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6   **A comparison of facial expression properties in five hylobatid species**

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8   **(Short title: Facial expressions in hylobatids)**

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10   Linda Scheider[1], Katja Liebal[1,2], Leonardo Oña[3], Anne Burrows[4,5] and Bridget Waller[2]

11

12   1 Dept. of Psychology, Freie Universität of Berlin, Germany

13   2 Dept. of Psychology, University of Portsmouth, Portsmouth, United Kingdom

14   3 Dept. of Natural Science and Mathematics, University of Groningen, The Netherlands

15   4 Dept. of Physical Therapy, Duquesne University, Pittsburgh, Pennsylvania

16   5 Dept. of Anthropology, University of Pittsburgh, Pittsburgh, Pennsylvania

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21   Correspondence to:

22

23   Linda Scheider

24   Freie Universität Berlin

25   Cluster Languages of Emotion

26   Department of Education and Psychology

27   Habelschwerdter Allee 45

28   14195 Berlin

29   Germany

30   Email: lindascheider@gmail.com

31   Phone: +31622902646

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38   Abstract

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

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62   *Keywords: gibbons, GibbonFACS, facial expression, FACS, monogamy index*

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71   INTRODUCTION

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73   It has been suggested that the complexity of primate communicative repertoires is

74   closely connected to living in social groups, because increased social complexity acts as a

75   driver for increased communicative complexity [e.g. Freeberg et al., 2012]. For example,

76   there is evidence for a positive correlation between group size and facial expressions in a

77   sample of 12 primate species [Dobson, 2009]. Furthermore, the specific social structure of

78   primates and the dominance hierarchy was found to influence the use and repertoire of facial

79   expressions [van Hooff, 1976; Preuschoft and van Hooff, 1997; de Waal and Luttrell, 1985;

80   Thierry et al. 1989; Maestripieri, 1999]. The extent to which species differences in facial

81   expression can be attributed to socio-ecological variables, therefore, is important to fully

82   understand the evolutionary function of facial expressions. Although, in hylobatids, there is

83   yet not much known about whether facial expressions have true communicative, or even

84   expressive, function, preliminary data suggests that this is the case [Liebal et al., in

85   preparation]. In order to investigate facial expressions and their specific function in

86   communicative contexts, a detailed investigation describing certain properties of facial

87   expressions in hylobatids is highly relevant. Here, for ease of description, facial expression is

88   defined as any single or combination of more than one facial movement (Action Unit [AU])

89   or more general head/eye movement (Action Descriptor [AD]), but without the assumption

90   that these movements are necessarily communicative.

91   Together with humans and great apes, hylobatids belong to the superfamily Hominoidae

92   [e.g. Geissmann, 2002; Mootnick, 2006]. Comprising up to 16 species, they represent the

93   most diverse group within this superfamily [Thin et al., 2010], and they are closely related to

94   both great apes and Old World Monkeys. Hylobatids are characterized by a similar set of

95   morphological, ecological and social features. They have prolonged extremities adapted to a

96   brachiating style of locomotion, they are arboreal and usually live in small groups comprising

97   of the mated pair and their offspring [Rowe, 1996]. However, there is some variability in their

98   social organization. Although they are commonly described as monogamous species, recent

99   studies have challenged this view. Thus, it has been demonstrated that the social organization

100   of gibbons is much more variable [e.g. Palombit, 1994; Reichard, 1995; Lappan, 2005] and

101   that the strength of social bonds varies between different hylobatid species [Fischer &

102   Geissmann, 1990]. In this regard, it is important to differentiate between sexual monogamy,

103   which means that female and male have only a single partner of the opposite sex at a time

104   [Black, 1996; Gowaty, 1996], and social monogamy, which refers to cooperation in the

105 acquisition of other resources, e.g. shared use of a territory, proximity between male and

106 female, behaviors favoring pair cohesion [Reichard, 2003]. Thus, the latter can include sexual

107 monogamy but also refers to social organization. One strong indicator against sexual

108 monogamy is the engagement in extra pair copulations [e.g. Westneat, 1987]. For the white-

109 handed gibbon (*Hylobates lar*) and siamangs (*Symphalangus syndactylus*) extra pair

110 copulations have been observed in their natural habitats [Reichard & Sommer 1997; Fuentes,

111 2000; Reichard, 2003; Reichard & Barelli, 2008], as well for the yellow-cheeked crested

112 gibbon (*Nomascus gabriellae*), although to a slightly lesser extent [Kenyon et al. 2011]. For

113 siamangs there is most evidence of desertion and re-pairing with other individuals [Chivers &

114 Raemaekers, 1980; Brockelman, 1998; Palombit 1994], whereas in other species it has not

115 been observed [Mootnick 1984; Zhou et al. 2008; Fan & Jiang, 2010]. Although from these

116 observations one could argue that for example siamangs might be less monogamous than

117 other hylobatid species, there is also evidence for siamang males investing in paternal care

118 [e.g. Lappan, 2008], which is rather an indication favouring monogamy, whereas for other

119 species only a few observations of paternal care were reported [e.g. *Hylobates lar*: Berkson,

120 1966; Fischer & Geissmann, 1990; *Hylobates pileatus*: Srikosamatara, 1980]. However,

121 paternal care might not be the strongest indicator for monogamy. Thus, by considering

122 different behaviors related to either sexual and/or social monogamy we aim to rank species by

123 different degrees of monogamy.

124 Despite the variability in the strength of monogamy, the social group structure of

125 Hylobatidae is characterized by small stable family groups consisting of one pair and their

126 offspring, with no pronounced hierarchy between the two adult individuals [Brockelman et

127 al., 1998; Preuschoft et al., 1984]. Following the line of argument by Freeberg and colleagues

128 [2012], therefore, gibbons should use less facial signals compared to other primate species

129 that live in more complex groups, e.g. chimpanzees and macaques. Indeed, Chivers [1976]

130 concluded that wild siamangs only show a limited communicative repertoire (facial

131 expressions and gestures). In addition, given that they live in densely foliated environments,

132 we might expect them to rely mostly on vocal rather than visual communication. However,

133 very little is known about the communicative behavior of gibbons, with the exception of

134 studies investigating their exceptional vocal duetting repertoires [Raemaekers et al., 1984;

135 Haimhoff, 1986; Geissmann, 2002]. There are some studies that report facial expressions in

136 the behavioral repertoire of hylobatids [Fox, 1972, 1977; Orgeldinger 1999; Liebal et al.,

137 2004], and some report detailed descriptions about those expressions. Liebal et al. [2004], for

138 example, described three different facial expressions, one of which was observed in two

139   varieties. A 'grin' was described as facial expression where the mouth is "slightly opened and

140   the corners of the mouth are withdrawn with the teeth scarcely visible between the lips". The

141   facial expression 'Mouth open' was observed in two different varieties: 'Mouth-open half' is

142   when "the mouth is opened slightly, so that the canine teeth are almost completely covered by

143   lips; the shape of the mouth is oval with the corners of the mouth withdrawn very little" and

144   'Mouth-open full' when "mouth is opened to the full extent with the canine teeth and the

145   palate visible". The last facial expression was labeled 'Pull a face' and described as "upper

146   and lower jawbones are closed; the lips are protruded and slightly opened, forming an

147   elliptical shape".

148   However, a comparison across these studies is difficult because they did not use a

149   standardized, objective method to classify different types of facial expressions. This lack of

150   standardized methodology has recently been tackled by the establishment of a Facial Action

151   Coding System for gibbons [GibbonFACS: Waller et al., 2012], which is a modified version

152   of the HumanFACS [Ekman & Friesen, 1978], similar to other versions that were previously

153   developed for other primate species [ChimpFACS for chimpanzees: Vick et al., 2007;

154   MaqFACS for rhesus macaques: Parr et al., 2010; OrangFACS for orangutans: Caeiro et al.,

155   2012]. This method relies on the identification of muscular movements underlying facial

156   expressions. The development of these different versions of FACS consists of various steps,

157   including anatomical dissections [Burrows et al., 2006, 2009; Diogo et al., 2009],

158   intramuscular stimulation techniques [Waller et al., 2006, 2008], and descriptions of the

159   associated observable movements from video footage of spontaneous behavior.

160   This study aimed to investigate facial expressions in hylobatids by testing whether

161   differences between hylobatid species relate to differences in socio-ecological variables. One

162   hypothesis is that facial expressions vary between different hylobatid species as a function of

163   their maximum group sizes [Chivers, 1976; Dobson, 2010]. The results by Dobson [2009]

164   support the hypothesis that natural selection favors increased facial expressions (i.e. the

165   number of different AUs a species can produce) in larger groups, in order to more effectively

166   manage conflict behavior and increase bonding between individuals within a group [e.g.

167   Waller & Dunbar, 2005, Flack & de Waal 2007]. Therefore, one possible function of facial

168   expressions might be group cohesion [Thierry et al. 1989; Maestripieri, 1999; Parr et al.

169   2002].

170   However, a second socio-ecological factor that could also be influential on facial

171   expressions is the strength of monogamy. It has been shown that monogamous species might

172   be associated with higher behavioral complexity and greater cognitive processing demands

173 than polygamous species [Dunbar, 1992; Dunbar & Shultz, 2007; Shultz & Dunbar, 2010a,

174 2010b; Dunbar, 2011], which might suggest that signal repertoires are more complex than

175 would be predicted by group size alone.

176   Another hypothesis is that facial expressions are subject to phylogenetic inertia [e.g.

177 Chan, 1996; Thierry et al. 2000; Blomberg & Garland, 2002] and, thus, highly conservative

178 so that marked differences between species cannot be observed.

179   In this study we aimed to 1) characterize and compare the repertoires, the rates and the

180 diversity of facial expressions of five hylobatid species by using a newly developed objective

181 coding system [GibbonFACS: Waller et al., 2012] and 2) to investigate whether socio-

182 ecological factors (group size and monogamy) are linked to these facial expression

183 characteristics. Furthermore, we investigate whether females and males differ in certain

184 properties of their facial expressions. Some sex differences in other respects have been

185 observed, for example, many hylobatid species are dichromatic and some are known for their

186 sex-specific songs [e.g. Rowe, 1996; Chivers, 2000]. However, other aspects might be more

187 important in this regard. Compared to other primate species, hylobatids are monogamous and

188 there is no explicit dominance hierarchy between pair partners, which might suggest that there

189 are no pronounced differences in facial expression between females and males.

190

191

192 METHODS

193

194 *Subjects*

195

196   Five different species comprising a total of 16 individuals were observed: three

197 mated pairs of *Symphalangus syndactylus*, two pairs of *Hylobates pileatus*, one pair of

198 *Hylobates lar*, one pair of *Nomascus gabriellae* and one pair of *Nomascus siki*. A detailed

199 list of the individuals is shown in Table 1. The pairs were housed in enclosures in groups

200 of different sizes depending on the number of offspring present. All pairs except one were

201 housed together with their offspring (1-3 individuals) in the enclosures (for details of the

202 group composition see Table S1 in the Supplementary Material S1). The study was carried

203 out in compliance with respective animal care regulations and principles of the American

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

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206

207   **------ Table 1 ------**

208

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210   *Data collection and coding*

211

212   Data collection took place between March 2009 and July 2012 in different zoos in

213   the UK (Twycross), France (Mulhouse), Switzerland (Zurich) and Germany (Rheine,

214   Westphalia). The behavior of each pair was video recorded in 15 min bouts using the focal

215   animal sampling method [Altmann, 1974] (with both animals always in view) resulting in

216   a total of 1080 bouts. Recordings took place at different times of the day on several

217   different days resulting in a total amount of 21 hours of observation (9h (43%) for

218   *Symphalangus*, 7h (33%) for *Hylobates* and 5h (24%) for *Nomascus*). Mean observation

219   time per individual was 158 minutes (SD = 34 min). Recordings were taken only when the

220   pair was in reaching distance and so had the opportunity to closely interact. We measured

221   the number of facial expressions, the repertoire and diversity per individual of each pair.

222   Since the recording time differed between pairs, a correction for each of these

223   measurements was performed by dividing each of these measurements by the recording

224   time per individual (for details see section *Measurements of the facial expressions*). The

225   video footage was coded using the software Interact (Mangold International GmBH,

226   Version 9.6). Facial expressions were identified using GibbonFACS [Waller et al., 2012].

227   A facial expression was coded when it clearly showed the apex of a signaling action, i.e.

228   when the action is strongest for that event. We conducted a reliability analysis on 10 % of

229   the data, which was calculated using Wexler's Agreement as for the human FACS and all

230   other non-human primate FACS systems [Ekman et al., 2002]. Agreement was 0.83,

231   which in FACS methodology is considered good agreement [Ekman et al., 2002].

232

233   *Measurements of the facial expressions: rates, corrected repertoire and corrected diversity*

234

235   Three measurements were used to examine the use of facial expressions across the

236   three gibbon genera. One facial expression can consist of a single facial movement

237   (AU/AD) or a combination of more than one. First, we calculated the overall frequency of

238   facial expressions, which is the total number of facial expressions produced independent

239   of their type for each genus. *Rates* were obtained by correcting for the observation time

240   for each individual, and then taking the mean for each genus.

241   Second, the *repertoire* of facial expressions was established for each genus, which

242   comprises the number of different types of facial expressions observed during the

243   recording time in the context of social interactions. The 'repertoire' in the present study

244   should not be confused with the 'facial repertoire' as an inventory of facial signals in the

245   ethogramme of a species, which is usually defined as an ensemble of (not objectively

246   defined) facial patterns, regardless of the context in which they are observed. The

247   observed repertoire in the present study is therefore a 'standardized repertoire', for the

248   sake of ease labeled only 'repertoire' here.

249   The corrected repertoire for the *m* genera (R_{Cm}) was calculated as $R_{Cm} = \sum_{i=1}^{k} \frac{R_i}{t_i}$,

250   where *k* is the number of individuals belonging to the *m* genera, τ_i is the recording time of

251   the individual *i* belonging to the *m* genera, R_i is the repertoire of the individual *i*,

252   belonging to the genera m without time correction and R_m is the repertoire of the *m* genera

253   without time correction. Thus, the corrected repertoire of an individual was calculated by

254   dividing the number of different types of facial expressions that an individual produced

255   (repertoire of that individual) by its recording time.

256

257   Third, the *diversity* of the facial expressions takes into account both the repertoire

258   and the rates. It should be interpreted as a weighted repertoire. The diversity measurement

259   incorporates information about how many types of facial expressions are observed and

260   how evenly those types are represented [Hill, 1973]. For a given number of types, the

261   value of a diversity index is maximized when all types are equally present. In other words,

262   the more different types there are and the more they are evenly represented, the higher the

263   diversity measurement. Thus, if the number of facial expressions of an individual is given

264   by *S*, we first calculated the *Shannon Information* [Shannon, 1984] for the n-individual as:

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

265   .

266   Here p_i represents the ratio between the number of each facial expressions and the total

267   number of facial expressions for a given individual.

268

269   The diversity of facial expressions is given by:

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

270   .

271   The *corrected diversity index* (D_{nt}) [Hill, 1973] of the facial expressions for each

272   individual is then calculated by: $D_{nt} = \dfrac{e^{H_n}}{t_n} = \dfrac{e^{-\sum_{i=1}^{S} p_i \log(p_i)}}{t_n}$.

273

274

275   *Socio-ecological variables (Group size and monogamy)*

276

277   We correlated the three properties of facial expressions (rates, corrected repertoire and

278   corrected diversity) with the two socio-ecological variables group size and monogamy

279   (Indices I, II and III) for each species using regression models. Information about group size

280   was taken from the literature (see Table 2). We used the maximum numbers of reported group

281   size for further analysis. For this analysis we used the rates, corrected repertoire and the

282   corrected diversity for each species. We incorporated phylogenetic information into the

283   regression analysis because interspecific data are prone to violating assumptions of

284   independence [Cohen & Cohen, 1983]. Each regression was performed using a phylogenetic

285   general least squares (PGLS) analysis in the software 'R' (packages 'caper' and 'ape') with

286   each property of facial expression as a dependent variable and the socio-ecological factors as

287   predictor variables. For a detailed description of this analysis see the Supplementary

288   Information S1.

289

290   ------ Table 2 ------

291

292

293   We included the following socio-ecological variables for the creation of the

294   monogamy index: extra pair copulation (EPC), polyandry (PA) and polygyny (PG), proximity

295   at day (Pd), proximity at night (Pn), desertion (D), group composition (Gc) and paternal care

296   (Pc) (see Table 3). Information about these behaviors was obtained from a literature survey on

297   85 publications between years 1976 and 2012 (see reference list in Supplementary Materials

298   S1 and S2). We divided behaviors either referring to sexual monogamy (SeM) or social

299   monogamy (SoM); see Table 3. We considered sexual monogamy, where an individual has

300   only a single partner of the opposite sex at a time [Black, 1996; Gowaty, 1996], as stronger

301   indicators of monogamy than behaviors of social monogamy, which refers to cooperation in

302   the acquisition of other resources, e.g. shared use of a territory, proximity between male and

303   female, behaviors favoring pair cohesion [Reichard, 2003]. In order to create an index, each

304   behavior was ranked to calculate the monogamy indices (for details see Supplementary
305   Material S1). To investigate whether variables of both sexual and social monogamy have a
306   different impact on the outcome of the indices, we created three different indices. Assuming
307   that those variables deriving from sexual monogamy are stronger predictors of monogamous
308   behavior, the first index contains only variables of SeM (Index I). The second and third
309   indices also include those variables of social monogamy but with the weights (given by α)
310   distributed differentially in both cases (Index II − all variables of SeM + SoM weighted
311   equally; Index III – SeM weighted with α = 1 and SoM weighted with α = 0.5). For a detailed
312   description of this procedure see S1.
313
314
315   ------- Table 3 ------
316
317
318   RESULTS
319
320   **Rates, Corrected Repertoires and Corrected Diversity of Facial Expressions**
321
322   We coded a total of 1080 instances of facial expressions (movements of single Action
323   Units or Action Descriptors or a combination of two or more AUs/ADs): 878 from
324   *Symphalangus,* 118 from *Nomascus* and 93 from *Hylobates* (uncorrected by recording time).
325   Table 4 shows which types of facial expressions were observed for each of the three genera
326   Symphalangus (*S. syndactylus*), Hylobates (*H. pileates*, *H. lar*) and Nomascus (*N. gabriellae*
327   and *N. siki*) and their frequency of use. For statistical analyses we corrected the three
328   measurements by dividing the measurements of each individual by the individual's recording
329   time.
330
331   ------ Table 4 ------
332
333   *Repertoire*
334   To examine whether the three genera differ significantly from each other in the
335   types of different facial expressions, we conducted a Kruskal-Wallis test. The comparison
336   of the corrected repertoires did not reveal significant differences between the genera
337   (Kruskal-Wallis test: H = 5.30, df = 2, P = 0.071) (see Figure 1).

338

339

340   ------ Figure 1 ------

341

342   *Rates*

343   The rates for Symphalangus, Nomascus and Hylobates are 0.79, 0.20 and 0.11

344   facial expressions per minute, respectively. In order to examine whether the three genera

345   differ from each other in the rates of facial expressions we conducted a Kruskal-Wallis

346   test and found significant differences between the three genera (Kruskal-Wallis test: H =

347   11.25, df = 2, P < 0.001). We performed a non-parametric post-hoc test for the difference

348   between pairs. Following Conover, we used the critical difference of the mean ranks test

349   [Conover, 1999; Sprent, 2001; Bewik, 2004]. We found that Symphalangus was

350   significantly different than Nomascus and Hylobates (P < 0.05, see Supporting Material

351   1), but no significant differences were found between Nomascus and Hylobates (P >

352   0.05); see Figure 2.

353

354

355

356   ------ Figure 2 ------

357

358

359   *Diversity*

360   In order to examine whether the three genera differ from each other in their

361   diversity of facial expressions we conducted a Kruskal-Wallis test, which revealed

362   significant differences between genera (Kruskal-Wallis test: H = 6.22, df = 2, P = 0.045.

363   We performed a non-parametric post-hoc test for the difference between pairs. We used

364   Conover's critical difference of the mean ranks test [Conover, 1999; Sprent, 2001; Bewik,

365   2004]. We found that Symphalangus was significantly different than Nomascus and

366   Hylobates (P < 0.05, see Supporting Material 1), but no significant differences were found

367   between Nomascus and Hylobates (P > 0.05); see Figure 3.

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369

370   ------ Figure 3 ------

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374   **Comparison of males and females**

375

376   When combining the three genera, there were 15 combinations, which we only

377   observed in males, while an additional 13 combinations were only present in females (see

378   Table 5). The remaining combinations were shared by both genders. However, statistical

379   analyses found no differences between males and females in regard to the rates (Mann

380   Whitney U test: $Z = 0.32$; $P = 0.753$), the corrected repertoires (Mann Whitney U test: $Z =$

381   -1.33; $P = 0.185$), or corrected diversity (Mann Whitney U test: $Z = 0.63$; $P = 0.574$).

382

383   ----- Table 5 ------

384

385

386   **Relationship between facial expressions and socio-ecological factors**

387

388   We correlated the three measurements of facial expressions (rates, corrected

389   repertoire and corrected diversity) with the two socio-ecological variables group size and

390   monogamy (Indices I, II and III; see Table 6) using regression models. The models

391   revealed no significant relationship of facial expression properties and the socio-

392   ecological factors (see Results in Table 7).

393

394

395   ------ Table 6 ------

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397

398   ------ Table 7 ------

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401

402   DISCUSSION

403

404   This is the first study to systematically investigate the use of facial expressions across

405   different gibbon genera based on an objective, standardized method to identify and classify

406 facial expressions (GibbonFACS). We studied the facial expressions of eight pairs of five
407 hylobatid species belonging to the three genera in regard to the rate of signaling, the repertoire
408 of facial expressions, and the diversity of signals. While the three genera did not differ in
409 regard to their repertoires of facial expressions, siamangs differed from other gibbons in their
410 more frequent use of facial expressions and a higher diversity of facial expressions. A facial
411 expression is defined as a single or a combination of more than one facial movement (so-
412 called Action Unit or Action Descriptor), regardless whether used communicatively or not.

413   In previous studies siamangs were found to show more synchronized activities and a
414 special form of songs within the pair (duetting), which is thought to strengthen the pair-bond
415 [Geissmann & Orgeldinger, 2000], compared to other hylobatid species. It was also found
416 that their diet contains more leaves compared to the smaller species [Chivers, 1972; Rowe,
417 1996]. The observation that the defense of the territory was less intensive than in smaller
418 species [Gittins & Raemaekers, 1980] could be connected to the more folivorous diet. Thus,
419 there seem to exist some differences between siamangs and other hylobatid species
420 concerning their behavior and ecology. However, how these different morphological, social
421 and ecological factors differentiating siamangs from other gibbons regarding their facial
422 communication, needs to be addressed in further studies.

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

438   Although Dobson's [2009] findings support the 'social complexity hypothesis',
439 Freeberg et al. [2012] mentioned that group size is not necessarily implying social complexity

440 and that there are several other aspects which have to be taken into account when assessing
441 social complexity, e.g. the social network, the strength of bonding between individuals, other
442 and/or additional channels of communication, etc. Freeberg and colleagues define social
443 complex systems as "those in which individuals frequently interact in many different contexts
444 with many different individuals, and often repeatedly interact with many of the same
445 individuals over time" [Freeberg et al., 2012].

446   There is some contradiction about whether the level of monogamy implies a high
447 [Dunbar, 1992; Dunbar & Shultz, 2007, Shultz & Dunbar, 2010a, 2010b; Dunbar, 2011] or
448 low social complexity [e.g. Kroodsma, 1977]. Although little is known about the relationship
449 between a species' social system and the size of facial expression repertoire [Freeberg et al.,
450 2012], we discuss both scenarios. Thus, if we consider a high level of monogamy to be of low
451 social complexity and siamangs to exhibit a low level of monogamy (based on the results of
452 our monogamy index), their social system would be consequently highly complex. In this
453 scenario the higher rate and diversity of facial expressive behavior would support the 'social
454 complexity hypothesis for communicative complexity' argument mentioned by Freeberg et al.
455 [2012]. Alternatively, if we consider a high level of monogamy to be of high social
456 complexity, siamangs' social system would be characterized by low complexity. In this latter
457 example our results would contradict the social complexity hypothesis. Future studies have to
458 be conducted to address this issue in more detail by e.g. increasing the sample size of the
459 species and also considering a multimodal analysis of the communicative system as well as an
460 analysis of the species' social network and therefore including various measurements when
461 defining complexity.

462   We could not observe significant differences between males and females in regard to
463 their repertoires, rates of signaling or diversity of facial expressions. This suggests that social
464 communication through facial expressions in both males and females do not exhibit specific
465 roles in their social structure and consequently that there is no hierarchical order between the
466 mated pairs, which is in line with previous findings [Brockelman et al., 1998; Preuschoft et
467 al., 1984]. However, we observed 13 facial expressions, which were exclusively used by
468 females and 15 different facial expressions exclusively used by males. Further investigations
469 need to clarify what specific functions those expressions have and whether their use is indeed
470 due to sexual differences.

471   Taken together, the examination of the repertoire, rate and diversity of facial
472 expressions of five hylobatid species by using an objective coding system revealed a richer
473 repertoire than previously reported for gibbons [Fox, 1972, 1977; Chivers, 1976; Liebal et al.,

474   2004]. Interestingly, siamangs differed from other gibbon species regarding the rates and

475   diversity of facial expressions and thus confirm previous results showing siamangs to be

476   outstanding when compared to other gibbon species. A relationship between the facial

477   expressions and socio-ecological factors such as group-size and monogamy level, however,

478   was not found, suggesting that despite these small species differences, on the whole facial

479   expressions have been subject to phylogenetic inertia.

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508 ACKNOWLEDGEMENTS

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759   **TABLES**

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762   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

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789   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]

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Species	Maximal number of group size	

826   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 ($\alpha = 0.5$)**

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Sexual monogamy (SeM)	Social monogamy (SoM)

861   Table 4: Repertoire (uncorrected) of facial expressions in the three Hylobatid genera and their
862   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]		

863 (*AU1/2 resembles AU1+2 from Waller et al. 2012; **AUEye resembles either AU43 (eye closure) or
864 AU45 (eye blink), we did not differentiate between the two AUs here.
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895   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

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917 Table 6: Monogamy indices of the five species. Index I only includes behavioral variable of
918 sexual monogamy (SeM); Index II includes behavioral variable of both, sexual and social
919 monogamy (SoM); Index III includes behavioral variables of SeM and SoM, but with
920 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

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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

975 **FIGURES**
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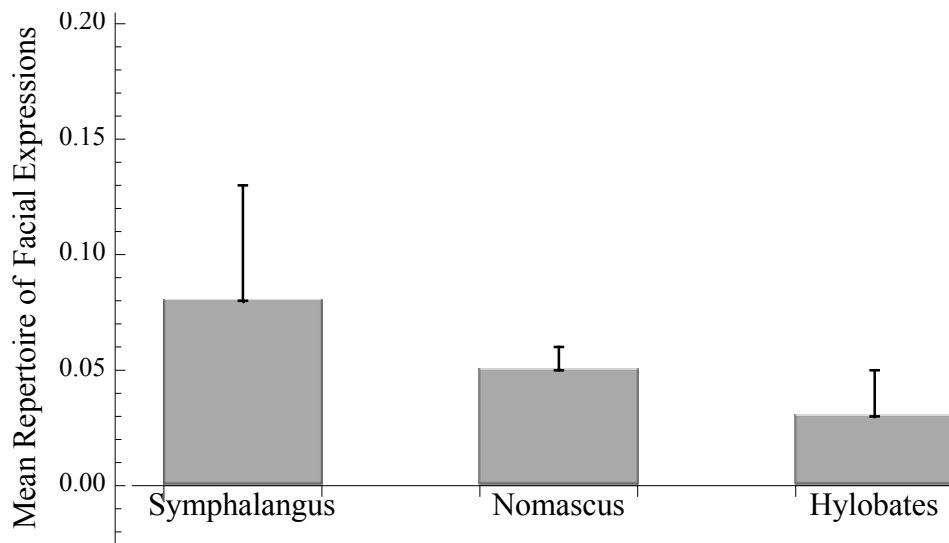
978
979 Figure 1: Mean corrected repertoire for all three genera (± SD.). There is no significant
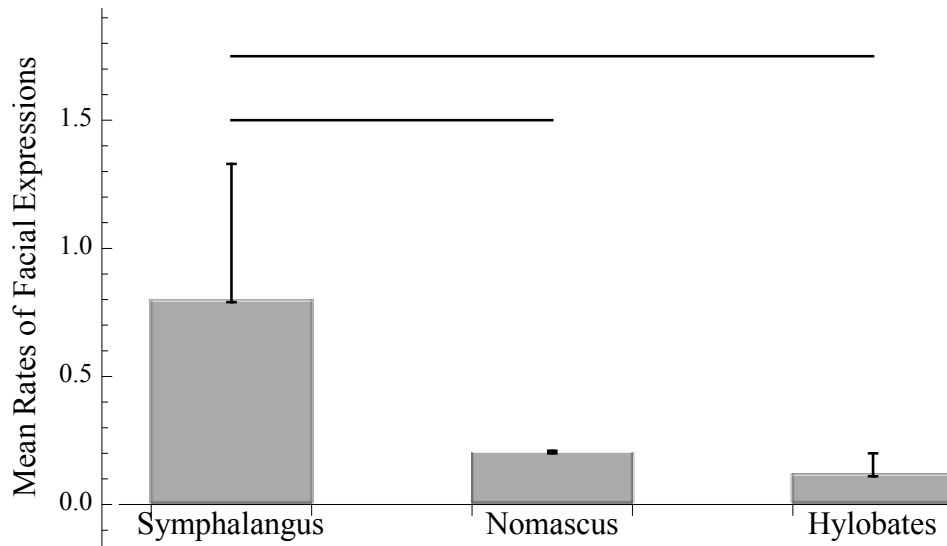980 difference between the three genera.
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Figure 2: Mean rates (number of facial expressions per minute corrected by recording time) of the three genera (± SD). * represents P-values < 0.05.
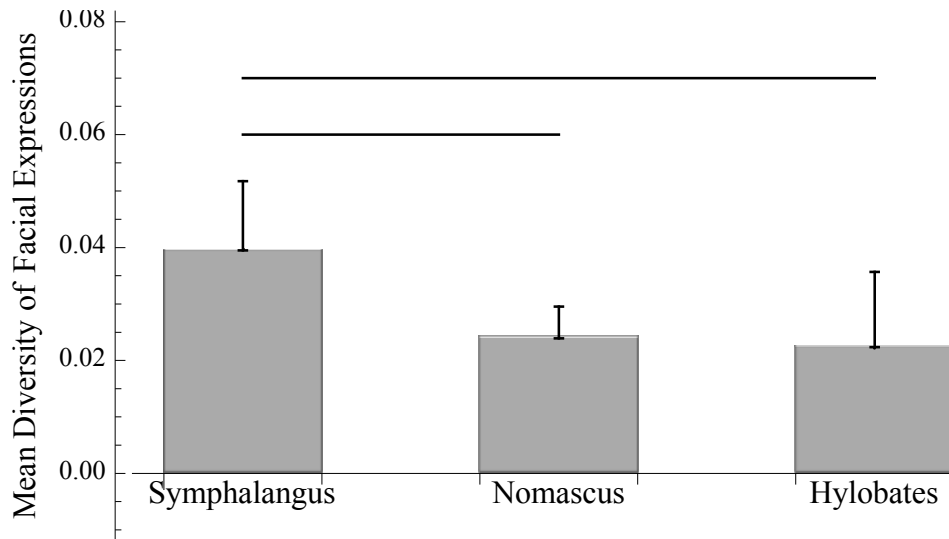
Figure 3: Mean diversity (corrected by recording time) of the three genera (± SD). * represents P-values < 0.05.