

## RESEARCH ARTICLE

### A Comparison of Facial Expression Properties in Five Hylobatid Species

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Little is known about facial communication of lesser apes (family Hylobatidae) and how their facial expressions (and use of) relate to social organization. We investigated facial expressions (defined as combinations of facial movements) in social interactions of mated pairs in five different hylobatid species belonging to three different genera using a recently developed objective coding system, the Facial Action Coding System for hylobatid species (GibbonFACS). We described three important properties of their facial expressions and compared them between genera. First, we compared the rate of facial expressions, which was defined as the number of facial expressions per units of time. Second, we compared their repertoire size, defined as the number of different types of facial expressions used, independent of their frequency. Third, we compared the diversity of expression, defined as the repertoire weighted by the rate of use for each type of facial expression. We observed a higher rate and diversity of facial expression, but no larger repertoire, in *Symphalangus* (siamangs) compared to *Hylobates* and *Nomascus* species. In line with previous research, these results suggest siamangs differ from other hylobatids in certain aspects of their social behavior. To investigate whether differences in facial expressions are linked to hylobatid socio-ecology, we used a Phylogenetic General Least Square (PGLS) regression analysis to correlate those properties with two social factors: group-size and level of monogamy. No relationship between the properties of facial expressions and these socio-ecological factors was found. One explanation could be that facial expressions in hylobatid species are subject to phylogenetic inertia and do not differ sufficiently between species to reveal correlations with factors such as group size and monogamy level. *Am. J. Primatol.* 76:618–628, 2014. © 2014 Wiley Periodicals, Inc.

**Key words:** gibbons; GibbonFACS; facial expression; FACS; monogamy index

#### INTRODUCTION

It has been suggested that the complexity of primate communicative repertoires is closely connected to living in social groups, because increased social complexity acts as a driver for increased communicative complexity [e.g., Freeberg et al., 2012]. For example, there is evidence for a positive correlation between group size and facial expressions in a sample of 12 primate species [Dobson, 2009]. Furthermore, the specific social structure of primates and the dominance hierarchy was found to influence the use and repertoire of facial expressions [de Waal & Luttrell, 1985; Maestriperi, 1999; Preuschoft & van Hooff, 1997; Thierry et al., 1989; van Hooff, 1976]. The extent to which species differences in facial expression can be attributed to socio-ecological variables, therefore, is important to fully understand the evolutionary function of facial expressions. Although, in hylobatids, there is yet not much known about whether facial expressions have true communicative, or even

expressive, function, preliminary data suggests that this is the case [Liebal et al., in preparation]. In order to investigate facial expressions and their specific function in communicative contexts, a detailed investigation describing certain properties of facial expressions in hylobatids is highly relevant. Here, for ease of description, facial expression is defined as any single or combination of more than one facial

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movement (Action Unit [AU]) or more general head/eye movement (Action Descriptor [AD]), but without the assumption that these movements are necessarily communicative.

Together with humans and great apes, hylobatids belong to the superfamily Hominoidea [e.g., Geissmann, 2002; Mootnick, 2006]. Comprising up to 16 species, they represent the most diverse group within this superfamily [Thin et al., 2010], and they are closely related to both great apes and Old World Monkeys. Hylobatids are characterized by a similar set of morphological, ecological, and social features. They have prolonged extremities adapted to a brachiating style of locomotion, they are arboreal and usually live in small groups comprising of the mated pair and their offspring [Rowe, 1996]. However, there is some variability in their social organization. Although they are commonly described as monogamous species, recent studies have challenged this view. Thus, it has been demonstrated that the social organization of gibbons is much more variable [e.g., Lappan, 2005; Palombit, 1994; Reichard, 1995] and that the strength of social bonds varies between different hylobatid species [Fischer & Geissmann, 1990]. In this regard, it is important to differentiate between sexual monogamy, which means that female and male have only a single partner of the opposite sex at a time [Black, 1996; Gowaty, 1996], and social monogamy, which refers to cooperation in the acquisition of other resources, for example, shared use of a territory, proximity between male and female, behaviors favoring pair cohesion [Reichard, 2003]. Thus, the latter can include sexual monogamy but also refers to social organization. One strong indicator against sexual monogamy is the engagement in extra pair copulations [e.g., Westneat, 1987]. For the white-handed gibbon (*Hylobates lar*) and siamangs (*Symphalangus syndactylus*) extra pair copulations have been observed in their natural habitats [Fuentes, 2000; Reichard, 2003; Reichard & Barelli, 2008; Reichard & Sommer 1997], as well for the yellow-cheeked crested gibbon (*Nomascus gabriellae*), although to a slightly lesser extent [Kenyon et al., 2011]. For siamangs there is most evidence of desertion and re-pairing with other individuals [Brockelmann et al., 1998; Chivers & Raemaekers, 1980; Palombit, 1994], whereas in other species it has not been observed [Fan & Jiang, 2010; Mootnick, 1984; Zhou et al., 2008]. Although from these observations one could argue that for example siamangs might be less monogamous than other hylobatid species, there is also evidence for siamang males investing in paternal care [e.g., Lappan, 2008], which is rather an indication favoring monogamy, whereas for other species only a few observations of paternal care were reported [e.g., *Hylobates lar*: Berkson, 1966; Fischer & Geissmann, 1990; *Hylobates pileatus*: Srikosamatar, 1980]. However, paternal care might not be the strongest indicator for monogamy. Thus, by considering different behaviors related to

either sexual and/or social monogamy we aim to rank species by different degrees of monogamy.

Despite the variability in the strength of monogamy, the social group structure of Hylobatidae is characterized by small stable family groups consisting of one pair and their offspring, with no pronounced hierarchy between the two adult individuals [Brockelmann et al., 1998; Preuschoft et al., 1984]. Following the line of argument by Freeberg et al. [2012], therefore, gibbons should use less facial signals compared to other primate species that live in more complex groups, for example, chimpanzees and macaques. Indeed, Chivers [1976] concluded that wild siamangs only show a limited communicative repertoire (facial expressions and gestures). In addition, given that they live in densely foliated environments, we might expect them to rely mostly on vocal rather than visual communication. However, very little is known about the communicative behavior of gibbons, with the exception of studies investigating their exceptional vocal duetting repertoires [Geissmann, 2002; Haimhoff, 1986; Raemaekers et al., 1984]. There are some studies that report facial expressions in the behavioral repertoire of hylobatids [Fox, 1972, 1977; Liebal et al., 2004; Orgeldinger, 1999], and some report detailed descriptions about those expressions. Liebal et al. [2004], for example, described three different facial expressions, one of which was observed in two varieties. A “grin” was described as facial expression where the mouth is “slightly opened and the corners of the mouth are withdrawn with the teeth scarcely visible between the lips.” The facial expression “Mouth open” was observed in two different varieties: “Mouth-open half” is when “the mouth is opened slightly, so that the canine teeth are almost completely covered by lips; the shape of the mouth is oval with the corners of the mouth withdrawn very little” and “Mouth-open full” when “mouth is opened to the full extent with the canine teeth and the palate visible”. The last facial expression was labeled “Pull a face” and described as “upper and lower jawbones are closed; the lips are protruded and slightly opened, forming an elliptical shape”.

However, a comparison across these studies is difficult because they did not use a standardized, objective method to classify different types of facial expressions. This lack of standardized methodology has recently been tackled by the establishment of a Facial Action Coding System for gibbons [GibbonFACS: Waller et al., 2012], which is a modified version of the HumanFACS [Ekman & Friesen, 1978], similar to other versions that were previously developed for other primate species [ChimpFACS for chimpanzees: Vick et al., 2007; MaqFACS for rhesus macaques: Parr et al., 2010; OrangFACS for orangutans: Caeiro et al., 2013]. This method relies on the identification of muscular movements underlying facial expressions. The

development of these different versions of FACS consists of various steps, including anatomical dissections [Burrows et al., 2006, 2009; Diogo et al., 2009], intramuscular stimulation techniques [Waller et al., 2006, 2008], and descriptions of the associated observable movements from video footage of spontaneous behavior.

This study aimed to investigate facial expressions in hylobatids by testing whether differences between hylobatid species relate to differences in socio-ecological variables. One hypothesis is that facial expressions vary between different hylobatid species as a function of their maximum group sizes [Chivers, 1976; Dobson, 2009]. The results by Dobson [2009] support the hypothesis that natural selection favors increased facial expressions (i.e., the number of different AUs a species can produce) in larger groups, in order to more effectively manage conflict behavior and increase bonding between individuals within a group [e.g., Flack & de Waal, 2007; Waller & Dunbar, 2005]. Therefore, one possible function of facial expressions might be group cohesion [Maestripieri, 1999; Parr et al., 2002; Thierry et al., 1989].

However, a second socio-ecological factor that could also be influential on facial expressions is the strength of monogamy. It has been shown that monogamous species might be associated with higher behavioral complexity and greater cognitive processing demands than polygamous species [Dunbar, 1992; Dunbar, 2011; Dunbar & Shultz, 2007; Shultz & Dunbar, 2010a,b], which might suggest that signal repertoires are more complex than would be predicted by group size alone.

Another hypothesis is that facial expressions are subject to phylogenetic inertia [e.g., Blomberg & Garland, 2002; Chan, 1996; Thierry et al., 2000] and, thus, highly conservative so that marked differences between species cannot be observed.

In this study we aimed to (1) characterize and compare the repertoires, the rates and the diversity of facial expressions of five hylobatid species by using a newly developed objective coding system [Gibbon-FACS: Waller et al., 2012] and (2) to investigate whether socio-ecological factors (group size and monogamy) are linked to these facial expression characteristics. Furthermore, we investigate whether females and males differ in certain properties of their facial expressions. Some sex differences in other respects have been observed, for example, many hylobatid species are dichromatic and some are known for their sex-specific songs [e.g., Rowe, 1996; Chivers, 2000]. However, other aspects might be more important in this regard. Compared to other primate species, hylobatids are monogamous and there is no explicit dominance hierarchy between pair partners, which might suggest that there are no pronounced differences in facial expression between females and males.

## METHODS

### Subjects

Five different species comprising a total of 16 individuals were observed: three mated pairs of *Symphalangus syndactylus*, two pairs of *Hylobates pileatus*, one pair of *Hylobates lar*, one pair of *Nomascus gabriellae*, and one pair of *Nomascus siki*. A detailed list of the individuals is shown in Table I. The pairs were housed in enclosures in groups of different sizes depending on the number of offspring present. All pairs except one were housed together with their offspring (1–3 individuals) in the enclosures (for details of the group composition see Table SI in the Supplementary Material S1). The study was carried out in compliance with respective animal care regulations and principles of the

TABLE I. Subjects

Pair	Individual	Species	Birth	Sex	Zoo
1	Daniel	<i>Symphalangus syndactylus</i>	26.05.1996	m	Twycross
	Tango	<i>Symphalangus syndactylus</i>	27.03.1994	f	Twycross
2	Kane	<i>Symphalangus syndactylus</i>	02.11.1990	m	Twycross
	Sheena	<i>Symphalangus syndactylus</i>	30.01.1991	f	Twycross
3	Spike	<i>Symphalangus syndactylus</i>	25.11.2000	m	Twycross
	Tarragona	<i>Symphalangus syndactylus</i>	18.11.2000	f	Twycross
4	Khmer	<i>Hylobates pileatus</i>	28.11.1984	m	Zurich
	Willow	<i>Hylobates pileatus</i>	06.05.1987	f	Zurich
5	Iaman	<i>Hylobates pileatus</i>	1959	m	Zurich
	Iba	<i>Hylobates pileatus</i>	1974	f	Zurich
6	Dan	<i>Nomascus gabriellae</i>	1991	m	Mulhouse
	Chloe	<i>Nomascus gabriellae</i>	06.01.1990	f	Mulhouse
7	Dorian	<i>Nomascus siki</i>	23.12.1989	m	Mulhouse
	Fanny	<i>Nomascus siki</i>	13.06.1993	f	Mulhouse
8	Bert	<i>Hylobates lar</i>	01.05.1982	m	Rheine
	Lissy	<i>Hylobates lar</i>	ca. 1981	f	Rheine

American Society of Primatologists for the ethical treatment of nonhuman primates.

**Data Collection and Coding**

Data collection took place between March 2009 and July 2012 in different zoos in the UK (Twycross), France (Mulhouse), Switzerland (Zurich), and Germany (Rheine, Westphalia). The behavior of each pair was video recorded in 15 min bouts using the focal animal sampling method [Altmann, 1974] (with both animals always in view) resulting in a total of 1,080 bouts. Recordings took place at different times of the day on several different days resulting in a total amount of 21 hr of observation (9 hr (43%) for *Symphalangus*, 7 hr (33%) for *Hylobates*, and 5 hr (24%) for *Nomascus*). Mean observation time per individual was 158 min (SD = 34 min). Recordings were taken only when the pair was in reaching distance and so had the opportunity to closely interact. We measured the number of facial expressions, the repertoire, and diversity per individual of each pair. Since the recording time differed between pairs, a correction for each of these measurements was performed by dividing each of these measurements by the recording time per individual (for details see *Measurements of the facial expressions* section). The video footage was coded using the software Interact (Mangold International GmbH, Version 9.6). Facial expressions were identified using GibbonFACS [Waller et al., 2012]. A facial expression was coded when it clearly showed the apex of a signaling action, that is, when the action is strongest for that event. We conducted a reliability analysis on 10% of the data, which was calculated using Wexler's Agreement as for the human FACS and all other nonhuman primate FACS systems [Ekman et al., 2002]. Agreement was 0.83, which in FACS methodology is considered good agreement [Ekman et al., 2002].

**Measurements of the Facial Expressions: Rates, Corrected Repertoire, and Corrected Diversity**

Three measurements were used to examine the use of facial expressions across the three gibbon genera. One facial expression can consist of a single facial movement (AU/AD) or a combination of more than one. First, we calculated the overall frequency of facial expressions, which is the total number of facial expressions produced independent of their type for each genus. *Rates* were obtained by correcting for the observation time for each individual, and then taking the mean for each genus.

Second, the *repertoire* of facial expressions was established for each genus, which comprises the number of different types of facial expressions observed during the recording time in the context

of social interactions. The “repertoire” in the present study should not be confused with the “facial repertoire” as an inventory of facial signals in the ethogram of a species, which is usually defined as an ensemble of (not objectively defined) facial patterns, regardless of the context in which they are observed. The observed repertoire in the present study is therefore a “standardized repertoire,” for the sake of ease labeled only “repertoire” here.

The corrected repertoire for the *m* genera ( $R_{Cm}$ ) was calculated as  $R_{Cm} = \sum_{i=1}^k R_i / \tau_i$ , where *k* is the number of individuals belonging to the *m* genera,  $\tau_i$  is the recording time of the individual *i* belonging to the *m* genera,  $R_i$  is the repertoire of the individual *i*, belonging to the genera *m* without time correction, and  $R_m$  is the repertoire of the *m* genera without time correction. Thus, the corrected repertoire of an individual was calculated by dividing the number of different types of facial expressions that an individual produced (repertoire of that individual) by its recording time.

Third, the *diversity* of the facial expressions takes into account both the repertoire and the rates. It should be interpreted as a weighted repertoire. The diversity measurement incorporates information about how many types of facial expressions are observed and how evenly those types are represented [Hill, 1973]. For a given number of types, the value of a diversity index is maximized when all types are equally present. In other words, the more different types there are and the more they are evenly represented, the higher the diversity measurement. Thus, if the number of facial expressions of an individual is given by *S*, we first calculated the *Shannon Information* [Shannon, 1948] for the *n*-individual as:

$$H_n = - \sum_{i=1}^S p_i \log(p_i)$$

Here  $p_i$  represents the ratio between the number of each facial expressions and the total number of facial expressions for a given individual.

The diversity of facial expressions is given by:

$$D_n = e^{H_n} = e^{- \sum_{i=1}^S p_i \log(p_i)}$$

The *corrected diversity index* ( $D_{n\tau}$ ) [Hill, 1973] of the facial expressions for each individual is then

$$\text{calculated by: } D_{n\tau} = \frac{e^{H_n}}{\tau_n} = \frac{e^{- \sum_{i=1}^S p_i \log(p_i)}}{\tau_n}$$

**Socio-Ecological Variables (Group Size and Monogamy)**

We correlated the three properties of facial expressions (rates, corrected repertoire and corrected diversity) with the two socio-ecological variables

**TABLE II. Maximum Group Size for Each of the Five Species (From the Literature)**

Species	Maximal number of group size
<i>Symphalangus syndactylus</i>	10 [Fuentes, 2000]
<i>Hylobates pileatus</i>	5 [Fuentes, 2000]
<i>Hylobates lar</i>	12 [Fuentes, 2000]
<i>Nomascus gabriellae</i>	7 [Kenyon et al., 2011]
<i>Nomascus siki</i>	5 [Roos, personal communication]

group size and monogamy (Indices I, II, and III) for each species using regression models. Information about group size was taken from the literature (see Table II). We used the maximum numbers of reported group size for further analysis. For this analysis we used the rates, corrected repertoire and the corrected diversity for each species. We incorporated phylogenetic information into the regression analysis because interspecific data are prone to violating assumptions of independence [Cohen & Cohen, 1983]. Each regression was performed using a phylogenetic general least squares (PGLS) analysis in the software R (packages “caper” and “ape”) with each property of facial expression as a dependent variable and the socio-ecological factors as predictor variables. For a detailed description of this analysis see the Supplementary Material S1.

We included the following socio-ecological variables for the creation of the monogamy index: extra pair copulation (EPC), polyandry (PA), and polygyny (PG), proximity at day (Pd), proximity at night (Pn), desertion (D), group composition (Gc), and paternal care (Pc) (see Table III). Information about these behaviors was obtained from a literature survey on 85 publications between years 1976 and 2012 (see reference list in Supplementary Materials S1 and S2). We divided behaviors either referring to sexual monogamy (SeM) or social monogamy (SoM); see Table III. We considered sexual monogamy, where an

**TABLE III. Behaviors Used for the Creation of the Monogamy Indices**

Sexual monogamy (SeM)	Social monogamy (SoM)
Extra pair copulations (EPC)	Proximity of the pair at day (Pd)
Polyandry (PA)	Proximity of the pair at night (Pn)
Polygyny (PG)	Desertion (D)
	Group composition (>2 adults) (Gc)
	Paternal care (Pc)
Index I = SeM	Index II = SeM + SoM;
	Index III = SeM ( $\alpha = 1$ ) + SoM ( $\alpha = 0.5$ )

individual has only a single partner of the opposite sex at a time [Black, 1996; Gowaty, 1996], as stronger indicators of monogamy than behaviors of social monogamy, which refers to cooperation in the acquisition of other resources, for example, shared use of a territory, proximity between male and female, behaviors favoring pair cohesion [Reichard, 2003]. In order to create an index, each behavior was ranked to calculate the monogamy indices (for details see Supplementary Material S1). To investigate whether variables of both sexual and social monogamy have a different impact on the outcome of the indices, we created three different indices. Assuming that those variables deriving from sexual monogamy are stronger predictors of monogamous behavior, the first index contains only variables of SeM (Index I). The second and third indices also include those variables of social monogamy but with the weights (given by  $\alpha$ ) distributed differentially in both cases (Index II – all variables of SeM + SoM weighted equally; Index III – SeM weighted with  $\alpha = 1$  and SoM weighted with  $\alpha = 0.5$ ). For a detailed description of this procedure see S1.

## RESULTS

### Rates, Corrected Repertoires, and Corrected Diversity of Facial Expressions

We coded a total of 1,080 instances of facial expressions (movements of single Action Units or Action Descriptors or a combination of two or more AUs/ADs): 878 from *Symphalangus*, 118 from *Nomascus*, and 93 from *Hylobates* (uncorrected by recording time). Table IV shows which types of facial expressions were observed for each of the three genera *Symphalangus* (*S. syndactylus*), *Hylobates* (*H. pileatus*, *H. lar*), and *Nomascus* (*N. gabriellae* and *N. siki*) and their frequency of use. For statistical analyses we corrected the three measurements by dividing the measurements of each individual by the individual’s recording time.

### Repertoire

To examine whether the three genera differ significantly from each other in the types of different facial expressions, we conducted a Kruskal–Wallis test. The comparison of the corrected repertoires did not reveal significant differences between the genera (Kruskal–Wallis test:  $H = 5.30$ ,  $df = 2$ ,  $P = 0.071$ ) (see Fig. 1).

### Rates

The rates for *Symphalangus*, *Nomascus* and *Hylobates* are 0.79, 0.20 and 0.11 facial expressions per minute, respectively. In order to examine whether the three genera differ from each other in the rates of facial expressions we conducted a

**TABLE IV. Repertoire (Uncorrected) of Facial Expressions in the Three Hylobatid Genera and Their Frequency of Occurrence**

No.	Facial expression	Symphalangus	Nomascus	Hylobates
1	AU1/2 <sup>a</sup>	[2]	[8]	[2]
2	AU8	[1]		
3	AU12	[1]		
4	AU17			[1]
5	AU18	[1]	[10]	[1]
6	AU25	[14]	[1]	[1]
7	AU41	[8]	[2]	[1]
8	AUEye <sup>b</sup>	[2]	[3]	
9	AD37	[1]		
10	AD500	[5]		
11	AU1/2 + AU18			[2]
12	AU10 + AU25	[1]		
13	AU16 + AU27			[1]
14	AU16 + AU25	[3]		
15	AU25 + AU26	[165]	[6]	[23]
16	AU25 + AU27	[37]	[1]	[4]
17	AU25 + AD19	[2]		
18	AU25 + AD37	[3]		
19	AU41 + AUEye	[2]		
20	AU7 + AU25 + AU26	[5]		
21	AU8 + AU25 + AU26	[12]		
22	AU8 + AU25 + AD37	[1]		
23	AU10 + AU25 + AU26	[17]		
24	AU10 + AU25 + AU27	[15]		
25	AU12 + AU25 + AU26	[7]		
26	AU12 + AU25 + AU27	[6]		
27	AU16 + AU25 + AU26	[52]	[1]	[1]
28	AU16 + AU25 + AU27	[38]	[4]	[1]
29	AU18 + AU25 + AU26	[3]		[1]
30	AU25 + AU26 + AD19	[5]		
31	AU25 + AU26 + AD37	[328]	[60]	[42]
32	AU25 + AU27 + AD19			[7]
33	AU1/2 + AU5 + AU25 + AU26			[1]
34	AU7 + AU9 + AU18 + AU22	[1]		
35	AU8 + AU25 + AU26 + AD19	[1]		
36	AU8 + AU25 + AU26 + AD37	[34]		
37	AU9 + AU10 + AU25 + AU27		[2]	
38	AU10 + AU12 + AU25 + AU27	[3]		
39	AU10 + AU16 + AU25 + AU26	[10]	[2]	
40	AU10 + AU16 + AU25 + AU27	[55]	[14]	[1]
41	AU12 + AU16 + AU25 + AU26	[4]		
42	AU12 + AU16 + AU25 + AU27	[4]	[1]	
43	AU12 + AU25 + AU26 + AD37	[1]		
44	AU16 + AU18 + AU25 + AU26	[1]		
45	AU18 + AU25 + AU26 + AD19	[1]		
46	AU18 + AU25 + AU26 + AD37	[1]		
47	AU25 + AU26 + AUEye + AD37	[1]		
48	AU25 + AU26 + AD37 + AD500	[1]		
49	AU1/2 + AU10 + AU16 + AU25 + AU27		[1]	
50	AU9 + AU10 + AU16 + AU25 + AU27	[1]		
51	AU10 + AU12 + AU16 + AU25 + AU26	[5]		[1]
52	AU10 + AU12 + AU16 + AU25 + AU27	[11]	[2]	
53	AU10 + AU12 + AU16 + AU25 + AU27 + AUEye	[2]		

<sup>a</sup>AU1/2 resembles AU1 + 2 from Waller et al. [2012].

<sup>b</sup>AUEye resembles either AU43 (eye closure) or AU45 (eye blink), we did not differentiate between the two AUs here.

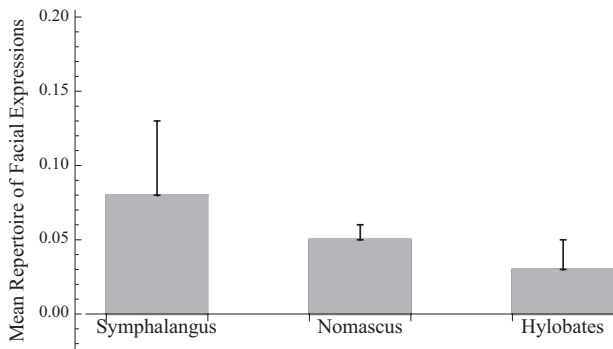


Fig. 1. Mean corrected repertoire for all three genera ( $\pm$ SD). There is no significant difference between the three genera.

Kruskal–Wallis test and found significant differences between the three genera (Kruskal–Wallis test:  $H = 11.25$ ,  $df = 2$ ,  $P < 0.001$ ). We performed a non-parametric post-hoc test for the difference between pairs. Following Conover, we used the critical difference of the mean ranks test [Conover, 1999; Sprent and Smeeton, 2001; Bewick et al., 2004]. We found that *Symphalangus* was significantly different than *Nomascus* and *Hylobates* ( $P < 0.05$ , see Supporting Material 1), but no significant differences were found between *Nomascus* and *Hylobates* ( $P > 0.05$ ); see Figure 2.

### Diversity

In order to examine whether the three genera differ from each other in their diversity of facial expressions we conducted a Kruskal–Wallis test, which revealed significant differences between genera (Kruskal–Wallis test:  $H = 6.22$ ,  $df = 2$ ,  $P = 0.045$ ). We performed a non-parametric post-hoc test for the difference between pairs. We used Conover's critical difference of the mean ranks test [Conover, 1999; Sprent and Smeeton, 2001; Bewick et al., 2004]. We found that *Symphalangus* was significantly different than *Nomascus* and *Hylobates* ( $P < 0.05$ , see Sup-

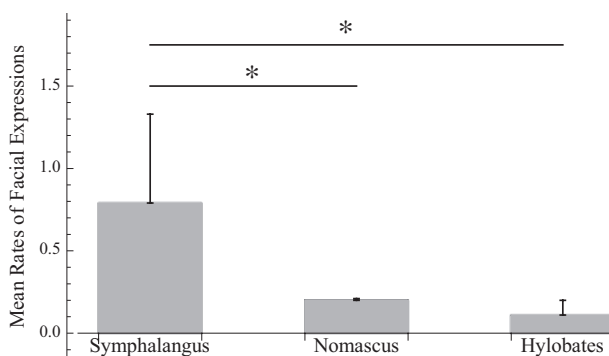


Fig. 2. Mean rates (number of facial expressions per minute corrected by recording time) of the three genera ( $\pm$ SD). \* Represents  $P$  values  $< 0.05$ .

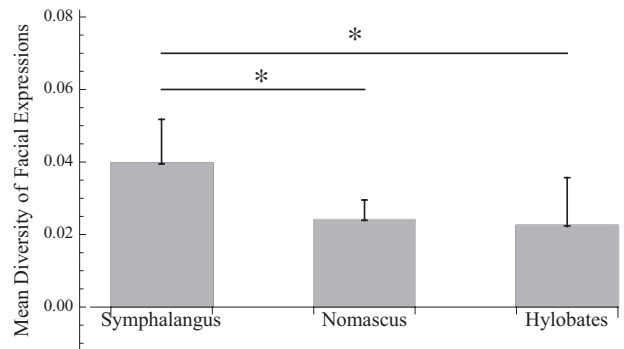


Fig. 3. Mean diversity (corrected by recording time) of the three genera ( $\pm$ SD). \* Represents  $P$  values  $< 0.05$ .

porting Material 1), but no significant differences were found between *Nomascus* and *Hylobates* ( $P > 0.05$ ); see Figure 3.

### Comparison of Males and Females

When combining the three genera, there were 15 combinations, which we only observed in males, while an additional 13 combinations were only present in females (see Table V). The remaining combinations were shared by both genders. However, statistical analyses found no differences between males and females in regard to the rates (Mann–Whitney  $U$ -test:  $Z = 0.32$ ;  $P = 0.753$ ), the corrected repertoires (Mann–Whitney  $U$ -test:  $Z = -1.33$ ;  $P = 0.185$ ), or corrected diversity (Mann–Whitney  $U$ -test:  $Z = 0.63$ ;  $P = 0.574$ ).

### Relationship Between Facial Expressions and Socio-Ecological Factors

We correlated the three measurements of facial expressions (rates, corrected repertoire, and corrected diversity) with the two socio-ecological variables group size and monogamy (Indices I, II, and III; see Table VI) using regression models. The models revealed no significant relationship of facial expression properties and the socio-ecological factors (see Results in Table VII).

### DISCUSSION

This is the first study to systematically investigate the use of facial expressions across different gibbon genera based on an objective, standardized method to identify and classify facial expressions (GibbonFACS). We studied the facial expressions of eight pairs of five hylobatid species belonging to the three genera in regard to the rate of signaling, the repertoire of facial expressions, and the diversity of signals. While the three genera did not differ in regard to their repertoires of facial expressions, siamangs differed from other gibbons in their more

**TABLE V. Facial Expressions Exhibited by Males and Females for All Species**

Exclusive for	Facial expression	
Males	AD37	
	AU16 + AU25	
	AU16 + AU27	
	AU8 + AU25 + AD37	
	AU18 + AU25 + AU26	
	AU25 + AU27 + AD19	
	AU7 + AU9 + AU18 + AU22	
	AU8 + AU25 + AU26 + AD19	
	AU9 + AU10 + AU25 + AU27	
	AU18 + AU25 + AU26 + AD37	
	AU18 + AU25 + AU26 + AD19	
	AU25 + AU26 + AD37 + AD500	
	AU25 + AU26 + AUEye + AD37	
	AU10 + AU12 + AU16 + AU25 + AU26	
	AU10 + AU12 + AU16 + AU25 + AU27 + AUEye	
	Females	AU8
		AU12
AU17		
AU26		
AU1/2 + AU18		
AU10 + AU25		
AU41 + AUEye		
AU7 + AU25 + AU26		
AU1/2 + AU5 + AU25 + AU26		
AU12 + AU25 + AU26 + AD37		
AU16 + AU18 + AU25 + AU26		
AU1/2 + AU10 + AU16 + AU25 + AU27		
AU9 + AU10 + AU16 + AU25 + AU27		

frequent use of facial expressions and a higher diversity of facial expressions. A facial expression is defined as a single or a combination of more than one facial movement (so-called Action Unit or Action Descriptor), regardless whether used communicatively or not.

In previous studies siamangs were found to show more synchronized activities and a special form of songs within the pair (duetting), which is thought to strengthen the pair-bond [Geissmann & Orgeldinger, 2000], compared to other hylobatid species. It was also found that their diet contains more leaves compared to the smaller species [Chivers, 1972; Rowe, 1996]. The observation that the defense of the territory was less intensive than in

smaller species [Gittins & Raemaekers, 1980] could be connected to the more folivorous diet. Thus, there seem to exist some differences between siamangs and other hylobatid species concerning their behavior and ecology. However, how these different morphological, social and ecological factors differentiating siamangs from other gibbons regarding their facial communication, needs to be addressed in further studies.

According to the prediction of Freeberg et al. [2012] and Dobson [2009] we should also expect differences between species in the repertoire of facial expressions as a function of their varying social organization as found already by Dobson [2009] for a variety of other primate species. We explored this hypothesis by testing for a potential correlation between different properties of facial expressions of each species with the socio-ecological factors group size and level of monogamy; both were found to differ between siamangs as compared to the other species. However, in the current study we could not observe any relationship between facial expressions and those socio-ecological factors. One possibility is that only a comparison between a relatively large number of species belonging to a group which members are phylogenetically separated by a longer time scale in evolutionary history can reveal such differences [Dobson, 2009], whereas a group consisting of a smaller number belonging to a smaller and closer related group of species can not, even though we corrected for phylogeny in our sample. Therefore, facial expressions in hylobatid species may be subject to evolutionary constraint and do not differ enough between species to reveal correlations between factors such as group size and monogamy level.

Although Dobson's [2009] findings support the "social complexity hypothesis," Freeberg et al. [2012] mentioned that group size is not necessarily implying social complexity and that there are several other aspects which have to be taken into account when assessing social complexity, for example, the social network, the strength of bonding between individuals, other and/or additional channels of communication, etc. Freeberg et al. [2012] define social complex systems as "those in which individuals frequently interact in many different contexts with many different individuals, and often repeatedly interact with many of the same individuals over time."

**TABLE VI. Monogamy Indices of the Five Species**

Species	Index I = SeM	Index II = SeM + SoM	Index III = SeM ( $\alpha = 1$ ) + SoM ( $\alpha = 0.5$ )
<i>Nomascus siki</i>	0.5	0.5	0.38
<i>Nomascus gabriellae</i>	0.483	0.54	0.36
<i>Hylobates lar</i>	0.185	0.36	0.21
<i>Hylobates pileatus</i>	0.417	0.46	0.31
<i>Symphalangus syndactylus</i>	0.18	0.45	0.26

Index I only includes behavioral variable of sexual monogamy (SeM); Index II includes behavioral variable of both, sexual and social monogamy (SoM); Index III includes behavioral variables of SeM and SoM, but with differently distributed weights on each indicated by  $\alpha$ .



TABLE VII. Results of Phylogenetic Generalized Least Square (PGLS) Analysis

Predictor	Response	$R^2$	Slope ( $b$ )	Standard error	$P$ values
Group size	Rate	-0.06	0.037	0.042	0.444
Group size	Repertoire	0.59	$6.1 \times 10^{-3}$	$2.4 \times 10^{-3}$	0.081
Group size	Diversity	0.41	$2.0 \times 10^{-3}$	$1.0 \times 10^{-3}$	0.149
Index I	Rate	0.25	-1.3	0.85	0.222
Index I	Repertoire	0.35	-0.11	0.06	0.175
Index I	Diversity	0.38	$-3.9 \times 10^{-2}$	0.021	0.160
Index II	Rate	-0.15	-1.53	2.25	0.545
Index II	Repertoire	-0.25	-0.078	0.17	0.684
Index II	Diversity	-0.27	0.028	0.071	0.721
Index III	Rate	-0.18	-1.53	2.47	0.580
Index III	Repertoire	-0.33	$-8.02 \times 10^{-6}$	$3.5 \times 10^{-4}$	0.983
Index III	Diversity	0.05	-0.065	0.059	0.348

Predictor variables are the socio-ecological factors group size and level of monogamy reflected by Index I, II, and III. Response variables are the measured properties of facial expressions.

There is some contradiction about whether the level of monogamy implies a high [Dunbar, 1992; Dunbar, 2011; Dunbar & Shultz, 2007; Shultz & Dunbar, 2010a,b] or low social complexity [e.g., Kroodsma, 1977]. Although little is known about the relationship between a species' social system and the size of facial expression repertoire [Freeberg et al., 2012], we discuss both scenarios. Thus, if we consider a high level of monogamy to be of low social complexity and siamangs to exhibit a low level of monogamy (based on the results of our monogamy index), their social system would be consequently highly complex. In this scenario the higher rate and diversity of facial expressive behavior would support the "social complexity hypothesis for communicative complexity" argument mentioned by Freeberg et al. [2012]. Alternatively, if we consider a high level of monogamy to be of high social complexity, siamangs' social system would be characterized by low complexity. In this latter example our results would contradict the social complexity hypothesis. Future studies have to be conducted to address this issue in more detail by, for example, increasing the sample size of the species and also considering a multimodal analysis of the communicative system as well as an analysis of the species' social network and therefore including various measurements when defining complexity.

We could not observe significant differences between males and females in regard to their repertoires, rates of signaling or diversity of facial expressions. This suggests that social communication through facial expressions in both males and females do not exhibit specific roles in their social structure and consequently that there is no hierarchical order between the mated pairs, which is in line with previous findings [Brockelmann et al., 1998; Preuschoft et al., 1984]. However, we observed 13 facial expressions, which were exclusively used by females and 15 different facial expressions exclusively used

by males. Further investigations need to clarify what specific functions those expressions have and whether their use is indeed due to sexual differences.

Taken together, the examination of the repertoire, rate, and diversity of facial expressions of five hylobatid species by using an objective coding system revealed a richer repertoire than previously reported for gibbons [Chivers, 1976; Fox, 1972, 1977; Liebal et al., 2004]. Interestingly, siamangs differed from other gibbon species regarding the rates and diversity of facial expressions and thus confirm previous results showing siamangs to be outstanding when compared to other gibbon species. A relationship between the facial expressions and socio-ecological factors such as group-size and monogamy level, however, was not found, suggesting that despite these small species differences, on the whole facial expressions have been subject to phylogenetic inertia.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

# Supplementary Information (S1)

from: “A comparison of facial expression properties in five hylobatid species”

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## 1. Group composition

Table S1: Group composition of the individuals.

Pair	Individuals	Species	Additional individuals (name, sex, birth)	Zoo
1	Daniel (m), Tango (f)	<i>Symphalangus syndactylus</i>	1 - Infant, 10.02.2010	Twycross
2	Kane (m), Sheena (f)	<i>Symphalangus syndactylus</i>	0 - no other individual	Twycross
3	Spike (m), Tarragona (f)	<i>Symphalangus syndactylus</i>	1 - Stig, infant male, 15.07.2009	Twycross
4	Khmer (m), Willow (f)	<i>Hylobates pileatus</i>	1 - Fayar, subadult male, 04.06.2005; 2 - Hantu, juvenile male, 23.07.2007; 3 - Jantan, baby male, 29.10.2009	Zurich
5	Iaman (m), Iba (f)	<i>Hylobates pileatus</i>	1 - Gadis, juvenile female, 04.04.2006; 2 - Ibu, infant female, 05.10.2008	Zurich
6	Dan (m), Chloe (f)	<i>Nomascus gabriellae</i>	1 - Banguin, adult, 13.10.2006; 2 - Bebe, baby female, October, 2010; 3 - Petit, baby male, 19.09.2010	Mulhouse
7	Dorian (m), Fanny (f)	<i>Nomascus siki</i>	1 - Anoie, subadult female, 25.10.2005; 2 - Chanchi, juvenile, 13.11.2007; 3 - Tiny, infant, 20.03.2010	Mulhouse
8	Bert (m), Lissy (f)	<i>Hylobates lar</i>	1 - Lilly, juvenile, 08.06.2004	Rheine

## 2. Recording times

Table S2: Individual recording times and average recording time per genera.

Genera	Subject	gender	Recording time (min)	Recording time (hours)	Average hours per gender
Symphalangus	Spike	m	240.53	4	3
Symphalangus	Tara	f	240.53	4	
Symphalangus	Daniel	m	138.96	2.3	
Symphalangus	Tango	f	138.96	2.3	
Symphalangus	Kane	m	159.3	2.7	
Symphalangus	Sheena	f	159.3	2.7	
Nomascus	Dan	m	148.28	2.5	2.6
Nomascus	Chloe	f	148.28	2.5	
Nomascus	Dorian	m	159.12	2.7	
Nomascus	Fanny	f	159.12	2.7	
Hylobates	Khmer	m	143.84	2.4	2.3
Hylobates	Willow	f	143.84	2.4	
Hylobates	Iaman	m	144.06	2.4	
Hylobates	Iba	f	144.06	2.4	
Hylobates	Bert	m	127.4	2.1	
Hylobates	Lissy	f	127.4	2.1	

### 3. Non-Parametric Post-hoc Test for the Kruskal-Wallis test

If the null hypothesis of no difference between groups is rejected, then it is possible to identify which pairs of groups differ by calculating a least significant difference (Conover 1999, Sprent 2001, Bewick 2004). Groups  $i$  and  $j$  are significantly different at the 5% significance level if the difference between their mean ranks is greater than the least significant difference (i.e. if the following inequality is true):

$$\left| \frac{R_i}{n_i} - \frac{R_j}{n_j} \right| > t \sqrt{S^2 \left( \frac{N-1+T}{N-k} \right) \left( \frac{1}{n_i} + \frac{1}{n_j} \right)}$$

Where  $t$  is the value from the t distribution for a 5% significance level and  $N - k$  degrees of freedom. Here  $T$  is defined as:

$$T = \frac{12}{N(N+1)} \sum_{j=1}^k \frac{R_j^2}{n_j} - 3(N+1)$$

Where  $R_j$  is the total of the ranks for the  $j^{\text{th}}$  sample,  $n_j$  is the sample size for the  $j^{\text{th}}$  sample,  $k$  is the number of samples, and  $N$  is the total sample size. This is approximately distributed as a  $\chi^2$  distribution with  $k - 1$  degrees of freedom. If  $r_{ij}$  is the rank for the  $i^{\text{th}}$  observation in the  $j^{\text{th}}$  sample,  $S^2$  is given by the following equation:

$$S^2 = \frac{1}{N-1} \left( \sum_{j=1}^k \sum_{i=1}^{n_j} r_{ij}^2 - \frac{N(N+1)^2}{4} \right)$$

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#### 4. Justification for the time correction

In order to understand to what extent the correction proposed in the present paper can or cannot be justified, we need to understand the properties of the process that generated the data collected. One would expect the production of facial expressions through time to be described as a Poisson process. If so, the time between each pair of consecutive events has an exponential distribution with parameter  $\lambda$  and each of these inter-arrival times should be independent of other inter-arrival times. Formally, the process can be defined as:

$$P(a(t + \tau) - a(t) = k) = \frac{e^{-\lambda\tau} (\lambda\tau)^k}{k!} \quad k = 0, 1, \dots$$

where  $a(t + \tau) - a(t) = k$  is the number of events in the interval  $(t, t + \tau]$ . The rate parameter  $\lambda$  gives the expected number of "events" that occur per unit time.

One of the fundamental properties of a Poisson process is that increments are stationary. This means that the probability distribution of the number of occurrences counted in any time interval only depends on the length of the interval. Therefore, the cumulative distribution of number of events in time is linear (See Figure 1 below, blue line B.).

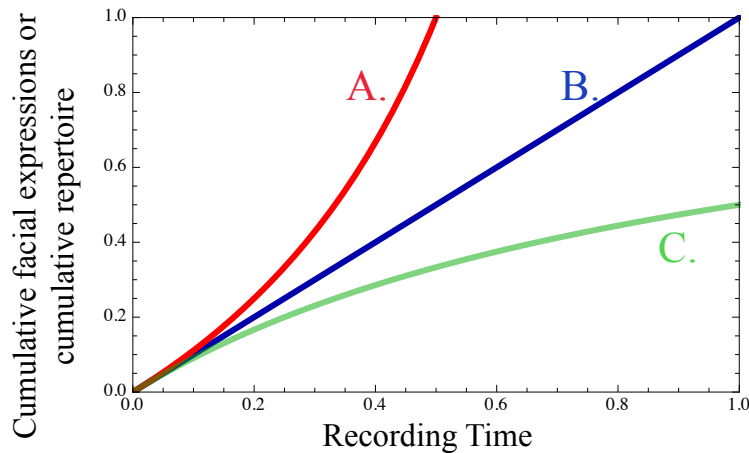


Figure S1: Different Scenarios describing the cumulative distribution of facial expressions or types of facial expressions through Recording Time.

We checked if this expected behavior is actually observed in our data. As an example, we plotted the cumulative distribution in the number of facial expressions vs. recording time in individuals from different genera, and used maximum likelihood methods to parameterize (by finding the adjusted numerical value of parameter  $\lambda$ ) a Poisson model.

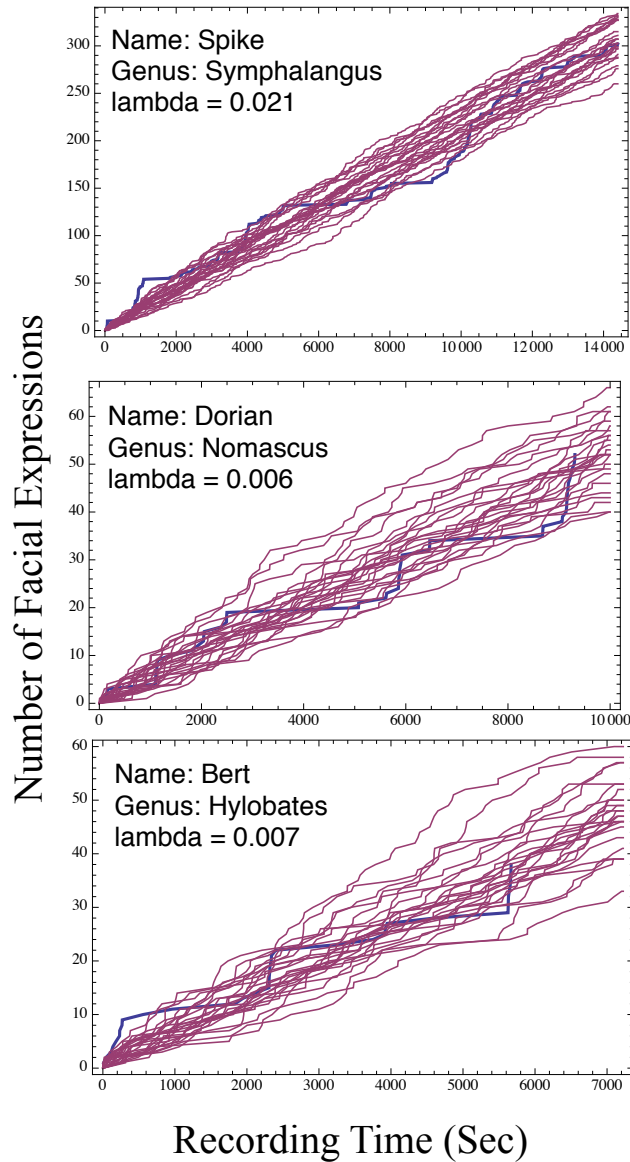


Figure S2: Cumulative number of facial expressions in different individuals as a function of the recording time. The empirical data is given by a blue thick line and simulated data are given by 25 red thin lines in each case. Detailed information contains the name of the individual, the Genus and the lambda parameter defining the stochastic Poisson Process, estimated using maximum likelihood methods.

As expected, we observed that the data could be well described following a Poisson Process. Given that increments are stationary, and as a consequence, the probability distribution of the number of occurrences counted in any time interval only depends on the length of the interval, dividing by recording time as a correction method is justified.

In which scenario dividing by recording time would imply errors by over or under-estimation of the facial expressions or type of facial expressions? Under the scenario described by the red curve A. in Figure 1, correcting the data by simply dividing by recording time will clearly lead to over-estimation of the real value observed (i.e. more recording time, will lead to much more than expected increase in facial expressions or types of facial expression observed). On the other hand, in the scenario described by the green curve C. in Figure 1, correcting the data by simply dividing by recording time will lead to an under-estimation of the real data



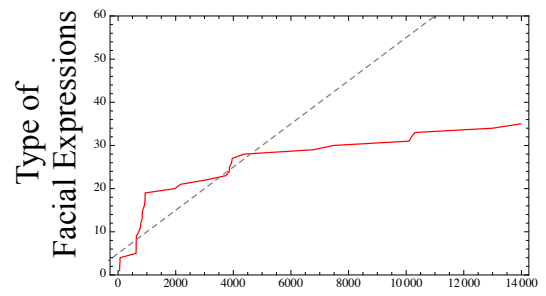
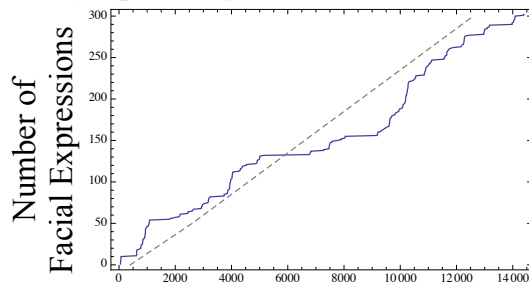
observed. Therefore estimation of the corrected (by time) values under scenario given by the C. curve will imply a highly conservative estimation.

The distribution of the type of facial expressions (repertoire) can be clearly situated in the scenario described by the green curve C in Figure 1. This is because, in the beginning, each facial expression that is generated is going to be of a new given type, as times goes by, facial expressions belonging to the same type are going to start appearing. Eventually, after some given recording time each new facial expression will have high chances to be of a type that already appeared, leading to a plateau in the curve (see examples in Figure 3 – red lines -). As a consequence, in groups where the recording time was larger than others, dividing by recording time is strongly conservative. It implies to punish too strongly cases where the recording time was longer.

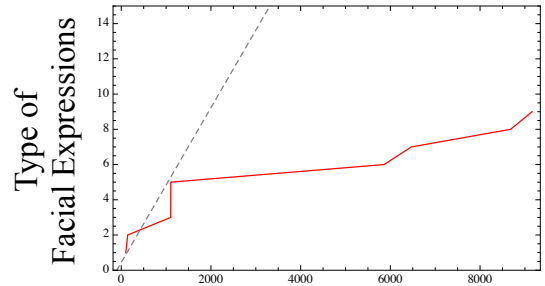
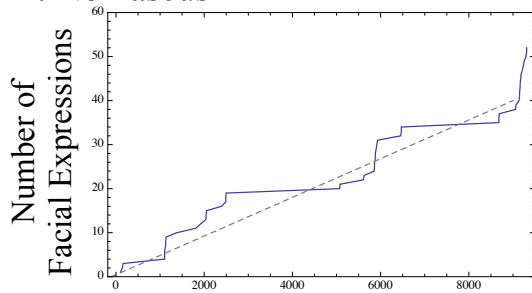
To clarify, let us take a guided step-by-step example, following the data from Figure 3. In order to eliminate the variation in recording time, let us do the calculation for the rates in the examples till time 5000 (check blue curves for the different individuals in Figure 3). In the example of *Symphalangus*, at time 5000, the number of facial expressions performed are ~ 130. This leads to a value in rates of  $130/5000 = 0.026$ . The number of facial expressions performed in time 12000 are ~ 260. This leads to a value in rates of  $260/12000 = 0.02167$ . As one can observe, the difference is really small (in the order of 0.005). Given that the relationship is linear, increasing the recording time, only allows to “fine-tuning” the correct value of the slope. With this simple example, we provide validity of the correction used for the estimation of the rates.

For the case of type of facial expressions (repertoire) we will show that correcting by time, will not lead to higher repertoire for species where the recording time was longer. On the contrary we will show that dividing by time is a conservative correction method. Imagine that we take the cumulative type of facial expressions observed for each genus till time 5000. The corrected value for *Hylobates*, *Nomascus* and *Symphalangus* will be  $6/5000=0.0012$ ,  $6/5000=0.0012$ ,  $28/5000=0.0056$ , respectively. Note that for the last case, if we consider all the recording time for *Symphalangus* (14000) we will obtain a value for the corrected type of facial expressions equal to  $32/14000=0.0023$ . This value, as can be easily observed, is smaller than the previous estimation (0.0056).

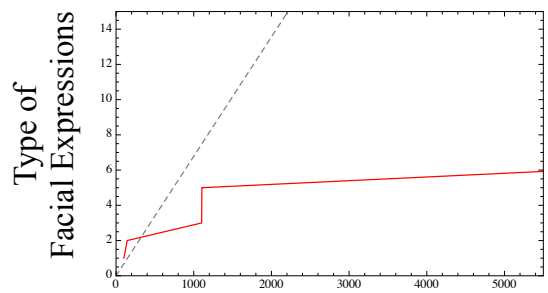
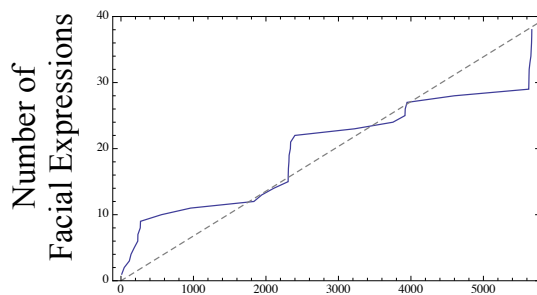
### A. Symphalangus



### B. Nomascus



### C. Hylobates



Recording Time (Sec.)

Recording Time (Sec.)

Figure S3: Number (blue line) and type (repertoire –red line-) of the individuals Spike (Symphalangus), Dorian (Nomascus) and Bert (Hylobates) vs. Recording Time.

## 5. Explanation of Action Units and Action Descriptors

Table S3: Detailed description of the observed Action Units and Action Descriptors.

AU/AD	Description (partially taken from Waller et al. 2012 and GibbonFACS Manual)
1+2	<b>Inner and Outer Brow Raiser:</b> during movement, a greater part of skin of the frontal region becomes visible as the scalp retracts.
AU7	<b>Lids Tight:</b> The lower lid is raised and tightened, covering more of the eyeball. The curvature of the lower eyelid is straightened and the eye aperture is narrowed. Visibility of the sclera and/or iris is reduced.
AU8	<b>Lips Towards Each Other:</b> The jaw is dropped, but the teeth are not visible due to the lips being rolled inwards. The lower face appears elongated vertically.
AU41	<b>Glabella Lowerer:</b> general lowering of the complete brow, reducing visibility of the underbrow region.
AU9	<b>Nose Wrinkler:</b> horizontal wrinkles appear at the root of the nose, extending toward the brow region, and the skin along the side of the nose is raised, shortening the distance to the upper face region.
AU10	<b>Upper Lip Raiser:</b> muscle action pulls the upper lip upward, which appears to thicken slightly. The distance between upper lip and tip of nose is shortened.
AU12	<b>Lip Corner Puller:</b> The lip corners are pulled backward and slightly upward, the shape of the mouth is slightly crescent-like in the corners and wrinkles, in the lip corners may appear.
AU16	<b>Lower Lip Depressor:</b> the lower lip is being pulled downward medially and the lower teeth become exposed.
AU17	<b>Chin Raiser:</b> movement causes the skin of the mental region to be pushed upward with a shortening of the distance between the upper lip and the tip of nose. The medial portion of the upper lip is pushed up as the lower lip becomes more protruded. The lip corners stay down and appear angled downward relative to the rest of the mouth.
AU18	<b>Lip Pucker:</b> the lips protrude slightly and vertical wrinkles appear above the upper lip. The lip corners are drawn to the middle and the medial portion of the upper lip becomes scallop-shaped.
AU25	<b>Lips Parted:</b> In this movement the lips part and may expose teeth, gums and tongue.
AU26	<b>Jaw Drop:</b> The muscles holding the jaw are relaxed. As the lips part (AU25), a gap between upper and lower teeth are visible.
AU27	<b>Mouth Stretch:</b> The lips are parted (AU25) and the jaw is not only lowered but actively pulled downwards by several muscle actions.
AD19	<b>Tongue Show:</b> The tongue is visible, not just lying relaxed in the mouth cavity, but protruding or turning and twisting.
AD37	<b>Lip Wipe:</b> The tongue is parting the lips, touching them either from side to side or in forwards and backward movement.
AD500	<b>Throat Sac Inflation:</b> This is an action unit exclusively observed in one hylobatid species, the siamang gibbon. This is caused by the throat sac filling with air, so that it takes on a balloon-like appearance.
AUEye	Either AU43 ( <b>Eye Closure</b> ) or AU45 ( <b>Blink</b> ), not specified here.

## 6. Creation of the monogamy index

We conducted a literature survey (see reference list below and Supplementary Material 2) and searched for information about variables related to monogamy for the five species: strong variables predicting sexual monogamy (SeM) = extra pair copulation (EPC), polyandry (PA) and polygyny (PG) and variables which predict social monogamy (SoM) = proximity at day (Pd), proximity at night (Pn), desertion (D), group composition (Gc), paternal care (Pc). For the creation of the indices we conducted the following steps and ranked the variables on a scale from 0-1:

Suppose there are  $k$  variables in the population related with monogamy. For each variable we have information about the 5 Gibbon species: *Symphalangus syndactylus*, *Hylobates pileatus*, *Hylobates lar*, *Nomascus gabriellae* and *Nomascus siki*. In some cases the behavioral information for a given species is missing, and therefore we do not have any positive nor negative association between that variable and monogamy. If no information is provided, the variable given for this variable is 0.5. The variables can increase or decrease beginning from this value, and therefore the index reflects the information we have about monogamy rather than the actual monogamy level (this index should not be interpreted as if a value of 1 represents fully monogamous, and 0 fully polygamous). In order to combine different variables we can assume that they are independently contributing to the monogamy index, and therefore we can generate the index by a linear combination of the  $k$  variables. In this way the value of the monogamy

index for a given species  $S_1$  will be given by  $S_1 = \sum_{i=1}^k b_i$ . Assuming that some variables are

more likely to reflect monogamy than others (SeM > SoM), we can modify the previous values by including weights ( $\alpha_i$ ) to each variable. The value of the monogamy index for a

given species  $S_1$  will be given then by  $S_1 = \sum_{i=1}^k \alpha_i b_i$ . This way provides the possibility to

propose scenarios (different values of  $\alpha_i$ ). For instance, imagine that we want to combine quantitative information related to SeM with variables related to SoM. It is possible to assign less strength to the more qualitative and indirect measurements of monogamy, e.g. from paternal care (PC) behavior. Note that the inclusion of weight in the calculation will not generate any bias in the relationship between species, because the weights will affect each species in the same way.

We created three indices. The first one (Index I) includes only variables predicting SeM and the second and third one includes variables of both, SeM and SoM. Index II weights every variable equally. Index III distributes full weight ( $\alpha = 1$ ) on the variables of SeM and less weight ( $\alpha = 0.5$ ) on variables of SoM.

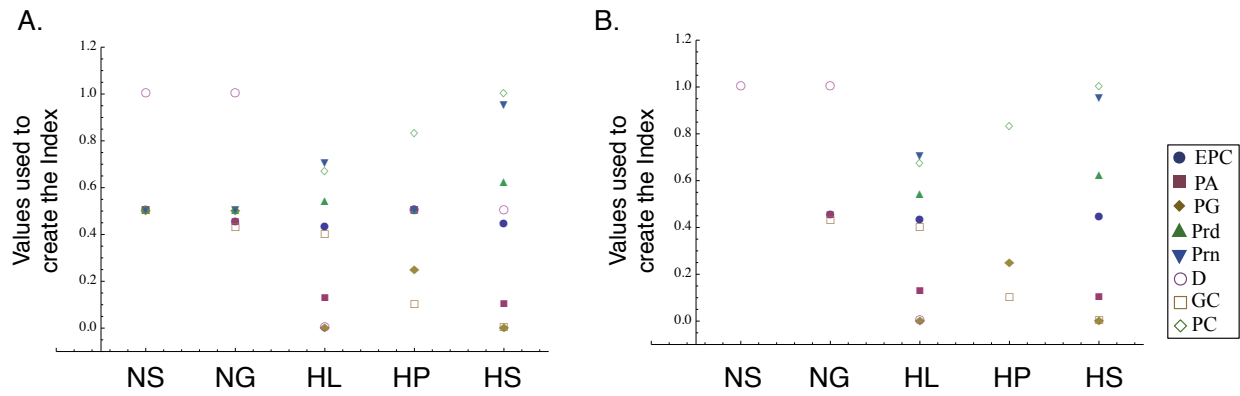


Figure S4: Single values used for generating the monogamy indices plotted (EPC=Extra Pair Copulation; PA=polyandry; PG=polygyny; Pd=Proximity at day; Pn=Proximity at night; D=Desertion; Gc=Group Composition (i.e. more than two adult individuals); PC=Paternal Care) for all five species (NS=*Nomascus siki*, NG=*Nomascus gabriellae*, HL=*Hylobates lar*, HP=*Hylobates pileatus*, SS=*Symphalangus syndactylus*). A. All values (including 'no information' = 0.5). B. Exclusion of 'no information'.

Table S4: Values for each of the variables reflecting monogamy for each of the five species. In red = variables reflecting sexual monogamy (SeM); in green = variables reflecting social monogamy (SoM). Values (percentages and yes/no) taken from the literature (for details see Table S3) and ranked to values (red and green numbers) in order to create the indices I, II and III (I=values from only SeM; II=values taken from both SeM and SoM; III=values taken from both SeM and SoM but weighted by  $\alpha=1$  for SeM and  $\alpha=0.5$  for SoM).

	<i>Nomascus siki</i>	<i>Nomascus gabriellae</i>	<i>Hylobates lar</i>	<i>Hylobates pileatus</i>	<i>Symphalangus syndactylus</i>
<b>Extra Pair Copulation (max)</b>	unknown 0.5	10% 0.45	13% 0.43	unknown 0.5	12% 0.44
<b>Polyandry (max)</b>	unknown 0.5	unknown 0.5	75% 0.125	unknown 0.5	80% 0.1
<b>Polygyny</b>	unknown 0.5	unknown 0.5	yes 0	yes (also no) 2/1 0.25	yes 0
<b>Index I</b>	<b>0.5</b>	<b>0.483</b>	<b>0.185</b>	<b>0.417</b>	<b>0.18</b>
<b>Proximity of the mated pair during night</b>	unknown 0.5 0.25	unknown 0.5 0.25	40% 0.7 0.35	unknown 0.5 0.25	90% 0.95 0.475
<b>Proximity of the mated per during day</b>	unknown 0.5 0.25	unknown 0.5 0.25	8% 0.54 0.27	unknown 0.5 0.25	23% 0.62 0.31
<b>Desertion</b>	no 1 0.5	no 1 0.5	yes 0 0	unknown 0.5 0.25	yes/no 0.5 0.25
<b>Group composition (&gt; two adults)</b>	unknown 0.5 0.25	22% 0.43 0.215	18% 0.4 0.2	yes (> <i>H.synd.</i> ) 0.1 0.05	yes (< <i>H.p.</i> ) 0 0
<b>Paternal care</b>	unknown 0.5 0.25	unknown 0.5 0.25	yes, not much 0.67 0.335	yes 0.83 0.415	yes, much 1 0.5
<b>Index II</b>	<b>0.5</b>	<b>0.54</b>	<b>0.36</b>	<b>0.46</b>	<b>0.45</b>
<b>Index III</b>	<b>0.38</b>	<b>0.36</b>	<b>0.21</b>	<b>0.31</b>	<b>0.26</b>

## Example for EPC:

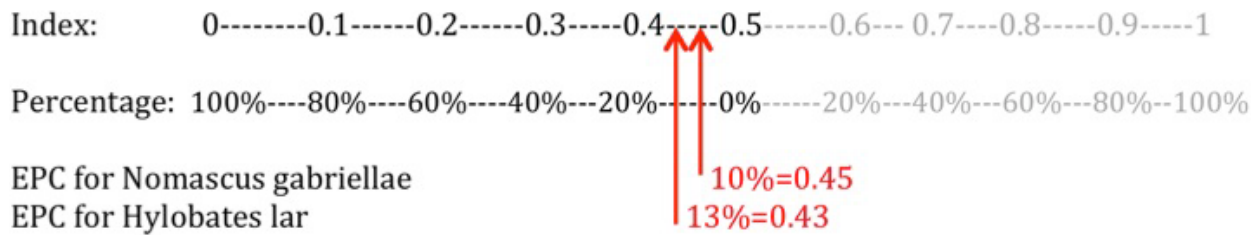


Figure S5: Example how the information from the literature was ranked to create the values of the monogamy index. Values 10% and 13% ranked from the literature (see Table S1 in Supplementary Material 2) to values of the indices. If no information is provided, the variable given for this variable is “0.5”. The variables can increase or decrease beginning from this value, and therefore the index reflects the information we have about monogamy rather than the actual monogamy level (this index should not be interpreted as if a value of 1 represents fully monogamous). If we consider “0” in the index as ‘least monogamous’, then the higher the percentage for e.g. extra pair copulation is, the closer it is to the value “0”, starting from 0.5 (=0%). 10% in the direction to 100% (=0 in the Index) resembles 0.45 in the Index. Quantitative information (yes/no) has been transformed into numbers, depending on the strength/quantity of information found (“yes, not much (=0.67)” is ranked less strong than “yes (=0.83)” and numbers depend on whether information is in direction favoring monogamy (=1) not (=0) etc.).

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## Supplementary Information (S2)

from: “A comparison of facial expression properties in five hylobatid species”

Table S1: Information from the literature for each of the five species and values for ranking them to create the indices.

	<i>Hylobates lar</i>	<i>Symphalangus syndactylus</i>	<i>Nomascus gabriellae</i>	<i>Hylobates pileatus</i>	<i>Nomascus siki</i>
<i>Extra pair copulation (EPC)</i>	Reichard (2003) reported about 8.3% EPC in <i>Hylobates lar</i> , whereas Fuentes (2000) and Reichard & Sommer (1997) both reported 12% EPC. Reichard & Barelli (2008) observed EPC in the range of 0-13%. By taking the maximum of this range (13%), summing all values together and dividing them by 4 we have a mean value of 13% EPC. We used the mean value of all values (9.95%) to rank this behaviour for the indices.	For this species there is only one study reporting about 12% EPC (Fuentes 2000). This value will be used to create the indices.	Kenyon et al. (2011) analysed DNA from faecal samples of 10 infants and juveniles and identified 1 case of extrapair paternity - Paternity was genetically confirmed to a lone male, with no territory. The value for creating the indices is 10% because one out of 10 infant was shown to come from EPC.	no information found	no information found
<i>Polyandry (PA)</i>	Studies found that polyandrous groups constituting more than 20% of the groups in a population (Savini et al. 2009). Others report a range of 16–42% of groups, which are consistently polyandrous (Savini et al. 2009). Barelli et al. (2007) found that 5 out of 12 (42.16%) groups each comprised a second adult male that was unrelated to the female of the group. These social units are best characterized as multimale or socially polyandrous. Reichard (2009) reports about 15.8 + 10.4% multimale-singlefemale groups in Khao Yai. Lappan (2007) observed polyandrous mating patterns in 75% of the groups with more than a single adult male (n=4). Out of all values we calculated the mean, which is 75% (taking the mean from ranges: 46.16%) to create the indices. Barelli et al. (2007) found that 5 out of 7 groups comprised a second adult male additional to the first one that was unrelated to the female of the group.	Lappan (2007) reported a high proportion of multimale groups (4 out of 5), both males were observed to copulate with the female, they were matrilineally not related to each other or to the female. This resulted in a value of 80%, which we used to create the indices.	no information found	no information found	no information found

<p><i>Polygyny</i> (PG) (yes/no)</p>	<p>YES Studies reveal the presence of polygyny in this species (Reichard 2009; Reichard and Barelli 2008; Fuentes 1998; Brockelmann and Srikosmatara 1984). As a value to create the indices we used 0.</p>	<p>YES Brockelmann and Srikosmatara (1984) observed formation of a polygynous group and in another study they reported about groups with <math>\geq 2</math> females (Srikosmatara and Brockelmann 1987). As a value to create the indices we used 0.</p>	<p>no information found</p>	<p>(2x YES/1x NO) Srikosmatara and Brockelmann (1987) and Brockelmann and Srikosmatara (1984) found evidence for polygyny, whereas Rutberg considers the species to be monogamous (Rutberg 1983). As a value to create the indices we used 0.5 since we have contrasting observations. As a value to create the indices we used 0.25 because we have more evidence for yes than no.</p>	<p>no information found</p>
<p><i>Proximity</i> (day)</p>	<p>Adults spend 4-8% of daytime activity in close proximity (grooming, sitting in contact with each other; Palombit 1992,1994; Whitten 1980). To create the indices we used the maximum value of 8%.</p>	<p>Adults spend 9-23% of daytime activity in close proximity (grooming, sitting in contact with each other; Palombit 1992, 1994; Whitten 1980). To create the indices we used the maximum value of 23%.</p>	<p>no information found</p>	<p>no information found</p>	<p>no information found</p>
<p><i>Proximity</i> (night)</p>	<p>Individuals spend approximately 40% of nights in the same tree (Palombit 1994). We used 40% as a value to create the indices.</p>	<p>Individuals spend nearly 90% of nights in the same sleeping tree (Whitten 1980). We used 90% as a value to create the indices.</p>	<p>no information found</p>	<p>no information found</p>	<p>no information found</p>
<p><i>Desertion</i> (yes/no)</p>	<p>(YES) Observations revealed that individuals of this species desert and that the disappearance of former mate possible (Brockelmann, W. 1998). They were observed to terminate current partnerships and re-pair (Chivers and Raemaekers 1980, Palombit 1994). Savini et al. (2009) reported about two secondary males leaving a polyandrous groups during the observation period and that males do not desert females but are ousted by other males or may leave the (polyandrous) group after a while. As a value to create the indices we used 0.</p>	<p>(YES/NO) For this species we found contrasting information. One study observed an adult leaving the mate ("deserted") to exploit new reproductive opportunities (Palombit 1994) but according to Chivers (1974) adult siamangs are thought to pair for life. As a value to create the indices we used 0.5.</p>	<p>(NO) Pair-bonds in <i>Nomascus</i> are thought to be stable, lasting for as many years as investigators have been able to observe known groups in the wild (Fan and Jiang 2010; Mootnick 1984; Zhou et al. 2008b), and often lifelong in captivity (Mootnick 1984; Schilling 1984). As a value to create the indices we used 1.</p>	<p>no information found</p>	<p>(NO) Pair-bonds in <i>Nomascus</i> are thought to be stable, lasting for as many years as investigators have been able to observe known groups in the wild (Fan and Jiang 2010; Mootnick 1984; Zhou et al. 2008), and often lifelong in captivity (Mootnick 1984; Schilling). As a value to create the indices we used 1.</p>
	<p>(YES, not much) For this species we found evidence that males care for their young, but to a low degree, e.g., (male was actually observed to carry the infant around, albeit in most groups for short distances only (Berkson 1966). It is repeatedly reported to have shown a "determined effort" to take the infant</p>	<p>(YES, much) Observations show that the male carries infants from the age of 12-15 months until they become independent in their third year of life. Infants in monogamous groups received substantially more male care than infants in polyandrous groups, males</p>	<p>no information found</p>	<p>(YES) Some evidence for paternal care was found. Adult males spend more time than their mates playing and grooming with their young (Srikosmatara 1980). As a value for creating the indices we used 0.83.</p>	<p>no information found</p>

<p><i>Paternal care</i> (yes/no)</p>	<p>offspring from the female (e.g. Crandall, 1945; Bertsson, 1966), but female most often did not allow the father to take the infant (captive groups, Fischer and Geissmann 1990). As a value for creating the indices we used 0.67.</p>	<p>often engaged in babysitting behavior (remain in close proximity to the infant while the others forage or defend the territory; Lappan 2008). Other observations found siamang fathers carrying their offspring at some time during ontogeny (Alberts, 1987; Ms. S. Fowmes, pers. comm.; Dr. Dr. U. Hollih, pers. comm.; Mr. R. Opitz, pers. comm.), others were never observed to do so (Ms. S. Fowmes, pers. comm.; Orgeldinger, 1989, p. 70; own observations on three pairs) (captive groups, Fischer and Geissmann 1990). Chivers (2000) also found evidence for paternal care. As a value for creating the indices we used 0.</p>	<p>Kenyon et al. 2011 found that 13 groups fitted with social monogamy, with a pair of adults, while 5 gibbon groups contained 2 blonde females. In 1 group, the second female was confirmed genetically as a daughter of the breeding pair and in a second group a female was confirmed to be the daughter of the male (but no DNA was available from the possible mother). To calculate the indices we used the value <math>4/18 = 22\%</math>.</p>	<p>Fuentes (2000) observed at least three greater-than-2 adult group. As a value we used 0.1 (&gt;H.s.) since with three observed groups is considered to be less monogamous than H.s.</p>	<p>no information found</p>
<p><i>Group composition</i> (&gt;2 adults)</p>	<p>Fuentes (2000) observed greater-than-2 adult groups ranging from 10-18%. Other studies support that greater-than-2 adult groups exist (Carpenter 1940, Reichard and Barelli 2008, Nettelbeck 1998, Lappan 2007). For creating the indices we used the maximum value of 18%.</p>	<p>Fuentes (2000) observed at least one greater-than-2 adult group. As a value for creating the indices we used 0 (&lt;H.p.).</p>	<p>Kenyon et al. 2011 found that 13 groups fitted with social monogamy, with a pair of adults, while 5 gibbon groups contained 2 blonde females. In 1 group, the second female was confirmed genetically as a daughter of the breeding pair and in a second group a female was confirmed to be the daughter of the male (but no DNA was available from the possible mother). To calculate the indices we used the value <math>4/18 = 22\%</math>.</p>	<p>Fuentes (2000) observed at least three greater-than-2 adult group. As a value we used 0.1 (&gt;H.s.) since with three observed groups is considered to be less monogamous than H.s.</p>	<p>no information found</p>