A comparison of facial expression properties in five hylobatid species

(Short title: Facial expressions in hylobatids)

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Abstract

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.

Keywords: 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 [van Hooff, 1976; Preuschoft and van Hooff, 1997; de Waal and Luttrell, 1985; Thierry et al. 1989; Maestripieri, 1999]. 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 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 Hominoidae [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. Palombit, 1994; Reichard, 1995; Lappan, 2005] 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, e.g. 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 [Reichard & Sommer 1997; Fuentes, 2000; Reichard, 2003; Reichard & Barelli, 2008], 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 [Chivers & Raemaekers, 1980; Brockelman, 1998; Palombit 1994], whereas in other species it has not been observed [Mootnick 1984; Zhou et al. 2008; Fan & Jiang, 2010]. 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 favouring 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*: Srikosamatara, 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 [Brockelman et al., 1998; Preuschoft et al., 1984]. Following the line of argument by Freeberg and colleagues [2012], therefore, gibbons should use less facial signals compared to other primate species that live in more complex groups, e.g. 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 [Raemaekers et al., 1984; Haimhoff, 1986; Geissmann, 2002]. There are some studies that report facial expressions in the behavioral repertoire of hylobatids [Fox, 1972, 1977; Orgeldinger 1999; Liebal et al., 2004], 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., 2012]. 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, 2010]. 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. Waller & Dunbar, 2005, Flack & de Waal 2007]. Therefore, one possible function of facial expressions might be group cohesion [Thierry et al. 1989; Maestripieri, 1999; Parr et al. 2002].

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 & Shultz, 2007; Shultz & Dunbar, 2010a, 2010b; Dunbar, 2011], 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. Chan, 1996; Thierry et al. 2000; Blomberg & Garland, 2002] 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 [GibbonFACS: 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 1. 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 S1 in the Supplementary Material S1). The study was carried out in compliance with respective animal care regulations and principles of the American Society of Primatologists for the ethical treatment of nonhuman primates.

------ Table 1 ------

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 1080 bouts. Recordings took place at different times of the day on several different days resulting in a total amount of 21 hours of observation (9h (43%) for *Symphalangus*, 7h (33%) for *Hylobates* and 5h (24%) for *Nomascus*). Mean observation time per individual was 158 minutes (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 section *Measurements of the facial expressions*). 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, i.e. 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 non-human 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 ethogramme 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 $R_{Cm} = \sum_{i=1}^{k} \frac{R_i}{\tau_i}$, where *k* is the number of individuals belonging to the *m* genera, τ_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, 1984] for the n-individual as:

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

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:

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

The *corrected diversity index* (D_{nt}) [Hill, 1973] of the facial expressions for each individual is then calculated by: $D_{nt} = \frac{e^{H_n}}{t_n} = \frac{e^{-\sum_{i=1}^{S} p_i \log(p_i)}}{t_n}$.

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 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 2). 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 Information S1.

------ Table 2 ------

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 3). 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 3. We considered sexual monogamy, where an 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, e.g. 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 α) 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.

------- Table 3 ------

RESULTS

Rates, Corrected Repertoires and Corrected Diversity of Facial Expressions

We coded a total of 1080 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 4 shows which types of facial expressions were observed for each of the three genera Symphalangus (*S. syndactylus*), Hylobates (*H. pileates*, *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.

------ Table 4 ------

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 Figure 1).

------ Figure 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 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, 2001; Bewik, 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.

------ 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, 2001; Bewik, 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 3.

------ 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 5). 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: $Z = 0.63$; $P = 0.574$).

----- Table 5 ------

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 6) using regression models. The models revealed no significant relationship of facial expression properties and the socio-ecological factors (see Results in Table 7).

------ Table 6 ------

------ Table 7 ------

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 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, e.g. the social network, the strength of bonding between individuals, other and/or additional channels of communication, etc. Freeberg and colleagues 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” [Freeberg et al., 2012].

There is some contradiction about whether the level of monogamy implies a high [Dunbar, 1992; Dunbar & Shultz, 2007, Shultz & Dunbar, 2010a, 2010b; Dunbar, 2011] 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 e.g. 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 [Brockelman 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 [Fox, 1972, 1977; Chivers, 1976; 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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TABLES

Table 1: Subjects.

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

Table 2: Maximum group size for each of the five species (from the literature).

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

Table 3: 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 ($\alpha = 0.5$)**

Table 4: Repertoire (uncorrected) of facial expressions in the three Hylobatid genera and their frequency of occurrence.

No.	**Facial Expression**	**Symphalangus**	**Nomascus**	**Hylobates**
1	AU1/2*	[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**	[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]		

(*AU1/2 resembles AU1+2 from Waller et al. 2012; **AUEye resembles either AU43 (eye closure) or AU45 (eye blink), we did not differentiate between the two AUs here.

Table 5: 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

Table 6: Monogamy indices of the five species. 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 α.

Species	**Index I = SeM**	**Index II = SeM + SoM**	**Index III = SeM (α = 1) + SoM (α = 0.5)**
Nomascus siki	0.5	0.5	0.38
Nomascus gabriellae	0.483	0.54	0.36
Hylobates lar	0.185	0.36	0.21
Hylobates pileatus	0.417	0.46	0.31
Symphalangus syndactylus	0.18	0.45	0.26

Table 7: Results of Phylogenetic Generalized Least Square (PGLS) Analysis. 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.

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 10^{-3}	2.4 10^{-3}	0.081
Group size	Diversity	0.41	2.0 10^{-3}	1.0 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 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 10^{-6}	3.5 10^{-4}	0.983
Index III	Diversity	0.05	-0.065	0.059	0.348

FIGURES

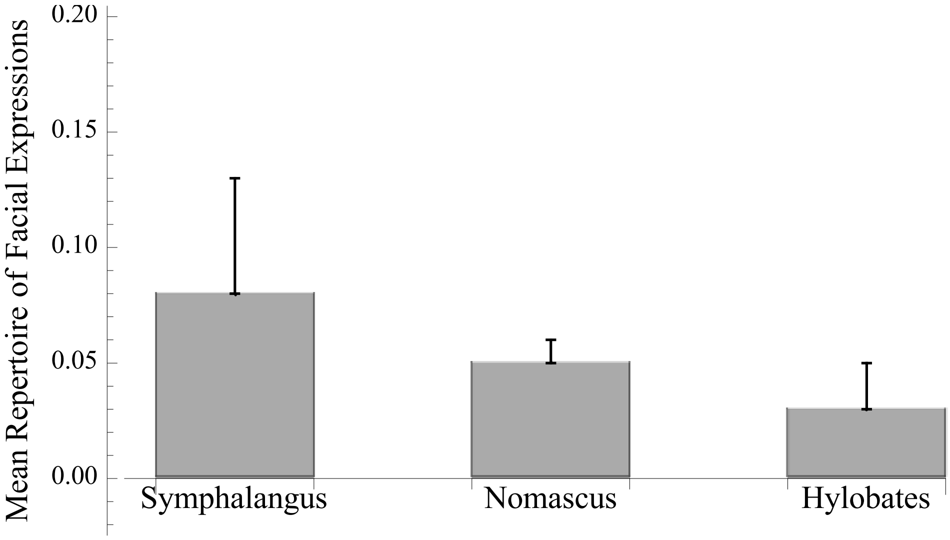

Figure 1: Mean corrected repertoire for all three genera (± SD.). There is no significant difference between the three genera.

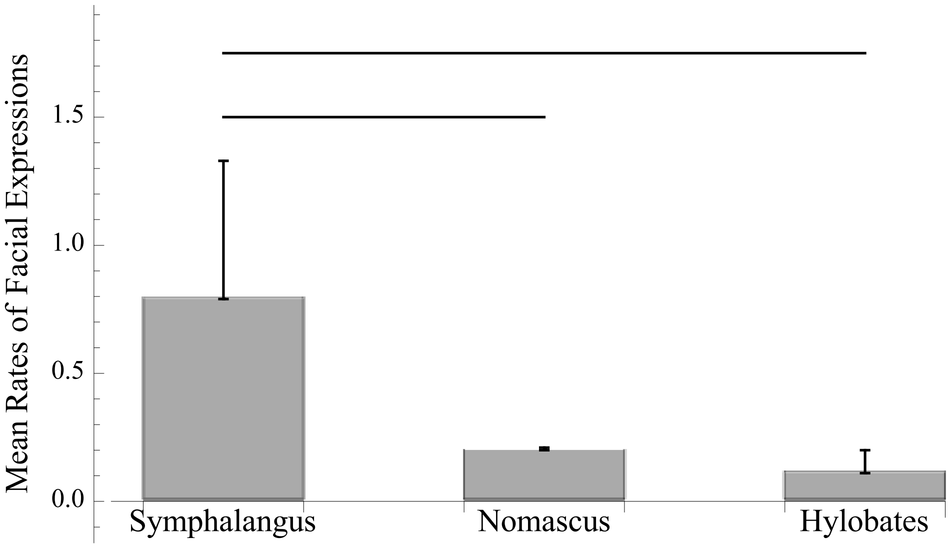

Figure 2: Mean rates (number of facial expressions per minute corrected by recording time) of the three genera (± SD). * represents P-values < 0.05.

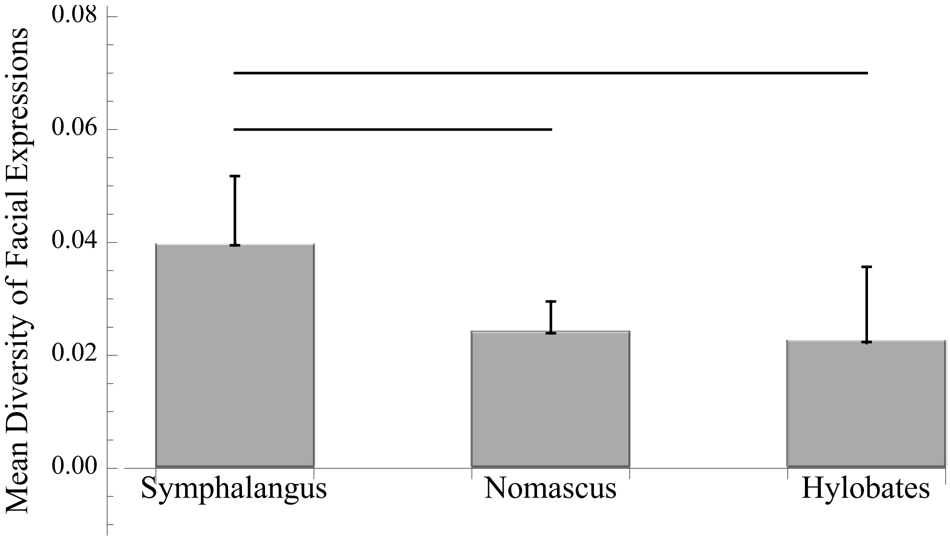

Figure 3: Mean diversity (corrected by recording time) of the three genera (± SD). * represents P-values < 0.05.