Singing Patterns of White-Cheeked Gibbons (Nomascus sp.) in the Annamite Mountains of Laos

C. N. Z. Coudrat, C. Nanthavong, D. Ngoprasert, P. Suwanwaree & T. Savini

International Journal of Primatology
The Official Journal of the International
Primatological Society

ISSN 0164-0291

Int J Primatol
DOI 10.1007/s10764-015-9849-x

Springer

Your article is protected by copyright and all rights are held exclusively by Springer Science +Business Media New York. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com”.

Springer

Author's personal copy

Int J Primatol
DOI 10.1007/s10764-015-9849-x

Singing Patterns of White-Cheeked Gibbons (*Nomascus* sp.) in the Annamite Mountains of Laos

C. N. Z. Coudrat[1] **· C. Nanthavong**[2] **·**
D. Ngoprasert[3] **· P. Suwanwaree**[2] **· T. Savini**[3]

Received: 6 November 2014 / Accepted: 25 May 2015
© Springer Science+Business Media New York 2015

Abstract Studying the structure and patterns of vocalizations in primates is important to understand their evolution, responses to changing environments, and social behavior, and to design efficient vocalization-based survey techniques. Gibbons (Hylobatidae) are small arboreal apes known for their stereotyped songs. Data on their vocalization patterns remain limited, especially for crested gibbons (*Nomascus* spp.). We recorded songs of white-cheeked gibbons (*Nomascus* sp.) heard from listening posts at a site in Nakai–Nam Theun National Protected Area, central-eastern Laos, during a cold dry and a warm dry season, from November 2013 to May 2014, along with weather data. Males typically initiated the duet songs at a mean time of 06:14 h. Duet song bouts lasted a mean of 16 min. Song bout length was relatively constant throughout the study but decreased with the occurrence of wind. On a given day, the first male song started at a mean of 12 min before sunrise and all songs ceased at a mean of 13 min after sunrise. The start time of the first song relative to sunrise did not differ significantly between the two seasons but we found a significant negative relationship between the start time of the first song and both time of sunrise and temperature. The mean number of song bouts heard was significantly larger during the cold dry season than the warm dry season, and we found a significant negative relationship between the number of song bouts heard and temperature. Song rates also increased during days with no rain relative to rainy days. Our findings provide a preliminary understanding of song patterns in *Nomascus* spp. and can aid the planning and interpretation of surveys that rely on documenting their calls.

✉ C. N. Z. Coudrat
camillecoudrat@gmail.com

[1] Project Anoulak, Ban Oudomsouk, Nakai District Khammouan Province, Lao PDR

[2] Suranaree University of Technology, School of Biology, Institute of Science,
NakhonRatchasima 30000, Thailand

[3] King Mongkut's University of Technology Thonburi, School of Bioresources & Technology,
Bangkok 10150, Thailand

Published online: 04 August 2015

Author's personal copy

Keywords Calls · Conservation · Listening posts · Meteorological variables · Seasonality · Sunrise · Survey · Vocalizations

Introduction

Studying the structure and patterns of vocalizations in primates is important for our understanding of their evolution, responses to changing environments, and social behavior, as well as for the design of vocalization-based surveys. Primates are known to alter their behavior in relation to environmental factors such as light intensity, temperature, humidity, precipitation, day/night length, moon phase, and weather induced by the geophysical solar and earth system (Erkert 2003). The behaviors affected include vocalization patterns. For example, indri (*Indri indri*) songs varied in rate and timing across the year, with peaks in song rates during midsummer, when they also started singing earlier in the morning (Pollock 1986), and buff-cheeked gibbons (*Nomascus gabriellae*) sang more during the dry season, but the songs were shorter than during the wet season (Rawson 2004).

Gibbons are one of the most threatened primate groups (Melfi 2012) as a result of hunting and habitat loss (Duckworth 2008; Rawson *et al*. 2011). They are notable for their stereotyped songs (Marshall and Marshall 1976). These vocalizations have implications for inter- and intragroup communication for resource defense, predation avoidance and pair-bonding (Clarke *et al*. 2006; Cowlishaw 1992; Fan *et al*. 2009), their response to human disturbance (Johns 1985), and their taxonomy (Geissmann 1993; Konrad 2004; Thinh *et al*. 2010a, 2011). Gibbons typically sing every morning, either as male or female solo bouts or in duets (Dooley *et al*. 2013; Geissmann 2002; Geissmann and Nijman 2006; Tenaza 1976; Whitten 1982). Among gibbon species, songs vary in timing patterns, e.g., start time, length etc., and in intra- and intergroup coordination (Tenaza 1976). Songs also include species-, sex- and individual-specific acoustic characteristics (Dallmann and Geissmann 2001, 2009; Geissmann 1993; Heller *et al*. 2010; Keith *et al*. 2009; Konrad and Geissmann 2006; Thinh *et al*. 2011).

Although the function and evolution of gibbon songs have received attention from scientists, the effect of weather on the circadian and circannual rhythm of songs has rarely been investigated and such studies have focused mostly on the genus *Hylobates* (Cheyne 2008; Dooley *et al*. 2013; Geissmann 2002; Geissmann and Nijman 2006; Tenaza 1976; Whitten 1982). Crested gibbons (*Nomascus* spp.) are thought to differ from *Hylobates* in vocalization patterns (Geissmann 1993) and to have a more seasonal calling pattern (Fan *et al*. 2008, 2009). Crested gibbons share general sex-specific vocabulary characteristics (Geissmann 2002) but seasonality in their song patterns has not been well studied.

White-cheeked gibbons (*Nomascus siki* and *N. leucogenys*) are among the rarest and most threatened gibbon species (Rawson *et al*. 2011) but are almost unstudied ecologically. Gibbons are best surveyed by the detection of their songs from listening posts (Brockelman and Ali 1987) but wildlife surveyors have highlighted the paucity of current data on song patterns for *Nomascus* species as a constraint in survey design and interpretation (Duckworth *et al*. 2005). We studied the singing behavior of a population of white-cheeked gibbons for which the taxonomic identity remains uncertain (Thinh *et al*. 2010b) and could be any of *Nomascus siki*, *N. leucogenys*, or both, with or without hybrids, in Nakai–Nam Theun National Protected Area, central-eastern Laos,

Author's personal copy

where gibbon density is relatively high (Coudrat and Nanthavong 2014). We examined whether weather and time of sunrise affect singing rate and timing and differences between the cold dry and the warm dry seasons.

Methods

Study Site

Nakai–Nam Theun National Protected Area, which covers *ca.* 3500 km^2, is located in central-eastern Laos in the Annamite mountain range (Fig. 1). The area remains largely

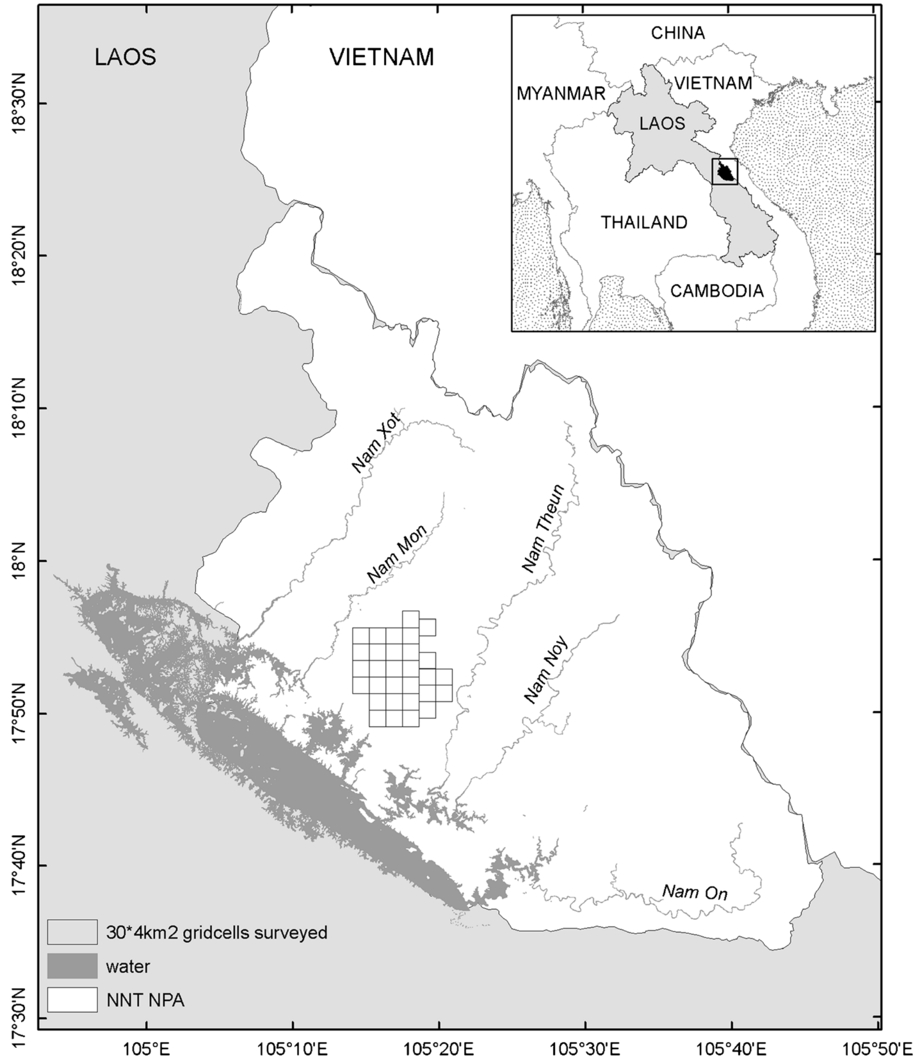

Fig. 1 Location of Nakai–Nam Theun National Protected Area (NNT NPA), Lao PDR, and the research site (4-km^2 grid of 30 cells) for this study of *Nomascus* sp. from November 2013 to May 2014.

Author's personal copy

forested (Robichaud *et al*. 2009) with mixed semi-evergreen/coniferous, upper montane, dry evergreen and wet evergreen forests (Timmins and Evans 1996). Elevation in the area ranges from *ca.* 500 m to 2300 m above sea level (asl). Measured annual precipitation ranges 1865–2620 mm but may be considerably higher in some of the wettest areas, given the complexity of relief and paucity of direct rainfall measurements within and around the area. Monthly mean temperatures range 14–24°C, with daily extremes of 4–32 °C (Hijmans *et al*. 2005). The area typically experiences four seasons based on average monthly rainfall and temperatures: a cold dry season in December–February, a warm dry season in March–May, a warm wet season in June–September, and a further warm dry season in October–November. Before data collection, the research site, in the central-west part of the NPA (17°34′–18°23′N 105°02′–105°46′ E) was divided into 4 km^2 grid cells (total, 30). Elevation at the research site varied from 579 to 1277 masl, based on remote sensing data (CGIAR Consortium for Spatial Information (http://srtm.csi.cgiar.org/).

Data Collection

Vocalization Records We conducted vocalization surveys of gibbons in Nakai–Nam Theun National Protected Area (Fig. 1) from November 2013 to May 2014 (*N* = 117 survey days). We set three listening posts in a line in each of the 30 contiguous grid squares spaced *ca.* 500 m apart, located from 596 m to 1128 m asl. We visited the three listening posts in each grid simultaneously before dawn for four consecutive days, arriving at a mean of 05:41 h (range: 04:55–06:38 h) and staying until all groups heard had stopped singing for ≥30 min, i.e., at a mean of 07:26 h (range: 06:00–09:40 h). We recorded all gibbon songs we heard, including both duets and songs where only males were heard, hereafter solos, and noted the following data: start time of male song, start time of female song, approximate end time of song bout (duet or solo). The listening records revealed that some songs were not heard from some listening posts, e.g., female songs, and some beginning times may not have been accurately recorded from distant groups. In those cases, the start time was either recorded approximately or not recorded at all. End times of the song bouts were recorded systematically (if the end time was not recorded that record was not used in the analysis of song duration).

We trained each team leader to differentiate male and female song sequences. Male and female songs in *Nomascus* species are sex-specific and easily distinguished (Geissmann 2002; Haimoff 1984; Konrad 2004; Konrad and Geissmann 2006; Marshall and Marshall 1976; Thinh *et al*. 2011).

Weather Variables We recorded the occurrence of rain, fog, and wind in the morning at the listening posts, and measured ambient temperature, dew point temperature, heat stress index, and relative humidity thrice a day (at a mean of 6:19 ± SD 0:32, 12:26 ± SD 0:44, and 18:18 ± SD 0:29 h) using a hand-held Kestrel 3000 weather station at one of the three listening posts. We obtained the official times of sunrise for our survey days from http://www.timeanddate.com/worldclock/sunrise.html. Throughout, we use “sunrise” to mean “official sunrise” rather than location-specific actual sunrise.

Author's personal copy

Data Analysis

We present song timings for all songs combined, duets only and male solos only. We tested the effect of weather variables (presence/absence of wind, fog, and rain; morning temperature) and time of sunrise on three dependent variables: start time of the first male song heard for duet calls relative only to sunrise time (mean of the three listening posts per day, hereafter, start time of first song relative to sunrise), song bout length for duet calls only (from start time of male song to end time of all songs in the bout, hereafter referred to as song bout length) and mean number of song bouts heard per day (mean of the three listening posts; including duets and solos, hereafter referred to as mean number of song bouts heard). To investigate seasonal variation, we combined months of December to February as the cold dry season and months of November and March to May as the warm dry season, based on weather data. We used the Mann–Whitney *U* statistic to test 1) differences in song timings between duet calls and solos; 2) differences in meteorological variables between the two seasons; 3) differences in mean number of song bouts heard, start time of first song relative to sunrise and song bout length between the two seasons; and 4) differences in mean number of song bouts heard, start time (clock-time) of first song, start time of first song relative to sunrise and song bout length between days with rain vs. no rain, fog vs. no fog, and wind vs. no wind. We used the chi-square statistic to test for differences in presence vs. absence of rain, fog, and wind between the two seasons. Finally, we used a linear regression R^2 to test the relationship between mean number of song bouts heard and temperature and the relationship between the start time of first song relative to sunrise and temperature. We performed all the above statistical tests (two-tailed) in SPSS v. 20.

Because the relationship between time of first song and temperature is confounded by changes in time of sunrise, we performed all analyses of song timings relative to sunrise (negative value for calls before sunrise and positive value for calls after sunrise). However, we present descriptive statistics using clock time for song timing for comparison with other studies, and compare clock time between duets and solos.

Ethical Note

The research adhered to the Code of Best Practice for Field Primatology (Riley *et al.* 2014) including ethical obligations to the study species.

Results

Gibbon Song Timing and Rates

We recorded a total of 1023 song bouts, including 922 duets, 101 male solos, and no female solos during the 117 survey days with a mean of 2.93 song bouts heard per day ($N = 90$ listening posts). Males typically initiated the duet songs (95.3%); the female started singing a mean of 3 ± SD 4 min after the male (range –27 to +44 min). On rare occasions ($N < 10$; not systematically recorded) we heard some songs after the data collection period, between 09:00 and 12:00 h (excluded from the analysis).

Author's personal copy

Combining all songs, 62% started before sunrise and 73% ended after sunrise (Table I). Of duets only, 62% started before sunrise and 74% ended after sunrise. When considering only the first group to duet, 83% occurred before sunrise and 67% ended after the sunrise (Table I; Fig. 2). Male solos began significantly earlier (Mann–Whitney $U = 39291.0$, $z = -2.058$, $P < 0.05$), bouts ended earlier ($U = 33983.5$, $z = -2.737$, $P < 0.01$), and call length was shorter ($U = 28692.5$, $z = -4.269$, $P < 0.001$) than duets. There were no significant differences the start time of the male relative to sunrise ($U = 40313.5$, $z = -1.682$, $P = 0.093$) and the end time of the group relative to sunrise ($U = 40955.0$, $z = -0.101$, $P = 0.920$) between male solos and duets.

Variation in Weather and Time of Sunrise Between Seasons

During the study period ($N = 117$ days), there were 13 days of rain, 30 days with fog, and 46 windy days (Table II). Temperature, heat stress index, dew point temperature, and relative humidity were all greater and the sun rose earlier during the warm season than during the cold season (Table II). There was no seasonal difference in the occurrence of wind and fog (Table II).

Seasonal Variation in Gibbon Songs

On days with no rain, there was a significant difference in mean number of song bouts heard between the two seasons (Mann–Whitney test: $U = 974.5$, $z = -2.456$, $P < 0.05$)

Table I Comparison of song timings (mean, SD, and range) for all songs combined, duets only, and male solos only for *Nomascus* sp. in Nakai–Nam Theun National Protected Area, Lao PDR from November 2013 to May 2014

		Mean	SD	Range
All songs	Start time male	06:13	±27 min	05:07–07:58
	Start time female	06:16	±26 min	05:12–08:02
	End time	06:29	±27 min	05:15–08:20
	Song bout length	16 min	±8 min	0–93 min
	Start time of male relative to sunrise	–2 min	±20 min	–53 to 93 min
	End time of group relative to sunrise	13 min	±20 min	–37 to 111 min
Duets only	Start time male	06:14	±26 min	05:07–07:58
	Start time female	06:16	±26 min	05:12–08:02
	Time end	06:29	±27 min	05:18–08:23
	Song bout length	16 min	±7 min	0–73 min
	Start time of male relative to sunrise	–2 min	±20 min	–53 to 93 min
	End time of group relative to sunrise	13 min	±20 min	–37 to 111 min
Male solos only	Start time male	06:08	±29 min	05:11–07:20
	Time end	06:21	±30 min	05:15–07:37
	Song bout length	15 min	±15 min	0–93 min
	Start time of male relative to sunrise	0 min	±22 min	–44 to 62 min
	End time of male relative to sunrise	13 min	±20 min	–30 to 86 min

Author's personal copy

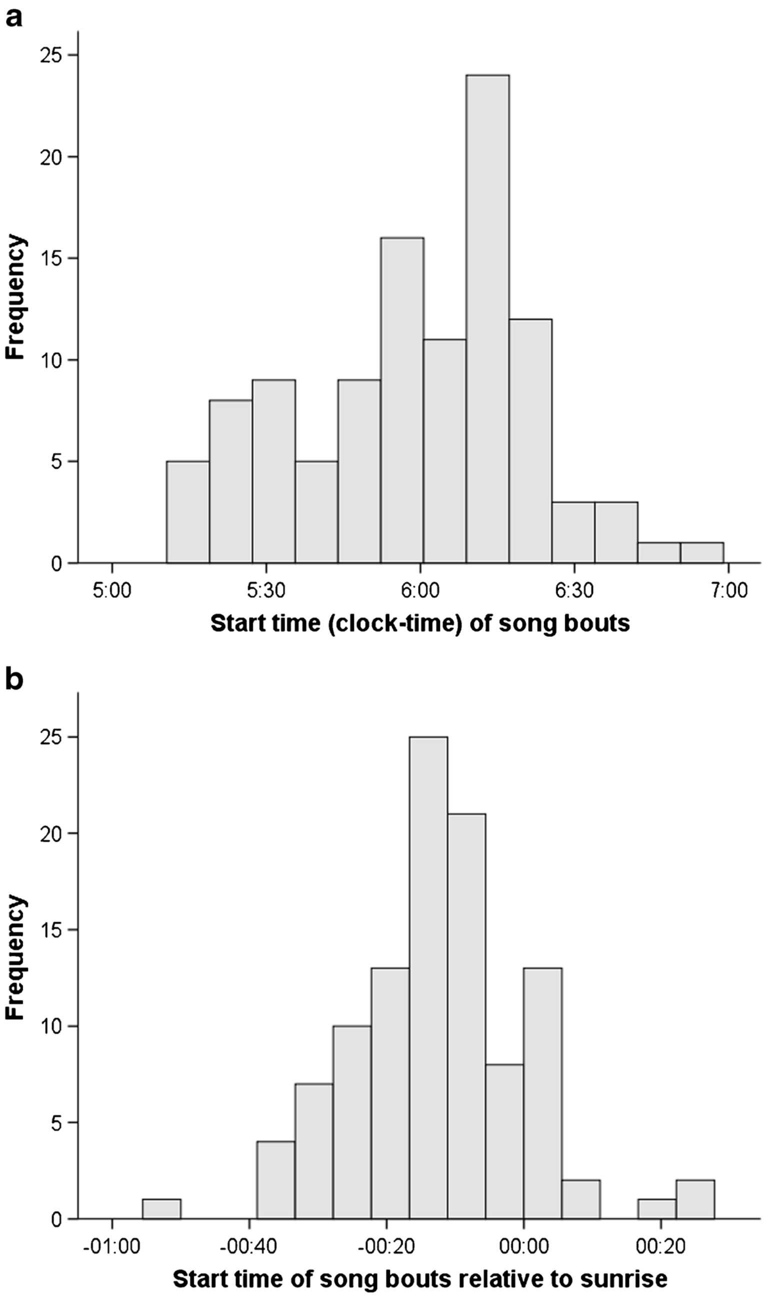

Fig. 2 Frequency of start time of male (hh:mm since midnight) **(a)** and start time of male relative to sunrise (in minutes) **(b)** for first duet calls for *Nomascus* sp. in Nakai–Nam Theun National Protected Area, Lao PDR, from November 2013 to May 2014.

(Fig. 3). The start time of the first song relative to sunrise and song bout length were not significantly different between the two seasons ($U = 1398.5$, $z = –0.141$, $P = 0.888$; $U = 1384.5$, $z = –0.228$, $P = 0.819$, respectively).

Author's personal copy

Table II Difference in meteorological variables between the warm dry (November 2013 and March–May 2014) and cold dry (December 2013–February 2014) season in Nakai–Nam Theun National Protected Area, Lao PDR, with the results of Mann–Whitney U and chi-square tests

Variables	Seasons [frequency/mean ± SE and (range)]		Statistical comparison
	Warm (N = 66 days)	Cold (N = 51 days)	
Frequency of occurrence of rain	13 days	0 days	$\chi^2 = 11.301$, d.f. = 1, $P < 0.001$
Frequency of occurrence of wind	12 days	23 days	$\chi^2 = 1.267$, d.f. = 1, $P = 0.320$
Frequency of occurrence of fog	11 days	17 days	$\chi^2 = 2.806$, d.f. = 1, $P = 0.134$
Sunrise (clock time)	5:55 ± 0:02 (5:30–6:13)	6:29 ±0:00 (6:13–6:33)	$U = 0.500$, $z = –9.255$, $P < 0.001$
Temperature (°C)	19.61 ±0.38 (12.8–25.0)	12.07 ±0.48 (5.40–20.50)	$U = 167.5$, $z = –8.246$, $P < 0.001$
Dewpoint temperature (°C)	18.78 ±0.38 (11.5–24.2)	11.09 ±0.54 (4.5–24.7)	$U = 193.5$, $z = –8.054$, $P < 0.001$
Heat stress index (°C)	20.57 ±0.46 (13.2–28.4)	12.56 ±0.53 (5.9–24.9)	$U = 188.5$, $z = –8.127$, $P < 0.001$
Mid-day relative humidity (%)	85.27 ± 1.31 (60.0–100.0)	75.08 ± 1.69 (47.7–100.0)	$U = 766.5$, $z = –4.286$, $P < 0.001$

Author's personal copy

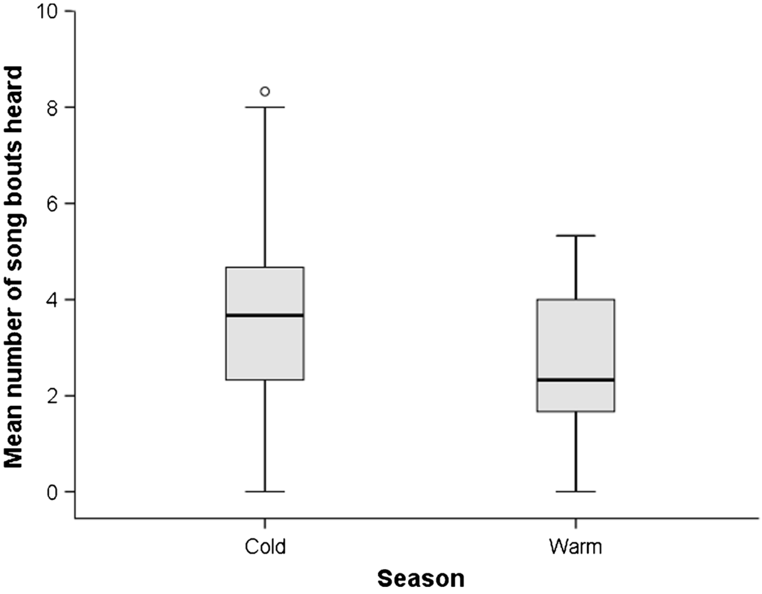

Fig. 3 Seasonal variation in the number of song bouts heard (including duets and solos). Plot shows median, lower and upper *quartile*, overall range of values excluding the outlier (o); $N = 117$ survey days for *Nomascus* sp. in Nakai–Nam Theun National Protected Area, Lao PDR, from November 2013 to May 2014.

Effect of Weather and Sunrise on Gibbon Songs

The mean number of songs was significantly greater on days with no rain than on rainy days, but there was no relationship between the mean number of songs and the occurrence of either wind or fog (Table III). Singing started earlier relative to sunrise on days with no wind and days with fog, but there was no effect of rain. Songs were significantly shorter on windy days than on days without wind, but there was no effect of fog or rain (Table III).

Excluding rainy days, the mean number of song bouts heard decreased significantly with temperature (Fig. 4). As temperature increased, the first songs started earlier relative to sunrise (Fig. 4). However, there was no significant relationship between song bout length and temperature ($R^2 = 0.011$, $P = 0.288$).

Discussion

Gibbon song timings recorded in Nakai–Nam Theun National Protected Area were consistent with general song patterns of other *Nomascus* species. Gibbons typically called between 05:00 h and 09:00 and song bouts lasted 11–15 min (Fan *et al*. 2009; Johns 1985; Johnson *et al*. 2005; Lan 1993; Rawson 2004; Rawson *et al*. 2009). Our study design does not allow us to determine whether the male solo songs recorded were produced by solitary individuals, by sexually mature offspring still resident in their natal group, or by males whose female mate did not sing. We did not record any solo female songs. Long-term follows of habituated groups may be more appropriate to

Author's personal copy

Table III Variation in the number of song bouts heard, time of first song, and song bout length in *Nomascus* sp. in relation to the occurrence of rain, wind, and fog and temperature in Nakai–Nam Theun National Protected Area, Lao PDR, from November 2013 to May 2014, with the results of Mann–Whitney U tests

Dependent variable Independent variable		Mean number of song bouts heard	Start time of first song bout (clock-time)	Start time of first song bout relative to sunrise (minutes)	Song bout length (minutes)
Wind (N days)	Yes (46)	2.8 ± 0.2	06:09 ± 2 min	–8 ± 1	16 ± 0
	No (71)	3.4 ± 0.2	05:52 ± 2 min	–15 ± 1	19 ± 0
Statistical comparison		$U = 1430.0$, $z = -1.135$, $P = 0.256$	$U = 829.5$, $z = -3.416$, $P < 0.01$	$U = 899.5$, $z = -2.970$, $P < 0.01$	$U = 976.5$, $z = -2.479$, $P < 0.05$
Fog (N days)	Yes (30)	3.5 ± 0.3	05:56 ± 3 min	–17 ± 2	19 ± 0
	No (87)	3.0 ± 0.2	06:00 ± 2 min	–10 ± 1	17 ± 0
Statistical comparison		$U = 1117.5$, $z = -1.173$, $P = 0.241$	$U = 1016.5$, $z = -0.634$, $P = 0.526$	$U = 670.0$, $z = -3.090$, $P < 0.01$	$U = 837.5$, $z = -1.903$, $P = 0.057$
Rain (N days)	Yes (13)	1.7 ± 0.3	05:41 ± 4 min	–9 ± 1	18 ± 1
	No (104)	3.3 ± 0.2	06:01 ± 2 min	–12 ± 1	18 ± 0
Statistical comparison		$U = 280.5$, $z = -3.437$, $P < 0.01$	$U = 217.5$, $z = -2.863$, $P < 0.01$	$U = 411.0$, $z = -0.792$, $P = 0.428$	$U = 452.5$, $z = -0.348$, $P = 0.728$

Author's personal copy

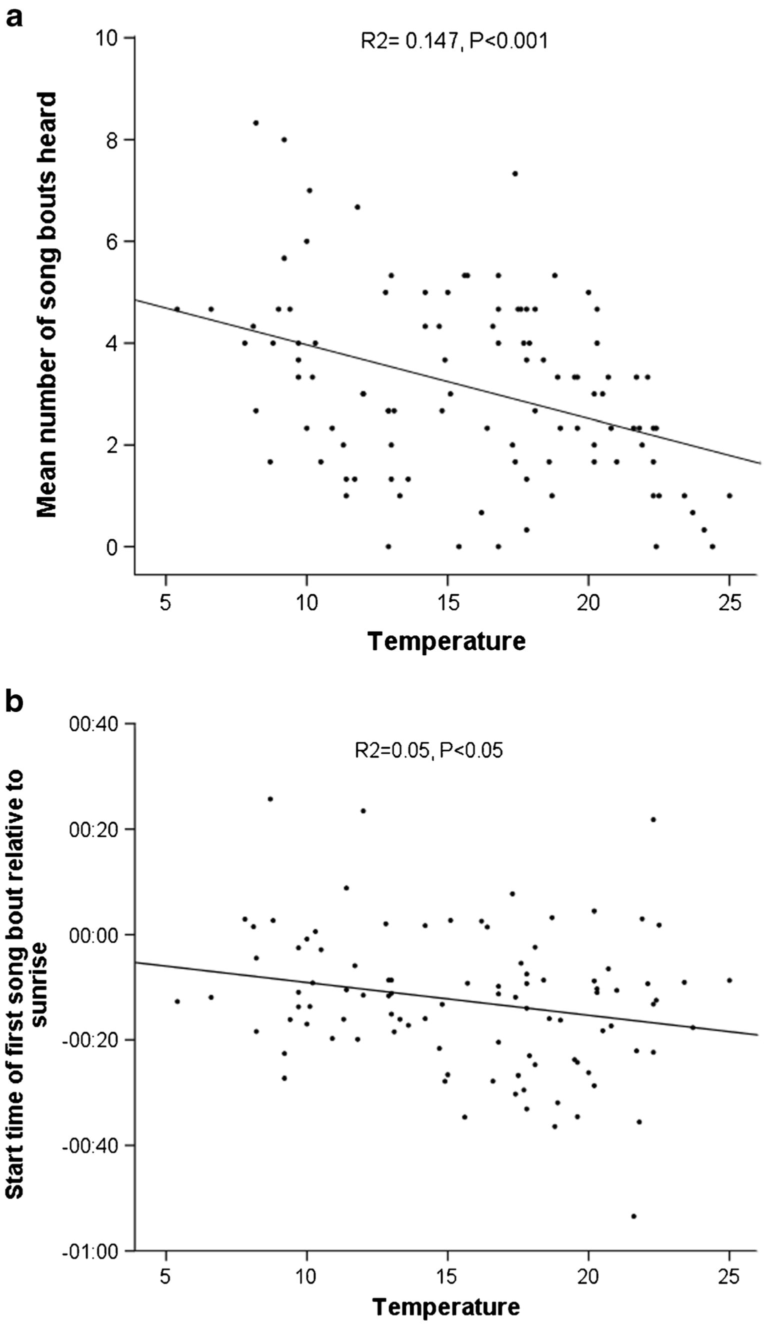

Fig. 4 Relationship between the mean number of song bouts heard and temperature **(a)** and between the start time of the first song relative to sunrise and temperature **(b)**. *N* = 117 survey days for *Nomascus* sp. in Nakai-Nam Theun National Protected Area, Lao PDR, from November 2013 to May 2014.

record such calls, but female solo songs seem generally infrequent in *Nomascus* species, although they have been recorded in other *Nomascus* species (Fan *et al.*

Author's personal copy

2009). Male solos started earlier and were shorter than duet songs. Shorter lengths of solo males compared to duet bouts have also been found in *Nomascus concolor* and *Hylobates pileatus* (Fan *et al*. 2009; Traeholt *et al*. 2006). These differences in timing may be explained by the different functions of solo songs and duets (Fan *et al*. 2009).

Song Timing

We found that first songs of duets occurred mainly within the 20 min before the sunrise, at around 06:15 h. The relatively consistent morning start times and song bout length reflect those in other *Nomascus* species (Fan *et al*. 2009; Johns 1985; Johnson *et al*. 2005; Lan 1993; Rawson 2004; Rawson *et al*. 2009), while variability seems generally greater in *Hylobates* species (Geissmann 1993).

The atmospheric conditions created by meteorological, astronomical, and biotic variables are important drivers of sound transmission by animals (Larom *et al*. 1997), including primates (Brown *et al*. 1995; Morrill *et al*. 2013; Van Bell *et al*. 2013). However, the effects of wind, rain, and fog on song transmission in primates have not been specifically tested. We found that the occurrence of wind reduced song length. If wind reduces song transmission, gibbons may shorten their song bout on windy days to conserve energy. Our study species also started singing earlier relative to sunrise on days with no wind and on days with fog, although rain did not affect their start time in relation to sunrise. These results differ from those for *Hylobates albibarbis* in Borneo, Indonesia, in which song onset occurred later than usual on rainy days when gibbons did sing (Cheyne 2008). In addition, we found that as temperature increased, the first songs started earlier relative to sunrise, while it was still dark. Warmer temperatures may allow gibbons to start their diurnal activity earlier with their first call initiated even before the sun rises.

Singing Rates

Gibbons sang less on rainy days, consistent with our original hypothesis and with previous studies. Rainfall has been identified most often as a factor inhibiting singing events in gibbons (Cheyne 2008; Dooley *et al*. 2013; Mitani 1988; Rawson 2004; Rawson *et al*. 2009; Whitten 1982) although it did not significantly affect singing rates of *Nomascus concolor jingdongensis* in two separate studies (Fan *et al*. 2009; Lan 1993). Rain the night before also has been found to be a factor decreasing probability of singing the following morning in gibbons (Mitani 1988; Rawson 2004; Whitten 1982) but our data did not allow us to test this factor. Rain may affect singing rates because it greatly reduces the audibility of calls (Dooley *et al*. 2013), rather than because of a reduction in body heat in the callers as previously suggested (Cheyne 2008; Whitten 1982), as we found that cold temperature does not inhibit singing.

When excluding rainy days from the analysis, the mean number of song bouts heard was significantly greater during the cold dry than during the warm dry season. Excluding rainy days, we also found a significant negative relationship between the mean number of song bouts heard and temperature. Other studies of the effect of temperature on singing rate have found inconsistent patterns. At one area in Lao PDR (Xe Pian NPA), in one year (1992–1993), *Nomascus* gibbons increased their song output markedly between December (cold season) and early May (hot season),

Author's personal copy

considering only dry mornings (Duckworth *et al.* 1995). However, temperature had no significant effect on song rates in other studies (Brockelman and Srikosamatara 1993; Cheyne 2008, Fan *et al.* 2009; Lan 1993; Mitani 1988), and its effect was inconsistent in other studies on some of the same species (Dooley *et al.* 2013; Whitten 1982). This suggests that temperature may not systematically affect gibbon song rates and that additional site-specific factors are likely to be involved. One possibility is the range of temperature at a site. For example, temperature in Nakai Nakai–Nam Theun National Protected Area, where we found a significant effect on gibbon song, are highly seasonal, within a range of 5°C–30°C depending on altitude.

We found no significant effect of fog or wind on gibbon singing rates. Fog did not influence singing rates in other studies, either (Cheyne 2008; Rawson *et al.* 2009). In contrast, wind inhibited singing in *Hylobates pileatus* in southeast Thailand (Brockelman and Srikosamatara 1993; Srikosamatara and Brockelman 1983) and in *Hylobates albibarbis* in Borneo (Cheyne 2008). Wind may affect singing rates differently in different habitat topography. In the former study, the research site was located in a steep-sided valley while in the latter, a lowland flat area. Wind in these habitats likely significantly reduces song transmission and would therefore make it a waste of energy to sing on windy days. In contrast, our site covered a larger area of highly rugged terrain where gibbons can sing from high points.

Other biotic and abiotic factors can influence singing frequencies in gibbons. For example, groups of *Hylobates lar* significantly reduced calling behavior when disturbed by loggers (Johns 1985). In Indonesia, where air quality varies seasonally with forest fires, *Hylobates albibarbis* reduced singing during months of intense atmospheric smoke (Harisson *et al.* 2007). Some studies suggest that gibbons sing more during periods of high fruit availability (Bartlett 2009; Fan *et al.* 2008; Rawson 2004; Tenaza 1976). The availability of figs —a major food item in gibbons' diet— is unpredictable, with no seasonal pattern in phenology. Future studies should investigate this hypothesis to understand better the relationship between food availability and song rates. Singing rates may also be density dependent; gibbons are likely to sing less in areas of low gibbon density, e.g., where hunting pressure has reduced a population, as intergroup communication is reduced (Brockelman and Srikosamatara 1993).

Understanding how gibbon species interact with their environment can provide insights into how they may adapt to climate change in the future; climate factors that may reduce song frequencies and/or alter their pattern may influence gibbon behavioral ecology by affecting inter- and intragroup communication. Although our findings for a *Nomascus* species can be used to inform design of gibbon survey for related species by choosing the best periods of the year and time of day to survey to maximize calling detection probabilities, our understanding of gibbon songs relative to biotic and abiotic factors remain too limited to conclude that the patterns observed in our study site and study species can be generalized to other sites and *Nomascus* species. Our study did not span the rainy season, to maximize call detection probability, known to be highest during the dry season for *Nomascus* spp. (Rawson 2004). However, the research covered two seasons (warm dry and cold dry) with distinctive solar timing and meteorological patterns, e.g., temperature, humidity. This allowed us to test for seasonal difference in gibbon song timings and rates, but study over the rainy season will be necessary to understand annual variation in the species' vocalizations. Future research

Author's personal copy

should also test the influence of fruit availability and gibbon density on singing patterns of gibbons.

Acknowledgments Permission to conduct this research was provided by the Ministry of Natural Resources and Environment of Lao PDR (authorization letter No. 5707, dated August 29, 2013) and the Nam Theun 2 Watershed Management and Protection Authority. Special thanks go to the field assistants from Ban Navang and Ban Nahao. Thank you to Project Anoulak's team for the support to make this gibbon project possible. Funding for this study was provided by Parc Animalier d'Auvergne/La Passerelle Association (France), Minnesota Zoo (USA), Mulhouse Zoo (France), Zoologische Gesellschaft Für Arten Und Populationsschutz e. V. (ZGAP) (Germany), Idea Wild (USA), Le Conservatoire pour la Protection des Primates/La Vallée des Singes (France), Primate Conservation Inc. (USA), Apenheul Primate Park (The Netherlands), American Society of Primatology (USA), Association Française des Parcs Zoologiques (France), and Suranaree University of Technology (Thailand). We are grateful to T. Q. Bartlett, W. Brockelman, W. J. Duckworth, anonymous reviewers, and the journal editor for their comments on earlier drafts, which substantially improved the manuscript.

References

Bartlett, T. Q. (2009). Territoriality and intergroup encounters. In T. Q. Bartlett (Ed.), *The gibbons of Khao Yai: Seasonal variation in behaviour and ecology* (pp. 103–119). Boston: Allyn & Bacon.

Brockelman, W., & Ali, R. (1987). Methods of surveying and sampling forest primate populations. In C. W. Marsh & R. A. Mittermeier (Eds.), *Primate conservation in the tropical rain forest* (pp. 23–62). New York: Alan R. Liss.

Brockelman, W., & Srikosamatara, S. (1993). Estimation of density of gibbon groups by use of loud songs. *American Journal of Primatology, 29*, 93–108.

Brown, C. H., Gomez, R., & Waser, P. M. (1995). Old world monkey vocalizations: adaptations to the local habitat? *Animal Behaviour, 50*, 945–961.

Cheyne, S. M. (2008). Effects of meteorology, astronomical variables, location and human disturbance on the singing apes: *Hylobates albibarbis. American Journal of Primatology, 70*, 386–392.

Clarke, E., Reichard, U. H., & Zuberbu, K. (2006). The syntax and meaning of wild gibbon songs. *PloS one*, e73.

Coudrat, C. N. Z., & Nanthavong, C. (2014). Gibbon survey and taxonomical status in Nakai-Nam Theun National Protected Area, Laos reveals one of the largest remaining populations of white-cheeked gibbons: Implications for their long-term conservation [Abstract]. Hanoi, Vietnam: *XXVIth International Primatological Society Congress*, August 11–16, 2014.

Cowlishaw, G. U. Y. (1992). Song function in gibbons. *Behaviour, 121*, 131–153.

Dallmann, R., & Geissmann, T. (2001). Different levels of variability in the female song of silvery gibbons (*Hylobates moloch*). *Behaviour, 138*, 629–648.

Dallmann, R., & Geissmann, T. (2009). Individual and geographical variability in the songs of wild silvery gibbons (*Hylobates moloch*) on Java, Indonesia. In S. Lappan & D. Whittaker (Eds.), *The gibbons: New perspectives on small ape socioecology and population biology* (pp. 51–72). New York: Springer Science+Business Media.

Dooley, H. M., Judge, D. S., & Schmitt, L. H. (2013). Singing by male and female Kloss gibbons (*Hylobates klossii*) in the Peleonan Forest, Siberut Island, Indonesia. *Primates, 54*, 39–48.

Duckworth, J. W. (2008). *Preliminary gibbon status review for Lao PDR 2008*. Vientiane, Laos: Fauna & Flora International.

Duckworth, J. W., Robichaud, W. G., & Eve, R. (2005). *Observations of birds and large mammals in Phongsaly province, Lao PDR, with particular reference to Phou Dendin National Protected Area*. Vientiane, Laos: WWF-Laos.

Duckworth, J. W., Timmins, R. J., Anderson, G. Q. A., Thewlis, R. M., Nemeth, E., Evans, T. D., Dvorak, M., & Cozza, K. E. A. (1995). Notes on the status and conservation of the gibbon *Hylobates (Nomascus) gabriellae* in Laos. *Tropical Biodiversity 3*, 15–27.

Author's personal copy

Erkert, H. G. (2003). Chronobiological aspects of primate research. In J. M. Setchell & D. J. Curtis (Eds.), *Field and laboratory methods in primatology* (pp. 252–270). Cambridge, UK: Cambridge University Press.

Fan, P.-F., Ni, Q.-Y., Sun, G.-Z., Huang, B., & Jiang, X.-L. (2008). Seasonal variations in the activity budget of *Nomascus concolor jingdongensis* at Mt. Wuliang, central Yunnan, China: Effects of diet and temperature. *International Journal of Primatology, 29*, 1047–1057.

Fan, P., Xiao, W. E. N., Huo, S., & Jiang, X.-L. (2009). Singing behavior and singing functions of black-crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, Central Yunnan, China. *American Journal of Primatology, 71*(7), 539–547.

Geissmann, T. (1993). *Evolution of communication in gibbons (Hylobatidae)*. Doctoral dissertation, Zurich University, Switzerland.

Geissmann, T. (2002). Duet-splitting and the evolution of gibbon songs. *Biological Reviews, 77*, 57–76.

Geissmann, T., & Nijman, V. (2006). Calling in wild silvery gibbons (*Hylobates moloch*) in Java (Indonesia): Behavior, phylogeny, and conservation. *American Journal of Primatology, 68*, 1–19.

Haimoff, E. H. (1984). The organization of song in the Hainan black gibbon (*Hylobates concolor hainanus*). *Primates, 25*, 225–235.

Harrison, M. E., Cheyne, S. M., Sulistiyanto, Y., & Rieley, J. O. (2007). Biological effects of smoke from dry-season fires in non-burnt areas of the Sabangau peat swamp forest, Central Kalimantan, Indonesia. In J. O. Rieley, C. J. Banks, & G. Radjaguk (Eds.), *Carbon-climate-human interaction on Tropical Peatland*: *Proceedings of the international symposium and workshop on Tropical Peatland*, *Yogyakarta*, *August 27–29, 2007* (pp. 1–5). Gadjah Mada University, Indonesia and University of Leicester, UK: EU CARBOPEAT and RESTOPEAT Partnership.

Heller, R., Sander, A. F., Wang, C. W., Usman, F., & Dabelsteen, T. (2010). Macrogeographical variability in the great call of *Hylobates agilis*: Assessing the applicability of vocal analysis in studies of fine-scale taxonomy of gibbons. *American Journal of Primatology, 72*, 142–151.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology, 25*, 1965–1978.

Johns, A. D. (1985). Behavioral responses of two Malaysian primates (*Hylobates lar* and *Presbytis melalophos*) to selective logging: Vocal behavior, territoriality, and nonemigration. *International Journal of Primatology, 6*, 423–433.

Johnson, A., Singh, S., Duangdala, M., Hedemark, M. (2005). The western black crested gibbon Nomascus concolor in Laos: new records and conservation status. *Oryx 39*, 311–317.

Keith, S. A., Waller, M. S., & Geissmann, T. (2009). Vocal diversity of Kloss's gibbons (*Hylobates klossii*) in the Mentawai Islands, Indonesia. In S. Lappan & D. Whittaker (Eds.), *The gibbons: New perspectives on small ape socioecology and population biology* (pp. 91–110). New York: Springer Science+Business Media.

Konrad, R. (2004). *Vocal diversity and taxonomy of the crested gibbons* (*genus* Nomascus) *in Cambodia*. PhD dissertation, University of Zurich, Switzerland.

Konrad, R., & Geissmann, T. (2006). Vocal diversity and taxonomy of *Nomascus* in Cambodia. *International Journal of Primatology, 27*, 713–745.

Lan, D.-Y. (1993). Feeding and vocal behaviours of black gibbons (*Hylobates concolor*) in Yunnan: A preliminary study. *Folia Primatologica, 60*, 94–105.

Larom, D., Garstang, M., Payne, K., & Raspet, R. (1997). The influence of surface atmospheric conditions on the range and area reached by animal vocalisations. *The Journal of Experimental Biology, 200*, 421–431.

Marshall, J. T., & Marshall, E. R. (1976). Gibbons and their territorial songs. *Science, 193*(4249), 235–237.

Melfi, V. A. (2012). Gibbons: Probably the most endangered primates in the world. *International Zoo Yearbook, 46*, 239–240.

Mitani, J. C. (1988). Male gibbon (*Hylobates agilis*) singing behavior: Natural history, song variations and function. *Ethology, 79*, 177–194.

Morrill, R. J., Thomas, A. W., Schiel, N., Souto, A., & Miller, C. T. (2013). The effect of habitat acoustics on common marmoset vocal signal transmission. *American Journal of Primatology, 75*, 904–916.

Pollock, J. I. (1986). The song of the Indris (Indri indri; Primates: Lemuroidea): Natural history, form, and function. *International Journal of Primatology 7*, 225–264.

Rawson, B. (2004). Vocalisation patterns in the yellow-cheeked crested gibbon (*Nomascus gabriellae*). In T. Nadler, U. Streicher, & H. T. Long (Eds.), *Conservation of primates in Vietnam* (pp. 130–136). Hanoi, Vietnam: Frankfurt Zoological Society; Endangered Primate Rescue Center.

Rawson, B. M., Clements, T., & Nut Meng Hor. (2009). Status and conservation of yellow-cheeked crested gibbons (*Nomascus gabriellae*) in the Seima Biodiversity Conservation Area, Mondulkiri Province,

Author's personal copy

Cambodia. In S. Lappan & D. Whittaker (Eds.), *The gibbons: New perspectives on small ape socioecology and population biology* (pp. 387–408). New York: Springer Science+Business Media.

Rawson, B. M., Insua-cao, P., Ha, N. M., Thinh, V. N., Hoang, D. M., Mahood, S., Geissmann, T., & Roos, C. (2011). *The conservation status of gibbons in Vietnam*. Hanoi, Vietnam: Fauna & Flora International and Conservation International.

Riley, E. P., Mackinnon, K. C., Fernandez-duque, E., Setchell, J. M., & Garber, P. A. (2014). Code of best practices for field primatology. International Primatological Society and American Society of Primatologists Steering Committee.

Robichaud, W., Sinclair, A., Odarkor-Lanquaye, N., & Klinkenberg, B. (2009). Stable forest cover under increasing populations of swidden cultivators in central Laos: The roles of intrinsic culture and extrinsic wildlife trade. *Ecology and Society, 14*, 33–60.

Srikosamatara, S., & Brockelman, W. Y. (1983). Patterns of territorial vocalization in the pileated gibbon (*Hylobates pileatus*). In P. K. Seth (Ed.), *Perspectives in primate biology* (pp. 19–22). New Delhi, India: T.T.P.P. Publishers.

Tenaza, R. (1976). Songs, choruses and countersinging of Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. *Zeitschrift für Tierpsychologie, 40*, 37–52.

Thinh, V. N., Mootnick, A. R., Geissmann, T., Li, M., Ziegler, T., Agil, M., Moisson, P., Nadler, T., Walter, L., & Roos, C. (2010a). Mitochondrial evidence for multiple radiations in the evolutionary history of small apes. *BMC Evolutionary Biology, 10*, 74–87.

Thinh, V. N., Rawson, B., Hallam, C., Kenyon, M., Nadler, T., Walter, L., & Roos, C. (2010b). Phylogeny and distribution of crested gibbons (genus *Nomascus*) based on mitochondrial cytochrome b gene sequence data. *American Journal of Primatology, 72*, 1047–1054.

Thinh, V. N., Hallam, C., Roos, C., & Hammerschmidt, K. (2011). Concordance between vocal and genetic diversity in crested gibbons. *BMC Evolutionary Biology, 11*, 36–44.

Timmins, R. J., & Evans, T. D. (1996). *Wildlife and habitat survey of the Nakai-Nam Theun National Biodiversity Conservation Area*. Vientiane, Lao PDR: Wildlife Conservation Society.

Traeholt, C., Bonthoeun, R., Virak, C., Samuth, M., & Vutthin, S. (2006). Song activity of the Pileated gibbon, *Hylobates pileatus*, in Cambodia. *Primate Conservation, 21*, 139–144.

Van Belle, S., Estrada, A., & Garber, P. A. (2013). Spatial and diurnal distribution of loud calling in black howlers (*Alouatta pigra*). *International Journal of Primatology, 34*, 1209–1224.

Whitten, A. J. (1982). The ecology of singing in Kloss gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *International Journal of Primatology, 3*, 33–51.