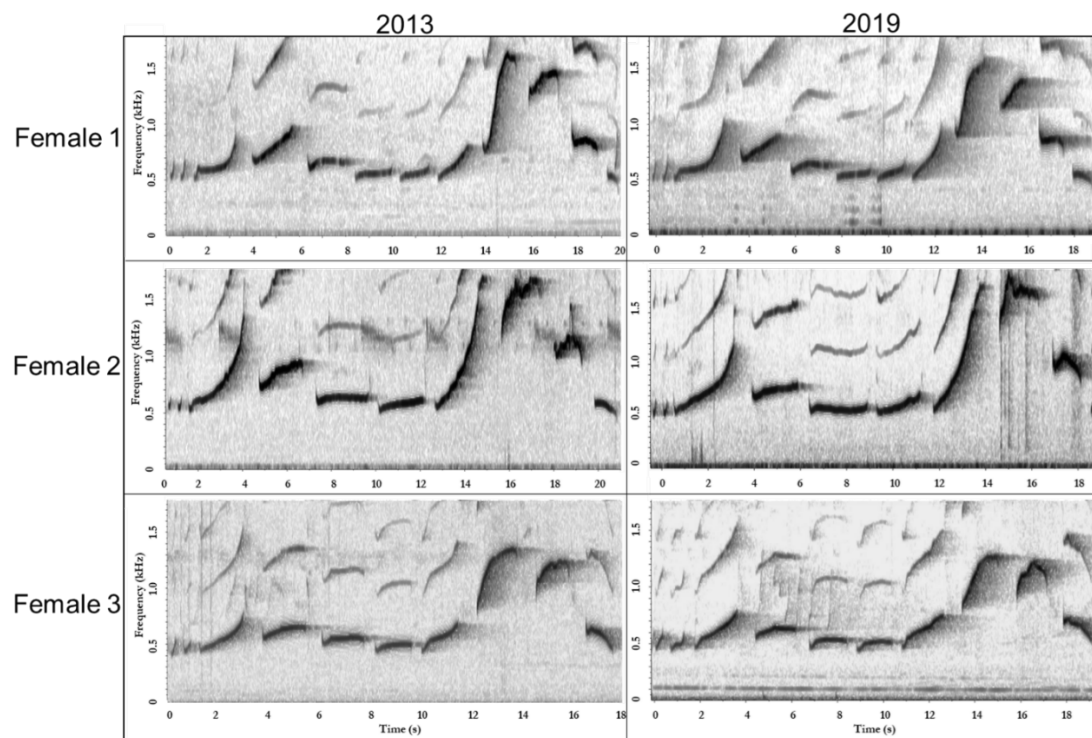
We made all recordings of wild gibbons at the Mo Singto—Klong E-Tau long-term research site at Khao Yai National Park, Thailand, in all years from 2013–2019, except for 2018. Estimated average age of the nine females at the start of the study was 19.3 years, range: 10.2–38.2 (Table 1). Recordings were made between June and August, in morning hours (6:00 AM to 12:00 PM), when females usually engaged in morning duets with males, often in response to the calls of direct neighbors and more distant gibbon groups' duet calling. We did not include great calls that were overlapped by other gibbon vocalizations (e.g., when females co-sing with their offspring).

Table 1*Subject Birthdates and Ages Throughout the Study*

Animal ID	Birth year/month \pm confidence (days)	Age during the study (years/months)
BD	2003/4*	10/2 – 16/2
W	2002/1 \pm 21	11/5 – 17/6
E	2001/2*	13/5 – 18/5
B	1999/7*	12/11 – 18/11
M	1996/10 \pm 2	16/8 – 22/9
N	1995/11 \pm 60	17/7 – 21/8
NOS	1988/3*	25/3 – 31/4
T	1987/11 \pm 120	27/6 – 33/7
S	1975/5*	38/2 – 42/2

Note. Asterisks denote subjects whose minimum ages were estimated, based on reproductive age at first observation (for details, see Terleph et al., 2016). All other subjects were aged based on direct observations shortly after birth (within the listed accuracy windows).

We avoided direct interaction with the animals, typically approaching close enough (<50 m) to be in direct line of sight of the vocalizing individuals. Most animals were habituated to our presence. We confirmed animal identities by territory location and individual pelage color and markings, based on long-term demographic and photo-records of individuals (Reichard, 2009). We used digital solid-state recorders (Marantz PMD661, Kanagawa, Japan) with Sennheiser microphones: K6 power module and ME67 recording head and windscreen (Sennheiser Electronic, Wedemark, Germany). All recordings were 24 bit, with a 48 kHz sample rate (examples: Figure 1).

Figure 1*Spectrograms of Representative Great Calls from Three Females*

Note. Spectrograms show recordings of female great calls from both 2013 and 2019, from three individuals.

To compare overall great call structure between years, we applied a bandpass filter (350-1750 Hz) to great call spectrograms, clipped all values below -60dB, and then removed additional noise and harmonics using smart erase and gamma adjustment tools in Photosounder 1.1.2 software (©2002-2022 by Michel Rouzic, Photosounder.com). We then used a spectrogram cross-correlation tool (Raven Pro 1.6 sound analysis software, Cornell Center for Conservation Bioacoustics, Ithaca, New York) to time shift spectrograms relative to each other, thus calculating maximum correlation value over a series of time increments (similarity index: 0 = no similarity, 1 = identical). These comparisons required recordings of complete great calls, recorded in the absence of extraneous noise (e.g., nearby birds, insects, or interruptions from other gibbons). We therefore visually inspected all spectrograms prior to the analysis, excluding all cases containing such noise. Each cross-correlation used 100 samples for the series of time shifts (Hanning window, 50% overlap, FFT size: 256 Hz).

To test if changes to overall great call structure accumulate over years, we first made all possible within-subject cross-correlation comparisons, both within and between years, for each of the 9 animals (mean comparisons per animal: 627, range: 210-861, total number of comparisons: 5,643). Then, to analyze great call structural change over time, we employed a Generalized Linear Mixed Model (GLMM), using the gap between years (0-6 years) as the fixed effect and both subject identity and the specific years that were compared for each gap as random effects.

Table 2

Number of Great Calls Used for the Analyses

Animal ID	2013	2014	2015	2016	2017	2019
BD	7/10	16/17	6/10	4/4	4/11	5/5
W	11/11	10/13	8/9	4/4	-/-	5/5
E	-/-	4/4	7/9	4/4	2/11	4/4
B	-/3	8/16	19/26	5/5	4/8	7/10
M	15/16	5/8	5/7	8/8	4/5	4/6
N	7/8	7/7	5/6	12/19	2/4	-/-
NOS	2/3	7/8	6/8	6/6	9/12	8/9
T	5/5	6/6	6/6	6/7	-/-	16/18
S	9/12	4/4	5/5	2/2	3/3	-/-

Note. The first number in each cell represents the number of great calls used for cross-correlation comparisons, the second number represents the number of great calls used for peak fundamental frequency (F0) comparisons.

We also measured the peak fundamental frequencies (F0) of great call climaxes from spectrograms (FFT size: 512 Hz), across all available years (mean per animal: 45.3 ± 12.5 , range: 26-68) and performed a GLMM analysis on these data, using recording years as the fixed effect and animals and their ages as random effects.

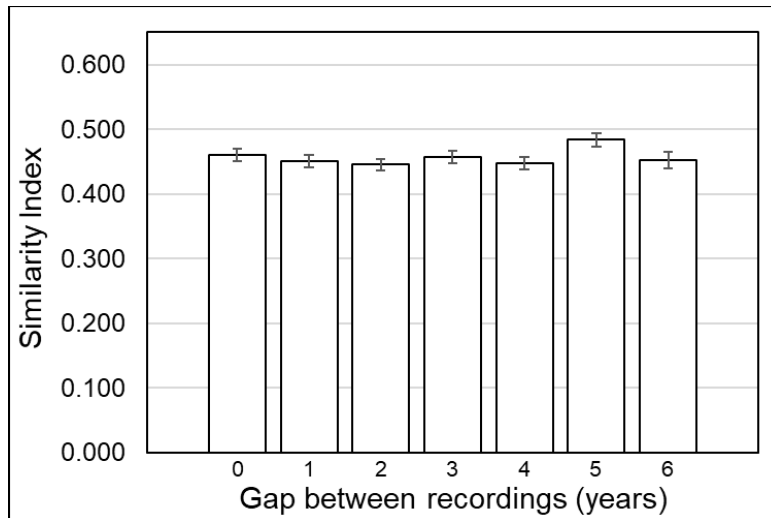
Results

Cross-correlation comparisons over the 0-6 years gaps revealed no significant difference in great call structure as a function of the time intervals between recordings $F(6, 5634) = .914, p = .484$ (Figure 2), and there was little between-subject (random effect) variability: $Z = 1.84, p = .066$.

The GLMM analysis used to compare peak F0 frequencies over separate years also showed no significant between-year differences: $F(5, 402) = 1.186, p = .315$ (Figure 3). There was a significant between-subject (random effect) variability: $Z = 1.981, p = .048$, but it did not differ significantly by year: $Z = .186, p = .852$.

Figure 2

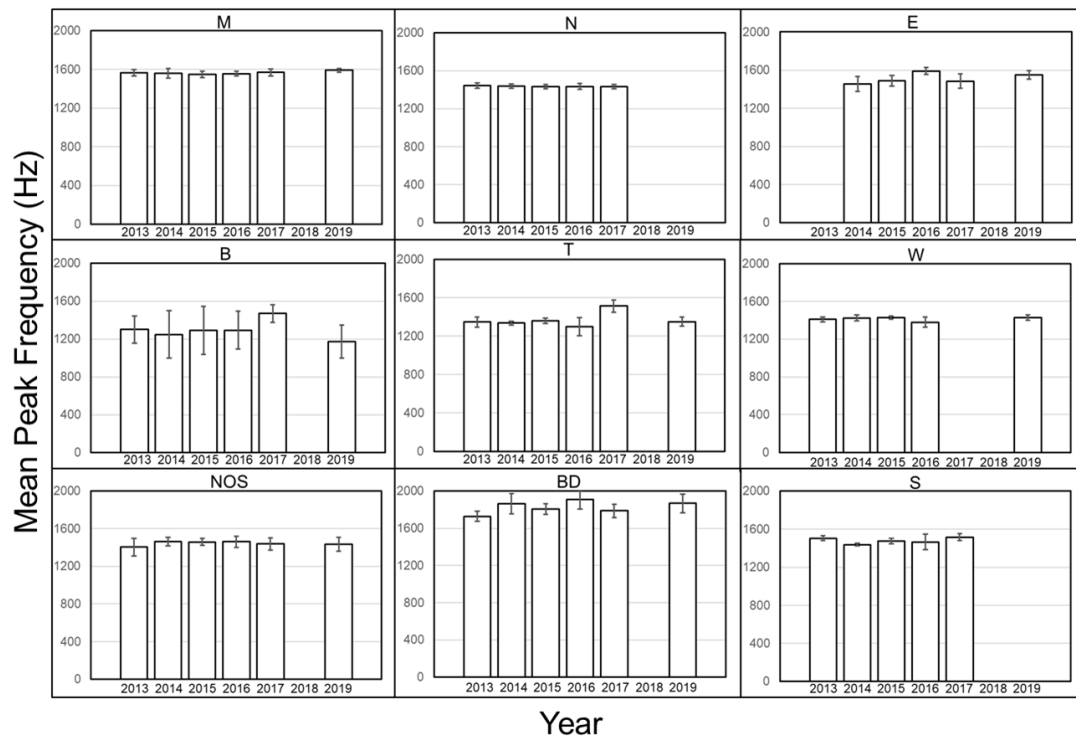
Mean Cross-Correlation Similarity Indices of Great Calls, As a Function of the Number of Years Between Recordings (N=9 Animals)



Note. Mean cross-correlation comparisons made between calls from the same year, and separated by 1, 2, 3, 4, 5 and 6 years (9 animals). Error Bars represent ± 1 SEM.

Figure 3

Mean Peak Fundamental Frequency (Peak F0) of Great Calls for Each Animal Across All Years



Note. Each animal was recorded for either 5 or 6 years, and no animals were recorded in 2018. Error Bars represent ± 1 SD.

Discussion

To our knowledge, the long-term individual vocal stability that we report here has not been previously documented to this degree for any other mammal, and has also not been reported for a complex, multi-note vocalization. Like gibbons, humpback whales (*Megaptera novaeangliae*) produce complex songs that can be highly stereotyped over the course of hours to days, but over longer time periods these songs show substantial change (Cholewiak et al., 2013; Fournet et al., 2018; Payne & McVay, 1971). This may be because, unlike gibbon great calls, that are developmentally fixed (Brockelman & Schilling, 1984; Geissmann, 1984), whale song is rapidly altered, either via learning/cultural transmission (Cholewiak et al., 2013) or by some other means (Mercado, 2022). Other studies of mammal vocal stability apply to much simpler one or two-note calls, and they have mostly failed to detect long-term stability. For example, ground squirrel calls (from three different species) reveal significant changes within most individuals' calls over a one-year period (Matrosova et al., 2009, 2010, Schneiderová et al., 2017). Reby et al. (1998) described more stable groans from fallow deer (*Dama dama*) across rutting periods, but they were able to only document long-term stability in a single animal. Similarly, Butynski et al. (1992) reported stability in the simple 'Pyow' call of a blue monkey (*Cercopithecus mitis stuhlmanni*) over ten years, but this was also documented for a single animal. An additional study of the simple 'phee' calls in common marmosets (*Callithrix jacchus*) (Jones et al., 1993) found individual vocal stability in five captive individuals, but over the course of only a single year. In contrast, we have documented vocal stability of a complex call (typically 8-10 notes, Terleph et al., 2015) for all individuals tested, and over a six-year period.

Contrary to one of our predictions, we did not find a decrease in F0 frequency of great call climaxes over the period that we analyzed. This finding does, however, provide further support for the prediction that great calls should remain highly stable within individuals, and suggests that selection pressure on great call stability has been high. The structural stability we found has the potential to reflect caller identity and possibly RHP to both direct and distant neighbors, over multiple years.

Over longer time periods than we measured, there may be subtle reductions to the pitch of call climaxes, as was suggested by our previous findings that employed a between-subjects design (Terleph et al., 2016); but we did not detect this within-subjects over a six-year period. The degree of vocal stability that we documented was remarkable because over half of the females in our study were over 20 years of age by the end of our data collection period (Table 1). If maintaining a high-pitched great call climax is physiologically demanding for these animals, then these older females would have been most likely to show a decrease in climax pitch. Additional long-term studies using more species would allow for a comparative analysis of the relevant ecological factors, such as long-term territory tenure, that may give rise to the evolution of stable vocal signals.

Author Contributions: TAT conceived the design of the study, analyzed the data and wrote the manuscript. All authors edited the manuscript and contributed to data collection and project administration.

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Conflict of Interest: The authors report no conflicts of interest.

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